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A Temperature-Dependent Development Model for Willow Beetle Species (Coleoptera: Chrysomelidae) in Ireland: Simulation of Phenology/Voltinism in Response to Climate Change

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For my parents, my family, my partner and my friends

DECLARATION

I, Ciarán Pollard, declare that this thesis titled, 'A Temperature-Dependent Development Model for Willow Beetle Species (Coleoptera: Chrysomelidae): Simulation of Phenology/Voltinism in Response to Climate Change' and the work presented in it are my own. I confirm:

- This work was done wholly or mainly while in the candidature for a research degree at this University.
- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.
- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

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A Temperature-Dependent Development Model for Willow Beetle Species (Coleoptera: Chrysomelidae): Simulation of Phenology/Voltinism in Response to Climate Change

Ciarán P. Pollard

Abstract

Rising fossil fuel prices, energy security and adherence to existing European Union (EU) climate/energy policies means that Ireland must look towards alternative energy sources to meet future demand. Woody biomass in the form of short rotation coppice willow (SRCW) is considered a viable option. SRCW is vulnerable to damage by a range of diseases and pests however. The blue (*Phratora vulgatissima*) and brown (*Galerucella lineola*) willow beetles (Coleoptera: Chrysomelidae) are identified economically as two of the most damaging insect pests of SRCW in Ireland. Policies which mandate levels of renewable energy use, to mitigate future climate change, fail to consider adaptation in the energy sector under increased levels of pestilence due to projected changes in the climate system.

The effects of abiotic and biotic factors, mainly temperature and photoperiod, but also host plant, on beetle development were investigated. Constant temperature experiments showed that development time for all assessed life-cycle stages decreased as temperature increased. *P. vulgatissima* oviposition period and total fecundity were influenced by temperature also. Development was not found to vary considerably when *P. vulgatissima* larvae were reared on different host plant varieties (*Tora, Resolution, Tordis* and *Inger*) across a similar range of constant temperatures. A critical daylength (CDL) for *P. vulgatissima* facultative reproduction was calculated.

The relationship between temperature and *P. vulgatissima* and *G. lineola* life-cycle stage development was represented by applying criteria satisfying non-linear deterministic and stochastic functions to development rates and development time distributions respectively. A combined phenology/voltinism model was constructed incorporating a *Salix. viminalis* degree-day budburst model, the temperature-dependent development rate and temperature-independent time distribution functions, and information regarding the reproductive diapause inducing CDL. Using observed temperature and statistically downscaled climate scenarios derived from different global climate models (GCMs) forced with different emission scenarios, model results suggested important spatio-temporal changes in the life cycle and voltinism of *P. vulgatissima*, including two annual generations for 5% and 50% beetle emergence proportions (E.P) at all observed locations nationally by the 2050s and three annual generations for 5% E.P for a percentage of years at certain

inland and south-westerly observed locations by the 2080s. The findings from this research may have implications for regional SRCW production, integrated pest and crop management and climate and energy policy in the future.

ACKNOWLEDGEMENTS

It seems quite usual to record acknowledgements for such works by declaring that there are so many people to thank. Fortunately for me, this is the situation. Unfortunately for all those who deserve acknowledgement, I have a terrible memory and I am bound to forget one or many, but please know that I am forever and truly grateful to all that contributed intellectually, financially and emotionally.

First and foremost, I would like to express my sincerest gratitude to my two supervisors Dr. Rowan Fealy and Dr. Christine Griffin for their endless dispersion of knowledge, exceptional guidance, and sustained encouragement throughout this lengthy process. Whether it was for a rare and dreaded 'progress update' meeting or a more frequent and benevolent "how are you doing" chat, the 'open door' policy was well and truly tested. I am indebted to have had you both on my side and always pushing me towards the finish line.

A wiser man once said "Surround yourself with people who make you happy. People who make you laugh, who help you when you're in need". I can confidently say that there was no shortage of happy and helpful individuals during my time in Maynooth. As I had the pleasure of working in both the Biology (Behavioural Ecology and Biocontrol Laboratory) and Geography (The Irish Climate Analysis and Research UnitS) departments, the list of such individuals is extensive but a special mention has to go to Catriona and Stephanie. Completing this thesis would have been a more daunting task had I not had you both to share the extreme up and down moments with. Thank you for allowing me share this experience with you.

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and aiding in the provision of suitable environments for me to carry out this work. Thank you to Philip Fanning for accompanying me to the many willow sites nationwide to access and capture the offending beetle species.

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List of Commonly used Abbreviations and Acronyms

AIC	Akaike information criterion
ANOVA	Analysis of variance
AR4	Fourth Assessment Report
AR5	Fifth Assessment Report
BIC	Bayesian information criterion
C.I	Confidence intervals
CCGCM2	Canadian Centre for Climate Modelling and Analysis, Canada, Mark 2
CDL	Critical Day-length
CMIPs	Coupled Model Intercomparison Projects
CO_2	Carbon dioxide
CSIROM2	Commonwealth Science and Industrial Research Organisation, Australia, Mark 2
DD	Degree Days
E.P	Emergence proportion
EPICA	European Project for Ice Coring in Antarctica
EREC	European Renewable Energy Council
EU	European Union
GCMs	Global Climate Models
GHGs	Greenhouse Gases
HadCM3	Hadley Centre for Climate Prediction and Research UK Coupled Model, Version 3
ILCYM	Insect Life Cycle Modelling software
IPCC	Intergovernmental Panel on Climate Change
IR	Infrared
K	Thermal constant
NOAA	National Oceanic and Atmospheric Administration
R^2	Coefficient of determination

R^2_{adj}	Adjusted coefficient of determination
RMSE	Root mean square error
RSS	Residual sum of squares
SEAI	Sustainable Energy Authority of Ireland
SIO	Scripps Institute of Oceanography
SLU	Swedish University of Agricultural Sciences
SRCW	Short rotation coppice willow
SRES	Special Report on Emission Scenarios
SSI	Sharpe-Schooldfield-Ikemoto model
T_l	Lower temperature threshold
T_{opt}	Optimal temperature threshold
T_u	Upper temperature threshold
UK	United Kingdom
USA	United States of America
WMO	World Meteorological Organisation

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1 INTRODUCTION

Climate change can be described as the greatest natural experiment in modern history. The consequential impacts of changes that have already occurred are widespread and substantial, affecting the major domains of sustainability in human society such as cultures (particularly in polar regions and low-laying nations), ecologies (food and energy security), economics (business and architecture) and politics (Ford, 2008; Lobell *et al*., 2011; de Vries *et al*., 2007; Dell *et al*., 2008; Kwok & Rajkovich, 2010; von Stein, 2008). Climate change impacts are however not restricted to humans, as an extensive range of flora and fauna species have exhibited alterations in their differing physiological and ecological patterns, and geographical distributions under unstable climate conditions (McCarty, 2001; Parmesan & Yohe, 2003; Root *et al*., 2003; Walther *et al*., 2002; Edwards & Richardson, 2004; Hickling *et al*., 2006; Post *et al*., 2009; Thomas, 2010). In truth, the numerous impacts of climate change have been documented on every continent, in every ocean, and almost every major taxonomic group (Parmesan, 2006).

The publication of the Fifth Assessment Report (AR5), by the Intergovernmental Panel on Climate Change (IPCC), provides a clear and unambiguous picture of a global climate that is becoming increasingly unstable. This report builds upon the findings of the preceding editions concluding that "warming of the climate system is unequivocal" and since the 1950s, many of the observed changes are unprecedented over decades to millennia: warming of the atmosphere and ocean, diminishing snow and ice, rising sea levels and increasing concentrations of greenhouse gases (GHGs) (IPCC, 2013). The report also states that radiative forcing, relative to preindustrial levels (1750), has increased (IPCC, 2013: 696). These changes are attributed with "very high confidence" to the emittance of GHGs through human activity (IPCC, 2013). The atmospheric concentrations of long-wave energy absorbing GHGs such as carbon dioxide (CO_2), methane, and nitrous oxide have

increased to levels unprecedented in the last 800,000 years with atmospheric CO_2 concentrations increasing by 40% since pre-industrial times, primarily from fossil fuel (coal, oil and gas) emissions and also from net land use change emissions (IPCC, 2013: 467). This has predominantly contributed to the globally averaged combined land and ocean surface temperature data warming by 0.85°C (0.65°C to 1.06°C, 90% confidence intervals) over the period of 1880 to 2012 (IPCC, 2013: 194).

Fossil fuels such as oil, natural gas and coal not only remain our major energy sources but they are also the primary material for a great variety of man-made materials and processes (Olah, 2005). The current world energy system, dominated by these fuels, is estimated to be at least a 1.5 trillion dollar market (Goldemberg, 2006). However, a global energy future based on fossil fuels usage is not sustainable. Reasons for this include (1) environmental degradation at local, national and international levels, (2) the external dependency and security of supply and (3) the continuously increasing purchase costs. This cost increase is due to the finiteness of the fuel supply, political unrest in producing countries and an increase in demand due to an exponentially increasing world population with emerging economies such as China, India and Middle Eastern countries (Dincer, 2000; Goldemberg, 2006; Tsoskounoglou *et al*., 2008; IEA, 2013: 1; CFR, 2014). Shifting society's dependence away from fossil fuel to alternative, renewable energy resources is viewed as an important contributor to the development of a sustainable industrial society and the effective management of important environmental issues such as GHG emissions (Ragauskas *et al*., 2006). Much attention has been focused on biomass – organic matter that may be converted into other forms of energy – as a substitute for conventional fossil fuels (McKendry 2002; Hoogwijk *et al*., 2003; 2008; Saxena *et al*., 2009). Types of dedicated energy crops grown exclusively for the purpose of energy production include eucalyptus, poplar, willow and non-woody perennial grasses such as miscanthus (Antizar-Ladislao & Turrion-Gomez, 2008; Karp & Shield, 2008; Evans *et al*., 2010).

As part of Ireland's compliance with the European Renewable Energy Directive 2009/28/EC and national targets set in the Government's Energy Policy Framework 2007-2020 White Paper, 16% of total final energy consumption must be delivered from renewables by 2020. Biomass production through the cultivation of short rotation coppice willow (SRCW) has been proposed as one option to help meet these environmental targets (Komor & Bazilian, 2005; Rourke *et al*., 2009; Connolly *et al*., 2011). Insect herbivores can consume significant amounts of plant biomass, particularly in agricultural systems and managed forest due to the loss of ecosystem services such as the natural control of insect pest populations (Haynes & Gage, 1981; Hare, 1990; Strauss *et al*., 2002; Gray *et al*., 2009). Changes in phenology (earlier and extended windows of presence in the field), life-cycle

duration (accelerated development time), mortality (increased survival), voltinism (additional generations) and population density (greater abundance) may occur under warmer climate scenarios (Cannon, 1998; Bale *et al*., 2002; Robinet & Roques, 2010; Cornelissen, 2011). These targets fail to account for a potential increase in insect herbivory as a consequence of climate change. With insect populations capable of causing a considerable amount of damage through defoliation under current conditions, extra generations and larger populations over longer development periods may limit or negate progress to achieve these future targets.

This study seeks to contribute to the existing discourse concerning the potential impacts of climate change on herbivorous insects in crop cultivation systems. The study focuses on *Phratora vulgatissima* (blue willow beetle) and to a lesser extent *Galerucella lineola* (brown willow beetle) – leaf-feeding chrysomelids identified as two of the most damaging insects of SRCW. With much research accounting for the effect of temperature and photoperiod on the life-cycle of insects, willow beetle are subject to these same effects in a changing climate. While photoperiod varies on a predictable cycle, significant spatial and temporal variations are evident in temperature across Ireland.

Laboratory-based experiments were conducted with different life stages to determine the effect these compounding elements have upon willow beetle development and their life-cycles. Temperature-driven life-cycle models were developed based on these results, with beetle emergence typically synchronised with the timing of budburst similar to field conditions and photoperiod being the key limiting factor of the reproductive season. With a better understanding of the relationship between beetle development and important abiotic environmental stimuli such as temperature and photoperiod, an evaluation of their effects on beetle phenology and voltinism under future climate scenarios throughout Ireland is presented.

1.1 Climate Change Overview

Climate change is recognised as one of the greatest challenges currently facing the international community. The recently published comprehensive IPCC AR5 detailing the world-wide impact of climate change reveals significant findings. Changes include: (1) global increases in temperature for land-surface, multiple upper ocean layers and the troposphere, (2) increases in precipitation in mid-latitudinal land areas of the Northern Hemisphere, (3) increases in extreme events such as heat wave frequency and heavy

precipitation events across North America and Europe, (4) increases in global mean sea levels, (5) increases in the rate of ice loss from the Antarctic and Greenland ice sheets, (6) decreases in Arctic sea ice extent and thickness, (7) decreases in glacier area, length, mass and volume and (8) the loss of snow cover and permafrost degradation in the Northern Hemisphere (IPCC, 2013).

These changes have been attributed to the enhanced atmospheric concentrations of long-wave energy absorbing GHGs, particularly CO_2 through the burning of fossil fuels since the Industrial Revolution during the late 18th century and early 19th century and the loss in land carbon storage through deforestation (Houghton *et al*., 2012; Boden *et al*., 2013). Concentrations of atmospheric CO_2 have been continuously monitored at Mauna Loa Observatory in Hawaii, United States of America (USA) since 1956. Collected air samples from intakes illustrate a greater than 25% increase in CO_2 levels from ~316 ppmv (parts per million volume) in 1956 to ~402 ppmv for present day (SIO, 2014) (Figure 1.1).

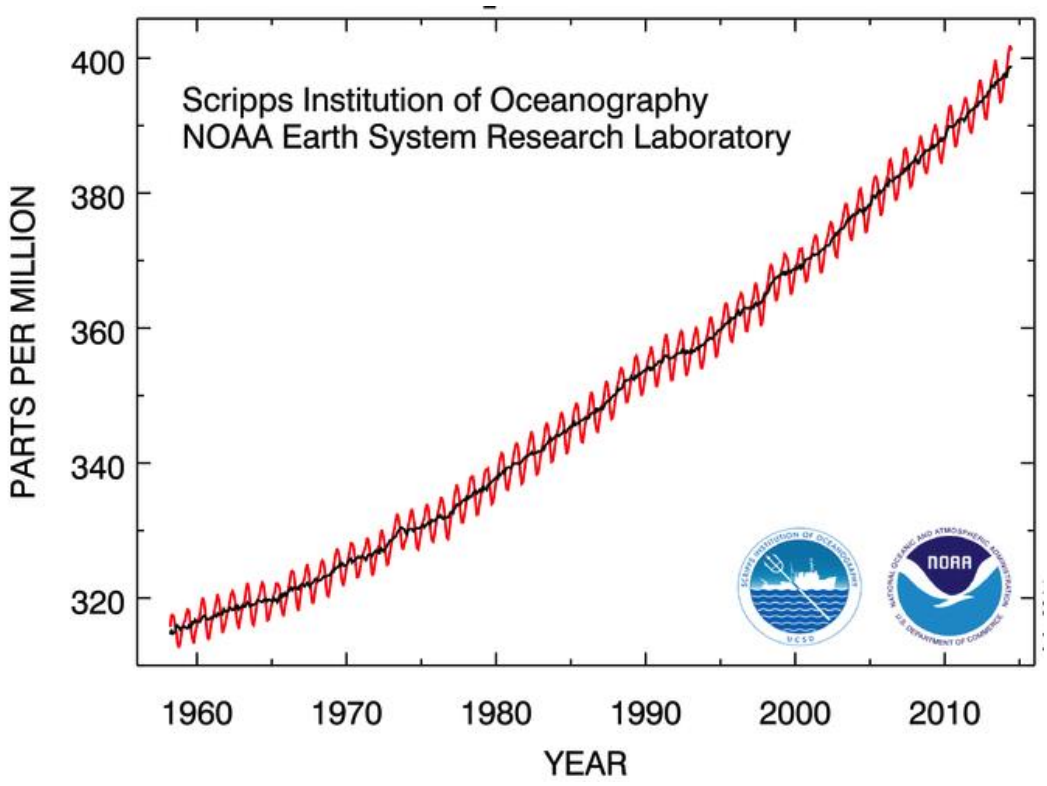


Figure 1.1 Atmospheric concentrations of carbon dioxide (CO2) sampled at Mauna Loa Observatory, Hawaii, USA, indicating a two parts per million per year increase (when corrected for seasonal variation) since record commencement in 1956 (Source: National Oceanic and Atmospheric Administration (NOAA), (2014): http://www.esrl.noaa.gov/gmd/ccgg/trends/, accessed 16/09/2014).

Ice cores have been used as a climate proxy indictor for paleoclimate reconstruction. Ice cores from the Vostok and European Project for Ice Coring in Antarctica

(EPICA) have provided a combined record of atmospheric CO_2 levels accounting for nine interglacial periods (including the current cycle) over the past 800,000 years (Petit *et al*., 1999; Lüthi *et al*., 2008) (Figure 1.2). Measuring the composition of air enclosed within the cores provides a direct record of past atmospheric CO_2 concentrations. Data from both cores suggest that current atmospheric CO_2 levels exceed normal concentration levels recorded during previous interglacial periods which varied between 180ppmv-300ppmv (Petit *et al*., 1999; Lüthi *et al*., 2008). The ice cores also provide details on global temperature through isotopic analysis. A corresponding pattern between CO_2 concentrations and temperature is evident – lower CO_2 concentrations and temperatures during glacial periods and higher CO_2 concentrations and temperatures during interglacial periods (Petit *et al*., 1999; Lüthi *et al*., 2008).

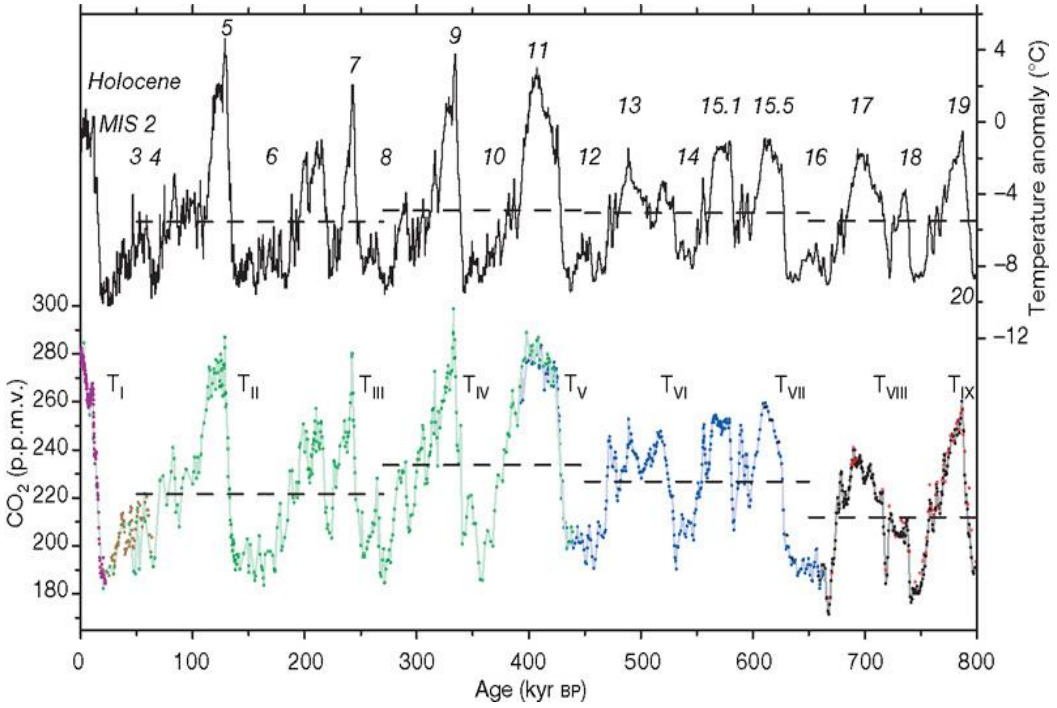


Figure 1.2 Compilation of CO_2 measurements from Antarctic ice coring projects (Dome C, Taylor Dome and Vostok) and EPICA (Dome C site) temperature anomaly over the past 800,000 years, appearing to show a strong covariance during the span of the ice core record (Source: Lüthi *et al*., 2008).

Besides the direct shortwave radiation in the form of ultraviolet rays and visible light from the sun, there is also indirect longwave radiation in the form of infrared (IR) rays resulting from the thermal radiation that is emitted from the earth's surface heating the earth's surface. IR radiation is absorbed by gases within the atmosphere and re-emitted, both upwards and downwards, heating the ground beneath and maintaining a hospitable planetary temperature gradient. The presence of these gases gives rise to the natural greenhouse effect. Without the natural radiative forcing supplied by non-condensing CO_2

which accounts for 20% of the total greenhouse effect, the global climate of earth would be ~33°C lower (Lacis *et al.*, 2010). Due to increasing anthropogenic emissions of GHGs however, a resulting increase in anthropogenic forcing (2.29 W m^{-2} with 1.13 W m^{-2} to 3.33 W m^{-2}, 90% confidence intervals) relative to 1750 has substantially enhanced this greenhouse effect, with CO_2 identified as the largest contributor (1.68 W m^{-2} with 1.13 W m^{-2} to 3.33 W m^{-2}, 90% confidence intervals) (IPCC, 2013: 696) (Figure 1.3). This warming is projected to persist on multi-century timescales even with an idealized complete suspension of GHG emissions, due to their long-lived atmospheric lifespan, along with enhanced alterations to the physical environment defined by an increasingly unstable global atmospheric state (Solomon *et al.*, 2009; Gillett *et al.*, 2011; Frölicher *et al.*, 2013).

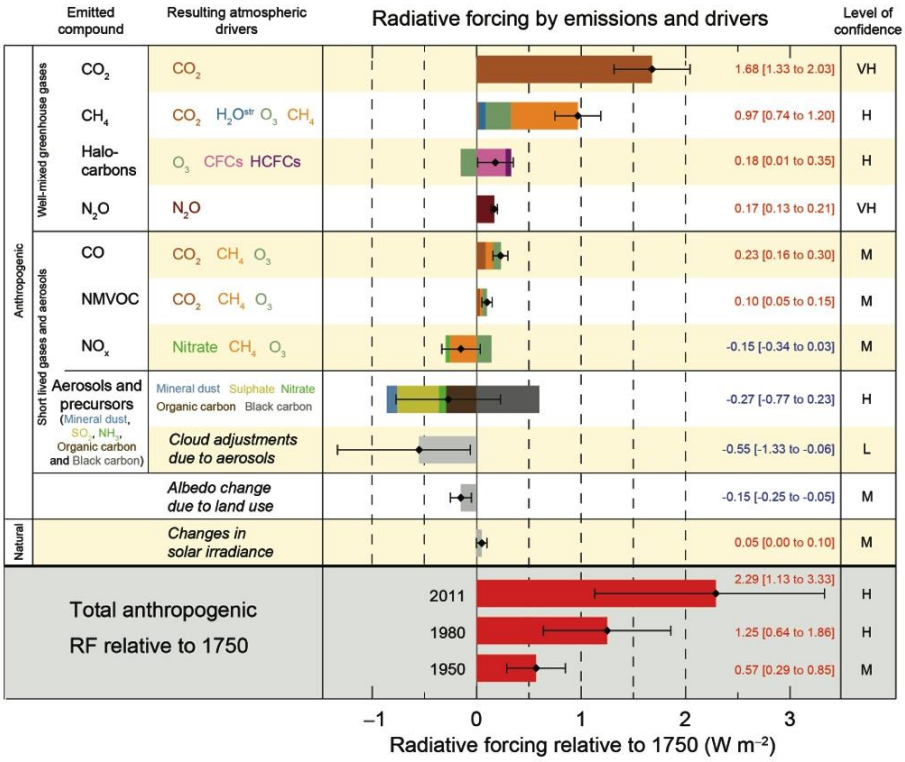


Figure 1.3 Radiative forcing estimates in 2011 relative to 1750 with positive (i.e. CO_2) and negative (i.e. cloud adjustments due to aerosols) components of radiative forcing presented (Source: IPCC, 2013).

1.1.1 Global Climate Observations and Projections: Temperature

The three prominent reconstructions of global surface temperature from instrumental data (Hadley Centre/University of East Anglia's Climatic Research Unit, National Aeronautics and Space Administration Goddard Institute for Space Studies and National Oceanic and Atmospheric Administration National Climatic Data Centre) all suggest that the Earth has

experienced significant warming since the latter decades of the 19th century (Hansen *et al*., 2010; Morice *et al*., 2012; Vose *et al*., 2012). The globally averaged combined land and ocean surface temperature has increased by 0.85°C (0.65°C to 1.06°C, 90% confidence intervals (C.I)) over the period 1880 to 2012, using these independently produced data-sets (IPCC, 2013: 194). Almost the entire globe has experienced surface warming over the longest period when calculation of regional trends is possible (1901-2012) (IPCC, 2013: 194) (Figure 1.4).

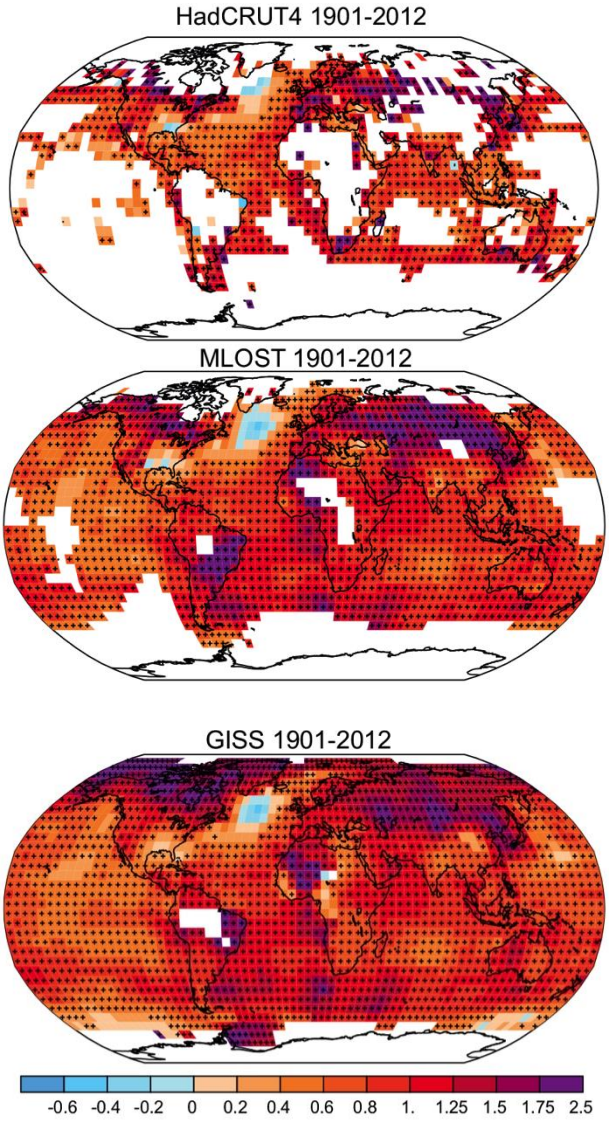


Figure 1.4 Trends in surface temperature from the three data-sets (Hadley Centre/University of East Anglia's Climatic Research Unit (top), National Aeronautics and Space Administration Goddard Institute for Space Studies (middle) and National Oceanic and Atmospheric Administration National Climatic Data Centre (bottom)) for 1901-2012 (Source: IPCC, 2013).

Although this warming has been calculated by a linear trend, it has been observed to occur over two periods since instrumental records began in 1850: beginning

around the 1900s to the 1940s and from around the 1970s onwards (Figure 1.5). The warming period in the early 1900s was largely a northern hemisphere mid to high latitude occurrence and the more recent warming period is a more global phenomenon (IPCC, 2013: 193). Each of the last three decades has been warmer than the one preceding it during this recent warming phase, with 2001-2010 registering as the warmest, and the ten warmest individual years occurring since 1997 (IPCC, 2013: 193). 2010 is ranked as the warmest year on record, together with 2005 and 1998, with no statistically significant difference between global temperatures for all years (WMO, 2013).

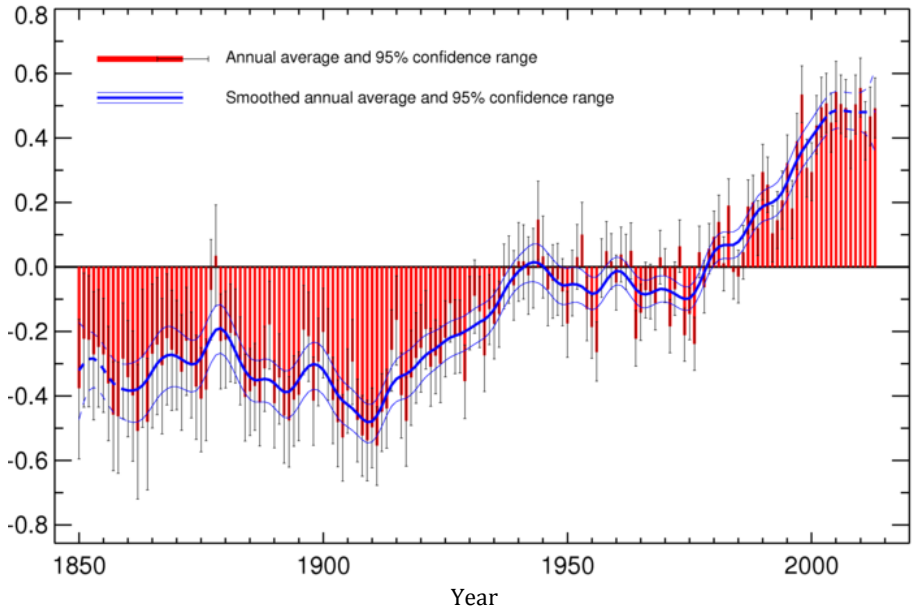


Figure 1.5 Global annual average near surface temperature anomalies for the period 1850-2013 (with the 95% confidence intervals on the annual averages) relative to the 1961-1990 average (Source: Met Office Hadley Centre (2014): http://www.metoffice.gov.uk/hadobs/hadcrut4/diagnostics.html, accessed 16/09/2014).

It is "virtually certain" that maximum and minimum temperatures over land increased on a global scale since 1950 with further definite changes in line with observed trends projected by the end of the current century (IPCC, 2013: 188). Multiple regional studies have reported on observed changes in a range of climate indices since the middle of the 20th century (Kunkel *et al.*, 2008; Choi *et al.*, 2009; Efthymiadis *et al.*, 2011; Donat *et al.*, 2013; Kruger & Sekele, 2013; Skansi *et al.*, 2013). With varying degrees of confidence attached to these results due to lack of instrumental data for some regions (such as Africa and the Middle East), the number of cold days and nights generally decreased and the number of warm days and nights mostly increased on the global scale (IPCC, 2013: 209-210). These warming trends were generally stronger for minimum temperatures and

colder seasons globally as the frequency of cold nights decreased by about 50% (18 days), the frequency of warm nights increased by about 55% (20 days) and the frequency of warmer days was greater during winter and transition seasons for both hemispheres since 1950 (Donet *et al*., 2013b). It is also "likely" that the frequency of heat waves has increased in large parts of Asia, Australia and Europe with further change "very likely" by the end of the current century (IPCC, 2013: 212-213).

Global climate models (GCMs) are the principal tools utilised for understanding shifts in the Earth's climatic processes in the past and identifying possible responses of the global climate system to changing conditions for the future. Atmosphere-Ocean GCMs (focusing on understanding the physical components of the climate system such as the atmosphere, oceans, land-masses and sea ice) were the main model types employed in the IPCC Fourth Assessment Report (AR4). Model experiments were used to project future climate conditions with differing atmospheric GHG concentrations as described in the Special Report on Emission Scenarios (SRES) (Nakićenović *et al*., 2000). Projected increases in global temperatures ranged from 1.8°C (1.1°C to 2.9°C range from a hierarchy of different models) for a B1 (low emission) scenario to 4°C (2.4°C to 6.4°C range from a hierarchy of different models) for an A1FI (high emission) scenario were suggested by the end of the 21st century (2090-2099) relative to 1980-1999 (IPCC, 2007:810) (Figure 1.6).

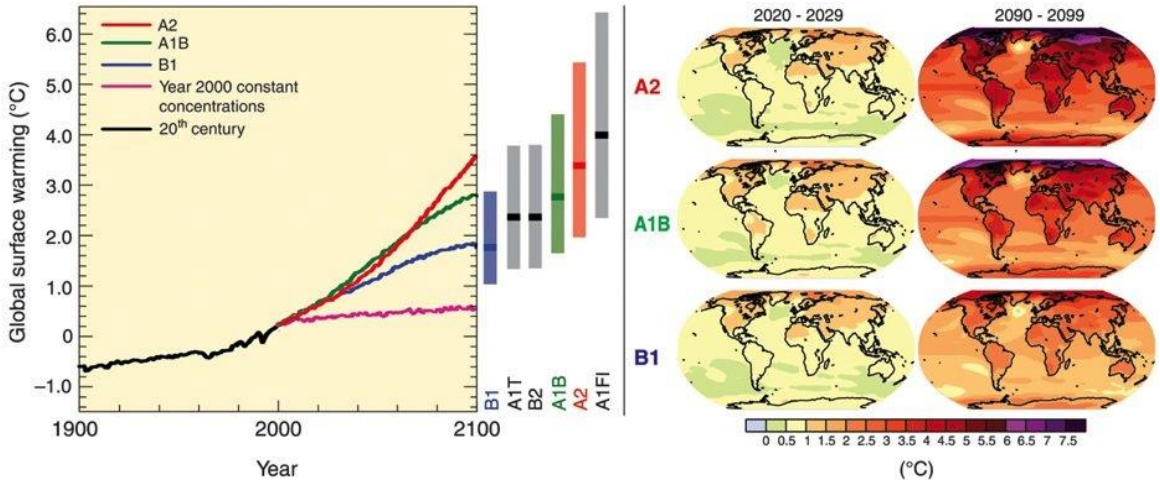


Figure 1.6 Projected global average surface temperature changes based on various scenarios of future GHG emissions relative to 1980-1999 with solid lines representing the best estimate while the bars show the likely range in temperature change (left) and projected surface temperature changes for the early and late 21st century relative to the period 1980-1999 with the panels showing the average projections for 3 scenarios (A2, A1B, B1) averaged over decades 2020-2029 and 2090-2099 (right) (Source: IPCC, 2007).

Earth System Models were the principle model type selected for use in AR5 and include representation of important biogeochemical cycles such as those involved in the carbon cycle, the sulphur cycle, and ozone. New model experiments were carried out as part of the worldwide collaborative Coupled Model Intercomparison Projects (CMIPs) (Taylor *et al*., 2012). Ensemble experiments were used to project future climate conditions for Representative Concentration Pathways (RCPs), four GHG concentration trajectories named after a possible range of radiative forcing values by the end of the 21st century relative to pre-industrial values (Moss *et al*., 2010). Projected increases in global temperatures ranged from 1°C (0.3°C to 1.7°C range based on CMIP ensemble) for RCP2.6 to 3.7°C (2.6°C to 4.8°C range based on CMIP ensemble) for RCP8.5 were suggested by the end of the 21st century (2081-2100) relative to 1986-2005 (IPCC, 2013) (Figure 1.7). Overall model consensus suggests a future global climate of more hot and fewer colder extremes (Sillmann *et al*., 2013). The degree of change however is unclear due to model and scenario uncertainty.

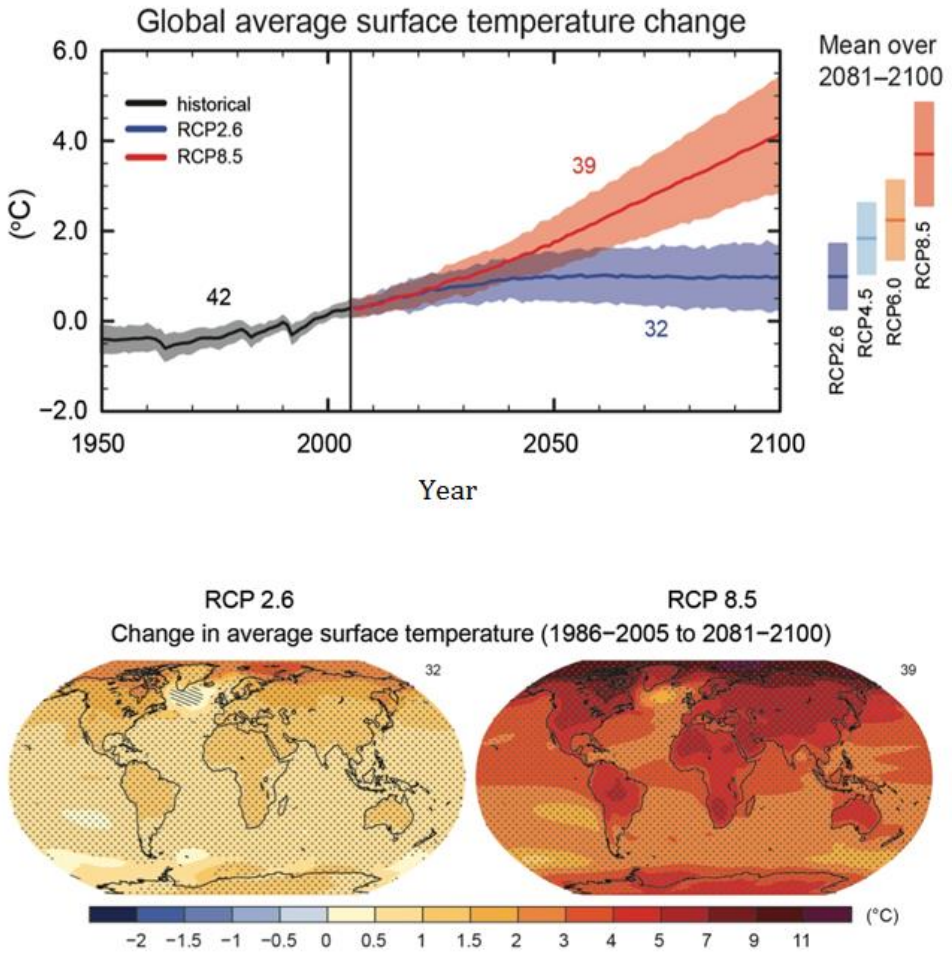


Figure 1.7 Coupled Model Intercomparison Projects (CMIPs) multi-model simulated time series from 1950 to 2100 for change in global annual average near surface temperature anomalies relative to 1986-2005 (with a measure of uncertainty defined by shading) (top) and maps of CMIPs results for Representative Concentration Pathways (RCPs) 2.6 and 8.5 in 2081-2100 for change in global annual average near surface temperature anomalies relative to 1986-2005 (bottom) (Source: IPCC, 2013).

1.1.2 Irish Climate Observations and Projections: Temperature

The temperate maritime climate of Ireland is predominantly defined by three interconnecting factors: (1) the country's positioning on the westernmost edge of the European continent; 2) the dominant influence of the North Atlantic Oscillation and (3) the prevailing south-westerly winds (Kiely, 1999). Ireland consequently does not experience extreme temperatures associated with other regions at similar latitudes such as Newfoundland and Labrador.

An average surface air temperature series for Ireland has been derived using data from five long-term weather stations: Malin Head, Co. Donegal; Valentia Observatory, Co. Kerry; Armagh Observatory, Co. Armagh; Phoenix Park, Co. Dublin and Birr, Co. Offaly (with weighted data from the nearby station at Gurteen used from 2009 after Birr station was officially closed) (McElwain & Sweeney, 2007; Dwyer, 2012). The annual national mean surface air temperature has increased by approximately 0.8°C during the period 1900-2011 (Dwyer, 2012) (Figure 1.8). Temperature variation has occurred over this time-series, consistent with the global record, with a notable cooling period from the 1940s through to the 1970s.

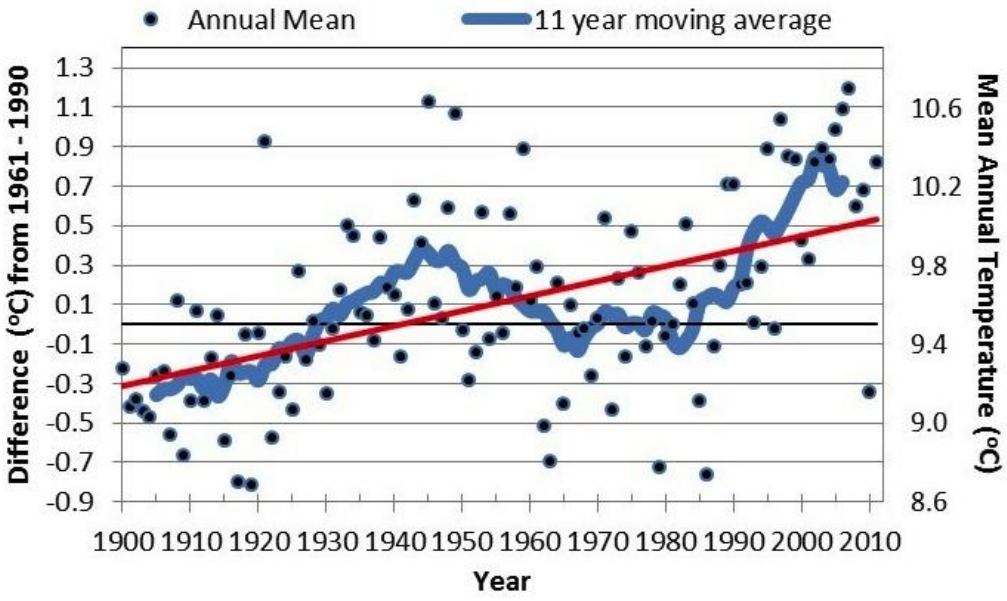


Figure 1.8 Mean annual surface air temperature for Ireland, derived using data from five long-term weather stations, during the period 1900 – 2011. The blue curve shows an 11 year moving average and the red line has been fitted to the annual anomalies (the difference between the mean annual temperature and the 1961 – 1990 normal or reference mean value) (Source: Dwyer, 2012).

The number of warm days has increased and the numbers of cold days has decreased, in line with observations across Western Europe (Dwyer, 2012). When additional synoptic stations were considered during the period 1961-2005, the majority of stations recorded a greater increase in mean temperatures at most stations in winter, with a greater increase in mean minimum temperatures in summer and a greater increase in mean maximum temperatures in winter (McElwain & Sweeney, 2007). The national trends are in agreement with the global patterns of temperature change.

Future projections in temperature have been derived for Ireland by Fealy & Sweeney (2007; 2008) and the Community Climate Change Consortium for Ireland (Dunne *et al*., 2008). Simulated results from both studies show warming everywhere relative to present conditions, particularly in the summer and autumn. Dunne et al. (2008) projected seasonal mean temperature increases of 1.2°C-1.4°C by the mid-century (2021-2060) increasing to 3.0°C-3.4°C by the end of the century (2060-2099) with different emission scenarios A1B, A2, B1 and B2. This warming is greatest in the east and southeast of the country.

Fealy & Sweeney (2008) projected an increase of 0.7°C-1.0°C for the early century (2020s), 1.4°C-1.8°C for the mid-century (2050s) and 2.0°C-2.7°C for the late century (2080s) with different emission scenarios A2 and B2. Spatial differences become more apparent during the 2050s, with an enhanced continental effect becoming visible by the 2080s (Figure 1.9). Projected changes in the frequency and magnitude of extreme events such as increases in hot day thresholds, heat wave duration, cold night temperatures and decreases in frost day occurrence are increasingly likely to have an impact on Irish society throughout the current century also (Fealy & Sweeney, 2008).

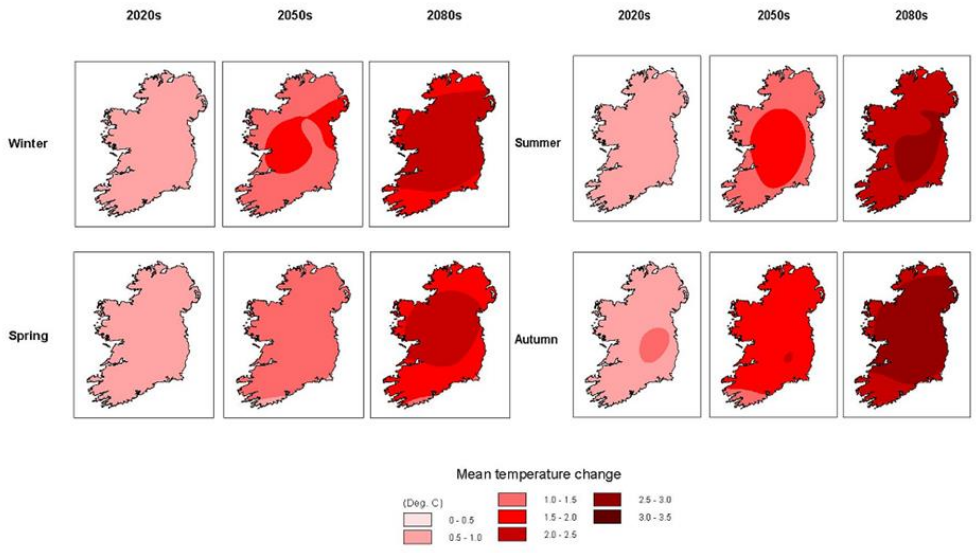


Figure 1.9: Projected seasonal temperature changes for Ireland for 2010-2039 (2020s), 2040-2069 (2050s) and 2070-2099 (2080s) relative to period 1961-1990 (Source: Fealy & Sweeney, 2007; 2008 & Sweeney *et al*., 2008).

1.2 **Insect Responses to Climate Change: Temperature**

Insects are ectothermic organisms. They are among the groups of organisms most likely to be affected by changes in climate because climate has a direct influence on their development, reproduction and survival (Bale *et al*., 2002). Insects generally have short generation times and high reproductive rates when compared to other animal phyla, so they are more likely to respond quicker to climate change on a measureable scale (Menéndez, 2007). Potential responses to changes in climate include phenological shifts due to physiological adaptation, distribution pattern expansion or contraction, and alterations in species interaction (species competition, herbivore host plant, predation and parasitism) (Figure 1.10).

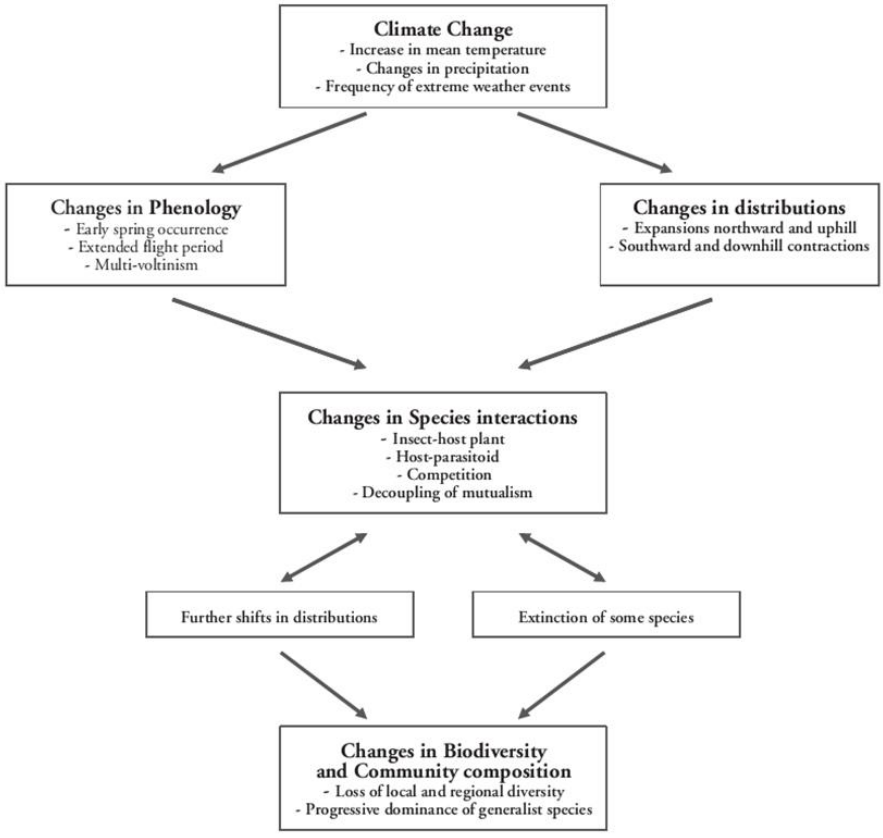


Figure 1.10 Potential effect of climate change on insect species leading to changes in biodiversity and community composition (Source: Menéndez, 2007, modified from Hughes, 2000).

Positive direct responses to increases in temperature have been documented globally for many insect groups. Advancements in flight activity for Lepidoptera species in the United Kingdom (UK) (Roy & Sparks, 2000), Europe (Peñuelas *et al*., 2002; Stefanescu *et al*., 2003) the USA (Forister & Shapiro, 2003) and Australia (Kearney *et al*., 2010) were

all found to be correlated with warming experienced over an assessed time frame. Earlier adult emergence has been recorded throughout the UK for Odonata species (Hassell *et al*., 2007), across Europe for Hemiptera species (Harrington *et al*., 2007) and throughout the Iberian Peninsula for Coleoptera species (Gordo & Sanz, 2005). Increases in temperature have reduced the time required for the completion of different life-cycle development stages. Berg *et al*. (2006) reported a doubling in the maturation rate for *Dendroctonus rufipennis* (spruce beetle) in the USA. Adjustments in CDL for delayed reproductive diapause induction due to thermal instability have been noted for Lepidoptera species in Japan (Gomi *et al*., 2007). Changes in voltinism have resulted from the combination of lengthened development seasons, prolonged periods for ovipositioning processes and the postponed onset of reproductive diapause inducing signals (Figure 1.11). Martín-Vertedor *et al*. (2010) corroborated a significant advance of *Lobesia botrana* (European grapevine moth) phenology and the occurrence of a fourth and partial fifth generation over three decades under a noteworthy trend towards local warming due to climate change. Further increases in generation numbers have been confirmed in multi-species studies confirming the general flexibility and high adaptability of insects to environmental change (Altermatt, 2009; Pöyry *et al*., 2011).

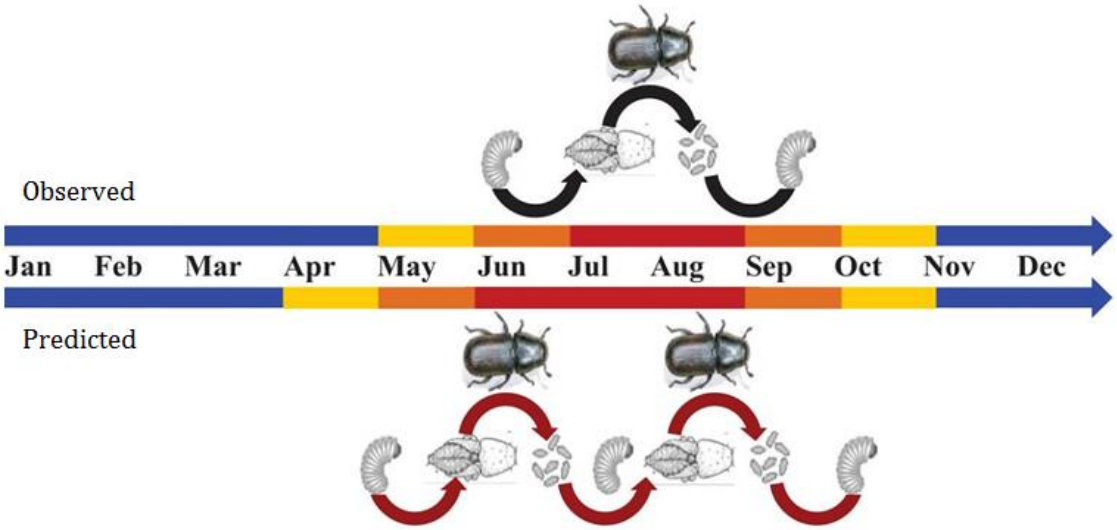


Figure 1.11 Observed and predicted changes in insect seasonal activity and voltinism due to climate change (Source: Mitton & Ferrenberg 2012).

Climate can also limit the geographic distributions of a species (Krebs, 2004). Projected increases in temperature are expected to promote shifts in species distributions, with range expansion at cool altitudinal and latitudinal limits as environments become suitable for occupation and range contraction at warm lower altitudinal and latitudinal

limits as previously suitable environments become uninhabitable (Cannon, 1998; Hughes 2000, Menéndez, 2007). Hickling *et al*. (2006) showed that the majority of insect groups (including Carabidae and Cerambycidae) were expanding their ranges polewards and to higher elevations in the UK over a thirty year period. A meta-analysis of Europe involving multiple species of non-migratory Lepidoptera showed there was a general polewards shift in response to temperature, with two-thirds of the species assessed retaining their lower latitudinal bounding limits (Parmesan *et al*., 1999). Contraction of southern and lower altitudinal ranges in the northern hemisphere have also been shown to drive local population and species extinction particularly species being gradually pushed towards geographical barriers (expansive water bodies or mountain peaks) (Wilson *et al*., 2005; Franco *et al*., 2006).

1.3 **Short Rotation Coppice and Leaf-Feeding Beetle**

Ireland is dependent on fossil fuel imports to meet current energy demands with the country's indigenous fossil fuel source limited to peat. Ireland's import dependence in 2012 was 85% which was a decrease from a peak of 90% in 2006 (Rourke *et al*., 2009; Howley & Holland, 2013). Numerous drivers such as fluctuations of fossil fuel prices, security of energy supply and the negative effects on different environmental dimensions highlight the necessity for Ireland to exploit indigenous renewable energy resources (Rourke *et al*., 2009).

As with other European Union Member States, Ireland's progression towards a renewable energy future has been primarily driven by EU legislation that pursues an overall reduction in GHG emissions and the promotion of energy from renewable sources. Building on the commitments made under the Kyoto Protocol, the EU's climate and energy Directive 2009/28/EC (so-called "20-20-20 targets") has set ambitious objectives for member states that have been designed to elicit change. The directive essentially aims to meet three targets by 2020: (1) a 20% reduction of GHG emissions compared to 1990 levels; (2) a 20% reduction in primary energy use – based on projected levels – through improved energy efficiency; and (3) a 20% share of energy consumption originating from renewable energy sources.

As part of Ireland's commitment to meet the targets set by the EU on energy efficiency, climate change and renewable energy, a mandatory national target of 16% for renewable energy shares of final energy consumption in 2020, which is calculated on the

basis of the 2005 share of each country (3.1% for Ireland), must be delivered (EREC, 2008). The share in 2012 stood at 7.1% (Howley & Holland, 2013). With many different indigenous renewable energy sources available to exploit in Ireland such as wind, wave and solar, biomass production through the cultivation of bioenergy crop such as short rotation coppice willow has been proposed as one option to help meet these environmental targets.

SRCW has several characteristics that make it suitable as a perennial biomass crop. It is recognised as a carbon neutral energy source (Grogan & Matthews, 2002; Rowe *et al*., 2009; Evans *et al.*, 2010), has the ability to resprout after harvests that take place every 3 – 4 years (Volk *et al*., 2004; Keoleian & Volk, 2005; Kuzovkina & Quigley, 2005) – and offers multiple social, rural and environmental benefits through planting and harvesting (Haughton *et al*., 2009; Rosenqvist & Dawson, 2005: Wickham *et al*., 2010).

Willow (*Salix*) has a rich genetic base, with breeding programs established in Sweden during the 1980s and the UK during the 1990s, to produce more varieties with greater yields over shorter time frames and increased resistance to pests and disease and extreme climatic conditions (Larsson, 1998; Wickham *et al*., 2010; Karp *et al*., 2011). SRCW yields vary depending on climatic, land quality and plot size (Searle & Malins, 2014). *S. burjatiea* and *Salix x Aquatica gigantean* grown on marginal agricultural land has achieved high annual yields of 13.5 and 17 oven dry tonnes per hectare in Ireland respectively (McElroy & Dawson, 1986; McCracken & Dawson, 1998). *Salix* is native to northern temperate zones with a preference for cooler, wetter conditions and largely heavy soils with a neutral pH at low altitude associated with most of Ireland (Dawson, 2007; Wickham *et al*., 2010). Figure 1.12 shows the location of SRCW sites in Ireland in 2009 and the suitability of land to support SRCW based on aspect, height, slope, rainfall and soil type (SEAI, 2014).

Insects commonly gain pest status in managed agricultural and forestry systems, particularly in monocultures such as SRCW when compared to less disturbed ecosystems (Dalin *et al*., 2009). These outbreaks are attributed to the changing of natural habitats into monocultures. Studies suggest that these changes result in the loss of ecosystem services, including the control of insect pest populations (Wilby & Thomas, 2002; Cumming & Spiesman, 2006). Dense monocultures lead to a reduction in competition for resources and a reduction in the time insects require to find their host plants and therefore increase their rate of dispersal from plant to plant aiding in the growth of the population (Root, 1973; Dalin *et al*., 2009). The planting of monocultures can also reduce biodiversity, and change the food web interactions at sites (Tylianakis *et al*., 2007). This can lead to an alteration in the interaction between herbivorous insects and their natural enemies.

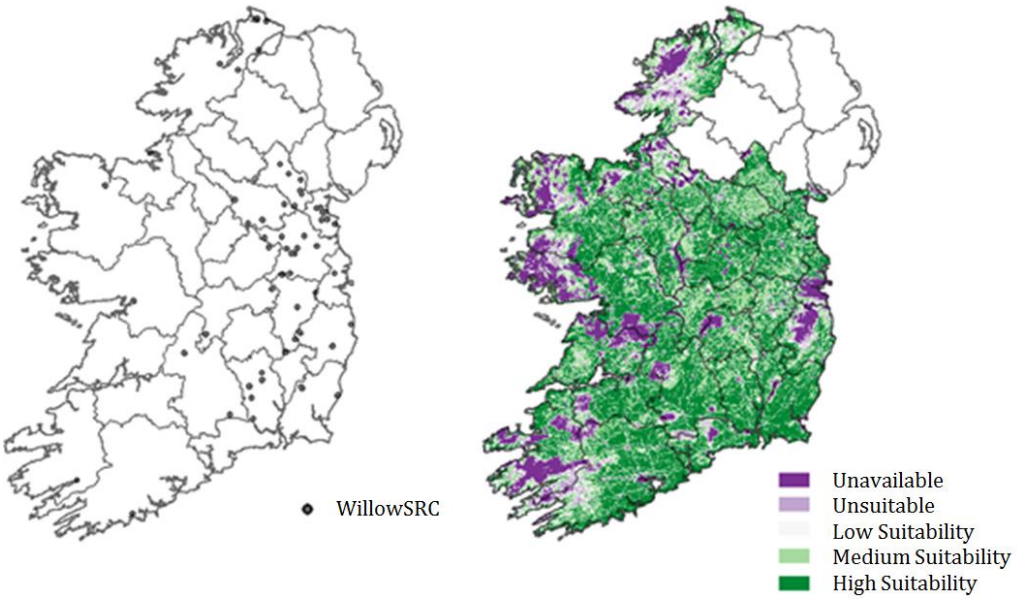


Figure 1.12 Location of SRCW sites in Ireland in 2009 (left) and the suitability of land to support SRCW based on aspect, height, slope, rainfall and soil type (right) (Source: Sustainable Energy Authority of Ireland (SEAI) (2009): http://maps.seai.ie/bioenergy/, accessed 16/09/2014).

The leaf-feeding blue willow beetle (*Phratora vulgatissima*) and the brown willow beetle (*Galerucella lineola*) are identified economically as two of the most damaging insect pests of SRCW in Ireland (Kelly & Curry, 1991a; 1991b; Sage & Tucker, 1998), the UK (Kendall e*t al*., 1996; Kendall & Wiltshire, 1998; Peacock *et al*., 1999) and other European countries (Larsson *et al*., 1997; Dalin & Björkman, 2003; Björkman *et al*., 2003) (Figure 1.13).

Figure 1.13 The leaf-feeding blue willow beetle (*P. vulgatissima*) (left) and the brown willow beetle (*G. lineola*) (right).

Both leaf-feeding beetles have similar life-cycles (Figure 1.14) (Kendall & Whitshire, 1998). During the winter, some adults remain within the plantation on willow shoots and stools or in dead vegetation, leaf litter on the plantation floor. Most beetles aggregate and hibernate in an array of sheltered places outside the crop such as loose bark and crevices on tree trunks and branches, hedgerows, weathered fence posts and gates, moss, leaf litter, weed vegetation and other ground debris (Kendall & Whitshire, 1998; Peacock *et al.,* 1999; Sage *et al.,* 1999; Karp & Peacock, 2004). The beetles tend to concentrate around the SRCW edges, within close proximity of the plantation (Kelly & Curry, 1991a; Sage & Tucker, 1998; Björkman & Eklund, 2006).

Adults emerge from overwintering around the middle of spring (April) and immediately colonise newly emerged *Salix* foliage (Caslin *et al*., 2010). Adults require a period of feeding to reach reproductive maturity (Karp & Peacock, 2004). Mating commences when sexual maturation is reached and this is followed by an oviposition period in May and June (Torp *et al*., 2013). *P. vulgatissima* typically oviposit on the underside of the leaves in small clusters near the base of the willow shoots (Kendall *et al.*, 1996). Egg clusters range in size from 2 to 50 eggs (Kendall & Whitshire, 1998; Sipura *et al*., 2002; Dalin, 2006). *G. lineola* position their brood on leaves at all levels on the shoots (Björkman *et al*., 2004).

Figure 1.14 Life-cycle for *P. vulgatissima* and *G. lineola*.

P. vulgatissima larvae hatch in synchrony and aggregate to feed together, becoming more solitary predators in latter larval stages (Björkman *et al*., 2004; Karp & Peacock, 2004). In contrast, newly hatched *G. lineola* larvae do not feed together (Björkman *et al*., 2004). In total, there are three larval developmental phases instars (Peacock *et al*., 2000, Kendall & Whitshire, 1998). Late third instars leave the foliage of host trees and make their way to the base of the willow rods to pupate in the soil near the base of the tree (Kendall *et al*, 1996; Sage *et al.*, 1998, Karp & Peacock, 2004; Sadeghi *et al*., 2004). Upon completion of the pupation stage in mid to late summer (late July to early August), the new generation of beetles return to the willow stems to start feeding before leaving the plantations in autumn (late August to early September) to seek suitable overwintering sites.

Reports of insect outbreaks in willow plantations are common (Sage & Tucker 1998). Feeding damage is consistent throughout the late spring, summer and early autumn with multiple phases of feeding attacks, beginning with overwintering adults returning to the willow plantations, followed by larvae and finally newly developed adults. Damage caused by these beetles can be substantial, particularly by the larvae due to their greater density and their restricted movement (SLU, 2014). Evidence of initial beetle damage can be observed when foliage becomes brown and skeletonised, reducing crop photosynthesis, leading to the stunted growth of SRCW, longer crop establishment rates and reduced yields (Figure 1.15). Reports in literature regarding damage extremes vary from 40% reduction in stem growth recorded by Björkman *et al.* (2000), to complete new shoot death throughout crop recorded by Mitchell (1995) and Kendall *et al*. (1996). Natural predators of the willow beetle are believed to overwinter at different life stages within willow plantations (Björkman *et al*., 2003; 2004). This important natural biological control process may be affected transitionally by disturbances such as winter harvesting every couple of years after initial cut-back, creating a short-term refuge for the leaf beetles before predator populations can recover. This is a problem as the application of insecticides to willow coppice is not optional due to economic, environmental and technical disadvantages although biological control is a plausible alternative.

Figure 1.15 Brown and skeletonised *Salix* foliage associated with willow beetle feeding damage.

1.4 General Aims and Objectives

The motivation for this thesis is driven by the challenges faced by countries to comply with binding targets of international directives such as 2009/28/EC under future climate conditions. Ireland's target under the Renewable Energy Directive is for 16% of the country's total energy consumption to be derived from renewable energy sources by 2020. Biomass production through the cultivation of SRCW has been proposed as option to help meet these energy/environmental targets. SRCW is susceptible to a number of diseases and pests, primarily leaf-feeding chrysomelids. Policies which mandate levels of renewable energy use to mitigate future climate change, such as Directive 2009/28/EC, fail to consider adaptation in the energy sector under increased levels of pestilence due to projected changes in the climate system. In light of this, the primary research objective was to account for the impact of abiotic and biotic factors, on the phenology and voltinism of native leaf-feeding willow beetles, specifically *P. vulgatissima* and *G. lineola*. The secondary research objective was to link these findings to climate model projections for Ireland in order to inform future policy in this area.

This thesis aimed to address these objectives by:

- Undertaking laboratory experiments to assess the effects of abiotic and biotic factors such as temperature and photoperiod, but also host plant, on the activity and development of *P. vulgatissima* and *G. lineola*

- Identify temperature-dependent deterministic and temperature-independent stochastic models to describe development data

- Constructing a process-based model for the estimation of beetle life-cycle stage emergence and voltinism

- Developing spatio-temporal maps of Ireland to illustrate estimated emergence and voltinism for future time periods by incorporating climate model projections

1.5 Thesis Structure

In addressing the research aims and objectives outlined in Section 1.4, this thesis is comprised of eight chapters, the content of which is described below.

Chapter 1: Introduction gives a brief overview of the science of climate change with an emphasis on changes in temperature at a local and global scale; the influence of temperature on insect phenology, life-cycles and distribution; biomass in the form of SRCW as a renewable energy resource and the leaf-feeding beetle pests *P. vulgatissima* and *G. lineola* that affect SRCW establishment and yield.

Chapter 2: General Materials and Methods describes the common practices carried out prior to and during the experimentation phase of this research. This included sourcing, maintaining and rearing of willow beetle for laboratory populations; establishing a greenhouse grown crop of *Salix* varieties and calibration of incubators. Details regarding statistical tests and software used during the research are described also.

Chapter 3: Experimentation provides background information on the experiments that were carried out to investigate the effects of temperature and photoperiod, and also host plant, on willow beetle life-histories. The materials and methods unique to each experiment set-up are described and the results from each experiment are presented with discussions regarding the findings.

Chapter 4: Insect Development Models reviews important empirical and biophysical models that have been formulated to describe insect development rate and development time distributions. A selection of these were fitted to development data obtained during the experimentation phase and final models were chosen based on predefined criteria with results discussed.

Chapter 5: Modelling Host Plant Phenology reviews important models (primarily mechanistic) that have been formulated to describe plant phenology. A selection of these were assessed to account for *Salix* budburst in the field using phenology records. A budburst model was chosen to be used as a biofix for willow beetle development and results are discussed.

Chapter 6: Phenology/Voltinism Model Construction reviews a selection of different phenology/voltinism models developed specifically for coleopteran species. This chapter describes the individual components of the constructed willow beetle

phenology/voltinism model. The model is subjected to validation and sensitivity analysis and the results from this are discussed.

Chapter 7: Phenology/Voltinism Model Results presents the results from the phenology/voltinism model using climate model projections as input. The results associated with five synoptic stations selected due to their locations at a national level (north, south, west, east, midlands) are compared before an overall national assessment of willow beetle life-cycle stage emergence and voltinism for future time periods is presented.

Chapter 8: Final Discussion summaries and discusses the findings and contributions of this bipartite study as well as highlighting limitations encountered during the research and possible avenues that could benefit from future investigation.

2 GENERAL MATERIALS AND METHODS

This chapter provides details of the preliminary work performed prior to the experimentation component of this research. In order to quantify the impact of environmental factors on willow beetle species, actions such as the collection of beetles and maintenance of laboratory cultures; the establishment of a greenhouse grown *Salix* crop, and climate room and incubator precision testing were required. Greater detail regarding these tasks is provided in the following sections.

2.1 Sourcing Beetle Populations

Semi-state and private organisations associated with SRCW production were contacted to seek information on outbreaks of *P. vulgatissima* and *G. lineola* populations within their crop. Site suitability for collections was based on beetle abundance, geographical distribution, site accessibility and distance from the research facility. The locations of these sites were 1) Lough Boora Parklands, Kilcormac, Co. Offaly (53°12'N, 7°43'W); 2) Pollardstown Fen, Newbridge, Co. Kildare (53°11'N, 6°51'W); 3) Rathcon Farm, Grangecon Co. Wicklow (53°00'N, 6°44'W); 4) Donard, Co. Wicklow c/o Rathcon Farm, Grangecon Co. Wicklow (53°01'N, 6°37'W); 5) Teagasc, Crops Research Centre, Oak Park, Carlow, Co. Carlow (52°52'N, 6°55'W); 6) Acorn Recycling Limited, Ballybeg, Littleton, Co. Tipperary (52°38'N, 7°14'W) and 7) Teagasc, Kildalton College, Piltown, Co Kilkenny (52°21'N, 7°19'W) (Figure 2.1).

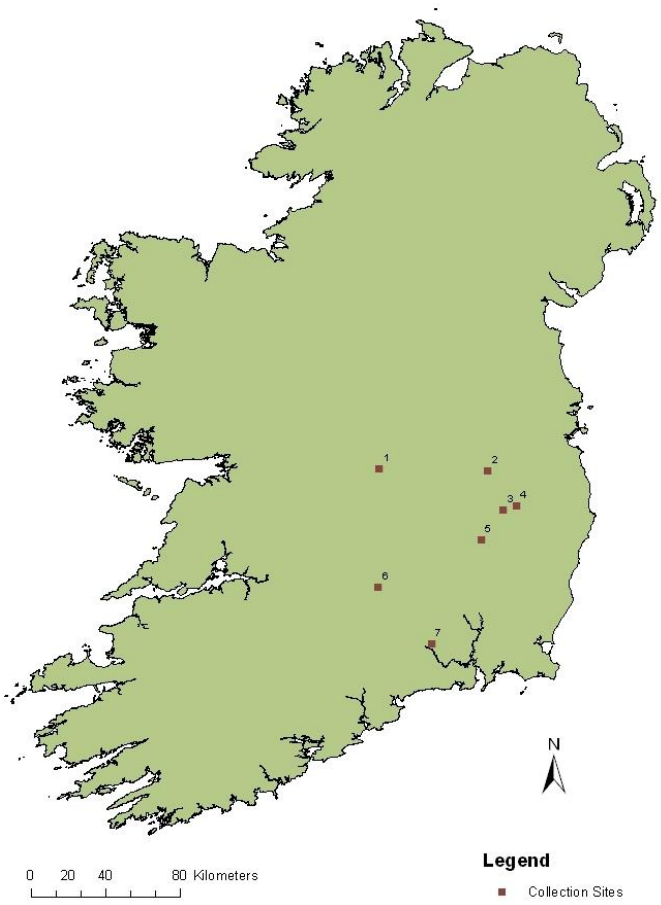


Figure 2.1 Beetle collection site locations.

Beetle collections were carried out at these SRCW plantations prior to and during the insect active season to set up laboratory cultures (Figure 2.2). Some sites had a single dominant species annually with *P. vulgatissima* found in greater numbers at Kilcormac from 2009 – 2011 and *G. lineola* expressing greater numbers at the Donard plantation from 2010 – 2013. Similar species distribution and dominance of *P. vulgatissima* or *G. lineola* has been observed in SRCW in Ireland and UK by Kendall & Wiltshire (1998), Sage & Tucker (1998), Batley *et al*. (2004) and Karp & Peacock (2004). Seasonal variation in species occurrence and abundance was evident at sites such as Littleton, Co. Tipperary, with *P. vulgatissima* more abundant in 2010 while *G. lineola* was more abundant in 2011.

Figure 2.2 Example of a collection site at Teagasc, Crops Research Centre, Oak Park, Co. Carlow (left) and active collecting at Donard, Co. Wicklow c/o Rathcon Farm, Grangecon Co. Wicklow (right).

All life-cycle stages, expect for pupae, were collected during frequent visits to the pre-selected sites. Field observations recorded by Kendall & Whitshire (1998) in the UK and Kelly & Curry (1991b; 1991c) in Ireland were used as a preliminary collecting guide regarding the seasonal presence of eggs, larvae and adults of *P. vulgatissima*. Eggs were collected during the months of May and June when female adult *P. vulgatissima* were ovipositing; larvae were collected from May to July and adults were collected regularly throughout the active season to replenish laboratory populations. Following the egg-laying in spring and early summer, adult numbers decreased until the new generation emerged in late summer and/or early autumn in accordance with life-cycle descriptions provided by Kendall & Whitshire (1998) and Sage & Tucker (1998). Life-cycle stage occurrence for *G. lineola* is similar to *P. vulgatissima* (Kendall & Wiltshire, 1998). *P. vulgatissima* and *G. lineola* eggs were usually found on the underside of leaves in small clusters as noted by Kelly & Curry (1991b) and Kendall & Wiltshire (1998). These were easily obtainable on the lower part of willow trees using the *search and find by hand* method. The eggs stick to trichomes on the underside of the leaf surface with an adhesive secretion coating the eggs (Hilker & Meiners, 2006). Numbers of eggs varied per cluster. These were collected by removing the whole leaf with attached eggs from the plant and placing them in sterilised 50 ml universal tubes (Sarstedt) with moistened cotton lining their conical bottoms (to maintain leaf condition and prevent damage from bending or breaking the midrib). *P. vulgatissima* and *G. lineola* hatching from egg batches normally aggregate together and feed on the same plant during their early stages of larval development. Therefore, neonate larvae were collected as per egg collection technique.

Field-collected adult beetles were obtained using different methods depending on various factors such as their abundance, their location on the plants and site

accessibility. The *search and find by hand* method previously used for egg and larvae collections was utilised. The beating technique was employed also. This collection technique was previously used by Sage & Tucker (1998). Adults were collected from within the canopy of SRCW plantations by shaking the tree stems and allowing the insects to fall into a white cotton sheet positioned on the ground between the *Salix* trees. The stems were knocked or shaken to displace insects in the crop canopy. Insect species were placed in 3.5 L food containers or 50 ml universal tubes. The number of stems disturbed depended upon crop height, crop spacing and the number of willow beetle required. This technique was useful around the perimeter of the plot and during the early period of the active season when ground vegetation within the SRCW plots was sparse. When vegetation was dense and canopy populations of willow beetle were low, a hand-held beating sheet was used. Using this collection equipment and method allowed for better accessibility within the *Salix* plots and rapid collections.

Another variation of the beating method was used for collecting adults, particularly at the beginning of the active season, when adults were emerging from overwintering sites surrounding the plot and relocating to the perimeter of *Salix* plots. Using a wide mouth plastic funnel and a 3.5 L food container, *Salix* stems were lowered and shaken over the funnel allowing insects to fall into the container. Predatory insects were removed from the container on site. These containers were provided with a *Salix* cutting for feeding. Applying the beating method in combination with the funnel and container or hand-held beating sheet techniques was effective as it also dislodged *P. vulgatissima* and *G. lineola* larvae. These collections took place on days with no precipitation to avoid water build-up within collection chambers.

2.2 Laboratory Beetle Cultures

Adult beetles collected in the field were maintained in different culture chambers: 36 cm (height) x 16 cm (width) x 16 cm (length) Bugdorms™, 55 cm (height) x 29 cm (width) x 30 cm (length) customized plastic storage boxes with mesh frontage and 9 cm (diameter) x 4 cm (height) plastic food tubs (Figure 2.3). The Bugdorms™ were used for larger populations of collected beetles while the plastic storage boxes and food tubs were used as mating and ovipositioning chambers. Adult populations maintained in all storage chambers were supplied with fresh *Salix* foliage every second day. To prevent excessive disturbance, old foliage was removed the day after new foliage was supplied to allow the

beetles to make their own transition between old and new material. At the same time, frass accumulations at the bottom and on the sides of the chambers were removed with a dry cloth or tissue while dead adults and leaf debris were removed. Eggs laid on leaves were removed and placed in 9 cm (diameter) x 1.5 cm (height) Petri dishes (Figure 2.3). Emerging larvae were reared in the Petri dishes also. Leaves were changed every 2-3 days. Dead larvae and frass accumulations were removed through the replacing of filter paper (Fisherbrand) at the bottom of the dishes. Prepupae larvae (larvae beginning to curl on base of containers) were transferred to food tubs with sterilised sand – washed and sieved to remove micro-material before being heated at >120°C for 24 hrs – moss peat substrate at a ratio of 1:1 by volume for pupation to occur.

Figure 2.3 Selection of containers used for maintaining insect cultures in the laboratory – Bugdorms™ (top-left), customized plastic storage boxes (top-right), plastic food tubs (bottom-left) and Petri dishes (bottom-right).

Field collected *P. vulgatissima* and *G. lineola* adults were maintained at room temperature (20°C ± 2°C). Chambers were kept in a quiet naturally lit area in the laboratory. Adult *P. vulgatissima* and *G. lineola* did not lay eggs in the rearing chambers but egg-laying did occur in the food tubs and these were used for life-stage experiments. Adult populations maintained in food tubs were supplied with fresh *Salix* foliage every second day. The end of

the feeding rods in the rearing chambers were placed in water-filled 100 ml Parafilm-sealed conical flasks and the leaf petioles in the Petri dishes were placed through holes in the lids of 1.5 ml safe-lock micro-centrifuge tubes with water. Relative humidity values were regularly recorded (>90% relative humidity using a Testo 635-2 thermohygrometer). Any excessive moisture accumulating on the inside of the Petri dishes was removed with a cloth or tissue when foliage was replaced. Similarly, during larval experimentation and rearing, a build-up of moisture needed to be avoided in smaller environments such as Petri dishes and food tubs as preliminary work with various life-stages of *P. vulgatissima* and *G. lineola* showed that drowning or the possible onset of pathogenic infections (i.e. fungi) was a potential threat. These were lined with moist filter paper as done in feeding preference experiments by Kendall *et al*. (1996) and Peacock *et al*. (2001) to allow foliage to remain fresh for the duration of each experiment and reduce moisture build-up on Petri dishes interiors.

P. vulgatissima and *G. lineola* have been found to express feeding preferences among willow varieties due to differing leaf morphology and levels of phenolic glycosides, condensed tannins, water content and nitrogen present in the leaves (Kelly & Curry, 1991c; Kendall *et al*., 1996; Rank *et al*., 1998; Torp *et al*., 2013). Research on host variety effects has shown that variety choice significantly impacts upon adult fecundity, survival and weight gain as well as larval development, mortality and weight gain under laboratory conditions (Peacock *et al*., 2004). During this research, *Salix* foliage cuttings were taken from sites where beetles were collected and found to predate heavily on host plants. In a study by Dalin & Björkman (2003), *P. vulgatissima* larvae on plants previously exposed to adult grazing consumed less total leaf area and showed more dispersed feeding than larvae on plants protected from grazing. Therefore, when possible, foliage with less feeding damage was obtained from the sites to feed to all stages of both beetle species so that host plant defences and plant condition had a minimal or no negative impact. Kelly & Curry (1991a) found adult *P. vulgatissima* expressed a preference for young leaves, with a higher level of feeding damage on upper than on mid shoot leaves also. Therefore, newly sprouted willow stems and shoots with sufficient foliage were collected for feeding purposes. Fresh foliage for feeding and oviposition medium was always available during experimental phases – either as collected and stored at 4°, directly from the sites where collections originally took place or from on-site greenhouse planted varieties (see Section 2.3). The same varieties and source of foliage provided to all beetle life cycle stages was consistent with the varieties found at the sites of collection except in experiments when effects of host plant varieties on beetle development and performance were been examined (see Section 3.3).

2.3 *Salix* Variety Collection and Planting

Salix foliage was acquired from the same plots during beetle collections, to be used for feeding and ovipositioning by laboratory cultures. Efforts were made to secure cuttings with young foliage that had not yet been predated upon by herbivorous insect species within the SRCW crop. This was to provide the maximum amount of feeding material with minimum induced plant defences (Dalin & Björkman, 2003) as explained in Section 2.2. Cuttings were taken from stems using secateurs. These were placed in black plastic bags with one litre of water added to the base of the bags to prevent foliage from drying out. They were stored at 4°C and usable for up to 4 weeks.

Different *Salix* varieties were obtained from the beetle collection sites. These were used for variety/temperature-dependent experimentation (see Section 3.3). 50 cm (length) rods were cut from different established varieties in late winter. These were transported back to research facilities, placed in 10 L buckets with 2-3 L water base and stored at 4°C. This was performed to replicate winter conditions and promote budding. Buckets with rods were removed from cold storage after 3-4 weeks and placed in a 20°C temperature controlled greenhouse. 15-20 rods per variety were planted in 10 L pots when rooting commenced. Pots contained a composition of moss peat, agricultural sand and vermiculite at a ratio of 2:1:1 by volume. The pots were placed in random order in black soil trays and placed on metal tables in the greenhouse under photoperiod conditions 16L:8D. The planted rods were watered regularly and allowed to establish over 3-4 months, developing through distinguishable phenological stages such as vegetative budburst, leaf expansion and stem elongation defined by Saska & Kuzovkina, (2010) (Figure 2.4).

Figure 2.4 *Salix* varieties planted and grown in greenhouse as feeding/oviposition medium for beetles.

2.4 **Incubator Calibration**

Numerous studies have been conducted measuring the effects of temperature on the development of insect species using controlled temperature environments such as growth chambers, climatic rooms and incubators to maintain different constant temperatures (Lapointe, 2000; Nava & Parra, 2003; Diaz *et al*., 2008). Although many studies refer to temperature conditions within these cultivation enclosures as being maintained within ±0.5°C of the set constant temperature, most studies provide minimum information regarding how constant temperatures are monitored. Some climatic chambers provide temperature monitoring details through inbuilt digital temperature display panels. However, these instantaneous readouts do not take into account micro-environments that may exist within the incubators with temperature measurements captured at a single or limited number of points within the chamber (Wagner, 1991). The occurrence of temperature fluctuations within these units and the importance of accounting and controlling for these conditions during temperature-dependent experimentation have been identified (Howe, 1967).

Figure 2.5 LMS Series Three Cooled Incubators (200W models) (left) with shelving lay-out used during experimentation (right).

During preliminary experimentation, external digital temperature readings for LMS Series Three Cooled Incubators (200W models) were accepted as the definite temperature at which different life-cycle stage development rate data for *P. vulgatissima* and *G. lineola* was being captured (Figure 2.5). Specifications for the cabinets allowed for temperature variation of ±0.5°C. However temperature data-loggers (Testo 175-T3 with external thermocouples) showed that incubator digital temperature readings were

inaccurate and these were used to validate temperatures within incubators for final experiments. Temperature probes in sealed containers such as Petri dishes and food tubs were placed at predetermined points, towards the front (closest to the door) and back of the four shelves in the cabinets, to identify any location-specific differences in temperatures experienced. The positioning of containers under Osram Lumilux L10W/827 Cool Daylight fitted fluorescent lights, directly above the shelves, was assessed as a possible factor promoting temperature fluctuation at points within the incubators also. Temperature validation was carried out at 2 minute intervals over a 96 hour period with photoperiods of 16:8 light:dark (L:D) at different constant temperatures – 15°C, 20°C, 25°C and 27°C.

Container positioning on the shelves from the front to the back of the cabinets did not result in differences in temperature. Additionally, temperature remained consistent across all four shelves. Temperature fluctuation was discovered to be higher than expected in the containers placed in the incubators. However, temperature variation was evident between the sequential light and dark phases (Figure 2.6). During the light phase, temperatures within containers increased by approximately 1.5°C-3°C above set temperatures. This was observed at all constant temperatures examined. During the dark phase, temperatures remained within ±0.5^{o}C of the set constant temperatures. To correct for this increase in temperature during the light phase, the set incubator temperature was adjusted to a lower temperature during this phase. When the set temperatures were offset by -1.4^{o}C (i.e. 13.6^{o}C, 18.6^{o}C, 23.6^{o}C and 25.6^{o}C) during the light phase, temperatures remained within ±0.5^{o}C of the required constant temperatures. It was established that temperature variation could be controlled for during the dark phase, by offsetting the required constant temperatures by +0.2 ^{o}C (i.e. 15.2^{o}C, 20.2^{o}C, 25.2^{o}C and 27.2^{o}C) also. Further measures to reduce minor temperature fluctuation and visible moisture build-up on the underside of the container lids within the cabinets involved removing two of the shelves with two attached fluorescent lights and doubling the distance between the light sources and the two remaining shelves.

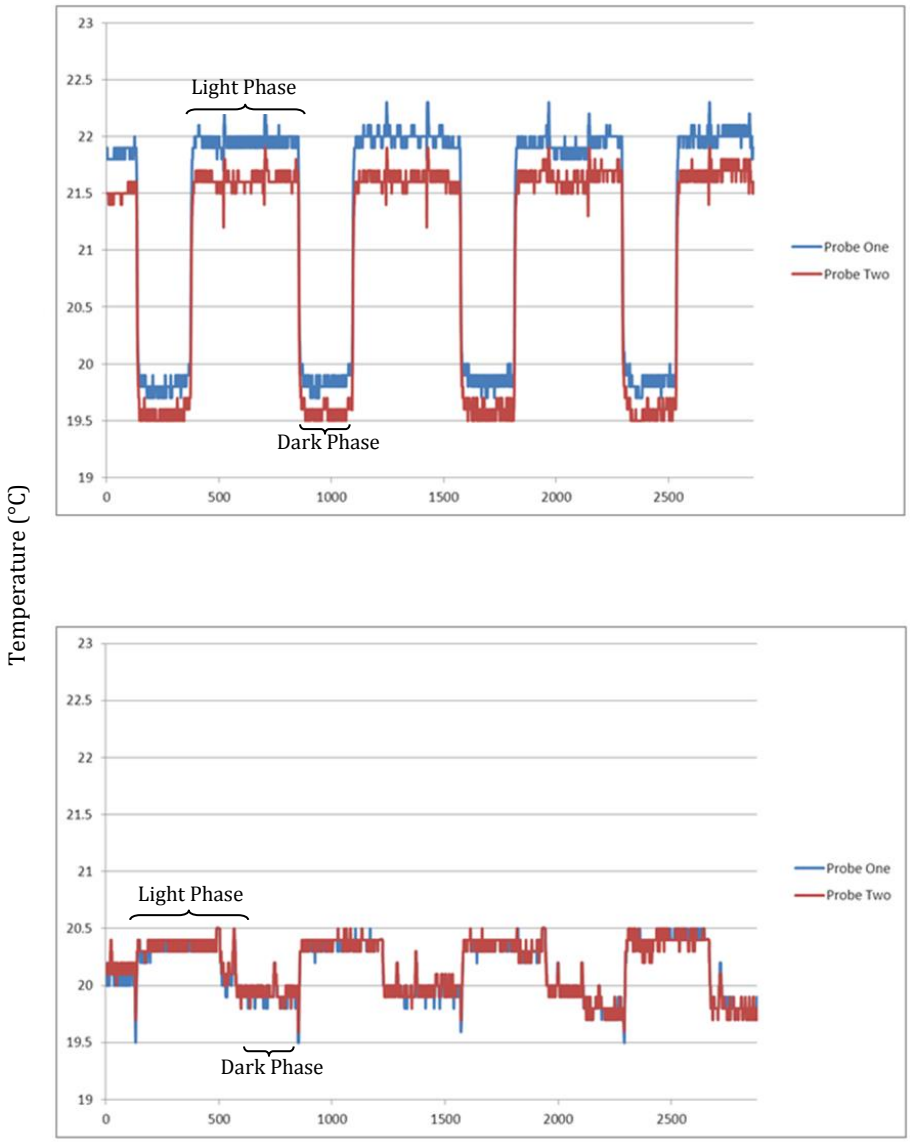


Figure 2.6 Temperature recorded in uncalibrated (top) and calibrated (bottom) incubators using temperature data-loggers.

2.5 Statistics and Software

All statistical tests were carried out (unless otherwise stated) using software packages Minitab v. 16 (Minitab Ltd.; Coventry, UK), IBM SPSS Statistics v. 20.0 (SPSS Ltd.; Hong Kong) and Statgraphics Centurion XVI (Statpoint Technologies, Inc.; Virginia, USA). Discrete data-sets for development and oviposition times were tested for normality using the Anderson-Darling method. These data-sets were significantly different from a normal distribution ($\alpha = 0.05$ – for all experimentation a p-value of ±0.05 was deemed statistically significant) and normality could not be achieved by transformation. The Mann-Whitney U-

test was used when comparing two data-sets and the Kruskal-Wallis test was used when comparing three data-sets or more. When multiple pairwise comparisons were made between data-sets using the Mann-Whitney U-Test, the level of significance was adjusted according to Bonferroni (p-value / number of comparisons). Discrete data-sets for total fecundity were tested for normality using the same method. This data-set conformed to a normal distribution and it was tested for equality of variances using Levene's test. No significant difference among the variances was found and data-sets were compared using a one-way ANOVA for multiple samples with Tukey's post-hoc test. Binomial data-sets (reproductive diapause – 1 for diapause, 0 for reproductive) were analysed using logistic repression using Statistical Analysis System v. 9.3 (PROC GENMOD, binominal, logit) (SAS Institute Inc., North Carolina, USA).

Insect and plant linear regression models were developed using Microsoft Office Excel 2010 (Microsoft, Washington, USA). The differences between the intercepts and differences between the slopes were assessed when the comparison of regression lines was required. Coefficients for empirical non-linear regression insect models were estimated through identified statistical packages using the Levenberg-Marquardt algorithm, with convergence criterion set to 0.00001 and the confidence level for all intervals set at 95.0. The algorithm is an ordinary least squares method based on successive iterations for parameter optimization (Marquardt, 1963). The method requires the provision of initial starting values for final parameter estimation. These values were based on coefficients estimations delivered in similar published studies. Parameters for biophysical non-linear regression model (Sharpe-Schoolfield-Ikemoto model (Ikemoto, 2005, 2008)) (see Section 4.1.2.5) were estimated using a function OptimSSI-P v. 2.7 (Shi *et al*., 2011a; 2011b; Ikemoto *et al*., 2013). This function runs on R statistical software v. 2.15.1(R Foundation for Statistical Computing, Vienna, Austria) and incorporates the optimization algorithm of Nelder & Mead (1965). This program was used to estimate coefficients for complex non-linear regression models such as the Unified model (Chuine, 2000) also (see Section 5.3.3), with selected initial starting values based on parameter estimations obtained from similar published studies aswell.

Model performance evaluation of linear and non-linear regressions models were made based on goodness-of-fit statistics: coefficient of determination (R^2), residual sum of squares (RSS), root mean square error (RMSE), Akaike information criterion (AIC) and Bayesian information criterion (BIC). These values were provided by the statistical software packages or calculated step-by-step using Microsoft Office Excel 2010 (Microsoft, Washington, USA).

All graphs were constructed using Microsoft Office Excel 2010 v.12.0 (Microsoft, Washington, USA) and Matlab version R2012a (Mathworks, Massachusetts, USA). Plant phenology models were constructed using Microsoft Office Excel 2010 v.12.0 (Microsoft, Washington, USA) and R statistical software version 2.15.1 (R Foundation for Statistical Computing, Vienna, Austria). The insect phenology/voltinism model was constructed using Matlab version R2012a (Mathworks, Massachusetts, USA). Phenology/voltinism maps were constructed using an inverse distance weighted technique in ArcGIS v.10.2 (ERSI, California, USA).

3 EXPERIMENTATION

This chapter presents and discusses the results of experiments that were carried out during this research, to investigate the effects of environmental factors such as temperature, photoperiod, but also host plant on willow beetle life-histories.

3.1 Experiment One: Temperature-Dependent Development and Survival of *Phratora vulgatissima* and *Galerucella lineola* – Eggs, Larval and Pupal Stages

Insects are poikilothermic; that is they do not regulate their body temperature which varies with ambient. Since body temperature of poikilotherms is usually very close to that of their surrounding environment, temperature is the driving force behind insect behaviour, ecology and physiology (Porter *et al*., 1991; Bale *et al*., 2002; Kontodimas *et al*., 2004). Many studies have investigated how temperature influences insect development and survival (Régnière, 1987; Bentz *et al*., 1991; Kim *et al*., 2001). In general, developmental time decreases as temperature increases within a range, between a lower and upper temperature threshold, with survival peaking at a point within the developmental window (usually around an optimum temperature for development) and dipping around the thermal thresholds (see Section 4.1.2).

Limited work has been conducted on the effects of temperature on *P. vulgatissima* and *G. lineola* with different studies commenting on the development time of various immature life-cycle stages at single constant temperatures. Focussing on the life-cycle and ecology of willow beetle on *Salix viminalis* in England, Kendall & Wiltshire (1998)

noted that the mean development time, from laying to hatching, for *Phratora vulgatissima* eggs in laboratory conditions at 15°C was 15 days while the mean development time of larvae and pupae instars at 15°C was 49 days; almost double the time at 25°C of 27 days. Similarly, Kelly & Curry (1991a) investigating the biology of *P. vulgatissima* on *S. viminalis* in Ireland, noted an egg hatch period at 20°C of 5-7 days; less than half the time at 15°C as recorded by Kendall & Wiltshire (1998).

The objectives of this experiment were to determine the effects of temperature on the developmental periods and survivorship of *P. vulgatissima* and *G. lineola* life-cycle stages – eggs, larvae and pupae – under controlled environmental conditions. Such information on the thermal requirements and limitations for development of willow beetles were to be used for constructing a phenology/voltinism model (see Chapter 6).

3.1.1 Materials and Methods

Egg clutches were obtained daily from *P. vulgatissima* and *G. lineola* adults that were collected in the field and stored as laboratory colonies (see Sections 2.1 and 2.2). Stock cultures were supplied daily with fresh field or greenhouse grown foliage removed from *Salix* clones with *S. viminalis* parentage. Egg clutches used were therefore always laid within a 24 hour period prior to set-up.

Leaves and attached egg clutches were placed in 9 cm (diameter) x 1.5 cm (height) Petri dishes (Figure 3.1). The petiole of the leaf was placed through the lid of a 1.5 ml micro-centrifuge tube containing water. One clutch containing a variable number of eggs was placed in each Petri dish. Petri dishes were base-lined with tap water moistened 90 mm filter paper. Relative humidity was monitored throughout the experiment using a Testo 635-2 thermohygrometer. Relative humidity was greater than 75% within the Petri dishes which was representative of conditions in the field. The Petri dishes were closed and sealed using Parafilm® (Pechiney Plastic Packaging; Menasha, USA) and placed in incubators set at different constant temperatures of 10°C, 12°C, 15°C, 20°C, 25°C, 27°C, 28°C, 29°C, 30°C, 31°C and 32°C ± 0.5°C depending on the species been analysed. Temperature in the Petri dishes was monitored using data-loggers. A photoperiod of 16:8 light:dark (L:D) was used. There was a minimum of ten dishes placed in each temperature treatment but the number of dishes per treatment varied due to differing numbers of eggs per clutch in each dish. Eggs were observed daily under a Leica EZ4 dissection microscope and the total number of larvae. Egg clutches that did not hatch were removed from the study as egg clutch viability

was not assessed. However single eggs that did not hatch from clutches that successfully produced larvae were classified as dead with the total survival percentage noted. Filter paper was replaced when necessary, excessive condensation was removed from the inside of the Petri dishes using tissue and water in the tubes was replenished.

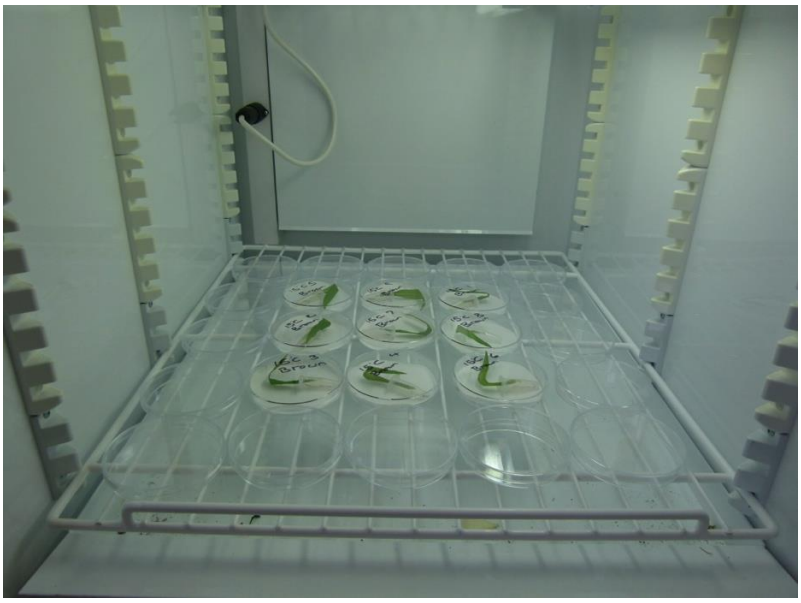


Figure 3.1 Petri dishes used for *P. vulgatissima* and *G. lineola* eggs development and survival experiments in incubators with surrounding buffers to reduce disturbance.

Leaf degradation occurred at the lower temperatures (10°C and 12°C) due to longer time requirements for development. Leaf-surface area surrounding the egg clutch was therefore trimmed before or during the experimental process using a laboratory scissors to remove decomposing leaf material. In preliminary experiments, the bacteria and fungi that colonise the leaves was suspected to inhibit hatching, particularly at the lower temperature treatments. The egg clutch and the surface of the leaf in each replicate at the lower temperature treatments were surface sterilised with 1% sodium hypochlorite (NaClO) and 16.5% sodium chloride (NaCl). Using a fine artist paint-brush, the sterilising fluid was applied and allowed to sit for a 2-3 minutes. The solution was washed off using tap water subsequently, before being delicately dried using laboratory paper towel.

After eggs hatched, neonate larvae were transferred to new foliage, from field or greenhouse grown stock, using a fine artist paint-brush. Stems with 3-4 attached leaves were used as feeding substrates. Similar to methods used for investigating eggs development, stems with attached leaves were placed through the lid of a 1.5 ml micro-centrifuge tube containing water. The foliage was placed in food tubs (Figure 3.2). Moistened filter paper was added to the base of the units. Larvae hatching from one batch

of eggs tend to aggregate together and feed in rows (Karp and Peacock, 2004). Therefore, larvae were placed in a group of 10-15 on the underside of a leaf in each tub. Emerging larvae were kept at the same temperature as the eggs from which they emerged. If numbers at a temperature treatment were low due to poor egg survival, additional eggs were reared at room temperature and emerging larvae were placed at the experimental temperature on day of emergence. A minimum of ten dishes were placed in each treatment but the number of dishes per treatment varied due to differing numbers of larvae in each dish. Larvae were observed daily. During observations, foliage and stem water were replenished. Filter paper was replaced when necessary and frass was removed. Excess moisture was also removed from the inside of the food tubs.

Figure 3.2 Tubs used for *P. vulgatissima* and *G. lineola* larval and pupal development and survival experiments in incubators with surrounding buffers to reduce disturbance.

When larvae reached late third instar phase, they began to withdraw from their feeding positions on the leaves to seek sheltered sites for pupation as they do in their natural environment (Sage & Tucker, 1998). When this behaviour was observed, filter paper was removed and a ratio of 1:1 by volume mixture of moss peat and sterilised sand was added to the food tubs. Depth of the mixture was ≤1 cm to facilitate observations. The total number of larvae completing stage development and the duration of development for each larva was recorded. Larvae that did not pupate were classed as dead with the total survival percentage noted. Pupae were observed daily until adult eclosion. The total number of pupae developing at each temperature treatment and the duration of development for each pupa was recorded.

3.1.2 Results

The mean development times and mean percentage survival rates for *P. vulgatissima* and *G. lineola* life-cycle stages are presented in Table 3.1 and Table 3.2. Graphs for mean development times with associated statistics regarding pairwise comparison amongst temperatures, relative frequency distributions for development times and percentage survival rate are provided in Appendix I. The duration and survival of different stages of *P. vulgatissima* and *G. lineola* development varied as a function of temperature with considerable differences between different constant temperature treatments.

P. vulgatissima development of eggs, larvae and pupae occurred over the range 10°C – 28°C. No development occurred at 29°C, 29°C or 28°C for eggs, larvae or pupae respectively. The mean number of days for the completion of life-cycle stages generally decreased as the temperature increased (eggs: Kruskal-Wallis test, $H = 1739.887$, d.f. = 6, $P < 0.001$; larvae: Kruskal-Wallis test, $H = 1733.558$, d.f. = 6, $P < 0.001$; pupae: Kruskal-Wallis test, $H = 537.223$, d.f. = 5, $P < 0.001$ (Table 3.1). The mean number of days for eggs to hatch decreased by approximately fivefold from 28.2 days at 10°C to 5.6 days at 27°C. The mean time required for larvae to develop decreased by more than fourfold from 61.0 days at 10°C to 14.2 at 27°C. The mean number of days for pupae to develop decreased threefold from 20.6 days at 10°C to 5.7 days at 25°C. Decreases in development times were much greater for all stages between 10°C and 20°C than for temperatures greater than 20°C.

Due to high mortality levels (likely in cases as a result of fungus establishing on degrading leaf material despite sterilisation, particularly during the eggs stage), development time at temperatures lower than 10°C are not presented for any life-cycle stage (Table 3.2). There was a slight increase in mean number of days required for development from 27°C to 28°C of 5.6 days to 5.8 days for eggs and 14.2 days to 14.5 days for larvae, and from 25°C to 27°C of 5.6 days to 5.8 days for pupae. Increases in development times at the higher temperatures indicated stressful conditions for the insects as percentage survival rates decreased and no complete development occurred at temperatures higher than these.

Table 3.1 Mean (± standard error (SE)) development times (in days) for *P. vulgatissima* and *G. lineola* life-cycle stages at different constant temperatures for number of samples (N) (no development denoted by -----). Different letters indicated a significant difference between temperatures (Kruskal-Wallis, P<0.001 and post hoc pairwise comparison, P=0.05).

Temperature (°C)	Eggs	N	Diff	Larvae	N	Diff	Pupae	N	Diff
P. vulgatissima									
10	28.20± 0.14	131	A	61.03± 0.35	38	A	20.64± 0.22	24	A
12	18.00± 0.14	471	B	48.42± 0.22	237	A	17.82± 0.08	49	A
15	13.18± 0.09	293	C	30.52± 0.21	430	B	11.36± 0.08	225	B
20	7.40± 0.03	337	D	21.34± 0.18	420	C	7.38± 0.06	136	C
25	6.06± 0.03	375	E	17.02± 0.14	376	D	5.69± 0.05	127	D
27	5.56± 0.04	226	F	14.19± 0.17	383	E	5.83± 0.12	29	D
28	5.81± 0.06	75	EF	14.47± 0.19	15	EF	------		
G. lineola									
10	------			76.76± 1.16	17	A	------		
12	28.90± 0.09	62	A	56.77± 0.73	26	A	18.56± 0.21	34	A
15	15.66± 0.09	243	A	28.52± 0.21	137	A	13.49± 0.07	84	AB
20	7.90± 0.03	309	B	16.25± 0.17	60	B	7.66± 0.08	59	B
25	6.08± 0.03	606	C	14.29± 0.09	298	C	5.48± 0.04	240	C
27	5.73± 0.05	351	D	13.05± 0.11	165	D	4.67± 0.07	87	D
29	6.22± 0.11	49	CD	15.14± 0.25	50	BC	4.63± 0.10	24	D
31	------			------			5.00± 0.00	3	BCDE

Percentage survival was greater than 65% for all *P. vulgatissima* life-cycle stages between and including 15°C and 25°C (Table 3.2). Percentage survival for eggs was greater than 70% at lower temperatures 10°C and 12°C, dropping to approximately 63% at the maximum temperature of 28°C. Percentage survival was approximately 60% and 79% for pupae at the lower temperatures of 10°C and 12°C respectively, decreasing to approximately 57% at the upper temperature 27°C. Due to longer developmental times experienced at the lower temperatures for the larvae stage, low survival percentages, when compared to other immature life-cycle stage survival percentages at similar temperatures, of approximately 42% and 45%, were observed at 10°C and 12°C respectively. At the other end of the constant temperature test range, similarly low survival percentages of approximately 46% and 13% were recorded at 27°C and 28°C, respectively.

Table 3.2 Mean percentage survival rates for *P. vulgatissima* and *G. lineola* life-cycle stages at different constant temperatures (no survival denoted by -----).

Temperature (°C)	Eggs	Larvae	Pupae
P. vulgatissima			
10	71.58	41.76	60.00
12	70.40	44.72	79.03
15	82.54	71.43	90.73
20	85.97	74.47	88.31
25	73.10	65.73	89.44
27	74.10	46.31	56.86
28	62.50	12.50	------
G. lineola			
10	------	41.46	------
12	70.45	31.33	54.84
15	87.41	69.19	96.55
20	71.86	72.29	98.33
25	75.94	64.92	94.49
27	65.00	48.39	84.16
29	39.20	41.67	58.54
31	------	------	30.00

Preliminary work suggested *G. lineola* developed at slightly higher temperatures than *P. vulgatissima*. Therefore, the effects of constant temperature on *G. lineola* eggs, larvae and pupae life-cycle stages were assessed at higher temperatures than for *P. vulgatissima. G. lineola* development of eggs, larvae and pupae occurred between and including 12°C and 29°C, 10 and 29°C and 12°C and 31°C respectively. No development occurred at 31°C, 31°C or 32°C for eggs, larvae or pupae respectively. The mean number of days for the completion of life-cycle stages generally decreased as the temperature increased (eggs: Kruskal-Wallis test, $H = 1215.203$, d.f. = 5, $P < 0.001$; larvae: Kruskal-Wallis test, $H = 511.356$, d.f. = 6, $P < 0.001$; pupae: Kruskal-Wallis test, $H = 428.188$, d.f. = 6, $P < 0.001$) (Table 3.1). The mean number of days for eggs to hatch decreased approximately fivefold from 28.9 days at 12°C to 5.7 days at 27°C. The mean time for larvae to develop decreased approximately sixfold from 76.8 days at 10°C to 13.1 days at 27°C. The mean number of days for pupae to develop decreased approximately fourfold from 18.6 days at 12°C to 4.6 days at 29°C. Decreases in development times were much greater for eggs and pupae between 12°C and 20°C and 10°C and 20°C for larvae than for temperatures greater than 20°C.

Similar to *P. vulgatissima*, high mortality levels (likely in cases as a result of fungus establishing on degrading leaf surfaces, particularly during the egg stage),

prevented development at temperatures less than 12°C for eggs and pupae(Table 3.2). Larvae obtained from eggs laid and reared at 20°C were placed at 10°C prior to hatch. Development time at temperatures lower than 10°C was not assessed at any life-cycle stage. No development occurred at 31°C, 31°C or 32°C for eggs, larvae or pupae respectively. Comparable with previous *P. vulgatissima* results at the higher temperatures, *G. lineola* eggs stage development period experienced an increase in days required for development at 29°C of 6.2 days. The mean number of days required for larval development days increased from 13.1 days at 27°C to 15.1 days at 29°C. Likewise, for pupae stage completion, the mean number of required development days increased from 4.6 days at 29°C to 5.0 days at 31°C. The higher temperatures indicated stressful non-optimal conditions as there was a decrease in the number of insects surviving, an increase in physical deformities for beetles that did complete development and no development at constant temperatures beyond these treatments.

For *G. lineola*, survival for the egg stage development period was greater than 70% from 12 to 25°C, dropping to 65% at 27°C and approximately 39% at 29°C (Table 3.2). Similar to *P. vulgatissima*, *G. lineola* larvae survival rates were lower when compared to other immature development stages due to longer required development times with lowest values of approximately 31% at 12°C and approximately 41% at 10°C and 42% at 29°C. However, from 15°C to 25°C, survival rates were greater than approximately 65%. For the pupae developmental stage, percentage survival was greater than 84% from 15°C to 27°C dropping to approximately 59% at 29°C, 30% at 31°C and 55% at 12°C.

3.1.3 Discussion

Temperature exerts a profound influence on the development of insects. The effects of temperature on the insect development may vary among species, but lower temperatures typically result in an increase in the duration of the time spent in each developmental stage. Results from this experiment showed that the developmental time for different stages of *P. vulgatissima* and *G. lineola* life-cycles declined with increasing temperature as expected. However, *P. vulgatissima* eggs and larvae did not complete development when the temperature treatment was greater than 28°C and *P. vulgatissima* pupae did not mature at temperatures higher than 27°C. *G. lineola* eggs and larvae completed stage development at slightly higher temperatures of 29°C while a limited number of pupae reached adulthood at 31°C. Comparing this data with the very limited published data on temperature-dependent

stage development of *P. vulgatissima,* there were slight differences in results. Kendall and Wiltshire (1998) recorded a mean development time for *P. vulgatissima* eggs at 15°C of 15 days compared to 13.2 days for this study. With large sample sizes for both data-sets, a difference of almost 2 days could have been due to a number of reasons ranging from unmanaged temperature variation in incubators used in experiments to genetic differences between different geographical populations (Grassberger & Reiter, 2002; Nabity *et al*., 2006). Kelly & Curry (1991a) noted an egg developmental period at 20°C of 5-7 days. A slightly greater mean development time of 7.4 days was recorded at the same temperature in this study. No temperature-dependent development data has been published for *G. lineola*.

Developmental times for these two beetle species can be compared as they frequently appear to operate within the same ecological niche. *G. lineola* egg stage development occurred over longer time periods, especially at 12°C and 15°C, with differences between the mean development times for the two species of 10.9 days and 2.5 days respectively. *G. lineola* larval stage development took longer at 10°C and 12°C, with differences of 15.7 days and 8.4 days respectively. However, for 15°C and higher, *P. vulgatissima* developmental times were larger, especially at 20°C and 25°C, with differences of 5.1 days and 2.7 days respectively. *G. lineola* pupae developed over longer time periods at the lower constant temperatures, with the greatest difference between developmental times occurring at 15°C of 2.1 days. Such differences in life-cycle stage completion for species operating within the same ecological niche have been recorded in other temperature-dependent development time studies despite the potential for interference competition (Blossey, 1995; Kontodimas *et al*., 2004).

Complications arise with insect development at unfavourable low and high temperatures. In a similar investigation on the developmental effects of various constant temperatures on another chrysomelid beetle's development, Lamb & Gerber (1985) acknowledged the tendency for *Entomoscelis americana* (red turnip beetle) to develop with visible abnormalities at temperature extremes, outside of the considered optimal range. In this experiment, it was demonstrated that constant exposure to high temperatures reduced the survival of *P. vulgatissima* and *G. lineola* eggs, larvae and pupae, with the incidence of malformed adults higher at temperatures greater than or equal to 28°C for both species. A small sample of *G. lineola* pupae were observed to complete development at 31°C with earlier immature life-cycle stages failing to do so, suggesting that suitable temperature ranges for development might differ between life-cycle stages. However, due to the fluctuation of temperatures under normal field conditions, a detailed study is needed to

determine the effects of exposure duration of the temperatures shown to be close to critical temperatures in this study.

The pattern of exposure to critical temperatures influences survival in many insect species. Although development times under constant temperatures are frequently similar to times under fluctuating temperatures (Campbell *et al*., 1974) some studies suggest that daily temperature cycles may play a role in insect development (Rock, 1985, Roltsch *et al*., 1990 Fornasari, 1995). Short-term exposure to low and high temperatures in daily temperature cycles may change mortality or development rates beyond those found with constant temperature studies, particularly when some constant temperatures go beyond the lower or upper temperature thresholds where complete stage development is rarely achieved (Beck, 1983). For example, *Plutella xylostella* (diamondback moth) development from egg to adult was recorded for constant temperatures within the range 8°C – 32°C only but for alternating temperatures 4°C – 12°C and 28°C – 38°C at 12L:12D, immature life-cycle development was completed also (Liu et al., 2002). Similarly no offspring of *Metopolophium dirhodum* (cereal aphid) survived as third instars when reared at 27°C but at a temperature of 31°C, survival was not reduced to zero if the exposure period was less than 8 hrs per day for up to 6 days (Ma *et al*., 2004).

Fungal infection of eggs at the lower temperatures of 10°C and 12°C was a study limitation, especially for *G. lineola*. In preliminary tests and experimental runs, it was found that fungal infection substantially reduced egg survival at temperatures less than or equal to 12°C for *P. vulgatissima*. However, when eggs were surface sterilised, results obtained enabled comparison of the temperature effects over a wider temperature range without confounding variables. This finding was similar to results in studies by Leppla *et al*. (1973), Connell (1981) and Byres (1995). Egg survival at the lowest temperatures tested in this experiment was 71.6% for *P. vulgatissima* at 10°C and 70.5% for *G. lineola* at 12°C which indicates that these temperatures were not unfavourable for egg survival and further development may be achieved for colder temperatures (< 10°C and 12°C respectively) under more natural conditions.

In conclusion, temperature was found to have pronounced effects on the development of *P. vulgatissima* and *G. lineola.* Results from this experiment showed that *P. vulgatissima* and *G. lineola* were sensitive to high constant temperatures greater than 28°C and 31° respectively. These temperatures are infrequent in their occurrence under current Irish climate conditions and would not be encountered constantly over a 24hr developmental period. Therefore under fluctuating summer temperature regimes, stage development is unlikely to be impeded.

3.2 Experiment Two: Temperature-Dependent Pre-Ovipositing Development of *Phratora vulgatissima*

Insects in temperate regions face seasonal challenges such as an absence of food, severe winter conditions and the necessity to synchronise reproduction with suitable environmental conditions (Goehring & Oberhauser, 2004). Various adaptations to these challenges include dormancy, migration and seasonal polyphenism, with combinations of these traits constituting a genetically programmed diapause syndrome (Tauber *et al*., 1986). Highlighting the dynamic aspects of the syndrome, Tauber *et al*. (1986) broadly defines diapause as

> *"a neurohormonally mediated, dynamic state of low metabolic activity. Associated with this are reduced morphogenesis, increased resistance to environmental extremes, and altered or reduced behavioural activity. Diapause occurs during a genetically determined stage(s) of metamorphosis, and its full expression develops in a species-specific manner, usually in response to a number of environmental stimuli that precede unfavourable conditions. Once diapause has begun, metabolic activity is suppressed even if conditions favourable for development prevail."*

Typical diapause among insects consists of several phases including induction, maintenance and termination (see Section 3.4). For many temperate insects, diapause termination is known to occur in mid-winter, before favourable conditions return in spring (Tauber *et al*., 1986; Hodek, 2002). Following this, most insects remain in a species-specific transitional state of post-diapause quiescence, with positive changes in limiting factors such as temperature, moisture and food availability allowing the organism to continue to a post-diapause direct development resumption phase (Tauber *et al*., 1986; Koštál, 2006). Where the diapausing life-cycle stage is the adults, the post-diapause transitional period that follows usually includes ovarian development leading to the initiation of oviposition by females while criteria for males include the resumption of mating behaviour and the capability to transfer sperm to females (Tauber *et al*., 1986).

Many studies have focused on insect diapause induction, maintenance and termination as well as their regulation mechanisms (Tauber *et al*., 1986; Hodek & Hodková 1988; Danks, 1992; Denlinger, 2002; Kostal, 2006). However, limited work has been devoted to post-diapause development and reproduction. Complexities arise in evaluating

the impact of individual environmental factors on post-diapause insects because many of these factors interact in a complex manner with each other, along with other biological factors, to determine behaviour, development and growth (Tauber *et al*., 1986). But similar to seasonal periods characteristic for normal development and growth, temperature is usually the primary governing environmental factor (Tauber *et al*., 1986). Because of this, many of the studies on post-diapause development and reproduction have focussed on the impact of temperature (Barker & Charlet, 1993; Kontodimas *et al*., 2004; Iranipour *et al*., 2010).

Studies have referred to *P. vulgatissima* emerging from overwintering sites and feeding for a period, before mating and ovipositing on the leaves (Kendall & Wiltshire, 1998; Karp & Peacock; 2004; Dalin, 2011). Additionally, the proportions of field-based *P. vulgatissima*, with immature, intermediate and mature ovaries at different stages during their post-diapause preoviposition stage were identified by dissection (Kelly & Curry, 1991a). These studies suggest that, like certain Coccinellidae species, *P. vulgatissima* require post-diapause feeding to initiate reproductive development leading to oviposition. However, the impact of environmental factors on *P. vulgatissima* post-diapause development has received limited attention in literature (Dalin, 2011). In this experiment, the effects of constant temperature on the post-diapause developmental period of adult *P. vulgatissima* (and to a lesser extent post eclosion developmental period) were explored to assess the time of first oviposition by females which is imperative for forecasting phenology and voltinism in response to climate conditions.

3.2.1 Materials and Methods

Stem cuttings collected in late winter from a plantation growing *Salix* clones with *S. viminalis* parentage were placed in individual pots containing a composition of soil, sand and vermiculate in a greenhouse with a 16L:8D photoperiod at a constant 20°C temperature (see Section 2.3). Foliage produced by the plants was used for adult insect feeding during experimentation. Overwintering adult *P. vulgatissima* were collected from resting sites in the field in late winter (February). Insects were transferred to the laboratory where they were distinguished by sex. This was achieved by examining the tarsus segments - in males, the second/third segments are wider and more round (leaf-shaped) than in females (P. Dalin, personal communication). Insects were placed in food tubs in groups of three – one female and two males – to allow for occasional male mortality.

The containers were base-lined with water-moistened 90 mm filter paper and replaced regularly between or during observations with excess moisture and frass within the container removed. Adults were provided with greenhouse-grown foliage every 2-3 days as per Section 3.1.1.

Insects were placed in climate chambers at constant temperatures of 10°C, 12°C, 15°C, 20°C, 25°C and 27°C ±0.5°C and photoperiod of 16L:8D with at least twenty replicates in each treatment. The beetles were assumed to have terminated diapause in the field but not initiated post-diapause development when collected as the mean temperature in the field had rarely increased above +5°C during the winter season. Some of the beetles were found to be parasitized by hymenopteran and tachinid species (Figure 3.3). Tubs in which the female died before oviposition were excluded from the study. In circumstances when a male died prior to the female ovipositing, the death was recorded and the male was replaced with another mature male. Tubs were monitored daily until eggs were recorded.

3.2.2 Results

The mean post-diapause development times for *P. vulgatissima,* but also mean post-eclosion development times for *P. vulgatissima* and mean post-diapause development times for *G. lineola* are presented in Table 3.3. Graphs for mean development times with associated statistics regarding pairwise comparison amongst temperatures and relative frequency distributions for development times are provided in Appendix II. Temperature had an effect on post-diapause preoviposition for *P. vulgatissima* (Kruskal-Wallis test, $H = 158.817$, d.f. = 5, $P < 0.001$). Female beetles laid eggs at all temperatures between and including 10 and 27°C. The mean number of days required for females to oviposit declined from 34.3 days at 10°C to 5.8 days at 25°C. As per *P. vulgatissima* immature life-stage developmental times, changes in required times before first oviposition were much greater between constant temperatures in the lower range of treatments when compared to constant temperatures in the upper range of treatments. The mean time for first egg-lay decreased from 34.3 days to 7.8 days between 10°C and 20°C respectively, a reduction of approximately 75%. The decrease in mean time to egg-lay from 7.8 to 5.8 days from 20°C to 25°C respectively was less pronounced.

Table 3.3 Mean (± SE) post-diapause development times (in days) and mean (SE not included due to low numbers) post-eclosion development times (in days) for *P. vulgatissima* at different constant temperatures, and mean (SE not included due to low numbers) post-diapause development times for *G. lineola* at different constant temperatures for number of samples (N) (no development denoted by -----). Different letters for post-diapause preoviposition development indicated a significant difference between temperatures (Kruskal-Wallis, P<0.001 and post hoc pairwise comparison, P=0.05).

Temperature (°C)	Post-diapause preoviposition	N	Diff	Post-eclosion imago preoviposition	N	Diff	Post-diapause preoviposition	N	Diff
	P. vulgatissima			***P. vulgatissima***			***G. lineola***		
10	34.26 ± 1.44	23	AB						
12	28.10 ± 1.39	21	B						
15	12.47 ± 0.29	36	BC	27.00	3		16.50	3	
20	7.79 ± 0.36	33	D	14.18	11		8.00	4	
25	5.78 ± 0.11	40	DE	15.17	6		5.50	2	
27	5.95 ± 0.24	39	E	12.71	7		-----		
28				14.00	2		6.67	6	

Temperature appeared to have an impact on post-eclosion preoviposition for *P. vulgatissima* also (Table 3.3).Graphs for mean development times are provided in Appendix II. The mean number of days required for first egg-lay decreased from 27.0 days at 15°C to 12.7 days at 27°C before rising to 14 days at 28°C. No adults survived long enough to reproduce at the lower temperatures of 10°C and 12°C. Tub numbers per temperature were much lower compared to post-diapause experiment.

3.2.3 Discussion

After diapause is terminated and environmental conditions become favourable, post-diapause development commences. Sufficient energy reserves must be accumulated before diapause to survive this process and enable post-diapause development that may involve metabolically expensive functions such as flight and reproduction (Hahn & Denlinger, 2011). Upon emerging from their overwintering sites in spring, *P. vulgatissima* fly from these sites back into the willow plantation and after a short feeding period, copulation and egg-laying commence (Kelly & Curry, 1991a; Kendall *et al*., 1996; Kendall & Whitshire, 1998; Sage & Tucker, 1998; Peacock & Herrick, 2000). Most of the published studies on the effects of environmental factors on insect development concentrate on the development of immature life-cycle stages and not the post-diapause and post adult eclosion stages.

However, more recent studies have accounted for these preoviposition stages as part of a complete biological cycle (Kontodimas *et al*., 2004; Eliopoulos *et al*., 2010; Stathas *et al*., 2011). The impact of individual physical factors on the organism at these times is not easily assessed because environmental factors including temperature, moisture and day-length interact to determine post-diapause development (Tauber & Tauber, 1976; Koštál, 2006; Hodek, 2012). However, with temperature playing a dominant role, as seen in Section 3.1, these are important stages of the biological cycle to be considered, that can ultimately define the occurrence of subsequent stages and emerging generations.

Parasitoid induced mortality had a major impact on insect numbers used in the experiment. Out of 192 groups set up for this experiment, over 30% were found to have been impacted upon by parasitoids, with obvious parasitization occurring without the need to perform dissections in the majority of cases (Figure 3.3). These parasitoids were identified as *Medina luctuosa* (Diptera: Tachinidae), *Centistes collaris* (Hymenoptera: Braconidae) and *Perilitus asper* (Hymenoptera: Braconidae), although the identification of the latter species was inconclusive with the possibility that it was a new undescribed species (Figure 3.3). These differed to other identified parasitoids of *P. vulgatissima* such as the tachinid *Degeeria luctuosa* in the UK, and the braconid *Perilitus brevicollis,* the tachinid *Anthomyiopsis nigrisquamata*, three species of Heteroptera (two mirids *Orthotylus marginalis* and *Closterotomus fulvomaculatus*, and the anthocorid *Anthocoris nemorum* and syrphids (Syrphis spp.) in Sweden (Kendall & Whitshire, 1998; Björkman *et al*., 2003; Dalin *et al*., 2011; Stenberg, 2012; Baffoe *et al*., 2012).

Figure 3.3 Adult *P. vulgatissima* with tachinid puparium protruding from abdomen (left) and adult *Medina luctuosa* (right).

Attempts were made to evaluate the mean length of time required by imago *P. vulgatissima* before first oviposition at different constant temperatures. Due to difficulties in rearing populations of insects, especially at the upper temperatures of the tested range where development with physical abnormalities was frequent, the number of groups for this experiment was low compared to numbers in the post-diapause experiment. However, time to first oviposition for post-eclosion *P. vulgatissima* was *at least* twice as long as that for post-diapause *P. vulgatissima* at each temperature. Although not quantified with a high degree of accuracy due to poor numbers and with no comparative published studies for similar or other insect species such an outcome was still of considerable importance for *P. vulgatissima* phenology/voltinism model construction (see Section 6.2). However, further comparative studies of these life-cycle processes would be beneficial for assessing future seasonal beetle occurrence.

Much like adult *P. vulgatissima*, adult *G. lineola* overwinter in sheltered places such as the bark crevices of mature trees, weathered fence-posts, leaf litter, hollow Phragmites species stems and in other similarly enclosed locations, within a few hundred metres of the coppice plantation with relatively few beetles remaining in the coppice fields during the winter (Kendall *et al*., 1996; Kendall & Whitshire, 1998; Sage *et al*., 1999; Sipura & Tahvanainen, 2000; Björkman *et al*., 2004). Few were found during field collections however. This presented a problem when trying to attain information on *G. lineola* post-diapause first oviposition. A small population of overwintering *G. lineola* was obtained and used to investigate this life-cycle process at a number of different temperatures, particularly for the higher end of the range. With restrictions due to low numbers of paired males and females, only crude assumptions could be made (Table 3.3). However, it did appear that *G. lineola* required a similar amount of time for post-diapause development to occur at these temperatures as *P. vulgatissima*.

3.3 Experiment Three: Temperature-Dependent Development and Survival of *Phratora vulgatissima* on Different Willow Varieties

Host plants can have direct or indirect effects on insect behaviour, ecology and physiology with defences including structures such as spines or trichomes, and secondary plant compounds which include alkaloids, phenolics and terpenoids (Gullan & Cranston, 2005). Additionally, host plant quality for insect herbivores is influenced by a range of nutritional

factors including nitrogen, carbon and elemental minerals (Awmack & Leather, 2002). Variation in development, survival, and fecundity of phytophagous insects is mainly due to variation in qualitative and quantitative amounts of these nutrients among host plants (Hough & Pimentel, 1978; Tsai & Wang, 1996; Roy & Barik, 2012). Plants with greater nitrogen content may have a preferable nutritional quality, potentially leading to increased fecundity but reduced survival levels for some insect species due to increased levels of defensive chemistry (Awmack & Leather, 2002). Furthermore, poor plant quality may lead to increases in development times, expanding the predation period for natural enemies to impact upon survival rates – the slow growth/high mortality hypothesis (Clancy & Price, 1987).

Recent studies have attempted to quantify the dual effect of temperature and host plant on insect development with example species including *Brachycaudus schwartzi* (peach aphid) on different commercial orchard trees (Satar & Yokomi, 2002), *Mecinus janthinus* (European stem-mining weevil) on invasive toadflax species (McClay & Hughes, 2007), *Tetraneura nigriabdominalis* (the root aphid) on rice, corn, and sorghum seedlings (Kuo *et al.,* 2006), *Plutella xylostella* (diamondback moth) on brassicaceous plants (Golizadeh *et al*., 2007), *Altica litigate* Fall (flea beetle) on weedy and cultivated plants (Pettis & Braman, 2007) and *Bemisia tabaci* Q biotype (sweet potato whitefly) on different orchard fruit and vegetable plants (Han *et al*., 2013). Although many studies such as these do not thoroughly examine the underlying mechanisms that give rise to noted differences in insect performance when reared on different host plants, they do identify the variability under similar temperature regimes that can exist in insect development when present in polycultures. Similarly, the objective of this experiment was to assess *P. vulgatissima* development when larvae were reared on different willow varieties at different temperatures.

Native willow beetle species such as *P. vulgatissima* and *G. lineola* have expressed feeding preferences among willow varieties based on *Salix* species mainly due to leaf morphology and levels of phenolic compounds, water content and nitrogen content of the leaves (Kelly & Curry, 1991b; 1991c; Kendall *et al*., 1996; Rank *et al*., 1998). Host variety food source significantly impacts upon larval development and adult fecundity, as well as survival and weight gain under laboratory conditions (Peacock *et al*., 2002; Peacock *et al*., 2004). Using a similar methodology to that of Kendall *et al*. (2006), P. Fanning (personal communication) examined the susceptibility of new commercial willow varieties to herbivory by *P. vulgatissima* and *G. lineola* adults. The percentage of leaf disc area consumed over a 24 hour period varied depending on variety (see Appendix III). The choice of varieties that were used in this experiment were based on these results.

3.3.1 Materials and Methods

Salix foliage cuttings were taken from a willow genotype yield trial that had been established at Teagasc Crops Research Centre, Oak Park, Co. Carlow in May 2007. P. Fanning (personal communication) collected cuttings from the same site for their work. SRCW had not been cut-back between their experiment and this. Based on unpublished work performed by P. Fanning on the susceptibility of commercial *Salix* varieties to feeding damage by *P. vulgatissima*, four willow varieties – *Tora, Resolution, Tordis* and *Inger* – were chosen. These varieties were selected as all were predated upon during the feeding trial with two (*Tora* and *Tordis*) more predated upon compared to the other two (*Resolution* and *Inger*) (P. Fanning, personal communication). Varieties included in this trial were from the UK/Swedish European Willow Breeding Partnership. Willow rods were randomly cut from the outer guard rows of random blocks containing varieties been used for the trial during the winter of 2011/2012. These rods were placed individually in pots containing a composition of soil, sand and vermiculate in a greenhouse with a 16L:8D photoperiod at a constant 20°C temperature (see Section 2.3). Foliage produced by the plants was used for adult insect feeding during experimentation.

Larvae were collected from laboratory beetle cultures (see Section 2.2) within one day of hatch and they were distributed between food tubs, along with stem cuttings of the selected willow varieties that were placed through the lids of 1.5 ml micro-centrifuge tubes containing water. Tubs were provided with perforated lids and lined with 90 mm filter paper. Each dish contained ten larvae and each cutting had 3-5 leaves attached. Tubs were assigned to temperatures 12°C, 15°C, 20°C, 25°C and 27°C with eight tubs per variety. Stem cuttings were changed every 2-3 days while excess moisture and accumulations of frass removed. Additionally, mortality was assessed during observations by gently prodding discoloured or stationary larvae with a soft paintbrush. Dead larvae were removed and the date was recorded. Larval development was complete when pupation occurred.

3.3.2 Results

The development time and percentage survival rates for *P. vulgatissima* reared at five constant temperature treatments on four host plants are presented in Table 3.4 and Table 3.5. Graphs for mean development times for larvae reared on the different hosts at different temperatures with associated statistics regarding pairwise comparison amongst hosts, and percentage survival rates on the different hosts at different temperatures are provided in Appendix III. The number of days to pupation was affected by the willow variety fed to the larvae at all temperature treatments (12°C: Kruskal-Wallis test, $H = 27.626$, d.f. = 3, $P < 0.001$; 15°C: Kruskal-Wallis test, $H = 29.082$, d.f. = 3, $P < 0.001$; 20°C: Kruskal-Wallis test, $H = 8.903$, d.f. = 3, $P = 0.031$; 25°C: Kruskal-Wallis test, $H = 23.328$, d.f. = 3, $P < 0.001$; 27°C: Kruskal-Wallis test, $H = 19.835$, d.f. = 3, $P < 0.001$). The time required for larvae to pupate decreased as temperature increased; 45.4 to 49.0 days at 12°C, 31.0 to 32.5 days at 15°C, 19.5 to 20.2 days at 20°C, 14.0 to 14.9 days at 25°C and 13.7 to 14.3 days at 27°C.

Table 3.4 Mean (± SE) development times (in days) for *P. vulgatissima* larvae on different willow varieties at different constant temperatures for number of samples (N). Different letters indicated a significant difference between varieties (Kruskal-Wallis, P<0.001 and post hoc pairwise comparison, P=0.05).

Temperature (°C)	Tora	N	Diff	Resolution	N	Diff	Tordis	N	Diff	Inger	N	Diff
12	47.96±0.61	79	A	45.44±0.38	80	B	48.28±0.30	79	A	48.96±0.49	80	A
15	31.04±0.22	79	A	31.07±0.22	80	A	31.50±0.21	80	A	32.53±0.20	79	B
20	19.53±0.12	80	A	19.76±0.14	77	A	19.85±0.12	80	A	20.15±0.15	80	B
25	14.89±0.14	78	A	14.02±0.10	77	B	14.33±0.13	78	B	14.38±0.11	76	B
27	13.75±0.12	79	A	13.88±0.13	80	A	13.72±0.10	80	A	14.34±0.11	80	B

Overall, *P. vulgatissima* larvae took longer to develop on *Inger* variety but this was not consistent for all temperature treatments. Development was longer on *Inger* variety when compared against other varieties at 12°C, 15°C, 20°C and 27°C. Development was longer on *Tora* variety at 25°C. The greatest differences in development time between varieties occurred at 12°C. Mean larval development of 45.4 days at 12°C was shorter on *Resolution* variety when compared against the other three varieties.

Table 3.5 Mean percentage survival rates for *P. vulgatissima* larvae on different willow varieties at different constant temperatures.

Temperature (°C)	Tora	Resolution	Tordis	Inger
12	32.91	31.25	45.57	31.25
15	68.35	73.75	77.50	78.48
20	77.50	81.82	93.75	82.50
25	71.79	64.94	61.54	72.37
27	72.15	73.75	75.00	81.25

Assuming linear relationships between larval developmental rate values (reciprocal of development time – see Sections 4.1.1) on different varieties across the range of constant temperatures, a comparison of regression lines was performed (Figure 3.4). Multiple regression analysis showed there was no offset between the four lines as the slopes of the lines representing the different varieties did not vary significantly (P = 0.96) and the intercepts of the lines did not vary significantly (P = 0.89).

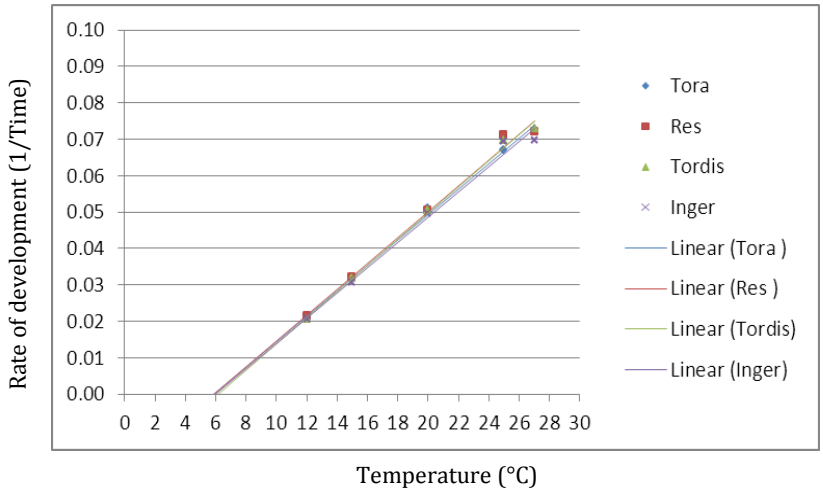


Figure 3.4 Multiple regression graph for *P. vulgatissima* larvae reared on different willow varieties at different constant temperatures.

Percentage survival was greater than 61% on all host plant varieties between and including 15°C and 27°C. Lower percentage survival between approximately 31% and 46% were recorded for larvae at 12°C which was similar to results obtained during previous larval stage development (see Section 3.1.2). Percentage survival rates on host plants were different depending on constant temperature, with higher values recorded for *Tordis* variety at 12°C and 20°C and *Inger* at 15°C, 25°C and 27°C. *Tora* variety provided the lowest percentage survival rates at 15°C, 20°C and 27°C, while percentage survival was lowest for *Resolution* and *Inger* varieties at 12°C and for *Tordis* variety at 25°C.

3.3.3 Discussion

Based on the results from this experiment, all varieties assessed were suitable host plants for *P. vulgatissima* larval development for all temperatures. The only consistent difference between varieties was the longer development time on *Inger*, except at 25°C where development was longer on *Tora* variety. As the different host plant varieties chosen were based on the work by P. Fanning (personal communication), where differences in consumption by adults were examined, it was hypothesised that *P. vulgatissima* larvae would feed and develop at an accelerated rate on one or two of the selected varieties (*Tora* and/or *Tordis* varieties) compared to the others. Host plant chemistry is considered to be one of the most important factors affecting the performance of herbivorous insects. Increased consumption by adult insects on a specific host would not necessarily reflect a preference in food source and performance of larvae however.

Temperature-dependent insect development studies are easiest to conduct in the middle range of temperatures, where the insect's higher survival rates allow results to be obtained from relatively large numbers of insects (Akey *et al*., 1988). For this reason, the effects of food on larval development were assessed at temperatures already identified as appropriate for complete development with survival rates greater than 40% (see Section 3.1.2). Although survival rates at the lowest temperature of 12°C were lower for larval cohorts reared on varieties *Tora*, *Resolution* and *Inger* when compared to survival rates of larvae in Section 3.1, numbers were sufficient for host and temperature comparison. Multiple regression analysis showed there was no significant difference between the regression lines representing the larvae developmental rate values on different varieties across the range of temperatures. This suggested that although there were differences between larvae development on varieties at different constant temperatures, the response of larval development to temperature was the same irrespectively of host plant variety. However, past studies have shown the impact of variety on *P. vulgatissima* larvae development (Peacock *et al*., 2002). Furthermore, the progeny of *P. vulgatissima* adults fed on different willow varieties exhibited differences in days to pupation when reared on a single *Salix* variety (*S. dasyclados*) or on the same variety as fed to adults (Peacock *et al*., 2004). Future work involving more recent varieties from the UK/Swedish European Willow Breeding Partnership being trailed for resistance and yield for future inclusion in polyculture plantations could reveal differences in larvae development times that would need to be accounted for during phenological and voltinism model construction. Such work could account for larvae development with *Doris* variety, as additional host plant experiments revealed that although this variety supposed a low survival rate of

approximately 30%, it offered a decreased larval development time of 30.4 days at 15°C, 2.1 days less than the assessed *Inger* variety at the same temperature (data not shown).

3.4 Experiment Four: Diapause Induction for *Phratora vulgatissima*

Diapause is an adaptive state of arrested development that helps synchronise active stages with suitable environmental conditions to increase survival potential during unfavourable seasons (see Section 3.2) (Tauber *et al*., 1986; Danks, 1987; Hodek, 2012). Many species are capable of diapause at one and less often several stages in their life-cycle, examples of the latter being *Nebria brevicollis* (European gazelle beetle) and *Patrobus atrorufus* (ground beetle) diapausing as larvae and adults (Thiele, 1969). Embryonic, larval, pupal and adult diapauses are documented and differences in stage-specificity of diapause within a single order and even within a single genus are recorded (Tauber *et al*., 1986). The typical diapause of insects consists of several phases including diapause induction, diapause maintenance, diapause termination and post-diapause development (Tauber *et al*., 1986). Although insect diapause may be influenced by abiotic factors, insect genetics or a combination of both, the environmental cues such as food, moisture and population density have been shown to have important regulating effects on insect seasonal cycles (Tauber *et al*., 1986). However, temperature and photoperiod are the prominent token stimuli governing diapause expression. Of these, photoperiod is the most dominant influence for temperate-zone species with temperature being the main diapause-inducing factor for species in equatorial and subterranean environments (Tauber *et al*., 1986). These environmental cues are perceived by the insect, often long in advance of the diapausing stage, sometimes spanning back to the grandparental generation for mulitvoltine insects such as aphids (Tauber *et al*., 1986). The duration of sensitivity to diapause-inducing stimuli can vary considerably, from days to months and over many life-cycle stages, an example of the latter being *Leptinotarsa decemlineata* (Colorado potato beetle) which is sensitive to photoperiod for determining adult diapause in both the larval and adult stages (De Wilde, 1969)

Photoperiodic reactions of insects are diverse and dynamic. While some species rely on photoperiod to regulate almost their entire life-cycle, other species require this predictable seasonal pattern to regulate a pivotal aspect of their life-cycle (Tauber *et al*., 1986). Since the early classical study of Kogure (1933) on the role of photoperiod in the

induction of embryonic diapause in *Botnbyx mori* (domesticated silkworm), day-length has been reported as a major inducing factor in the diapause of many other species (Beck, 1962). For many of these species, the photoperiodic responses are represented by the percentage of individuals entering or ending diapause as a function of stationary day-lengths. Critical photophase is obtained when the percentage diapause is plotted against a range of different naturally occurring day-lengths. It is defined as a day-length inducing diapause in 50% of a population. Photoperiodic response curves can be divided into short-day and long-day types with long-day types typically associated with insects that develop during long-day conditions.

The most distinct feature of adult diapause is the suppression of reproductive functions – reproductive diapause. The regulation of reproductive diapause has been studied extensively as it can be easily defined as an arrest of oocyte development in females and the absence of egg-laying (Pener, 1992). Reproductive diapause throughout this study refers to reproductive diapause in females; although much less investigated but nevertheless existent for male insects (Pener, 1992), it is female reproductive diapause that was of importance during this research. Reproductive adult diapause in the female has two major adaptive functions: it improves the chances of survival during unfavourable seasons and it directs and confines oviposition to a period of the year that is optimal for the survival of eggs and hatchlings (Pener, 1992).

Diapause during the adult stage for coleopteran species is the most common form of diapause with about 90% of beetle species belonging to the families of Chrysomelidae, Coccinellidae and Curculionidae (Danks, 1987). Hodek (2012) reviewed recently published studies dealing with reproductive diapause in coleopteran species and remarked that no break from the classic paradigm had been made with previous theories been further supported and extended. Such studies included the determination of photoperiod sensitive-stages and diapause inducing day-lengths for chrysomelids *Galerucella calmariensis* (black-margined loosestrife beetle) (Velarde *et al*., 2002) and *Plagiodera versicolora* (imported willow leaf beetle) (Ishihara & Hayashi, 2000).

Investigating the effects of photoperiod on the induction of diapause in insects is done using unchanging photophase (light phase) and scotophase (dark phase) at a constant temperature. The term photoperiod is used to refer to the total cycle composed of a period of light (photophase) and a period of dark (scotophase), following the terminology of Beck (1962). This was recommended as a means of avoiding the ambiguous use of the term photoperiod, commonly used to refer to both the total light/dark cycle, and the light portion of the total cycle. The following experiment investigated the effect of a declining

photophase on diapause incidence in *P. vulgatissima*. A similar methodology as that described by Bean *et al*. (2007) and Dalin (2011) were used to estimate critical photophase/day-length (CDL) in *P. vulgatissima* populations.

3.4.1 Materials and Methods

The insects were cultured from eggs to adults under six photoperiod treatments (17L:7D, 16L:8D, 15L:9D, 14L:10D, 13L:11D and 12L:12D and at a constant temperature of 20°C inside the climate chambers. The light-dark cycles chosen were based on photoperiod conditions that *P. vulgatissima* experience in the natural environment in Ireland (Figure 3.5). Characteristic of insects that develop and reproduce under long-day conditions, the proportion of females in diapause was expected to increase with declining photophase.

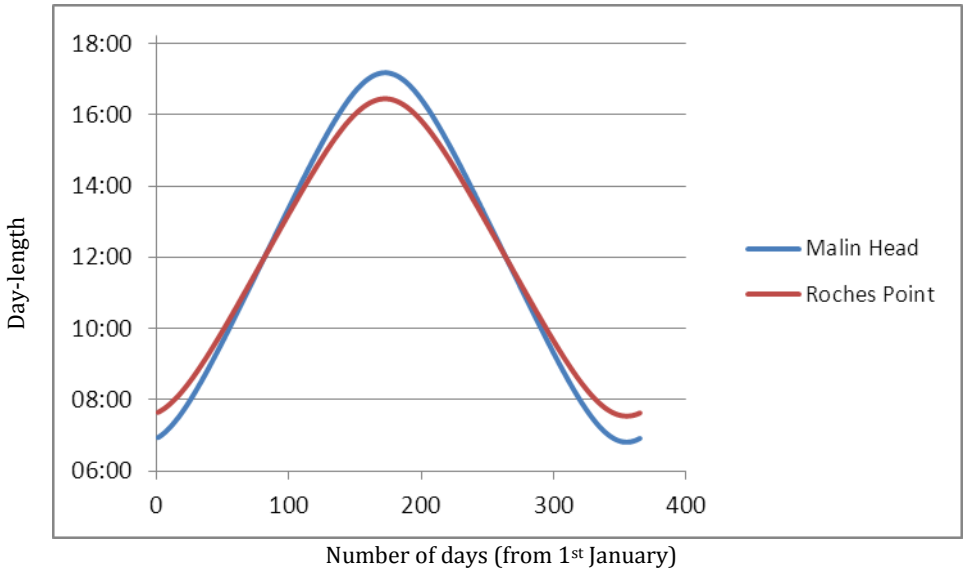


Figure 3.5 Difference in day-length (time between sunrise and sunset) between northern (Malin Head) and southern (Roche's Point) Irish synoptic stations.

Eggs were obtained from laboratory culture (see Section 2.2) and emerging larvae were reared in transparent snap on lid containers 19 cm (height) x 14 cm (width) x 5 cm (length) with 80-100 larvae in each container (Figure 3.6). Larvae were provided with fresh leaves from greenhouse-grown *Salix* (see Section 2.3) every second day while excess moisture and frass build-up within the container was removed. The bases of the containers were lined with tissue that was replaced regularly. Pre-pupae were observed approximately two weeks later with 3rd instar larvae actively moving off foliage and

beginning to curl under the tissue. Emerging adult beetles were provided with foliage. Individual beetles at each treatment were distinguished by sex after 3-4 days (see Section 3.2.1) and placed in pairs of one male and one female in food tubs. The number of pairs tested at each photoperiod was greater than fifteen. These paired adults were kept under experimental conditions for a further 20-25 days and if no oviposition occurred, the insects were scored as diapause. The propensity of diapause under different photoperiods was analysed using logistic regression (PROC GENMOD, binomial, logit) employing SAS institute software. Reproductive status was the dependent, binary response was the variable (1 for diapause, 0 for reproductive) and the light-hours the independent variable. Inverse prediction was used to calculate CDL.

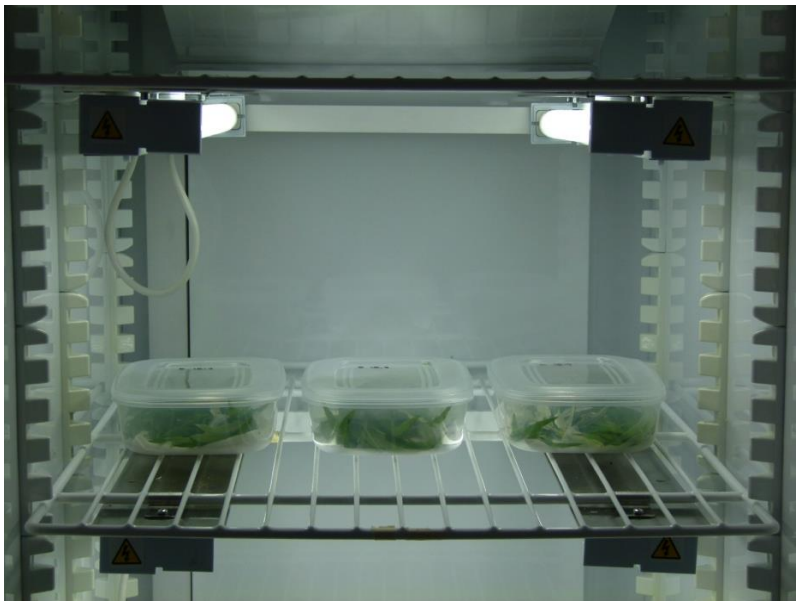


Figure 3.6 Snap on lid containers for *P. vulgatissima* diapause induction experiment.

3.4.2 Results

The proportion of female *P. vulgatissima* in diapause was affected by photoperiod (Figure 3.7). The CDL was estimated to be 14.92 hrs (95% CI: 14.46-15.41 hrs). The final numbers of insects in each photoperiod (N values) were lower than preferred due to natural mortality during immature life-cycle stage development. Pairs of beetles reared from eggs to adult under short days 12L:12D (N=19) failed to oviposit while one pair oviposited under short days 13L:11D (N=15). Almost 50% of pair kept under 14L:10D (N=15) and 30% of pairs observed under 15L:9D (N=17) oviposited. Under long days 16L:8D (N=15), 80% of pairs produced eggs while 100% of pairs produced eggs under long days 17L:7D (N=16).

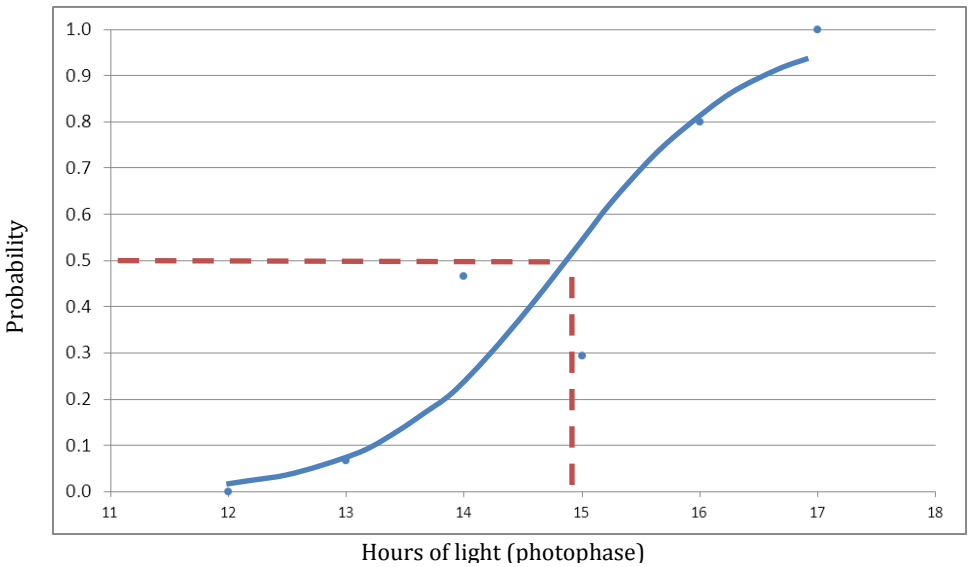


Figure 3.7 CDL for *P. vulgatissima.*

3.4.3 Discussion

The results from this experiment showed that *P. vulgatissima* has a reproductive diapause, induced by declining day-length (photophase after summer solstice) with a CDL of 14.9 hrs – approximately 14 hrs and 56 mins – under constant 20°C. These results are comparable with those by Dalin (2011) where CDL was estimated to be 18.1 hrs – approximately 18 hrs and 8 mins – for a Swedish population under similar test conditions. Based on these results and annual day-length cycles, and assuming that the adult phase is the photoperiod-sensitive stage, it is estimated that *P. vulgatissim*a will enter reproductive diapause within the first half of August in Ireland, similar to populations in the Sweden study conducted by Dalin (2011). Populations of the same species can differ in their responses to environmental conditions such as photoperiod, especially among species that occupy various geographic areas encompassing different latitudes such as *P. vulgatissima*. This kind of geographic variation in life-history is the result of natural selection while an insect species expands its distribution (Tauber *et al*., 1986, Danks, 1987). Examples include reproductive diapause for a northern strain (Ithaca, New York, 42°27′ N) of *Chrysopa carnea* (green lacewing) occurring at 13.75 hrs, one hour longer than a southern strain (Chandler, Arizona, 33°19′ N) at 12.75 hrs (Tauber & Tauber, 1976) and reproductive diapause for a northern population (Kentucky, 38°80′ N) of *Geocoris punctipes* (big-eyed bug) occurring at 13.20 hrs, 40 minutes longer than a southern population (Georgia, 31°82′ N) at 12.40 hrs (Ruberson *et al*., 2001). Wang *et al*. (2012) concluded that CDL for diapause induction in the *Sericinus montelus* (swallowtail butterfly) was positively correlated with

latitude and increased toward the north at a rate of about one hour for each 6.7 degrees of latitude also.

In many studies examining the seasonal adaptations of insects, the term facultative and obligatory have been used to categorize diapause. The term facultative diapause refers to diapause that could be averted under certain environmental conditions, when the environmental cues are known and alterable (Tauber *et al*., 1986). Obligatory diapause implies that diapause is expressed by all individuals in a population at some point throughout their generation, regardless of favourable environmental conditions (Tauber *et al*., 1986). *P. vulgatissima* has been classified as having a facultative reproductive diapause induced by declining day-length (Dalin, 2011). While decreasing day-length is accepted as the major inducing factor in the diapause of many species in temperate regions, the effect may be modified by other factors including temperature. For example, CDL induction for another chrysomelid *Diorhabda elongata* (tamarisk leaf beetle) ranged from 15 hrs and 4 mins at 22°C to 14 hrs and 14 mins at 34°C, a difference of 50 mins (Bean *et al*., 2007). Similar interactions between photoperiod and other factors, primarily temperature and host plant, have been reviewed (Tauber *et al*., 1986). Therefore, the effects of different environmental cues and their interactions on diapause induction in *P. vulgatissima* merit more attention.

The photoperiodic responses of insects are represented by the percentage of individuals entering or terminating diapause as a function of stationary photoperiods, with a resulting characteristic response curve. As the response curve usually rises very abruptly over the range (usually between two consecutive day-lengths), CDL is defined as a day-length inducing diapause in 50% of a population. An abrupt rise over the range of tested photoperiods did not occur for this experiment however. With the photosensitive life-cycle stage unidentified, all stages were treated as such with insects reared from eggs to adults under strict photoperiod regimes. Although observation and maintenance of the populations was carried out during daylight hours, disturbance in the laboratory environment outside of their set regimes in the form of light contamination may have occurred. The precision of the time measurement phenomena involved in the photoperiodic control of insect diapause has been demonstrated by Adkisson (1964) investigating diapause in *Pectinophora gossypiella* (pink bollworm) with discrimination between photoperiods differing by only 15 mins. Host plant quality was not considered to be an influencing factor in this experiment as all insects were reared on similar food stock and all photoperiod treatments would have been affected otherwise. Additionally, moisture was rejected as an environmental variable as all rearing chambers were set up and maintained in a standard manner. However, there was an outbreak of the

entomopathogenic fungus *Beauveria bassiana* in some of the containers, resulting in high mortality levels of larvae, pupae and adults, ultimately reducing numbers in every treatment. This may have produced stressful environments for adults to reproduce also as this fungus species has been shown to negatively impact upon reproduction in several insects including coleopteran species (Mulock & Chandler, 2001).

3.5 Experiment Five: Fecundity and Survival of *Phratora vulgatissima* at Different Constant Temperatures

Like development time, insect reproduction is governed by interactions between intrinsic life-history traits and extrinsic factors such as temperature, photoperiod, food quality and moisture (Tauber *et al*., 1986; Danks, 1994; Tauber *et al*., 1998; Awmack & Leather, 2002). Among the abiotic factors, temperature may be the most important because it directly affects reproductive parameters, such as duration of oviposition period, total fecundity and egg viability (Pervez & Omkar, 2004; Naves *et al*., 2006; Bonato *et al*., 2007). Optimal temperature ranges for egg production vary among insect species depending on geographic distribution, with these ranges generally reflecting the temperatures that a species normally encounters during its reproductive period (Engelmann, 1970). However, species-specific optimal temperatures for peak oviposition are greater than the highest environmental temperature experienced for many temperate-zone insects (Frazier *et al*., 2006). For some temperate-zone insects, these optimal temperatures for population growth are rarely reached, even during warmer summer conditions (Deutsch *et al*., 2008). Therefore, as many temperate-zone insects could show enhanced reproductive performance at higher temperatures, understanding the impact of temperature on reproduction is essential for estimating the timing of egg occurrence and explaining the annual phenology of *P. vulgatissima*. The goal of this study was to investigate the effects of different constant temperatures on the reproductive potential of *P. vulgatissima*.

3.5.1 Materials and Methods

Similiar methodology as that described by Son & Lewis (2005b) was used to investigate the effects of temperature on the reproduction and survival of the adult blue willow beetle. Copulating *P. vulgatissima* were collected in the field towards the end of spring (May, 2010) (see Section 2.1). No egg clutches for this species were observed on the crop foliage at the time of collection. Fresh foliage was collected from the same site on a weekly basis and stored in a 4°C cold room to be used for feeding and serve as an ovipositioning platform for the beetles.

In the laboratory, three beetles – two females and one male – were placed in food tubs with perforated lids. Methodology applied for unit set-up and maintenance was similar to that for previous experiments (see Sections 3.1.2, 3.2.2 and 3.3.2) Insects were incubated at constant temperature of 10°C, 12°C, 15°C, 20°C, 25°C and 27°C – with approximately 15 tubs per temperature. The experiment was run at a standard photoperiod of 16L:8D. Insects were monitored every 1-2 days to record first oviposition for each female beetle. Once oviposition commenced, eggs were collected approximately every 2-3 days. For calculation purposes, the oviposition events were assumed to have occurred at the midpoint between two consecutive observations (Roy *et al*., 2002). Egg viability was not assessed. When a death was recorded, the surviving beetle was sexed (see Section 3.2.1). If the dead beetle was male, it was replaced with another male from the stock collection. If the dead beetle was female, the death was noted and this replication was no longer observed. Observations of insects continued until all females were dead.

3.5.2 Results

Results for mean oviposition periods (defined as the number of days from first to last oviposition) and total fecundity (defined as the total number of eggs laid per female) under different constant temperatures for *P. vulgatissima* are presented in Table 3.6. Graphs for mean oviposition period and total fecundity with associated statistics regarding pairwise comparison amongst temperatures, and age-specific fecundity curves are provided in Appendix IV. Oviposition periods were affected by temperature (Kruskal-Wallis test, $H = 50.977$, d.f. = 5, $P < 0.001$). The duration of oviposition periods decreased from 78.9 days at 10°C to 22.5 days at 27°C. Temperature had an impact on total fecundity also (One-way ANOVA, $F = 3.965$, d.f. = 5, $P = 0.003$). Tukey's HSD (honestly significant difference) post-hoc test ($\alpha = 0.05$) showed that as constant temperature treatments increased from 10 to 15°C, total egg production significantly increased from 127.1 to 204.9 eggs per female.

Total fecundity did not increase significantly from 204.9 to 218.9 eggs per female for the mid constant temperature treatments of 15 and 20°C. Total egg production decreased from 218.9 to 151.3 eggs per female from 20°C to 27°C, although this was not a significant finding. Most of the eggs were laid in clutches on the leaves and sometimes on the sides of the containers.

Table 3.6 Mean (± SE) oviposition period (number of days from first to last oviposition) and total fecundity (total number of eggs laid per female) for *P. vulgatissima* at different constant temperatures for number of samples (N). Different letters indicated a significant difference between temperatures (Kruskal-Wallis, P<0.001 and post hoc pairwise comparison, P=0.05 for mean oviposition period and one-way ANOVA, P =0.003 and Tukey's post hoc test, P = 0.05 for total fecundity).

Temperature (°C)	Mean oviposition period	N	Diff	Total fecundity	N	Diff
10	78.86 ± 7.96	14	A	127.07 ± 12.38	14	A
12	61.36 ± 8.35	14	AB	164.21 ± 16.15	14	AB
15	48.58 ± 3.75	12	AB	204.92 ± 13.46	12	B
20	31.07 ± 2.41	14	BC	218.93 ± 22.01	14	B
25	23.00 ± 1.69	15	C	146.07 ± 20.91	15	AB
27	22.53 ± 1.41	15	C	151.33 ± 17.69	15	AB

3.5.3 Discussion

Life-history traits related to reproduction for *P. vulgatissima* across a range of different constant temperatures were assessed in this experiment. Temperature had a notable impact on *P. vulgatissima* reproduction. Significant differences were detected in both oviposition period and total fecundity. The results from this experiment were in general agreement with those found in other studies investigating temperature-dependent reproduction traits of coleopteran species (Wang *et al*., 2007; Zheng *et al*., 2008; Omkar *et al*., 2009).

Salix predated upon by adult beetles significantly affects the length of the oviposition period and the number of eggs laid per day (Peacock *et al*., 2004). *P. vulgatissima* were provided with fresh foliage from sites with high infestation levels. By and large, the majority of willow varieties planted in these SCRW sites were of *S. viminalis* parentage or grand-parentage. In the study by Peacock *et al*. (2004), *S. viminalis* proved to be a popular choice for egg-producing females, ranked within the top five out of thirty-five varieties

tested. Therefore, the reproductive outcomes from this study were believed to represent insects exposed to favourable crop conditions. Oviposition periods and total fecundity rates could fluctuate on different host plants however and further experimentation is required.

Age-specific fecundity curves for *P. vulgatissima* were constructed but as fecundity rates were checked approximately every 2-3 days and preoviposition period was not included as part of this experiment (see Section 3.2), curves were adjusted to reflect the mean number of eggs per female/per day from first day of egg-lay until final egg-lay (see Appendix IV). Based on the results from the previous experiments, along with the data from this experiment, it can be assumed that the peak oviposition period would occur earlier and shorten as temperatures increase within a suitable ovipositioning temperature range. This tendency for females to invest more in reproduction during the earlier phase of their lives, even at the cost of reducing their own potential longevity, has been discussed in other studies (Williams, 1996; Nedvěd & Honěk, 2012).

In the next chapter, the effects of temperature on the developmental and reproductive traits of *P. vulgatissima* will be explored by applying various mathematical models to results obtained from these experiments. Along with providing information regarding important biological parameters for temperature-dependent development such as lower and upper thresholds across suitable developmental ranges and optimum temperatures for development, the relationships between beetle development and important abiotic environmental stimuli will serve as a prerequisite for the construction of a process-based phenological/voltinism model.

4 MODELLING INSECT DEVELOPMENT

This chapter provides a literature review of important empirical and biophysical models that have been formulated to describe insect development rate and development time distributions. A number of these were fitted to development data obtained during the experimentation phase and final models are chosen based on predefined criteria with results discussed.

4.1 Modelling Temperature-Dependent Insect Development Rates

The effect of temperature on the development of insects has been well defined, through theoretical and experimental works, over the last three hundred years. The concept of degree-days (DD) – the total amount of thermal units required, between a lower and upper temperature threshold, for a temperature-dependent organism to develop from one point to another in its life cycle – was originally conceived by Réaumur (1735), when it was recognised that poikilothermic organisms develop quicker at higher temperatures, shortening the interval between sowing and harvesting of crops. Defined by De Candolle (1855) as the *law of total effective temperatures*, the above principle forms the basis for all modelling approaches linking heat and the velocity of development for plants and poikilothermic animals such as insects, that have been developed since then (Damos & Savopoulou-Soultani, 2012). The biophysical explanation for the temperature-development

relationship is that enzymes catalyse reactions, such as those responsible for development, within poikilothermic organisms (Sharpe & DeMichele, 1977; Ikemoto, 2005). Heating up these enzymes results in increased rate of chemical reaction. A greater understanding of the relationship between temperature, heat accumulation, and development is essential for understanding important phenological events for insects, such as emergence from diapause, immature stage development and reproduction.

The following section reviews important empirical and biophysical models that have been formulated to describe the rate of insect development. The process of model evaluation based on *a priori* features (the known model properties) and *a posteriori* features (the fit of the model to experimental data and the accuracy of estimates for biologically important species-specific parameters such as lower, optimal and upper temperature thresholds) are outlined.

4.1.1 Linear Development Rate Response to Temperature Using Degree Day Methods (Thermal Summation)

Temperature, as a measure of thermal energy, plays a major role in determining the rate of development of insects (Davidson, 1944; Messenger, 1959; Wigglesworth, 1972; Hoffmann, 1985). Poikilotherms have evolved to operate within defined species-specific temperature ranges associated with their local environment (Messenger, 1959; Sharpe & DeMichele, 1977, Wagner, 1984a,). Development beyond these limits – during sustained unseasonal weather conditions in their natural habitat or at extreme constant temperatures in a laboratory – can have deleterious effects (Campbell *et al*., 1974). This is based on the assumption that insect development is regulated by a series of enzymes along biochemical pathways whose temperature-dependent reaction rate determines the rate of the overall metabolic process of the organism (Johnson & Lewin, 1946). At temperatures below this range, the reaction rate decreases, suspending development and allowing the insect to survive during unfavourable conditions; referred to as the diapause period (Andrewartha, 1952; Tauber *et al*., 1986). At temperatures above this range, conformational change renders the enzymes inactive, arresting development, with irreversible inactivation if the heightened temperature is maintained for an extended period (Sharpe & DeMichele, 1977). Plotting the reciprocal of insect development times as development rates versus temperature produces a shallow sigmoid S-shaped curve that is widely accepted as being representative of the relationship between the rate of development for insects and

temperature (Davidson, 1944; Campbell *et al.*, 1974, Gilbert & Raworth, 1996). Figure 4.1 illustrates this typical temperature-dependent rate of development curve, which can be divided into three sections. The rate of development increases linearly in correspondence with increasing temperatures in range B. As temperatures decrease in range A, the rate of development decreases and becomes non-linear. As temperatures increase in range C, the rate of development declines sharply as an optimum temperature for development is exceeded and the conformation of enzymes responsible for metabolism is altered.

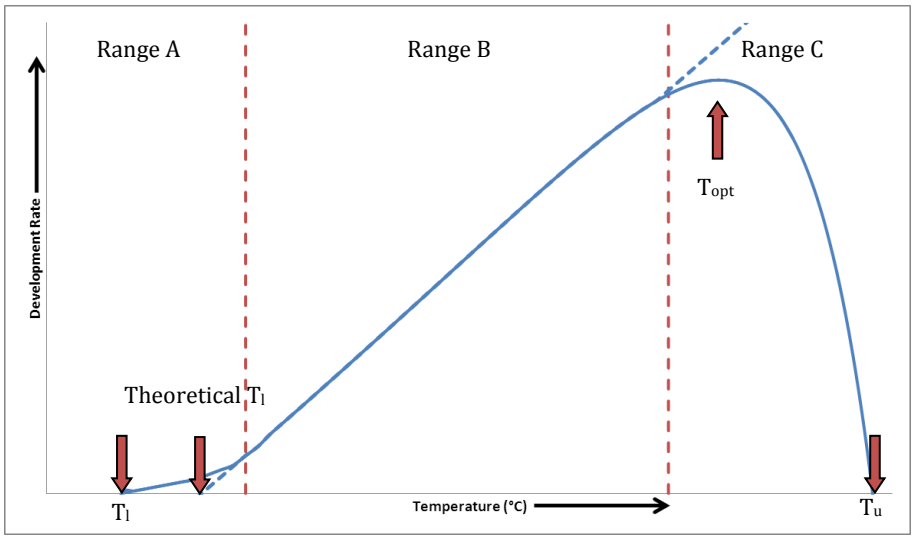


Figure 4.1 The relationship between the rate of development for insects and temperature, showing the linear (range B), non-linear portions (range A and C) and biologically important critical thresholds (Tl, Theoretical T_l, T_{opt} and T_u) (Campbell *et al.*, 1974).

Through the transformation of the development times to development rates plotted against temperature, the determination of biologically important species-specific development parameters is permitted. The calculation of these *critical thresholds* is essential for linking insect metabolic processes and thermal energy requirements. As can be observed from Figure 4.1, development increases from a base-line temperature – a lower temperature threshold (T_l) – where the full line intercepts the x-axis, below which no development occurs. Towards the upper end of the linear portion of the curve, development begins to slow down around a temperature associated with the fastest rate of development –an optimal temperature (T_{opt}). The rate of development decreases sharply beyond this point – reaching an upper temperature threshold (T_u) – and this can be numerically accounted for when the right side of the development curve reaches the x-axis. Increased mortality beyond the line boundaries of the development curve makes the study of development difficult (Uvarov, 1931; Howe, 1965; Wagner, 1984a). However, all

thresholds can be derived by fitting an appropriate model, to rate of development data for insects, obtained from laboratory-based experiments, under constant (or fluctuating) temperature conditions (Lactin *et al*., 1995, Briére *et al*., 1999; Ikemoto, 2005).

One approach to modelling insect development times uses the aforementioned linear portion of the rate of development curve. Campbell *et al*. (1974) suggest that the relationship between insect development rates and temperature can be represented by a straight line which cuts the x-axis to give an estimated but theoretically accepted T_l (Figure 4.1). The Campbell *et al*. (1974) model, hereafter referred to as the linear model, is based on linear regression:

$$d(T) = a + bT \qquad \textbf{Equation 4.1}$$

where d(T) is the rate of development, T is the temperature in degrees Celsius, a is the intercept of the line and b is the slope of the line. The T_l is calculated as:

$$T_l = \frac{-a}{b} \qquad \textbf{Equation 4.2}$$

and the thermal constant (K), defined as the number of days greater than T_l required for a life-cycle stage or generation to complete development which is the reciprocal of the slope b:

$$K = \frac{1}{b} \qquad \textbf{Equation 4.3}$$

As one of the oldest and most widely used models for describing insect development in relation to temperature, the simple linear model is an approach that has been utilised for many ectotherms. Since the work done by Campbell *et al*. (1974), many studies have solely used the linear model to account for the rate of development, T_l and K for various arthropod species, particularly pests and their natural enemies, within orders such as Acari (Bonoto, 1999; Broufas & Koveos, 2000; Kim *et al*., 2009a), Araneae (Li, 1998), Diptera (Duyck & Quilici, 2002; Grassberger & Reiter, 2002; Lefebvre & Pasquerault, 2004), Hemiptera (Blank *et al*., 2000; Satar & Yokomi, 2002; Diaz *et al*., 2007; Kivan, 2008), Hymenoptera (Hartley & Lester, 2003) and Lepidoptera (Zalucki, 1982; Howell & Nevin, 2000; Doerr *et al*., 2002). Regarding insect species of the order Coleoptera, linear temperature-dependent development has been described for *Laricobius nigrinus* (hemlock woolly adelgids predatory beetle) (Zilahi-Balogh *et al*., 2003), *Chysophtharta agricola* (southern eucalypt leaf beetle) (Nahrung *et al*., 2004) and *Hylobius abietis* (large pine weevil) (Inward *et al*., 2012).

The linear model – or thermal summation model – incorporates the degree-day theory and provides a direct estimate of the thermal constant. DD represents the accumulation of heat units above the estimated T_l – one degree-day per every degree above T_l – for a twenty-four hour period. By accruing the DD daily and relating these to K for a life-cycle stage, the time required for stage completion can be estimated. Different DD calculation methods have been developed. These include the averaging method, triangulation methods and sine wave methods, with all methods calculating DD from daily minimum and maximum temperatures, and a lower temperature threshold (Wilson & Barnett, 1983; Zalom *et al*., 1983). The averaging method uses daily minimum temperatures (T_{min}) and daily maximum temperatures (T_{max}) to estimate daily DD (Arnold, 1960):

$$DD = \left[\frac{T_{min} + T_{max}}{2} \right] - T_l \qquad \textbf{Equation 4.4}$$

and has been modified to:

$$DD = \left[\frac{T_l + T_{max}}{2} \right] - T_l \qquad \textbf{Equation 4.5}$$

to account for daily T_{min} below a T_l and avoid underestimation of DD during cooler periods (Damos & Savopoulou-Soultani, 2012). Triangulation and sine wave methods use daily T_{min} and T_{max} to produce a triangle and sine curve respectively and calculate daily DD values by determining the area above T_l and below the curve (Baskerville & Emin, 1969; Allen, 1976; Sevacherian *et al*., 1977; Zalom *et al*., 1983). While the averaging method solely utilises a T_l to allow for the calculation of daily DD, the triangulation and sine wave methods allows for the inclusion of T_u for more accurate DD accumulation estimations.

The linear model assumes that the development rate for insects is an increasing function of temperature. This highlights a central problem with this model. Although the linear functions allow us to calculate a theoretical T_l through extrapolation of the regression line in range A (Figure 4.1), this method has been recognised as inaccurate for estimating T_l (Baskerville & Emin 1969; Campbell *et al*., 1974, Wagner *et al*., 1984a). Outside the range of temperatures used to determine development rates during experimentation, the non-linearity of insect developmental response to low temperatures results in an overestimation of the lower temperature threshold through linear modelling. Another criticism of the linear model is the fact that it does not consider correctly the impact of extreme temperatures higher than T_{opt} on insect development in range C (Figure 4.1). The linear model works adequately over a range of favourable temperatures – usually

15-30°C – and within the optimum temperature range for a particular species (Campbell *et al*., 1974, Gilbert *&* Raworth, 1996, Honek, 1999). However, the function inaccurately models development in extreme temperatures. Some studies choose to ignore rate of development observations recorded at extreme temperatures to opt for the simplicity of the linear model. Examples for coleopteran species include the non-linear development of *Monochamus galloprovincialis* (pine sawyer beetle) post-dormancy larvae between 15°C and 32°C expressed as linear development between 15 and 30°C only (Naves & de Sousa, 2009), non-linear development of *Xyleborus fornicates* (shot hole borer) eggs and pupae between 15°C and 32°C expressed as linear development between 15°C and 30°C only (Walgama & Zalucki, 2007) and the non-linear development of *Anthonomus grandis grandis* (boll weevil) first instar larvae between 15°C and 35°C expressed as linear development over this temperature range when combined with other larval instar development (Greenburg *et al*., 2005). The response of the insect over the entire temperature range should be recognised for better accuracy of development rates.

4.1.2 Non-Linear Development Rate Response to Temperature Using Instantaneous Fractions of Development (Rate Summation)

The linear model provides a simple accessible method for describing development rates over a favourable temperature range. Additionally, this method is useful for estimating the biologically important theoretical T_l and providing the K parameter (Campbell *et al*., 1974). However, the linear model is inaccurate in describing development during extreme temperature conditions when the relationship between development rate and temperature becomes non-linear (Damos & Savopoulou-Soultani, 2012). Several empirical and biophysical non-linear models have been developed to describe developmental rate response curves over a wider range of temperatures with more accuracy than the limited linear model (Davidson, 1944; Janisch, 1932; Logan *et al*., 1976; Analytis, 1977; Sharpe & DeMichele, 1977; Huey & Stevenson, 1979; Taylor, 1981; Harcourt & Lee, 1982; Wang *et al*., 1982; Ratkowsky *et al*., 1983; Briére *et al*., 1999). While varying in complexity, these models do not account for thermal constants but many of these functions provide estimations for biologically important T_l, T_{opt} and T_u. While the linear model generally uses the thermal summation or DD approach for estimating predefined stage or generation completion, non-linear models apply the rate summation method with rate summation defined as:

$$D = \sum r(T(t))dt$$ **Equation 4.6**

where development (D) is a function of temperature (T), which in turn is a function of time (t) and r is the development rate that adjusts instantaneously to temperature (Worner, 1992; Liu *et al*., 1995; Baumgartner *et al*., 1998). Development rate is the reciprocal of mean or median development times used to construct rate versus temperature response curves. The rate represents the proportions of development occurring per unit time (per hour or day). These fractions are accumulated over discrete time increments, under constant temperatures, until they reach unity of one at which point the mean or median development time of the life-cycle stage or complete life-cycle is achieved (Curry *et al*., 1978; Worner, 1992; Liu *et al*., 1995). Although the application of the rate summation method through non-linear models is considered to give more accurate phenological responses, several studies have debated the biological realism of development rate assessment at constant temperatures (Hagstrum & Milliken, 1991; Worner; 1992; Liu *et al*., 1995).

The following sections provide reviews of some of the most frequently used non-linear models that have been applied to insect development (Figure 4.2). Based on *a priori* features and *a posteriori* features (see Section 4.1.3), a selection of these is subsequently used for defining *P. vulgatissima* and *G. lineola* development rates.

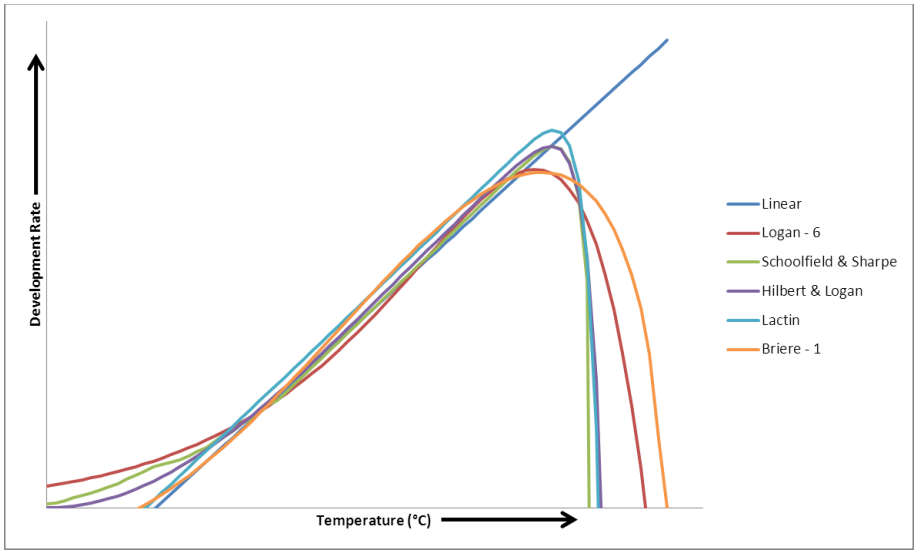


Figure 4.2 Relationship between temperature and development rate for a selection of described linear and non-linear models.

4.1.2.1 Stinner Model

In an attempt to correct for the considerable error from the linear function regarding T_u and account for the poor estimation of T_l from existent curvilinear functions, Stinner *et al*. (1974) proposed a modified sigmoid function of the form:

$$r(T) = \frac{c}{(1 + \exp^{(a+(b*T))})} \qquad \textbf{Equation 4.7}$$

where T is the temperature, and a, b and c are empirical constants, obtained through regression techniques. Although T_l and T_u cannot be estimated, T_{opt} can be obtained using this equation. The function assumes unrealistic symmetry around T_{opt} and the authors argued that the resultant errors are negligible, with mortality above this threshold rapidly approaching 100%. However, a number of studies suggest this underestimates the aforementioned threshold while poorly representing development at higher temperatures (Logan *et al*., 1976; Wagner, 1984a; Kontodimas *et al*., 2004). Nevertheless, this model has been selected over other functions to develop phenological models for coleopteran species such as *Dendroctonus ponderosae* (mountain pine beetle) (Logan & Bentz, 1999) and *Otiorhynchus ovatus* (strawberry root weevil) (Umble, 1999).

4.1.2.2 Logan Model

Recognising the limitations associated with linear models at low and high temperatures and responding to unsatisfactory non-linear equations due to symmetry at T_{opt} such as those derived by Stinner *et al*. (1974), Logan *et al*. (1976) employed two empirical models to describe asymmetrical temperature influenced rate of development for insects. Logan *et al*. (1976) proposed that the effect of temperature on life history parameters can be described in two phases: phase one describes the development period from some base to optimum temperature (mild incline) while phase two describes the period after the optimum development temperature has been exceeded (steep decline) (Figure 4.2). Phase one (Logan – 6) formula is:

$$r(T) = \Psi(\exp^{(\rho T)} - \exp^{\rho T_u - \frac{(T_m - T)}{\Delta T}}) \qquad \textbf{Equation 4.8}$$

where T is temperature above T_l, ψ is a rate of temperature-dependent physiological process at a base temperature, ρ is analogous to a Q_{10} value for critical enzyme-catalysed biochemical reactions, T_m is the lethal maximum temperature and ΔT is the number of

degrees above T at which thermal inhibition becomes predominant, and phase two (Logan – 10) formula is:

$$r(T) = \alpha((1 + k\exp^{(-pT)})^{-1} - \exp^{(-\frac{Tu-T}{\Delta T})}) \qquad \textbf{Equation 4.9}$$

where α and k are empirical values, and T, ρ, T_m and ΔT are as in Equation 4.8. With four and five fitted coefficients respectively, both derived equations provide an effective description of development over a complete range of temperatures offering broad application while remaining biologically acceptable. The Logan *et al*. (1976) models are more advantageous in this regard than the linear model as they cover temperatures above and below the optimum. Additionally, the Logan – 10 model can be used to estimate T_u. The formulated functions proposed by Logan *et al*. (1976) do not provide T_{opt} however. Furthermore, like many non-linear models, they both fail to estimate T_l as the curve of the Logan *et al*. (1976) models do not cross the x-axis. Therefore, the linear model needs to be incorporated with the Logan *et al*. (1976) models. Such an approach has been applied for modelling temperature-dependent development of coleopteran species such as *Coccinella septempunctata* (seven-spotted lady-beetle) (Xia *et al*., 1999), *Otiorhynchus sulcatus* (black vine weevil) (Son & Lewis, 2005a) and *Chilocorus bipustulatus* (armored-scale lady-beetle) (Eliopoulos *et al*., 2010).

4.1.2.3 Sharpe & DeMichele Model

Sharpe & DeMichele (1977) provided an alternative to the selection of existing empirical models available in the form of a biophysical model, theoretically based on the enzyme(s) reaction rate-controlling theory. Derived from the Eyring equation (1939) (based on the transition-state theory and used to describe the relationship between reaction rate and temperature) which resembles the Arrhenius (1915) equation (a formula for the temperature dependence of the reaction rate constants that quantifies the speed of a chemical reaction), Sharpe & DeMichele (1977) described the relationship between development and temperature in terms of the underlying physiological mechanisms. The six fitted coefficient model describes a non-linear response of developmental rate of insects exposed to low and high temperatures as well as a linear response at intermediate temperatures with all coefficients possessing a thermodynamic biochemical interpretation:

$$r(T) = \frac{T(\exp^{((\phi-\Delta Ha/T)/R)})}{1+\exp^{((\Delta Sl-\Delta Hl/T)/R)}+\exp^{(\Delta Sh-\Delta Hh/T)/R)}}$$

Equation 4.10

where R is the universal gas constant (1.987 cal degree $^{-1}$ mole $^{-1}$), Ø is the summarization term measuring the total concentration of control enzyme(s) and substrate (conversion factor with no thermodynamic meaning), ΔHa is the enthalpy of activation of the reaction catalysed by a rate-controlling enzyme(s), ΔSl and ΔSh are the changes in entropy associated with low and high temperature inactivation of the enzyme(s) respectively, and ΔHl and ΔHh are the changes in enthalpy associated with low and high temperature inactivation of the enzyme(s). According to Wagner *et al*. (1984a), this biophysical law based modelling approach qualifies it as being superior for describing development rates at both low and high temperatures, as well as the linear response at intermediate temperatures. However, the Sharpe & DeMichele (1977) model is similar to the Stinner *et al*. (1974) and the Logan *et al*. (1976) models as it fails to estimate T_l. Hilbert & Logan (1983) described the model as symmetrical about T_{opt} leading to less accurate estimation of development rates at higher temperatures also. Due to the large number of fitted coefficients, there is an increase in complexity associated with the fitting of this function (Kontodimas *et al*., 2004). Further studies highlight the high levels of correlation between the fitted coefficients, rendering non-linear estimation techniques unsatisfactory (Briére *et al*., 1999; Schoolfield *et al*., 1981).

4.1.2.4 Sharpe-Schoolfield Model

Schoolfield *et al*. (1981) modified the Sharpe & DeMichele (1977) model to allow for non-linear estimation techniques (Figure 4.2):

$$r(T) = \frac{p(25°C)\frac{T}{298}\exp^{(\frac{\Delta Ha}{R}(\frac{1}{298}-\frac{1}{T})}}{1+\exp^{(\frac{\Delta Hl}{R}(\frac{1}{T_{1/2l}}-\frac{1}{T}))}+\exp^{(\frac{\Delta Hh}{R}(\frac{1}{T_{1/2h}}-\frac{1}{T}))}} \qquad \textbf{Equation 4.11}$$

where p(25°C) is the development rate at 25°C assuming no enzyme inactivation, $T_{1/2l}$ is the temperature (°C) at which the rate-controlling enzyme is half active and half low-temperature inactive and $T_{1/2h}$ is the temperature (°C) at which the rate-controlling enzyme is half active and half high-temperature inactive with all other coefficients similar to those in the original model (Equation 4.10). The reciprocal of the denominator in the model represents the probability of enzyme(s) being in the active state. The Schoolfield *et al*. (1981) model can be transformed to eliminate high temperature enzyme inactivation effect by removing the last exponential term, eliminate low temperature inactivation effect by removing the first exponential term (both requiring only four fitted coefficients) or eliminating both inactivation effects by removing the exponential effects altogether

(requiring only two fitted coefficients), allowing development to be studied at different parts of the temperature range. The reformulated Sharpe & DeMichele (1977) model has been used to assess the coleopteran egg development for *Diabrotica virgifera virgifera* (western corn rootworm) (Schaafsma *et al*., 1991) and egg to adult development for *Dendroctonus frontalis* (southern pine beetle) (Wagner *et al*., 1984b). This function is described as providing more intuitive biological and graphical interpretation, more convenient initial parameter estimates and reduced correlation between parameter estimates (Schoolfield *et al*., 1981). However, the practicality of applying this model is limited, as it requires a high number of fitted coefficients and lacks the functionality of estimating T_l.

4.1.2.5 Sharpe-Schooldfield-Ikemoto Model

Schoolfield *et al*. (1981) highlighted issues regarding the application of the thermodynamic Sharpe & DeMichele (1977) model such as the undescribed interrelationships existing between model parameters and estimation of reasonable initial parameter estimates for fitted coefficients to begin interactions with not been readily available. Furthermore, Schoolfield *et al*. (1981) assumed that the probability of developmental enzyme(s) being in the active state should reach its maximum at 25°C. Later studies by van Straalen (1994), Ikemoto (2005) and de Jong (2010) found that the optimum temperature for the probability of enzyme(s) being in the active state could be significantly greater. Consequently, Ikemoto (2005) modified the Schoolfield *et al*. (1981) function to ensure that the probability of the developmental enzyme(s) being in an active state can be maximal at the intrinsic optimum temperature. This was in agreement with the primary assumption of Schoolfield *et al*. (1981) that little enzyme inactivation occurs at a particular temperature, which they assumed to be 25°C (Shi *et al*., 2011a; 2011b; Ikemoto *et al*., 2013). The modified Sharpe-Schoolfield model known as Sharpe-Schooldfield-Ikemoto model and hereafter referred to as SSI model is:

$$r(T) = \frac{p\Phi\left(\frac{T}{T\Phi}\right)\exp^{\left(\frac{\Delta Ha}{R}\left(\frac{1}{T\Phi}-\frac{1}{T}\right)\right.}}{1+\exp^{\left(\frac{\Delta Hl}{R}\left(\frac{1}{T_{1/2l}}-\frac{1}{T}\right)\right)}+\exp^{\left(\frac{\Delta Hh}{R}\left(\frac{1}{T_{1/2h}}-\frac{1}{T}\right)\right)}} \qquad \textbf{Equation 4.12}$$

where TΦ is the intrinsic optimum temperature at which no enzyme inactivation is hypothesized, pΦ is the mean development time at the intrinsic optimum temperature and R, ΔHa, ΔHl, ΔHh, Th and Tl are as described in Schoolfield *et al*. (1981) model. Although only recently presented as another biophysical model option, the SSI model has been

applied successfully in different studies (Jafari *et al*., 2012; Ullah *et al*., 2012; Padmavathi *et al*., 2013; Sreedevi *et al*., 2013). Further interpretation of this equation and the development of computer programs/functions for estimating all parameters in the SSI model has increased the functionality and ease of application of this non-linear model (Shi *et al*., 2011a; 2011b; Ikemoto *et al*., 2013).

4.1.2.6 Hilbert & Logan Model

Identifying the analytic nature of the model proposed by Logan *et al*. (1976), over a wide range of temperatures and its reflection of an observed asymmetry about T_{opt}, Hibert & Logan (1983) sought to use the developmental rate approaching zero asymptotically and account for T_l estimation. Through the combination of a sigmoid equation and an exponential equation, based on the functional responsive curves formulated by Holling (1965) and the exponential portion of the Logan *et al*. (1976) (Logan - 6) model respectively, a four fitted coefficient model was formulated (Figure 4.2):

$$r(T) = \Psi\left(\left(\frac{T^2}{T^2 + D^2}\right) - \exp^{\frac{-(Tm-T)}{\Delta T}}\right) \qquad \textbf{Equation 4.13}$$

where T_a is the air temperature, T_b is an arbitrary base temperature, T is T_a minus T_b, D is an empirical constant, ΔT is the width of the high temperature boundary area and ψ and T_m is as in previous equations. The Logan *et al*. (1976) (Logan - 6), Sharpe & DeMichele (1977) and the Hilbert & Logan (1983) models were fitted to a compiled data-set from various sources for *Melanoplus sanguinipes* (F.) (migratory grasshopper) (Hilbert & Logan, 1983). The Sharpe & DeMichele (1977) model proved to be the best at representing the data based on statistical tests while the Logan *et al*. (1976) (Logan - 6) model depicted the data poorly with overestimation of developmental rates at low temperatures. Although employing biological concepts, the Schoolfield *et al*. (1981) model overestimated insect development at low and high lethal temperatures, even describing positive development at 0°C with associated symmetrical development around T_{opt}. The Hilbert and Logan (1983) model is chosen as the function of choice for this species. This model has been fitted to data for coleopteran species such as *Otiorhynchus ovatus (*strawberry root weevil) (Fisher & Edwards, 2002) and *Diorhabda elongata (*Asian leaf beetle) (Herrera *et al.,* 2005).

In a study by Sánchez-Ramos *et al*. (2007), development rates for *Acarus farris* and *Tyrophagus neiswanderi* (cheese mites) were examined by fitting a selection of models to experimental data. The Hilbert & Logan (1983) model was the model selected to describe the relationship between developmental rate and temperature for *A. farris,* whereas the

Lactin *et al*. (1995) model (see Section 4.1.2.7) provided the best results for *T. neiswanderi* (based on coefficient of determination values) with T_l and T_u estimated for each stage of *A. farris,* 3-4°C lower than those estimated for *T. neiswanderi*. Despite such species being from the same region in Northern Spain, this showed that different model selection is often required, even when dealing with similar species from similar geographical locations.

Unlike the other empirical non-linear models discussed, the Hilbert & Logan (1983) model is capable of estimating T_l for development. However, Lactin *et al*. (1995) highlights the model as being biologically unrealistic as developmental rates rise without limitation as temperatures fall below estimated T_l.

4.1.2.7 Lactin Model

In a move to improve upon the aforementioned models formulated by Logan *et al*. (1976) and Hilbert & Logan (1983), Lactin *et al*. (1995) proposed a modification of the Logan *et al*. (1976) (Logan - 6) model that accounts for the non-linear development response to temperature and T_l while avoiding the unrealistic increase in the developmental rate at temperatures below the developmental threshold. This was achieved by removing the coefficient ψ defining the rate of temperature-dependent physiological process at a base temperature and adding an intercept coefficient λ to allow for the curve to intersect the abscissa at suboptimal temperatures for estimation of T_l (Figure 4.2):

$$r(T) = \exp^{pT} - \exp^{(pTu - \frac{(Tm - T)}{\Delta T})} + \lambda \qquad \textbf{Equation 4.14}$$

Temperature-dependent developmental rate data-sets for several coleopteran, dipteran and orthopteran insect species were examined that had been analysed successfully by previous studies, with the suggested modifications to the Logan *et al*. (1976) (Logan – 6) model, offering an improved fit of the curve to the development data in the majority of cases, based on various statistical tests (Lactin *et al*., 1995). Although these improvements were not significantly different, the cessation of development below the lower developmental thresholds were acknowledged. Thereafter, representation of the temperature-dependent development using the Lactin *et al*. (1995) model (hereafter referred to as the Lactin model) has been performed for various coleopteran species such as *Ips typographus* (spruce bark beetle) (Wermelinger & Seifert, 1998) and *Acalymma vittatum* (striped cucumber beetle) (Ellers-Kirk & Fleischer, 2006). Another temperature-dependent coleopteran development study involving *Adalia bipunctata* (two-spotted ladybeetle) has noted the same model to overestimate T_u however (Jalali *et al*., 2010).

4.1.2.8 Briére Model

Briére *et al*. (1999) proposed a simplified non-linear model to describe the relationship between the development rate and temperature whilst providing biologically meaningful parameters. Two models were developed (Figure 4.2):

$$r(T) = aT(T - T_l)\sqrt{(T_u - T)} \qquad \textbf{Equation 4.15}$$

a three fitted coefficient model (Briére – 1 hereafter referred to as the Briére model) with a non-linear component at low and high temperatures and a linear portion at intermediate temperatures where *a* is an empirical constant and T_l and T_u are as previously defined and:

$$r(T) = aT(T - T_l)(T_u - T)^{\frac{1}{m}} \qquad \textbf{Equation 4.16}$$

a four fitted coefficient model (Briére – 2) with an additional parameter m, developed to improve the fit of the model, and a, T_u and T_l are as in equation 4.15. The Briére *et al*. (1999) functions are favourable amongst entomologists because, like the Logan *et al*. (1976) models, when they are used together, they are capable of estimating all three biologically important temperatures. Furthermore, they require less fitted coefficients than Logan *et al*. (1976), Hilbert & Logan (1983) and the more complex biophysical equations. Incorporating data sources previously used in model-testing studies such as Stinner *et al*. (1974), Sharpe *et al*. (1981), Hilbert & Logan (1983), Lamb (1982), Lamb *et al*. (1985) and Briére & Pracros (1998), statistical testing indicated a better fit of the curves to the data than previous models – except in the case of *Melanoplus sanguinipes* (migratory grasshopper) (Orthoptera: Acrididae) with better statistical values obtained using the Hilbert & Logan (1983) function (Briére *et al*., 1999). Son & Lewis (2005a) described the relationship between temperature and development rate for coleopteran species *Otiorhynchus sulcatus* (black vine weevil) using the Logan *et al*. (1976) (Logan - 6) model. However, the reproductive maturation rate is modelled as a function of temperature using a combination of the Briére *et al*. (1999) (Briére - 2) model and the linear model. Keena (2006) used the same model to describe the relationship between temperature and mean rate of hatch for cohorts of eggs from different populations of another coleopteran species *Anoplophora glabripennis* (Asian long-horned beetle).

4.1.3 Model Selection Criteria for Development Rate

Multiple linear and non-linear models have been developed for the purposes of describing insect development rates in relation to temperature. Advances in computation and information processing capabilities have assisted in the construction and ease of use of these models. As no single model has emerged as superior, numerous studies assess a selection of these models to describe the relationship between temperature and the rate of development for arthropod species within orders such as Acari (ticks and mites) (Roy *et al*., 2002; Sánchez-Ramos *et al*., 2007; Kim *et al*., 2009), Diptera (flies, midge and mosquitoes) (Grout & Stoltz, 2007; Haghani *et al*., 2007) Coleoptera (beetles) (Kontodimas *et al*., 2004; Walgama & Zalucki, 2006; Arbab *et al*., 2008; Jalali *et al*., 2010), Hemiptera (aphids, plant-hoppers, true-bugs and whiteflies) (Liu & Meng, 1999; Arbab et al., 2006; Nielsen *et al*., 2008; Shi & Ge, 2010) and Lepidoptera (moths and butterflies) (Golizadeh *et al*., 2007; Sandhu *et al*., 2010; Aghdam *et al*., 2011).

In order to find the best fitting model that describes the relationship between these two variables, suitable criteria involving *a priori* (the known model properties) and *a posteriori* (the fit of the model to experimental data and the accuracy of estimates for biologically important species-specific parameters such as T_l, T_{opt} and T_u) features are employed in these studies to compare these functions against one another. *A priori* evaluation is based on: 1) the complexity of the model (the number of fitted coefficients), 2) the estimation of parameters having biological significance and 3) the biological interpretation of the model components. *A posteriori* assessment is established on: 1) the fit of the function to the observed data and 2) the accuracy of the fit at biologically meaningful temperatures compared to the observed data. Although the selection of the best fitting model(s) to development rate data is ultimately at the discretion of the researcher, some or all of these strategies have been used for selection of final model choice in the aforementioned studies.

The models defined in Section 4.1.2 differ in the number of fitted coefficients. These range from the linear model that requires the estimation of two fitted coefficients and the SSI model which requires the estimation of seven. Fitted coefficients are estimated by non-linear regression with the Levenberg-Marquardt method (Marquardt, 1963) using a statistical software program seeded with initial parameter values.

A model may fit the selected data and estimate the preferred number of critical thresholds but these estimations need to be in agreement with experimental data. In a study by Golizadeh *et al*. (2007), high coefficient of determination values and residual sum

of squares values for the Briére and Lactin models suggested that both functions were suitable to estimate the temperature-dependent development rate of *Plutella xylostella* (diamondback moth). The two models determined the optimal temperature for development to be approximately 31°C and 36.5°C respectively. No individual insect developed to complete a full biological cycle beyond 32.5°C. Consequently the Briére model was acknowledged as the most appropriate model. Similar definitive model choices have been made based on these criteria in the coleopteran studies performed by Kontodimas *et al*. (2004) and Walgama & Zalucki (2006).

A posteriori indicators used to select the best describing function include the residual sum of squares (RSS), coefficient of determination (R^2), adjusted coefficient of determination (R^2_{adj}), root mean square error (RMSE), mean square error, Akaike information criterion (AIC), Bayesian information criterion (BIC), corrected Akaike information criterion (AICC) and Akaike weights. However these indicators are not always used to estimate a model's goodness of fit as can be seen in studies executed by Roy *et al*. (2002), Golizadeh *et al*. (2007) and Escobar *et al*. (2012), with higher values of R^2 and lower values of RSS solely used to evaluate accuracy. In a review of model selection in ecology, Johnson & Omland (2004) stated that neglecting the principle of parsimony by maximizing the fit of a model to data without any consideration for model complexity can result in imprecise parameter estimates and development rate estimates. Angilletta Jr. (2006) highlighted the issues with describing model fit using R^2 and RSS indicators only, stating that functions that describe 100% of the variation do not actually describe a true performance curve. To avoid selecting a model that over-fits the data, choosing a model based on their AIC values, with its foundation in Kullback-Leibler information theory (Akaike, 1978; Burnham & Anderson, 2002), was recommended as it is dependent on the model's complexity. The AIC is calculated as:

$$\mathrm{AIC} = -2\mathrm{L} + 2\mathrm{K} + \frac{2\mathrm{K}(\mathrm{K}+1)}{\mathrm{N}-\mathrm{K}-1} \qquad \textbf{Equation 4.17}$$

where K is the number of parameters, N is the sample size and L is the maximized log-likelihood value of the model, calculated from the model's RSS as:

$$\mathrm{L} = \log\left(\frac{\mathrm{RSS}}{\mathrm{N}}\right)\frac{-\mathrm{N}}{2} \qquad \textbf{Equation 4.18}$$

Model selection based on BIC may be considered also as it is structurally similar to AIC but it is not based in Kullback–Leibler information theory and includes a penalty term

dependent on sample size and consequently tends to favour simpler models (Schwarz, 1978; Zucchini, 2000; Johnson & Omland, 2004).

In order to select an optimum model, the linear degree day model, three non-linear development models – Briére, Lactin and SSI as described in Section 4.1.2 – and a quadratic polynomial function from the TableCurve 2D (SYSTAT Software Inc., San Jose, CA) equation list were fitted to rate of development data obtained from experimentation (see Sections 3.1, 3.2 and 3.5) and evaluated based on this model selection criteria. The linear model was used to estimate T_l and K. Due to the observed non-linearity of development rates, only the development times that increased with the constant temperatures were used for linear regression to estimate development rates. To describe the development rate over the complete range of temperatures used during experimentation, the different non-linear models were applied.

4.1.4 Results

4.1.4.1 Temperature-Dependent Development Rate Models for *Phratora Vulgatissima*

Five functions were selected, due to their variety and subsequent range in complexity (linear, non-linear and biophysical), frequency of use in literature and their ability to estimate parameters of biological significance, to fit to development rate data for *P. vulgatissima* life-cycle stages (Figure 4.3 – Figure 4.5 and Table 4.1 and Table 4.2). The linear function was fitted to the linear portion of the data for post-diapause development (10-25°C), egg development (10-27°C), larval development (10-27°C), the pupal development (10-25°C) and oviposition period (10-25°C). The Briére, Lactin and SSI functions were fitted to same data and sexual maturation development covering the full range of constant temperatures used during experimentation. The SSI and quadratic polynomial functions were fitted to the oviposition period data-set.

The linear model provided a good fit to the data for all life-cycle stages with high R^2 values ranging from 0.97 – 0.99 (Table 4.3 – Table 4.4). T_l was estimated for each stage by extrapolation of the line to the x-axis. Estimations for T_l decreased through the successive stages of development – 7.5°C for post-diapause development, 5.7°C for egg development, 5.1°C for larval development and 4.2°C for pupal development. K values estimated by the linear model were considerably lower for the post-diapause (100), egg

(116.3) and pupal (123.5) stages when compared to the estimated value for larval stage (321.5) due to greater larval development time requirements.

The Briére, Lactin and SSI equations provided estimations for the three biologically important critical temperatures (T_l, T_{opt} and T_u), either as regression outputs or through graphical interpretation. The Briére equation provided the lowest estimations for T_l (6.2°C, 3.0°C, -1.4°C and 1.2°C) in life-cycle stage order post-diapause, eggs, larval and pupal (from hereafter unless stated) and highest estimations for T_{opt} (26.1°C, 27.3°C, 30.6°C and 26.6°C) and T_u (31.7°C, 33.7°C, 38.5°C and 33.2°C). When critical thresholds for Lactin and SSI equations were assessed, T_l estimations for the Lactin equation were lower for all stages (7.5°C, 6.2°C, 5.0°C and 4.9°C) than estimations for the SSI equation (7.9°C, 8.5°C, 7.3°C and 5.1°C), with a difference of greater than 2°C between equation estimations for both the eggs and larval stages.

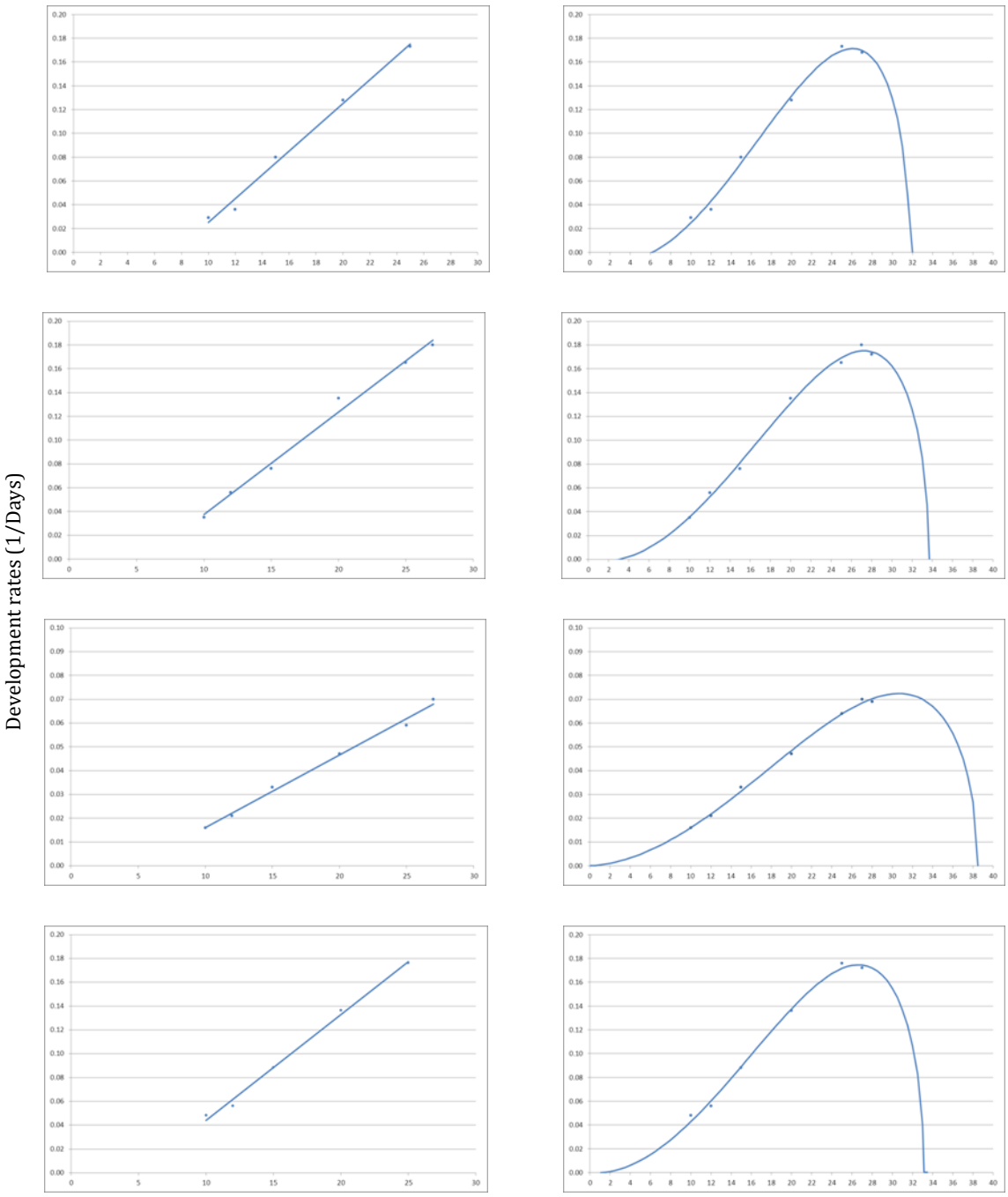


Figure 4.3 Linear model (left) and Briére model (right) fitted to *P. vulgatissima* post-diapause, eggs, larval and pupal development rates (top to bottom).

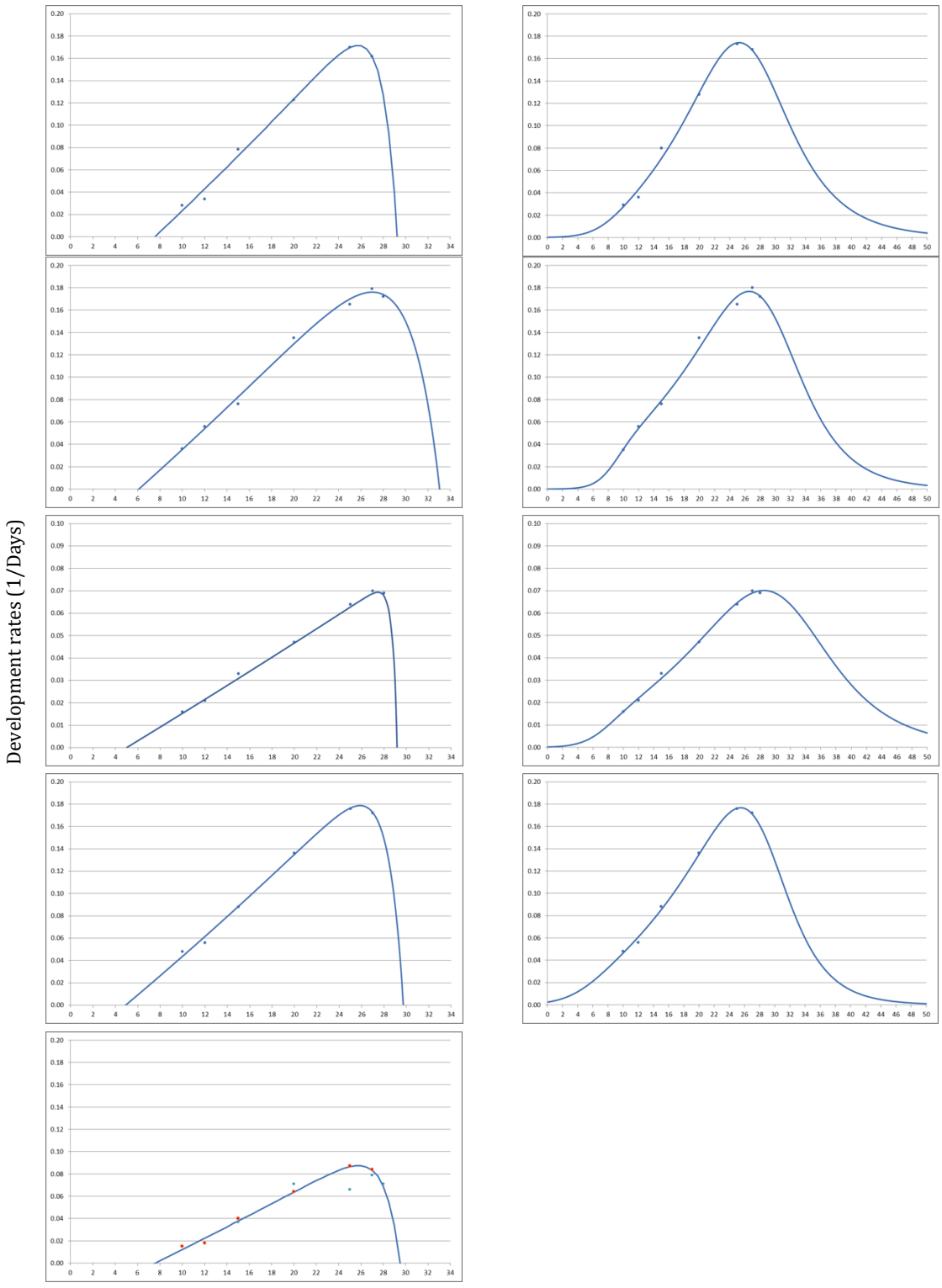


Figure 4.4 Lactin model (left) and SSI model (right) fitted to *P. vulgatissima* post-diapause, eggs, larval, pupal and sexual maturation development rates (top to bottom). Development rates for sexual maturation obtained during experimentation are denoted by the red dots to show their similarity to post-diapause development rate data increased by a factor of two to provide a representative data-set for modelling sexual maturation.

Table 4.1 Parameters and critical threshold estimations for models fitted to *P. vulgatissima* post-diapause, eggs, larval and pupal development rates (with all SSI outputs converted from Kelvin to Celsius).

Models	Parameters	Development Stage			
		Post-Diapause	***Eggs***	***Larval***	***Pupal***
Linear	a	-0.0749 ±0.0095	-0.0488 ±0.0082	-0.0163 ±0.0012	-0.0336 ±0.0113
	b	0.0100 ±0.0006	0.0086 ±0.0004	0.0032 ±0.0001	0.0081 ±0.0006
	k	100	116.28	312.50	123.46
	T_l	7.49	5.67	5.09	4.15
Briére	a	0.0001 ±0.00002	0.0001 ±0.00001	0.00003 ±0.00001	0.0001 ±0.00002
	T_l	6.20111 ±1.0511	3.0252 ±1.3588	-1.3475 ±2.2454	1.2326 ±1.7951
	T_u	31.6861 ±1.1088	33.6819 ±1.1351	38.4598 ±2.6497	33.1448 ±1.4166
	T_{opt}	26.05	27.27	30.64	26.64
Lactin	p	0.0091 ±0.0009	0.0086 ±0.0010	0.0030 ±0.0001	0.0081 ±0.0006
	T_m	32.9460 ±5.0468	37.7530 ±7.1617	30.3760 ±3.1378	32.0961 ±3.8104
	ΔT	1.6965 ±1.5545	2.8126 ±2.3182	0.4374 ±0.5885	1.3694 ±1.0925
	λ	-1.0714 ±0.0149	-1.0549 ±0.0149	-1.0151 ±0.0015	-1.0406 ±0.0093
	T_l	7.54	6.23	5.00	4.91
	T_u	30.04	33.21	29.21	29.74
	T_{opt}	25.77	27.02	27.47	25.86
SSI	TΦ	289.4082	289.3864	289.5169	290.1869
	pΦ	0.0881	0.0910	0.0361	0.1065419
	ΔHa	21391.91	15859.43	14513.24	15183.74
	ΔHl	-73517.22	-107065	-80363.22	-58166.06
	ΔHh	58858.5	59827.66	46695.45	67272.29
	T_l	7.86	8.47	7.25	5.06
	T_u	26.80	29.48	31.37	28.64
	T_{opt}	25.24	26.56	28.49	25.5

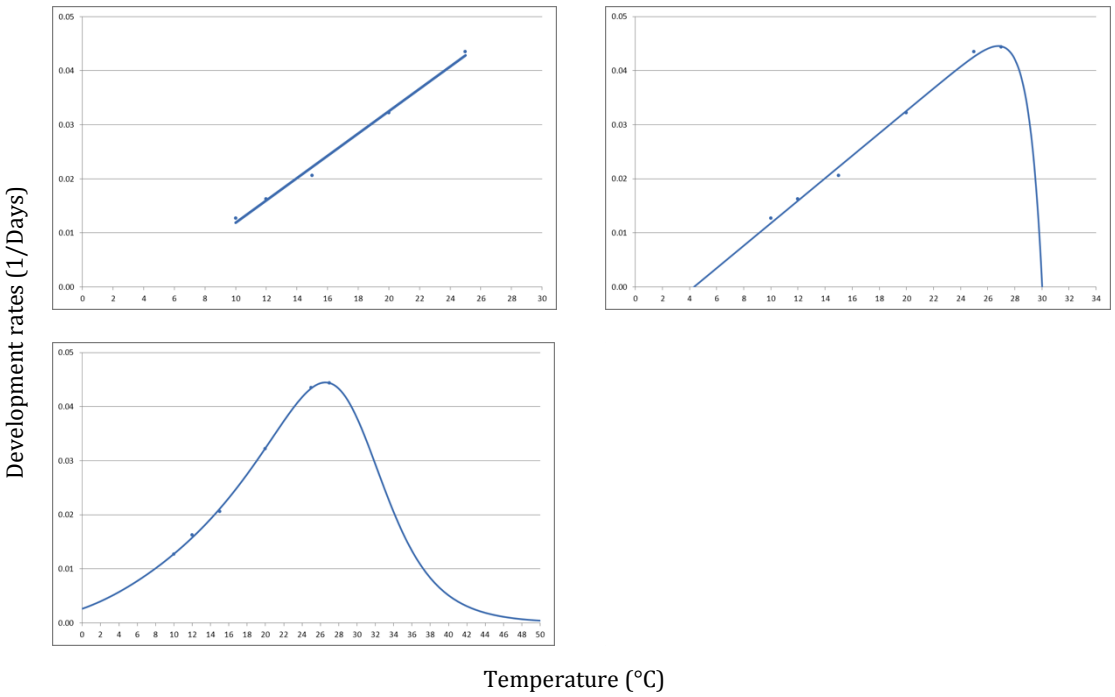


Figure 4.5 Linear model (top-left), quadratic polynomial model (top-right) and SSI model (bottom-left) fitted to *P. vulgatissima* oviposition period development rates.

Table 4.2 Parameter and critical threshold estimations for fitted models to *P. vulgatissima* oviposition period development rates (with all SSI outputs converted from Kelvin to Celsius).

Models	**Parameters**	**Development Stage**
		Oviposition period
Linear	a	-0.0088 ± 0.0016
	b	0.0021 ± 0.0001
Quadratic polynomial	a	-0.0090 ± 0.0018
TableCurve 2D	b	0.0021 ± 0.0001
eqn 1007	c	-4.9E-15 ± 3.5E-15
SSI	TΦ	290.7962
	pΦ	0.0275
	ΔHa	13752.69
	ΔHl	-36711.2600
	ΔHh	64765.63
	T_l	273.5444
	T_u	303.1696

T_u estimations for the Lactin equation were higher for all stages (30.0°C, 33.2°C, 29.2°C and 29.7°C) than estimations for the SSI equation (26.8°C, 29.5°C, 31.4°C and 28.6°C), except for larval stage, where the SSI equation estimation was greater than 2°C. T_{opt} estimations for the Lactin equation were higher for all stages (25.8°C, 27.0°C, 27.5°C and 25.9°C) than estimates for the SSI equation (25.2°C, 26.6°C, 28.5°C and 25.5°C), except for larval stage, where the SSI equation estimate was 1°C higher. Different models performed better for different stages depending on the choice of statistical test being employed (Table 4.3 – Table 4.4). The fitting of the Lactin model to the data-sets provided the lowest RMSE values for all life-cycle stages, expect the egg development stage, where the Briére model presented the marginally lower RMSE value (0.0038), compared to the Lactin (0.0040) and SSI (0.0047) model. AIC and BIC values for each development stage and model fluctuated in unison because they are based on the log-likelihood function. AIC/BIC values for the Briére model fitted to post-diapause (-41.9304/-42.5551) and egg (-51.0774/-52.2397) development stages were better than values for the Lactin model (-40.1472/-40.9802 and -49.4058/-49.6231 respectively) and the SSI model (-32.7049/-34.1626 and -41.1251/-41.5037 respectively). AIC/BIC values for the Lactin model fitted to larval data (-73.4830/-73.6994) were better than values for the Briére (-68.8950/-69.0573) and SSI (-61.5569/-61.9355) models. Fitting the SSI model to data for the pupal stage produced better AIC/BIC values (-51.2809/-51.6595) than the Briére and Lactin models (-44.7164/-45.3411 and -45.2713/-46.1043 respectively). The reciprocals of the oviposition period data-set were statistically better represented by the SSI model than the quadratic polynomial model due to a smaller RMSE value and higher AIC and BIC values when compared.

Table 4.3 Statistical results for models fitted to *P. vulgatissima* eggs, larval, pupal and post-diapause development rates.

Models	R^2	RSS	RMSE	AIC	BIC
	Eggs				
Linear	0.988	n/a	n/a	n/a	n/a
Briére	n/a	0.0001	0.0038	-52.0774	-52.2397
Lactin	n/a	0.0001	0.0040	-49.4068	-49.6231
SSI	n/a	0.0002	0.0047	-41.1251	-41.5037
	Larval				
Linear	0.998	n/a	n/a	n/a	n/a
Briére	n/a	0.00001	0.0011	-68.8950	-69.0573
Lactin	n/a	0.000004	0.0007	-73.4830	-73.6994
SSI	n/a	0.000008	0.0011	-61.5569	-61.9355
	Pupal				
Linear	0.974	n/a	n/a	n/a	n/a
Briére	n/a	0.0001	0.0035	-44.7164	-45.3411
Lactin	n/a	0.00005	0.0029	-45.2713	-46.1043
SSI	n/a	0.00004	0.0025	-51.2809	-51.6595
	Post-diapause				
Linear	0.988	n/a	n/a	n/a	n/a
Briére	n/a	0.0001	0.0045	-41.9304	-42.5551
Lactin	n/a	0.0001	0.0044	-40.1472	-40.9802
SSI	n/a	0.0001	0.0049	-32.7049	-34.1626

Table 4.4 Statistical results for models fitted to *P. vulgatissima* oviposition period development rates.

Models	R^2	RSS	RMSE	AIC	BIC
	Oviposition period				
Linear	0.9924	n/a	n/a	n/a	n/a
Quadratic polynomial	n/a	3.49E-06	0.0009	-61.7397	-62.3645
SSI	n/a	5.64E-07	0.0003	-66.0546	-67.5123

4.1.4.2 Temperature-Dependent Development Rate Models for *Galerucella Lineola*

Four functions were employed, due to their variety and subsequent range in complexity (linear, non-linear and biophysical), frequency of use in literature and their ability to estimate parameters of biological significance, to fit to development rate data for *G. lineola*

life-cycle stages (Figure 4.6 – Figure 4.7 and Table 4.5). The linear function was fitted to the linear portion of the data for the eggs development (12-27°C), the larval development (10-27°C) and the pupal development (12-29°C). The Briére, Lactin and SSI functions were fitted to the same data, covering the full range of constant temperatures used during experimentation.

The linear model provided a good fit to the data for all life-cycle stages with high R^2 values ranging from 0.96– 0.99 (Table 4.6). Estimations for T_l were 8.0°C, 6.4°C and 7.2°C for eggs, larval and pupal development respectively. K value estimations by the linear model were lower for eggs (104.2) and pupal (98.0) stages when compared to the estimated value for larval stage (256.4).

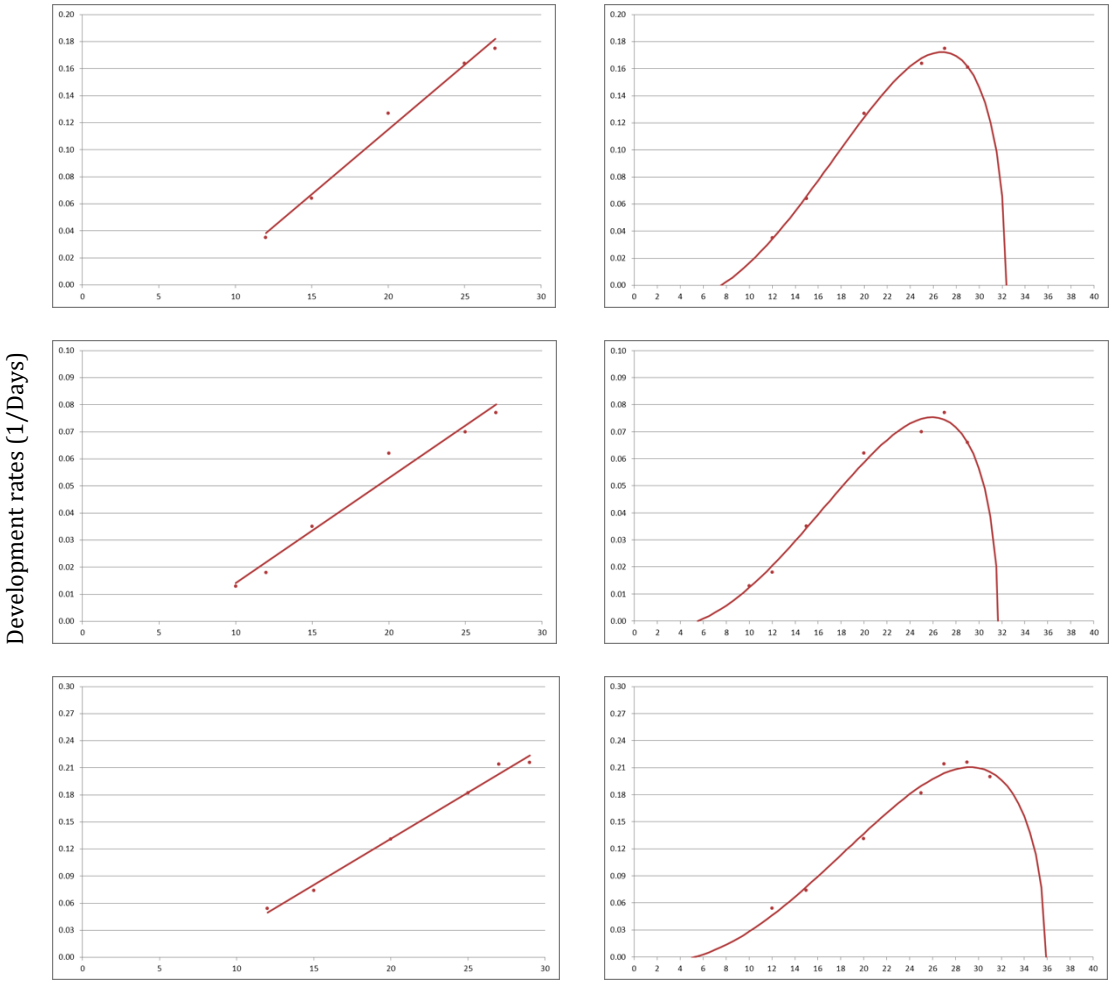


Figure 4.6 Linear model (left) and Briére model (right) fitted to *G. lineola* eggs, larval and pupal development rates (top to bottom).

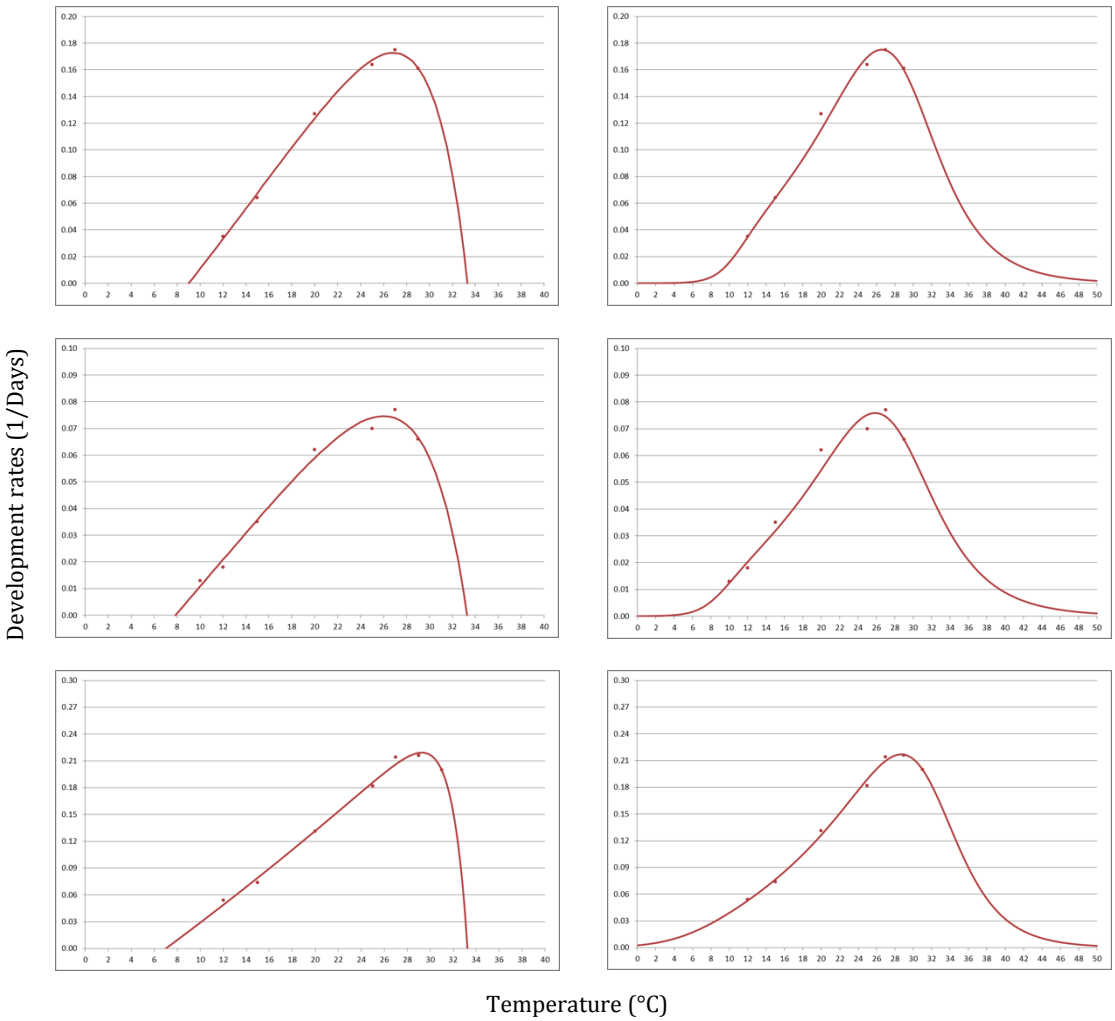


Figure 4.7 Lactin model (left) and SSI model (right) fitted to *G. lineola* eggs, larval and pupal development rates (top to bottom).

All non-linear equations provided estimations for all critical thresholds, either as regression outputs or through graphical interpretation. The Briére equation provided the lowest estimations for T_l (7.5°C, 5.6°C and 5.3°C) in stage order eggs, larval and pupal (from hereafter unless stated). Of the equation estimations for T_{opt} (26.8°C, 26.0°C and 29.3°C) and T_u (32.4°C, 31.7°C and 35.9°C), pupal stage estimations were highest for both biologically important thresholds when compared to other equation estimates. The Lactin equation provided the highest T_l estimation for the pupal development stage when outputs for all development stages were assessed (9.0°C, 7.9°C and 7.0°C). Additionally, the equation presented the highest T_{opt} and T_u estimates for eggs and larval development stages when T_{opt} (26.8°C, 26.0°C and 29.3°C) and T_u (33.3°C, 33.3°C and 33.3°C) estimations for both development stages were compared across all equations. The SSI equation stage estimates for T_l (10.5°C, 8.8°C and 6.1°C) were the highest with a 3.3°C difference between Briére and SSI equation estimates for the larvae development stage. In contrast, T_{opt} (26.6°C, 25.9°C and 28.7°C) and T_u (29.0°C, 28.3°C and 32.0°C) estimates by the SSI equation were

the lowest across the spectrum of reviewed models, with greater than 5°C difference between SSI and Lactin model estimates for the larvae development stages.

Table 4.5 Parameter and critical threshold estimations for fitted models to *G. lineola* eggs, larval and pupal development rates (with all SSI outputs converted from Kelvin to Celsius).

Models	Parameters	Development Stage		
		Eggs	***Larval***	***Pupal***
Linear	a	-0.0765 ±0.0137	-0.0248 ±0.0067	-0.0732 ±0.0112
	b	0.0096 ±0.0007	0.0039 ±0.0003	0.0102 ±0.0005
	k	104.17	256.41	98.04
	T_l	7.97	6.36	7.18
Briére	a	0.0001 ±0.00001	0.0006 ±0.00001	0.0001 ±0.0001
	T_l	7.5375 ±0.5323	5.5480 ±1.1633	5.2610 ±1.7533
	T_u	32.3513 ±0.3440	31.6748 ±0.5611	35.8809 ±1.1869
	T_{opt}	26.76	25.96	29.28
Lactin	p	0.0102 ±0.0012	0.0049 ±0.0010	0.0090 ±0.0005
	T_m	38.6591 ±3.2214	41.9895 ±6.7742	35.4547 ±2.4031
	ΔT	3.39048 ±1.3819	3.9771 ±2.5036	1.3939 ±0.7927
	λ	-1.0960 ±0.0175	-1.0390 ±0.0123	-1.0647 ±0.0116
	T_l	9.03	7.86	6.99
	T_u	33.33	33.30	33.25
	T_{opt}	26.84	26.01	29.27
SSI	TΦ	290.959	289.6829	293.8448
	pΦ	0.0932	0.0391	0.1384
	ΔHa	18532.37	18268.23	14664.19
	ΔHl	-106778.1	-98473.56	-45952.64
	ΔHh	67050.51	62682.47	71838.19
	Tl	10.48	8.80	6.10
	Th	29.03	28.26	32.01
	T_{opt}	26.57	25.86	28.68

Different models performed better for different stages depending on selected statistical test (Table 4.6). The Briére model provided the lowest RMSE value (0.0024) for the eggs development stage when compared to the Lactin (0.0027) and SSI (0.0053) models. The SSI model yielded the lowest RMSE value (0.0037) for the pupal stage when compared to the Briére (0.0069) and Lactin (0.0045) models. Both the Briére and Lactin model provided the lowest RMSE value (0.0026) for the larval development stage when compared

to the SSI model (0.0038). AIC/BIC values for the Briére model fitted to eggs (-49.3221/-49.9468) and larval (-57.6680/-57.8303) development stages were marginally better than values for the Lactin model (-46.0306/-46.8636) and -55.2428/-55.4592 respectively) and SSI model (-31.9191/-32.2968 and -44.0662 /-44.4448 respectively). AIC/BIC values for the Lactin model fitted to pupal data (-47.8391/-48.0554) were marginally better than values for the Briére (-43.7652/-43.9275) and SSI (-44.5270/-44.9056) model.

Table 4.6 Statistical results for fitted models to *G. lineola* eggs, larval and pupal development rates.

Nonlinear model	R^2	RSS	RMSE	AIC	BIC
	Eggs				
Linear	0.981	n/a	n/a	n/a	n/a
Briére	n/a	0.00003	0.0024	-49.3221	-49.9468
Lactin	n/a	0.00004	0.0027	-46.0306	-46.8636
SSI	n/a	0.0002	0.0053	-31.9181	-32.2968
	Larval				
Linear	0.962	n/a	n/a	n/a	n/a
Briére	n/a	0.00005	0.0026	-57.6680	-57.8303
Lactin	n/a	0.00005	0.0026	-55.2428	-55.4592
SSI	n/a	0.0001	0.0038	-44.0662	-44.4448
	Pupal				
Linear	0.988	n/a	n/a	n/a	n/a
Briére	n/a	0.0003	0.0069	-43.7652	-43.9275
Lactin	n/a	0.0001	0.0045	-47.8391	-48.0554
SSI	n/a	0.0001	0.0037	-44.5270	-44.9056

4.2 Modelling Temperature-Independent Insect Development Time

All of the models defined in Sections 4.1.1 and 4.1.2 are deterministic as they model insect development based on the mean or median of all individuals or cohorts per temperature treatment. These functions do not account for intrinsic differences among individuals in a population. However, insects reared under similiar environmental conditions develop at different times. This variation in development time is observed in Appendix I. A stochastic approach is required to describe the development times of proportions of individuals in a population (Stinner *et al*., 1975; Wagner *et al*., 1984c; Régnière, 1984). The integration of

deterministic development rate models and stochastic development time models is a fundamental requirement for all phenology models (Wagner *et al*., 1995; Ma & Bechinski, 2009).

4.2.1 Development Time Distribution Models

The following section provides a brief review of models considered in this study to describe variation of insect development observed during experimentation. The process of model evaluation is similar to that previously used for selecting development rate models.

4.2.1.1 Stinner Model

The distribution of development around the median rate of development for immature insect life-cycle stages or complete biological cycles is defined by Stinner *et al*. (1975) using a cumulative probability distribution function to describe proportion development in populations:

$$f(x) = (1 - z)^{\theta z^k} \qquad \textbf{Equation 4.19}$$

where f(x) is the cumulative probability of completing development by the normalized time x (time / median time), θ and k are empirical values, z is (B – t) / (B – A) where A and B are the times of development of the first and last individual(s) respectively, and t is the time from the start of development. Development times (1^{st} and 99^{th} percentiles considered the first and last individual(s) completing their development in a population respectively) and a selection of arbitrary values (i.e. 25^{th}, 50^{th} and 75^{th} percentiles) are calculated for each constant temperature distribution and converted to rates (Wagner *et al*., 1984c; Wagner *et al*., 1991). The percentile rates were plotted with respect to their associated temperatures and a non-linear temperature-driven development rate function such as Stinner *et al*. (1974) model, Schoolfield *et al*. (1977) model or Logan *et al*. (1979) model was fitted to each set of rates (Wagner *et al*., 1984c; Wagner *et al*., 1991).

4.2.1.2 Wagner Model

Wagner *et al*. (1984c) proposed a method to describe the distribution of development time based on the same-shape property theory discussed by Sharpe *et al*. (1977) and Curry *et al*.

(1978). This concept assumes that the inherent distributions of insect development times is of an identical shape, independent of temperature, meaning the distributions at different temperatures would fall on top of each other when normalised (Sharpe *et al*., 1977; Curry *et al*., 1978; Wagner *et al*., 1984c; Liu & Meng, 1999).

Development times at 1st, 5th, 10th, …, 90th, 95th and 99th percentiles are obtained from cumulative frequency distributions for each constant temperature treatment (Figure 4.8 – top) and divided by the median value of each distribution to produce normalised distributions for each temperature (Figure 4.8 – middle) (Wagner *et al*., 1984c; Wagner *et al*., 1991). A single cumulative distribution representing the normalised distributions for all temperature treatments is produced by averaging all the distributions that are weighted by the total frequency of each distribution (Figure 4.8 – bottom) (Wagner *et al*., 1984c; Wagner *et al*., 1991). A two (2P) or three parameter (3P) cumulative Weibull function is fitted to the combined curve (Figure 4.8 – bottom):

$$f(x) = 1 - \exp^{-[(x-y)/\eta]^{\beta}} \qquad \textbf{Equation 4.20}$$

where f(x) is as in equation 4.19 and γ is the lag in the onset of emergence, η is the emergence rate constant and β is the shape parameter that is an estimated regression parameter or:

$$f(x) = 1 - \exp^{[-(x/\alpha)]^{\beta}} \qquad \textbf{Equation 4.21}$$

where f(x) is as in equation 4.19, and α is a scale parameter and β is a shape parameter that is an estimated regression parameter respectively (Wagner *et al*., 1984c). A development rate model calculating the fraction of daily development combines with the Weibull equation to estimate the proportion of the population that completes development with each selected time step (Wagner *et al*., 1984c; Wagner *et al*., 1991).

The Weibull function describes development time distributions accurately using a direct methodology described by Wagner *et al*. (1984c) for many species including coleopterans such as *Aphthona lacertosa* and *A. nigriscutis* (flea beetles) (Skinner *et al*., 2004), and *Otiorhynchus sulcatus* (black vine weevil) (Son & Lewis, 2005a).

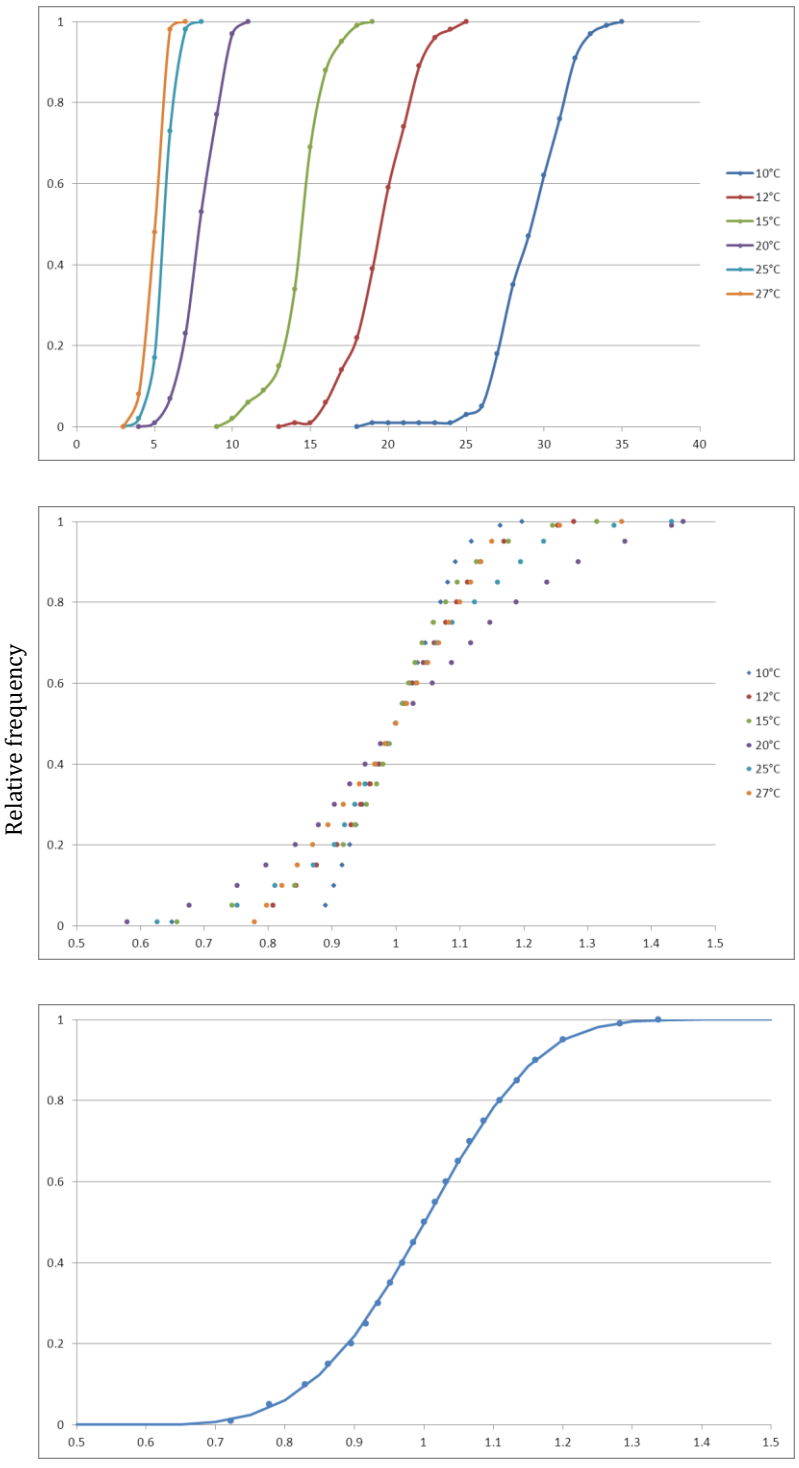


Figure 4.8 Hypothetical cumulative frequency distributions for an insect: cumulative probability distributions of development times at six constant temperatures (top) normalised development times at the 1st, 5th, 10th, ..., 90th, 95th and 99th percentiles for all distributions in the data-set (middle), and the cumulative Weibull distribution fitted to the weighted mean times at each percentile (bottom).

4.2.1.3 Régnière Model

Régnière *et al*. (1984) published a development time variability model around the same time as Wagner *et al*. (1984c). This function is conceptually developed on principles discussed by Sharpe *et al*. (1977) and Curry *et al*. (1978) and similar to the method of model application applied by Wagner *et al*. (1984c). A difference between this procedure and the previously reviewed applications is the use of the equation to describe the cumulative frequency distributions of development rates (instead of development time) relative to the median rate (instead of median time). The logistic model is defined as:

$$f(x) = \left\{1 + \exp^{[-k(x-1)]}(0.5^{-q} - 1)\right\}^{-1/q} \qquad \textbf{Equation 4.22}$$

where f(x) is as in equation 4.19, k is a shape parameter that determines the steepness of the curve and Q is a skew parameter that identifies a symmetric curve when equal to zero (a negative curve when greater than 0 and a positive curve when less than zero) (Régnière *et al*., 1984). The function is fitted to the development rates (relative to the median) for all experimental temperature treatments and resulting parameter estimates are examined for possible relationships with temperature (Régnière *et al*., 1984). The logistic equation is fitted to the pooled frequency data for all experimental temperature treatments if there is no relationship found (Régnière *et al*., 1984; Wagner *et al*., 1991). While this direct method and model are designed to be modified for small sample sizes and it is suitable for use with insects with multiple generations per season, it has not been as widely applied as the previous Weibull function via the Wagner *et al*. (1984c) technique. This is perhaps due to the less laborious application of the Wagner *et al*. (1984c) method and the accurate results obtained. The Régnière *et al*. (1984) approach has been employed successfully in different phenological studies including for coleopteran studies such as *Laricobius nigrinus* (hemlock woolly adelgid predatory beetle) (Zilahi-Balogh *et al*., 2003).

4.2.2 Model Selection Criteria for Development Time

Various stochastic approaches have been used in conjunction with deterministic rate functions to estimate the proportions of insect populations completing development through time. Differences in these approaches include the equation type (beta, Weibull and logistic), the choice of random variable modelled (development rate or development time) and the form of the frequency distributions used (averaged or pooled data). *A priori* and *a posteriori* features were employed to select a suitable approach. *A priori* assessment was

based on how distributions were obtained (direct (Wagner *et al*. (1984c) and Régnière *et al*. (1984) models) or indirect (Stinner *et al*. (1974) model) approaches – depending on the use of experimental data in the modelling process and use of several rate functions). *A posteriori* evaluation was established on the fit of the function to the observed data – similar to those utilised for development rate model selection.

4.2.3 Results

4.2.3.1 Temperature-Independent Development Time Models for *Phratora Vulgatissima*

Three distribution models – the two versions of the Weibull model describing the cumulative distribution of development times and the logistic model describing the cumulative distribution of development rates – were fitted to frequency distribution data-sets for all *P. vulgatissima* life-cycle stages and processes (Figure 4.9 –Figure 4.11 and Table 4.7 – Table 4.8). These models were chosen based on the direct methods used in obtaining the distributions to be modelled.

All functions were fitted successfully to the distribution data-sets (Table 4.9). The Weibull (3P) function performed best with RMSE values of 0.0087, 0.0053, 0.0112 and 0.0162 for post-diapause, eggs, larval and pupal life-cycle stages respectively when compared to results for the Weibull (2P) function (0.0165, 0.0408, 0.0136 and 0.0383) and the logistic function (0.0829, 0.0578, 0.0753 and 0.0797). The Weibull (3P) function was better for egg and pupae development time description based on AIC/BIC results (-140.3715/-137.0948 and -129.3160/-126.0429 respectively). The logistic function was the better function for larvae and post-diapause development time description based on AIC/BIC results (-233.6056/-228.7680 and -171.4185/-166.6796 respectively). Although the logistic model did not fit to the oviposition period development time data-set, both the Weibull (2P) function and Weibull (3P) function were fitted successfully and both were equally useful for representation with the Weibull (2P) model only slightly better with lower RSS and RMSE values and higher AIC and BIC values.

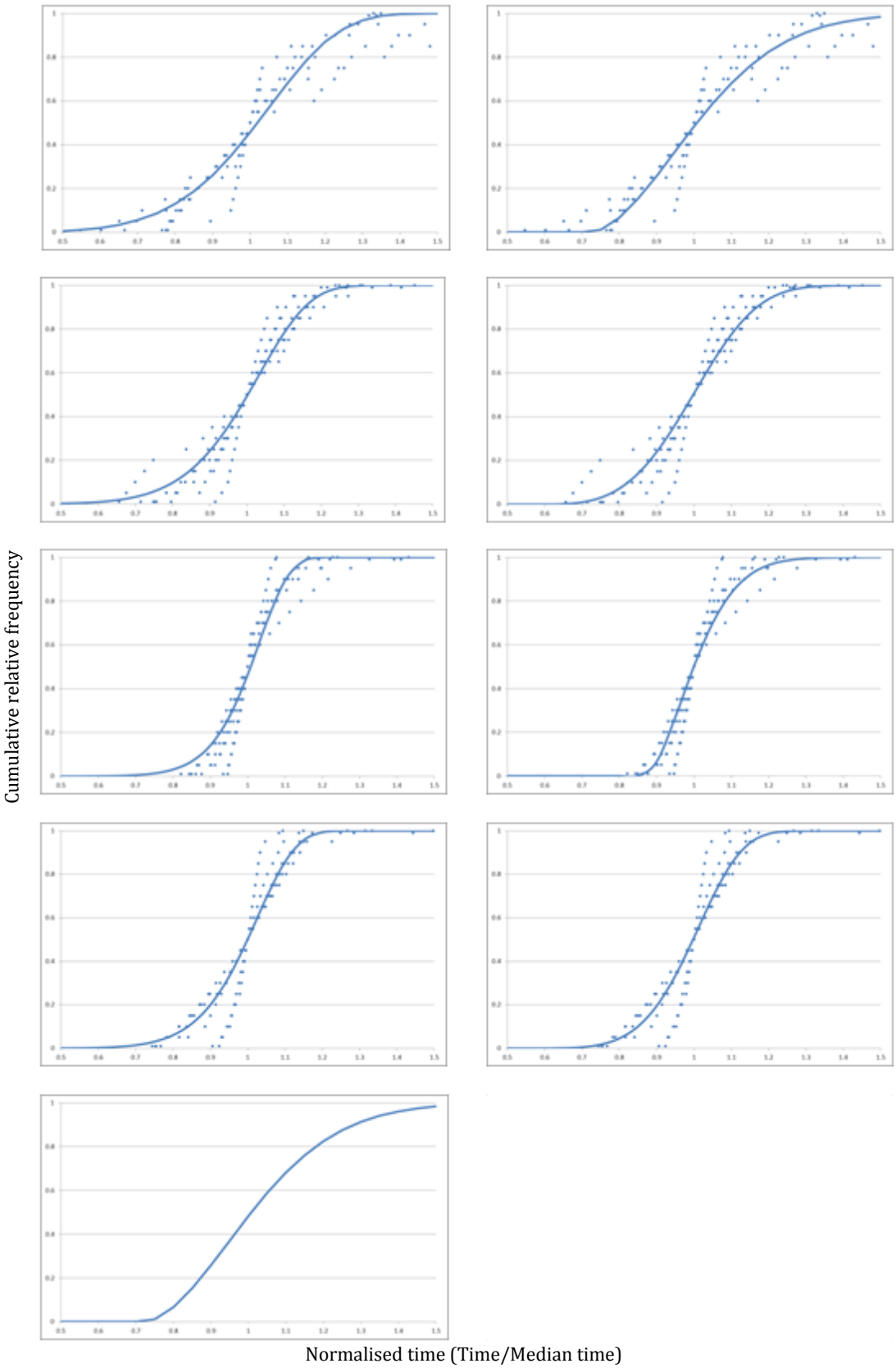


Figure 4.9 Weibull (2P) model (left) and Weibull (3P) model (right) fitted to *P. vulgatissima* post-diapause, eggs, larval, pupal and sexual maturation development distribution data-sets (top to bottom).

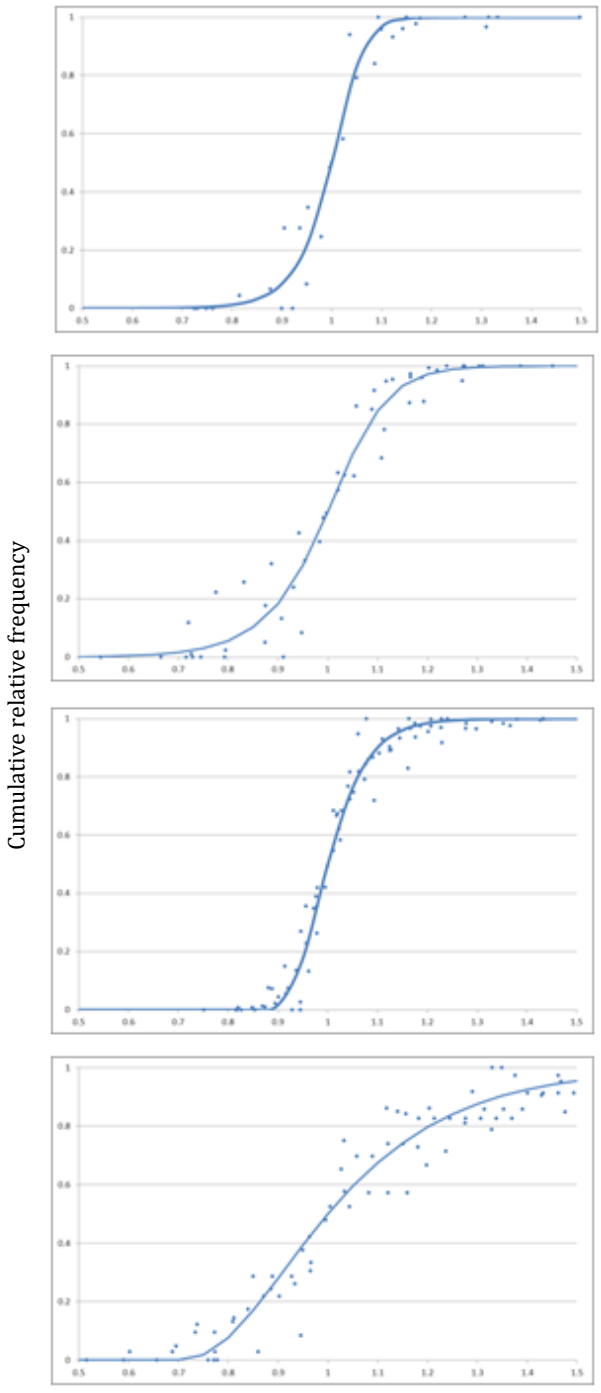


Figure 4.10 Logistic model fitted to *P. vulgatissima* post-diapause, eggs, larval and pupal development distribution data-sets (top to bottom).

Table 4.7 Parameter estimations for models fitted to *P. vulgatissima* post-diapause, eggs, larval and pupal development time distributions.

Models	Parameters	Development Stage			
		Post-Diapause	**Eggs**	**Larval**	**Pupal**
Weibull (2P)	a	1.0773 ±0.0063	1.0466 ±0.0019	1.0357 ±0.0032	1.0340 ±0.0012
	b	6.6274 ±0.3625	8.4924 ±0.1840	13.4234 ±0.7520	10.8076 ±0.1931
Weibull (3P)	g	0.7207 ±0.0190	0.5730 ±0.0323	0.8652 ±0.0027	0.4990 ±0.0778
	a	0.3517 ±0.0201	0.4706 ±0.0328	0.1661 ±0.0029	0.5335 ±0.0782
	b	1.7918 ±0.1324	3.5592 ±0.2821	1.7224 ±0.0393	5.3502 ±0.8538
Logistic	k	5.2256 ±0.5430	18.8371 ±3.7458	19.1673 ±1.7985	37.3918 ±11.8021
	q	-0.3073 ±0.2005	1.5407 ±0.6354	0.0799 ±0.2015	1.9359 ±1.0228

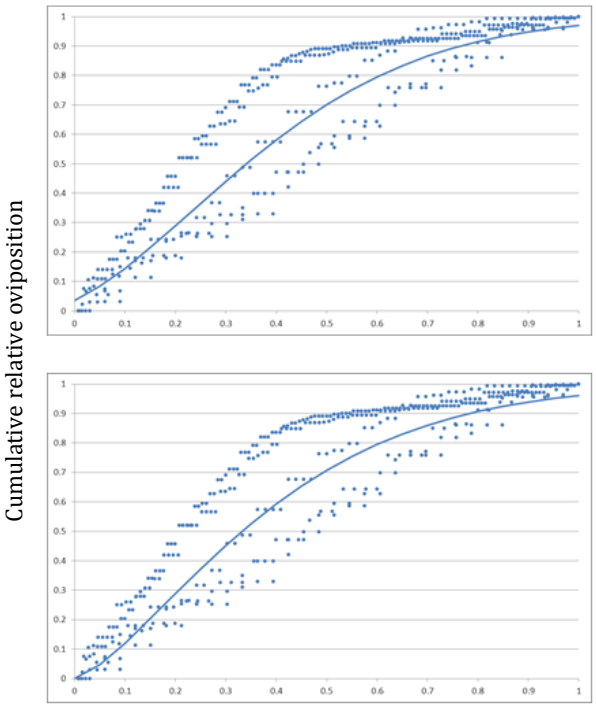


Figure 4.11 Relative oviposition of *P. vulgatissima* described using Weibull (2P) model (top) and Weibull (3P) model (bottom).

Table 4.8 Parameter estimations for models fitted to *P. vulgatissima* oviposition period data.

Models	Parameters	Development Stage
		Oviposition period
Weibull	a	0.4317 ± 0.0065
(2P)	b	1.4009 ± 0.0456
Weibull	g	-0.0716 ± 0.0394
(3P)	a	0.5117 ± 0.0434
	b	1.6997 ± 0.1708

Table 4.9 Statistical results for models fitted to *P. vulgatissima* eggs, larval, pupal, post-diapause development time distributions and oviposition period.

Models	RSS	RMSE	AIC	BIC
	Eggs			
Weibull (2P)	0.0060	0.0165	-114.2907	-112.1086
Weibull (3P)	0.0017	0.0087	-140.3715	-137.0984
Logistic	0.3364	0.0829	-101.0222	-97.2386
	Larval			
Weibull (2P)	0.0367	0.0408	-74.2919	-72.1098
Weibull (3P)	0.0006	0.0053	-162.2962	-159.0231
Logistic	0.2775	0.0578	-233.6056	-228.7680
	Pupal			
Weibull (2P)	0.0041	0.0136	-122.6617	-120.4796
Weibull (3P)	0.0027	0.0112	-129.3160	-126.0429
Logistic	0.1760	0.0753	-68.3340	-65.4660
	Post-Diapause			
Weibull (2P)	0.0322	0.0383	-77.1464	-74.9643
Weibull (3P)	0.0058	0.0162	-112.9868	-109.71369
	Oviposition period			
Weibull (2P)	6.0659	0.1210	-569.5136	-561.4619
Weibull (3P)	6.1012	0.1214	-565.1157	-553.0381
Logistic	0.5021	0.0797	-171.4185	-166.6796

4.2.3.2 *Galerucella lineola*

Three distribution models – the two versions of the Weibull model describing the cumulative distribution of development times and the logistic model describing the cumulative distribution of development rates – were fitted to frequency distribution data-

sets for all *G. lineola* life-cycle stages (Figure 4.12 – Figure 4.13 and Table 4.10). These models were chosen based on the direct methods used in obtaining the distributions to be modelled.

All functions were fitted successfully to the distribution data-sets (Table 4.11). The Weibull (3P) function performed best with RMSE values of 0.0135, 0.0031 and 0.0136 for egg, larvae and pupae life-cycle stages respectively when compared to results for the Weibull (2P) function (0.0325, 0.0336 and 0.0154) and the logistic function (0.0847, 0.0563 and 0.0154). The Weibull (3P) model was the choice function for egg and pupae development time description based on AIC/BIC results (-121.1368/-117.8636 and -120.7480/-117.4749 respectively). The logistic model was the choice function for larvae development time description based on AIC/BIC results (-240.7485/-235.9351).

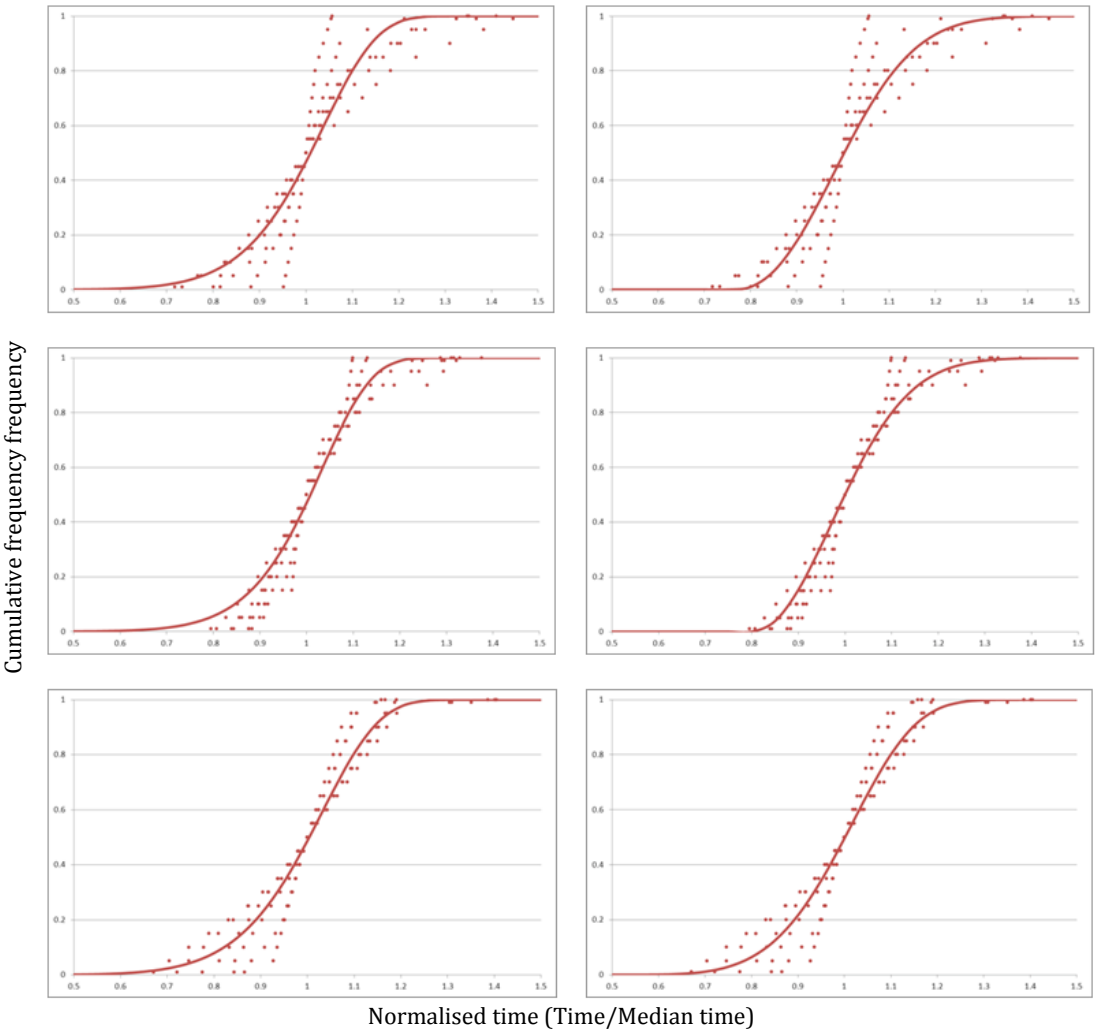


Figure 4.12 Weibull (2P) model (left) and Weibull (3P) model (right) fitted to *G. lineola* eggs, larval and pupal development distribution data-sets (top to bottom).

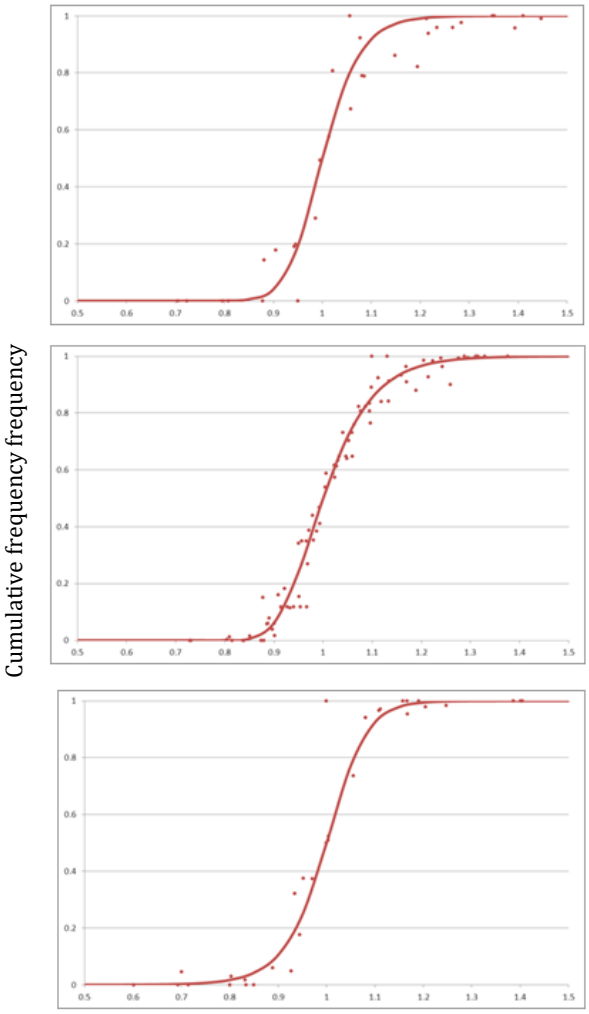


Figure 4.13 Logistic model fitted to *G. lineola* eggs, larval and pupal development distribution data-sets (top to bottom).

Table 4.10 Parameter estimations for models fitted to *G. lineola* eggs, larval and pupal development time distributions.

Models	Parameters	Development Stage		
		Eggs	***Larval***	***Pupal***
Weibull	a	1.0479 ± 0.0034	1.0434 ±0.0032	1.0436 ±0.0015
(2P)	b	9.8735 ± 0.4507	10.6468 ±0.4819	9.3598 ±0.1861
Weibull	g	0.7639 ± 0.0173	0.7995 ± 0.0029	0.4618 ±0.1012
(3P)	a	0.2809 ± 0.0178	0.2389 ± 0.0030	0.5800 ±0.1019
	b	2.2569 ± 0.1755	2.0699 ± 0.0330	5.0274 ±0.9604
Logistic	k	22.4446 ±5.8701	15.2462 ±1.2228	26.686 ±9.9477
	q	0.4943 ± 0.6278	0.1260 ± 0.1648	1.4433 ±1.0557

Table 4.11 Statistical results for models fitted to *G. lineola* eggs, larval and pupal development time distributions.

Models	RSS	RMSE	AIC	BIC
	Eggs			
Weibull (2P)	0.0232	0.0325	-84.3609	-82.1789
Weibull (3P)	0.0040	0.0135	-121.1368	-117.8636
Logistic	0.2437	0.0847	-67.4077	-64.3550
	Larval			
Weibull (2P)	0.0248	0.0336	-82.8625	-80.6804
Weibull (3P)	0.0002	0.0031	-185.7138	-182.4407
Logistic	0.2427	0.0563	-240.7485	-235.9351
	Pupal			
Weibull (2P)	0.0052	0.0154	-117.3346	-115.1525
Weibull (3P)	0.0041	0.0136	-120.7480	-117.4749
Logistic	0.0660	0.0454	-111.8480	-108.7953

4.3 **Discussion**

The curvilinear development rate – temperature relations for *P. vulgatissima* and *G. lineola* is typical of most insects (Rueda *et al*., 1990; Bentz *et al*., 1991; Muñiz & Nombela, 2001). It can be described by a plethora of models specifically adapted or constructed for development (Logan *et al*., 1976; Sharpe & DeMichele, 1977; Briére *et al*., 1999). The objective of this chapter was to select models that could best describe the relationship between temperature and development rates/time across all life-cycle stages for each species. The selection of a suitable fitting function was aided by employing model selection criteria based on *a priori* and *a posteriori* features (Kontodimas *et al*., 2004; Walgama & Zalucki, 2006). No single function efficiently satisfied the full range of criteria. In the interests of using a single model for describing development for each species, a degree of criteria compromise was considered justifiable (Roy *et al*., 2002; Walgama & Zalucki, 2006).

The linear model remains one of the easiest models to apply to development rate data with a minimum number of fitted coeffients required. The linear relationship between development rates and temperature applies to the mid-range of temperatures within which development can occur (Figure 4.1 – Figure 4.2). The fit of the equation to development rates associated with temperatures in this range for all life-cycle stages and processes was evident with high R^2 values. This statistic is a valid goodness-of-fit statistic for this type of model but it cannot be used to evaluate non-linear models as, unlike linear regression, the total sum of squares is not equal to the regression sum of squares plus the residual sum of

squares, and therefore lacks interpretation (Spiess & Neumeyer, 2010). The estimated values of K and T_l were obtained with the extrapolation of the line into a region where the relationship is unlikely to be linear. Furthermore, the development rate results showed that high temperatures in each life-cycle stage resulted in a decrease in development rates from an optimum development rate. This highlighted some of the inherent problems associated with estimating T_{opt} and T_u using this method. Estimating the developmental rates and suitable values of the critical thresholds for both species, across temperature ranges of 10-28°C and 10-31°C respectively, required the application of non-linear models. However, linear estimations for T_l were similar to estimations from non-linear models such as the Lactin model (7.5°C for linear estimation and 7.5°C for Lactin estimation for *P. vulgatissima* post-diapause development respectively, and 5.1°C for linear estimation and 5.0°C for Lactin estimation for *P. vulgatissima* larvae development respectively). Such differences between linear estimated values of K and T_l and more complex non-linear models have been acknowledged as negligible (Kontodimas *et al*., 2004; Forouzan *et al*., 2008).

The Briére model is the least complex of the three non-linear models fitted to development rates for life-cycle stages and provides estimates of three critical thresholds. Satisfying multiple *a priori* criteria, the Briére model was statistically adequate for describing development rates for both species compared to the other non-linear models, particularly for *P. vulgatissima* post-diapause and egg development and *G. lineola* egg and larvae development. However, the function provided unrealistically high critical threshold estimates when fitted to *P. vulgatissima* egg, larvae and pupae development rates (33.7°C, 38.5°C and 33.1°C respectively) and *G. lineola* pupae development rates (35.9°C) and compared to observed data. The model underestimated values when fitted to *P. vulgatissima* larvae development rates (-1.4°C) based on laboratory work also. This underestimation and overestimation of critical thresholds for insect development has been noted in other multi-model studies (Golizadeh *et al*., 2007; Jalali *et al*., 2010).

The SSI model, based on enzymatic reactions, was the only biophysical model tested. In contrast with the Briére model, the complex SSI model is similar in structure to preceding biophysical models of Sharpe & DeMichele (1977) and Schoolfield *et al.* (1981) requiring seven fitted coeffients. The model was therefore ranked negatively, prior to parameter estimation and statistical comparison, based on the model selection criteria. Estimated T_u for *P. vulgatissima* post-diapause development (26.8°C) was inappropriate as *P. vulgatissima* developed well at a constant higher temperature (27.0°). Similar underestimations of T_u were noted for *G. lineola* egg (29.0°C) and larvae (28.3°C) development due to good development at a constant higher temperature (29.0°). Other critical threshold temperatures across the life-cycle stages were considered reasonable for

both species. However, the other two non-linear models provided a better goodness of fit based on statistical comparisons.

Ultimately, the Lactin model was selected as the most appropriate model for describing development rates for both species across all life-cycle stages. This model is of medium complexity compared with the other two non-linear models. All biologically important species-specific parameter estimations (T_l, T_{opt} and T_u) were observed to be in general agreement with experimental results except for *P. vulgatissima* egg development T_u (33.2°C) which was considered to be marginally overestimated. Statistical analysis of the fitted non-linear models revealed the Lactin model to be the overall best-fitting function for *P. vulgatissima*. Although the Briére and Lactin models were both good fitting models for *G. lineola* development rates, statistically, the Briére function overestimated T_u for *G. lineola*. Also, the Lactin model captured the higher temperature range associated for *G. lineola* development, for egg, larvae and pupae life-cycle stages, when compared to *P. vulgatissima* also (see Section 3.1).

Consideration of the variability in development time among individuals of insect populations can greatly expand the information provided by phenology models (Curry *et al*., 1978; Régnière, 1984; Wagner *et al*., 1991). The Weibull (3P) function was the more complex of the three models assessed to describe variation in development time for both species in this study. The model satisfied other model selection criteria however as it provided an optimum fit to the distribution data-sets based on statistical analysis and the distributions were obtained using a direct approach.

The development rate data obtained for *P. vulgatissima* sexual maturation life-cycle stage was sparse in comparison to data acquired for the other life-cycle stages. Consequently, a non-linear model could not be applied to describe the data. Experiment outcomes suggested that imago *P. vulgatissima* required approximately twice as long as post-diapause *P. vulgatissima* to complete stage development and initiate first egg-lay (see Section 3.2). Based on these results, the Lactin function was fitted to post-diapause development rate data increased by a factor of two to provide a representative data-set for the sexual maturation. The Weibull (3P) equation with the same parameters as those used to describe post-diapause development time variability was employed to define sexual maturation development time variability. These were necessary assumptions required to construct a full life-cycle phenology/voltinism model for *P. vulgatissima*.

The oviposition period of *P. vulgatissima* was described using an adapted version of methods proposed by Wermelinger & Seifert (1998). The relative cumulative oviposition data (number of eggs per female per day divided by oviposition period for each

temperature treatment and adjusted for surviving females during each observation) was plotted against relative oviposition time (time divided by maximum oviposition period for each temperature treatment). The Weibull (3P) function was fitted to the data-set as the logistic function would not but Weibull (2P) version was equally practical based on statistical evaluation. This model was combined with the quadratic polynomial equation fitted to the temperature-dependent oviposition period rates to estimate the proportion of eggs laid within the oviposition period.

Due to a lack of information obtained for *G. lineola* life-cycle stages such as post-diapause development and processes such as ovipositioning, a full phenological model was constructed for *P. vulgatissima* only. Data-sets and fitted models for *G. lineola* are provided for two reasons: 1) to observe any synchrony based on temperature-dependent development between the two species that occupy similar ecological niches and 2) to provide information for future phenological modelling of *G. lineola.* The following chapter describes the development of a plant phenological model for *S. viminalis,* to be used as biofix for the willow beetle active season, and incorporated in the combined phenology/voltinism model.

5 MODELLING HOST PLANT PHENOLOGY

This chapter provides a literature review of important statistical, theoretical and mechanistic models that have been formulated to describe plant phenology. A number of these were considered to account for *Salix* budburst in the field using records obtained from a phenological garden network. A budburst model was chosen to be used as a biofix for willow beetle development and results are discussed.

5.1 Insect and Host Plant Synchrony

Environmental conditions limit the periods during which growth and reproduction cycles take place for flora and fauna species residing in temperate regions. For insect herbivores, the phenology – timing of periodic biological events in the animal and plant world as influenced by the environment – of their host plant species determines these cycles and it is therefore imperative for these species to be synchronised with their host plant's phenology. The commencement of specific life-cycle activities during this optimal period will vary with different species depending on dietary necessities. Development outside these transitory optimal conditions can have consequences on herbivore survival or fecundity (van Asch & Visser, 2007).

The degree of synchrony between insect herbivores and their hosts depends on the phenology of the herbivore and the host, and it is defined as the difference between the

phenological stadia of herbivore and host that are most relevant to the herbivore (van Asch & Visser, 2007). For many herbivorous species, feeding must begin just after leaf emergence and the time difference between appearance of feeding stages (post-diapause adults or newly hatched larvae) and host plant budburst is the degree of synchrony; perfect synchrony occurs when both events take place at the same time (van Asch & Visser, 2007). Such phenological events can be quantified using the first date of host budburst and the first date of herbivore appearance (van Asch & Visser, 2007).

The degree of synchrony between herbivore and plant phenologies is the result of two underlying processes: the response mechanism of the plant and the response mechanism of the herbivore (van Asch & Visser, 2007). As previously discussed in Chapters 3 and 4, temperature is the main factor affecting herbivore phenology, with photoperiod playing a role in species that have a diapause period. Temperate deciduous trees are subject to the same environmental controls as insects and temperature is recognised as the dominant abiotic factor influencing tree phenology. During colder winter months, tree buds are generally undeveloped and in a stage of rest, defined as the period in which buds remain dormant due to growth-arresting physiological conditions (Sarvas, 1974; Kramer, 1994). Such conditions are removed when buds are exposed to a period of low temperatures below a recognised baseline temperature – chilling phase (Sarvas, 1974; Kramer, 1994). After sufficient chilling, the quiescence period occurs; buds develop but remain dormant due to unfavourable environmental conditions. This developmental stage is temperature-dependent with budburst taking place when the buds have been exposed to warmer temperatures for an extended time period – forcing phase (Sarvas, 1974; Kramer, 1994) (Figure 5.1).

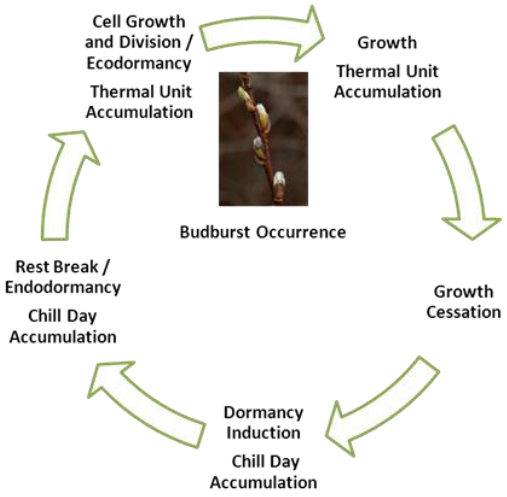


Figure 5.1 Integrated conceptual model of the annual cycle of growth and dormancy in boreal and temperate trees, identifying the ecophysiological phenomena that determine the timing of growth onset and cessation (Source: Hänninen & Tanino, 2011; Olsson *et al.*, 2013).

With a dependence on environmental conditions, the phenological responses of plants vary annually. To maintain synchrony with their host plants, many herbivorous insects have a plastic response to the same conditions – phenotypic plasticity (van Asch & Visser, 2007). However, there is the assumption that climate change will lead to a disruption of synchrony between insect herbivores and their host plants, which may impact on population dynamics if natural selection is insufficient to restore synchrony (Figure 5.2). Examples of such disruptions have been described in some insect herbivore populations such as *Operophtera brumata* (winter moth) and its host *Picea sitchensis* (Sitka spruce) (Dewar & Watt, 1992). In contrast to such studies showing increasing asynchrony, the phenology of *Anthocharis cardamines* (orange-tip butterfly) in the UK has fluctuated in precise synchrony with that of its crucifer host plant (Sparks & Yates 1997).

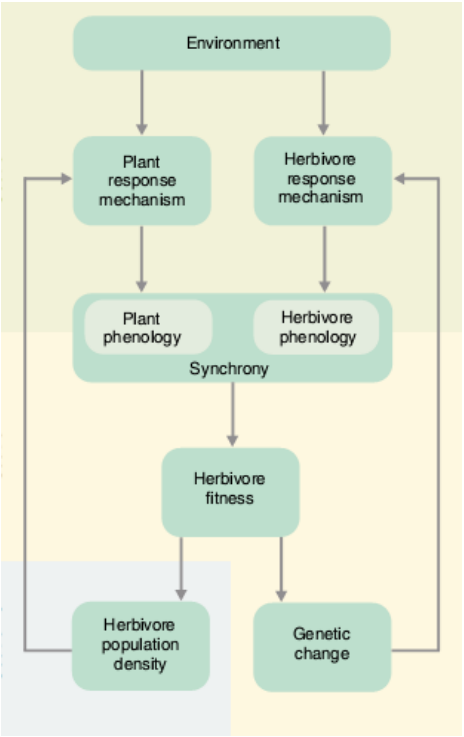


Figure 5.2 Schematic overview of the factors affecting and affected by synchronization of insect herbivore and plant phenology (Source: van Asch & Visser, 2007).

With *P. vulgatissima* and *G. lineola* post-diapause development dependent on *Salix* foliage emergence and observations in the field suggesting a close insect-host phenological interaction, budburst occurrence was subsequently used as a biofix for the initiation of post-diapause development in adult beetle populations. Thus the aim of this research was to examine models presented in the literature and select a model that adequately estimated the date of budburst for *S. viminalis* due to its use as a parent for variety development.

5.2 **Modelling Temperature-Dependent Budburst**

Many different plant phenology models have been developed to predict the dates of budburst and other important plant life-cycle events such as flowering and fruit maturation. Similar to the temperature-dependent insect development models discussed in Section 4.1, these models are based on the original 18th century findings of Reaumur (1735) who proposed that plant development is proportional to the sum of temperature over time namely the degree-day sum concept. Since then, three classes of plant phenology models have been developed – statistical, theoretical and mechanistic – with each type having associated advantages and disadvantages (Chuine *et al*., 2013; Zhao *et al*., 2013).

The Thermal Time or Spring Warming model (equation 5.1) based on the degree-day sum concept is the simplest form of a plant phenology model (Cannell & Smith, 1983; Hunter & Lechowicz, 1992). It is described as:

$$R_{force}(T) = \begin{cases} T - T_l & T \geq T_l \\ 0 & T < T_l \end{cases}$$

Equation 5.1

This commonly applied statistical model requires three parameters to be estimated: the arbitrary date from which to begin heat-unit accumulations, the lower base temperature threshold (T_l) and the required heat sum that signals an event occurrence when the required number of heat units have accumulated. T represents daily temperature. Although it has been used for modelling the budburst of many tree species in many boreal and temperate locations (Nizinski & Saugier, 1988; Wielgolaski, 1999; Schaber & Badeck; 2003), it fails to take dormancy into account by ignoring any chilling requirements, assumes an absolute photoperiod is required to initiate quiescence and describes a linear relationship between a phenological event such as the budburst and temperature above a set temperature threshold (Cannell & Smith, 1983).

Various theoretical models have been developed to understand the evolution of leaf strategies in trees rather than annual variation in plant phenology and these are based on the assumption of the cost-benefit trade-off involved in producing foliage to increase resource acquisition (Zhao *et al.,* 2013). Examples of such models include the carbon balance based model, based on the balance between carbon gain through photosynthesis and carbon loss through respiration; the survival and reproductive fitness based or niche based plant phenology model, based on the identification of traits that determine individual species fitness subjected to particular environmental conditions and the genetic behaviour

based plant phenology model, based on the links between genetic factors and phenological responses (Chuine & Beaubien, 2001; Arora & Boer, 2005; Wilczek *et al*., 2009). The advantages associated with such models include broader coverage, flexible application and realistic predictions. The disadvantages include greater complexity, technique-related confusion and a continued reliance on empirical relationships that occur between climatic variables and phenological events (Zhao *et al.,* 2013).

Mechanistic models are the most widely applied plant phenology model, describing relationships between biological processes and driving factors such as temperature in the plant's environment. Experimental approaches and statistical model-fitting techniques are often used for parameter estimations in mechanistic approaches (Zhao *et al.,* 2013). Established on the foundations of the Thermal Time model, these functions generally only consider what happens during quiescence, after dormancy has been broken, and development and cell growth are triggered by external thermal factors (Cleland *et al*., 2007). Many similar mechanistic models have been defined with dormancy chilling days and quiescence forcing temperature requirements accumulating at differing times and in differing formats. Examples of these include the Sequential model (Richardson, 1974; Sarvas, 1974), the Parallel model (Langsberg, 1974), the Deepening Rest model (Kobayashi *et al*., 1982), the Four Phase model (Vegis, 1964) and the Alternating model (Cannell & Smith, 1983; Murray *et al*., 1989).

Hänninen (1990) and Kramer (1994) reviewed the first four mechanistic models. For the Sequential model, the periods of dormancy and quiescence are considered to be independent phases, with no progression from rest to quiescence until the chilling stage requirements have been met and no transition from quiescence to budburst until the forcing stage requisites have occurred. In contrast, in the Parallel model, the accumulation of chilling and forcing units occurs together over time. The Deepening Rest model assumes two phases of rest during dormancy – a deepening rest and a decreasing rest – before the quiescence phase can be defined. The Four Phase model assumes three phases of rest during dormancy – pre-rest, true-rest and post-rest – before the initiation of quiescence, with an increasing temperature threshold for forcing during pre-rest, a decreasing temperature threshold for forcing during post-rest and no bud response to forcing temperature during true rest.

As described by Hänninen (1990) and Kramer (1994), all four models can be represented by the following equations with shared attributes: (1) the bud's potential to respond to forcing temperatures is dependent on the state of chilling; (2) during rest, the rate of chilling is assumed to have an optimum between minimum and maximum

temperature thresholds (equation 5.2); (3) during quiescence, the rate of forcing is assumed to be logistically related to temperature (equation 5.3) and (4) the states of chilling and forcing are the summation of the rates of chilling and forcing respectively using a variable time-step and a maximum of 1 day (equation 5.4 and 5.5):

$$R_{chill}(T) = \begin{cases} 1 & T \le T_{min} \\ \dfrac{T - T_{min}}{T_{opt} - T_{min}} & T_{min} < T \le T_{opt} \\ \dfrac{T - T_{max}}{T_{opt} - T_{max}} & T_{opt} < T \le T_{max} \\ 0 & T > T_{max} \end{cases}$$ **Equation 5.2**

$$R_{force}(T) = \begin{cases} 0 & T \le T_b \\ K\dfrac{a}{1 + e^{b(T+c)}} & T > T_b \end{cases}$$ **Equation 5.3**

$$S_{chill} = \sum_{t1}^{t} R_{chill}$$ **Equation 5.4**

$$S_{force} = \sum_{t2}^{t} R_{force}$$ **Equation 5.5**

where T_{min} is the minimum temperature for rate of chilling, T_{opt} is the optimal temperature for rate of chilling, T_{max} is the maximum temperature for rate of chilling, K is the buds potential to respond to forcing temperature, t1 is the date of onset of rest, t2 is the date of onset of quiescence and a, b, and c are empirical constants.

The Alternating model classifies each day as either a chilling day or a forcing day, depending on whether the mean daily temperatures are above or below a set temperature threshold (Cannell & Smith, 1983; Murray *et al.*, 1989). On forcing days, the temperature sum is accumulated as in the Thermal Time model. On a chilling day, the count of such days increases by one:

$$R_{chill}(T) = \begin{cases} 1 & T \le T_b \\ 0 & T > T_b \end{cases}$$ **Equation 5.6**

Due to the model's negative inverse relationship between the state of chilling and the state of forcing, the more chilling days that are received, the less forcing temperatures are needed for the budburst to ensue (Kramer, 1994).

The highly parameterised Unified model was formulated as a combination of the most relevant phenological modelling approaches previously discussed, simulating budburst for different species using the same equations but with species-specific parameter coefficients (Chuine, 2000):

$$\frac{1}{1+\exp^{a(x-c)^2+b(x-c)}} = \begin{cases} R_{chill} & \text{if } a = C_a \text{ and } b = C_b \text{ and } c = C_c \\ R_{force} & \text{if } a = 0 \text{ and } b = F_b \text{ and } c = F_c \end{cases} \quad \textbf{Equation 5.7}$$

$$R_{chill} = \frac{1}{1+\exp^{a(x-c)^2+b(x-c)}} \quad \textbf{Equation 5.8}$$

$$R_{force} = \frac{1}{1+\exp^{a(x-c)^2+b(x-c)}} \quad \textbf{Equation 5.9}$$

where C_a, C_b and C_c are chilling rate parameters, F_b and F_c are forcing rate parameters and C* and F* are chilling and forcing thresholds respectively. Similar to insect development models, an increase in the number of parameters increases the complexity of the model meaning responses are harder to obtain (Linkosalo *et al*., 2008; Fu *et al*., 2012a; 2012b; 2012c).

Recent studies have sought to assess these models on their predictive success (Kramer, 1994; Chuine, 1999; Linkosalo *et al*., 2008; Fu *et al*., 2012a; 2012b; 2013c). These models can be parameterised and validated against the whole data-set – internal validation – and/or parameterised on a randomly selected portion of the data-set to be tested against the other half – external validation – with model performances further evaluated using measures such as RMSE, Model Efficiency and AIC (Linkosalo *et al*., 2008; Fu *et al*., 2012a; 2012b).

5.3 **Materials and Methods**

The following section compares and tests (when possible) a number of the previously discussed models of leaf budburst in *Salix*, specifically *S. viminalis*, using budburst records sourced from a European phenological garden network and temperature records obtained from the Irish meteorological service.

5.3.1 Budburst Data

The International Phenological Gardens (IPG) is a European and individual network within the Phenology Study Group of the International Society of Biometeorology (ISB). It is a unique network for long-term phenological observations of plants representing the natural vegetation in Europe. Ranging across 28 degrees of latitude from Scandinavia to Macedonia and across 37 degrees of longitude from Ireland to Finland in the north and from Portugal to Macedonia in the south, the IPG consists of 93 stations in 19 countries (Chmielewski *et al*, 2013). The IPG network in Ireland has developed on the four sites which were originally planted in the early 1960s: Valentia Observatory, Co. Kerry; the National Botanic Gardens, Glasnevin, Co. Dublin; John F. Kennedy Arboretum; New Ross, Co. Wexford and Johnstown Castle, Co. Wexford. Fragmented budburst data-sets for *S. viminalis* and four other *Salix* species – *S. smithiana, S. acutifolia, S. aurita* and *S. glauca* – were obtained from the 1980s to 2010, except for *S. glauca* (Chmielewski *et al*, 2013) (Figure 5.3 – Figure 5.4). As per the Phenological Observation Guide of the International Phenological Gardens, budburst – or leaf-unfolding – was described as the date when the first regular surfaces of leaves were visible in several places (about 3 to 4) on the observed plant, with the first leaf of a plant pushed out of the bud up to its leaf stalk (petiole) (IPG, 2013).

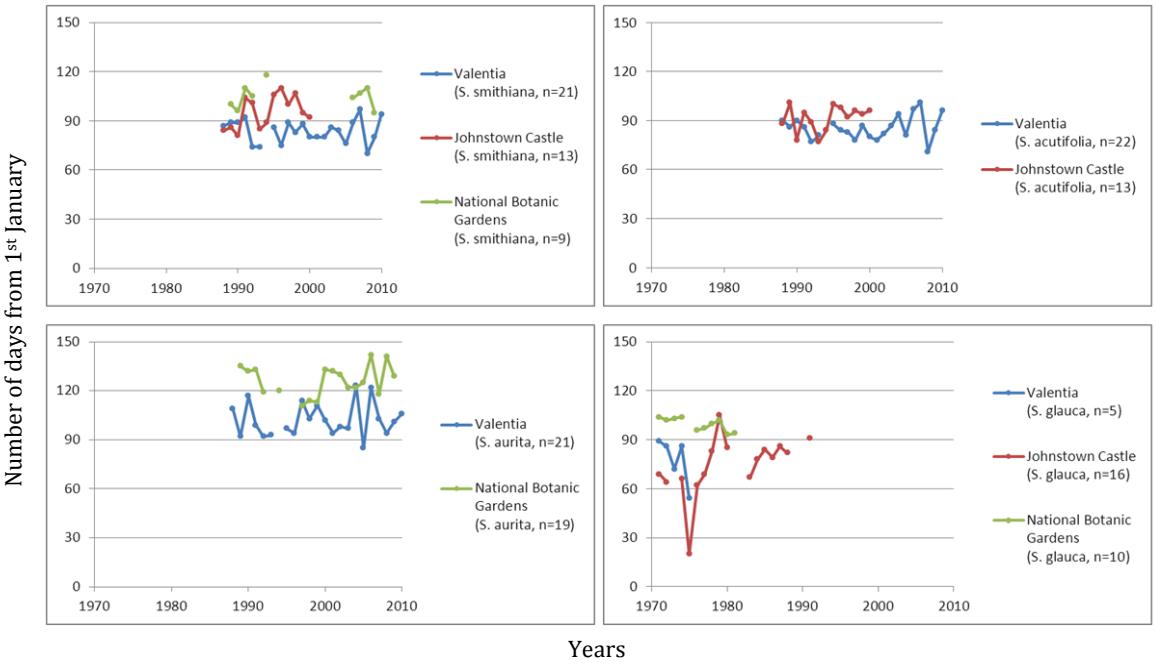


Figure 5.3 Recorded budburst observations for *S. smithiana* (top left), *S. acutifolia* (top right), *S. aurita* (bottom left) and *S. glauca* (bottom right) from IPG sites in Ireland.

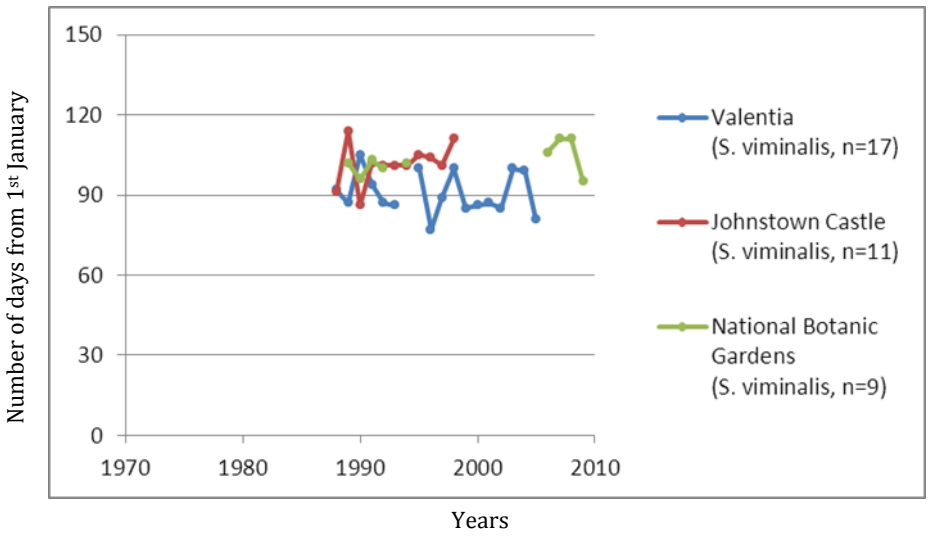


Figure 5.4 Recorded budburst observations for *S. viminalis* from IPG sites in Ireland.

The IPG network in Ireland was expanded in 2009 to include additional sites and new species (particularly native types) that were in close proximity to climate stations. Although a two to three year period of acclimation is suggested before monitoring (EPA, 2013), new *S. viminalis* budburst data for 2010-2012 became available towards the end of this study for sites at Carton House, Co. Kildare, Armagh Observatory, Co. Armagh, Millstreet County Park, Co. Cork, and Markree Castle, Co. Sligo. Additional recordings from the National Botanic Gardens and Johnstown Castle were obtained for this period also.

5.3.2 Temperature Data

Observed minimum and maximum daily temperatures were obtained from the national meteorological service, Met Éireann, to calculate mean daily temperature values for the periods and phenological observation sites related to the budburst recordings (Figure 5.5). These sites were located at Valentia. Co. Kerry; John F. Kennedy Arboretum, Co. Wexford; the National Botanic Gardens, Co. Dublin; Carton House, Co. Kildare; Armagh Observatory, Co. Armagh; Millstreet County Park, Co. Cork and Markree Castle, Co. Sligo. Valentia phenology garden (1) (51°56'N, 10°15'W) is located on the grounds of the Valentia Meteorological Observatory (1). Therefore, meteorological data corresponded well with the atmospheric conditions that the phenological garden experienced. For the phenological garden situated at Johnstown Castle (2) (52°18'N, 06°31'W), data collected at Rosslare synoptic station (2) (52°15'N, 06°20'W), which was officially closed in April 2008 and replaced by an automatic weather station beside the site, was used to provide an unbroken

data-set. Dublin Airport synoptic station (3) (53°23'N, 06°14'W) offered the best complete temperature data-set for the National Botanic Gardens site (3) (53°22'N, 06°16'W). For the newer phenological sites, temperature data from Casement Aerodrome, Co. Dublin (4) (53°18'N, 06°26'W), Cork Airport, Co. Cork (5) (51°51'N, 08°29'W) and Knock Airport (6) (53°55'N, 08°49'W) was utilised for Carton House, Co. Kildare (4) (53°22'N, 06°35'W), Millstreet County Park, Co. Cork (5) (52°04'N, 09°03'W), and Markree Castle, Co. Sligo (6) (54°11'N, 08°29'W) respectively, with the garden in Armagh (7) located near Armagh Observatory (7) (54°21'N, 06°38'W).

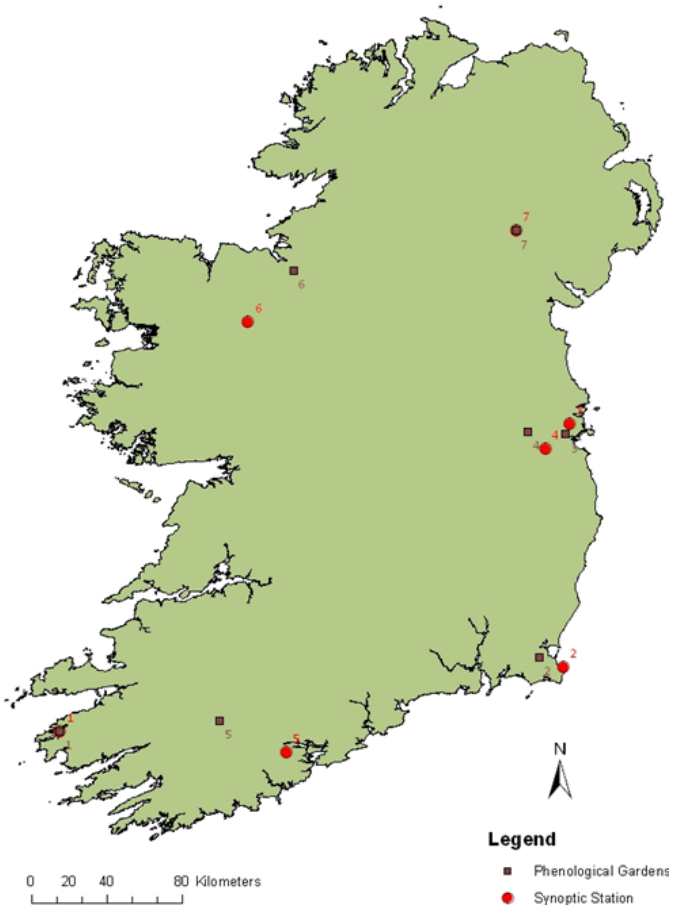


Figure 5.5 The location of Irish phenological gardens recording *S. viminalis* budburst and near-by synoptic stations.

5.3.3 Methods Used To Estimate Thermal Time Units And Chill Days For Models

Chilling (R_{chill}) time and thermal time (R_{force}) to budburst were calculated using the different phenology models and methods proposed by Cannell & Smith (1983), Murray (1989) and Chuine (2000):

1. the accumulation of thermal time units using the averaging method from arbitrary start dates and base temperatures – the Thermal Time method
2. the accumulation of thermal time units using the averaging method, and chill days from arbitrary start dates and base temperatures using the Alternating model method
3. the accumulation of thermal time units using the triangular method, and chill days from arbitrary start dates and base temperatures using the Alternating model method
4. the accumulation of thermal time units using the sine wave method, and chill days from arbitrary start dates and base temperatures using the Alternating model method
5. the accumulation of thermal time units and chill days applying the Unified method

Many studies choose 1st February as an arbitrary date for thermal time accumulation (Cannell & Smith, 1983). For methods 1-3, thermal time units were calculated from different start dates: 1st November; 1st December; 1st January and 1st February. Regarding chill days, 1st November was chosen as the starting date for chill day accumulation on the assumption that before this date, buds might be in a non-dormant state and for most years, few chill days occur before 1st November (Cannell & Smith 1983; Murray *et al*., 1989; Santini *et al*., 2004). For methods 1-3, various base temperatures – 3°C to 9°C – for thermal time units and chill days were investigated also. For methods 1-2, thermal time units were calculated using the average method:

$$R_{force} = \frac{T_{min} + T_{max}}{2} - T_{base}$$

Equation 5.10

where T_{min} was the daily minimum temperature, T_{max} was the daily maximum temperature and T_{base} was the arbitrary base temperature. For method 3, thermal times units were calculated using the single triangulation method, intercepted by the base temperature:

$$R_{force} = \frac{6(T_{max} + T_{base})^2}{T_{min} + T_{max}} \div 12$$ **Equation 5.11**

and the single sine method, intercepted by the base temperature:

$$R_{force} = \frac{1}{\pi}\left[\left(\frac{(T_{min} + T_{max})}{2} - T_{base}\right)\left(\frac{\pi}{2} - \theta_1\right) + \alpha\cos(\theta_1)\right]$$ **Equation 5.12**

where θ_1 was calculated as:

$$\theta_1 = \sin^{-1}\left[\left(T_{base} - \frac{(T_{min}+T_{max})}{2} \div \alpha\right)\right]$$ **Equation 5.13**

and the other equation components were the same for all equations, as per the averaging method. These different methods, using various starting dates and base temperatures, were assessed by means of the accuracy, expressed as R^2 values, with which a decreasing exponential function, of the form:

$$y = be^{mx}$$ **Equation 5.14**

adjusted to the data-set, explained the variance of the budburst date. The fit of the accurate models to the phenological data-set was assessed with the associated RMSE value:

$$\sqrt{\frac{\sum_{i=1}^{n}(z_i - x_i)^2}{n-1}}$$ **Equation 5.15**

where z_i is the model prediction, x_i is the observed date of the phenological event for year *i* and n is the number of years. For method 4, parameter estimation was undertaken by finding the parameter combination that minimized the RMSE with an optimisation technique – Nelder-Mead/Downhill Simplex method (Nelder & Mead, 1965). Traditional optimisation algorithms such as Nelder-Mead/Downhill Simplex and Newton's methods (Newton, 1736) have been noted to rarely converge towards a global optimum set of parameters (Kramer, 1994; Chuine, 1998; Chuine, 1999). However, the Nelder-Mead/Downhill Simplex method performed well when multiple starting points over 5000 program runs were tried – large run number chosen due to complication with the parameter space of the Unified Model – within starting point ranges for each parameters using R programming software (see Appendix V).

5.4 **Results**

There was a poor relationship between accumulated thermal time units and *S. viminalis* budburst dates using the Thermal Time model (method 1) based on low R^2 values (Table 5.1). There was no improvement in this relationship with varying starting dates (1st Nov – 1st Feb) and base temperatures (3°C – 9°C). When chill days were accounted for using the Alternating model (method 2), an inverse relationship between these and the accumulated thermal time units occurred with thermal time units to budburst decreasing exponentially with increasing values of chill days. R^2 values did not tend to vary between different base temperatures (5°C – 9°C). Base temperatures lower than 5°C were not assessed using the Alternating model as the accumulation of chill days for temperatures less than this was so low, particularly for years with warmer winters such as 1998. Over 70% of the years assessed for Valentia and Johnstown Castle had three or fewer chill days when chill day was characterised as less than 3°C. However, R^2 values decreased for the later arbitrary start dates (Table 5.1). When thermal time units were accrued from 1st November at temperatures greater than 7°C and chill days were accumulated from the same date at temperatures less than or equal to 7°C, the best R^2 value of 0.80 was obtained (Figure 5.6). This obtained model provided a RMSE value of 13.08 when fitted to the observed budburst data-set (Figure 5.7). Applying the empirical rule to the error values representing the difference between observed budburst days and estimated budburst days, 68% of the values lay within one standard deviation or 13 days of the mean.

Using the same model, thermal time units were accumulated using the single sine and single triangular methods (method 3 and method 4). R^2 values did not tend to vary between different temperatures and values decreased for later starting dates (Table 5.1). R^2 results did not improve when these methods were utilised. Chill day and thermal time unit accumulation was assessed for the additional *Salix* species (Table 5.2). These were *S. smithiana* (Valentia, Johnstown Castle and National Botanic Gardens, 1988-2010, n = 43), *S. acutifolia* (Valentia and Johnstown Castle, 1988-2010, n = 35), *S. aurita* (Valentia and National Botanic Gardens, n = 40) and *S. glauca* (Valentia, Johnstown Castle and National Botanic Gardens, 1971-1991, n = 31). R^2 values were highest for *S. smithiana* and *S. acutifolia* when base temperatures for both chill days and thermal units were equal to 7°C and accumulated from 1st November (0.75) and 1st December (0.68) respectively. R^2 values were highest for *S. aurita* and *S. glauca,* when base temperatures for both chill days and thermal time units were equal to 5°C and accumulated from 1st November (0.71) and 1st December (0.35) respectively. Therefore regression analysis of a combination of the budburst data for different species was considered inappropriate (Figure 5.8).

Table 5.1 Explained variance (R^2) of the exponential relationships between chill days and thermal time units, for *S. viminalis*, depending on calculation method: (1) the accumulation of thermal time units using the averaging method from arbitrary start dates and base temperatures or the Thermal Time method, (2) the accumulation of thermal time units using the averaging method, and chill days from arbitrary start dates and base temperatures using the Alternating model method, (3) the accumulation of thermal time units using the triangular method, and chill days from arbitrary start dates and base temperatures using the Alternating model method and (4) the accumulation of thermal time units using the sine wave method, and chill days from arbitrary start dates and base temperatures using the Alternating model method (best fit denoted by *).

Species	Method			Base Temperatures				
		November						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. viminalis	1	.00031	.00584	.01699	.02857	.03636	.03833	.03670
	2			.78700	.78098	.79715*	.78143	.72907
	3			.74855	.73591	.76014	.76017	.69446
	4			.74120	.72119	.75167	.75527	.69470
		December						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. viminalis	1	.00539	.00001	.00402	.01328	.02157	.02491	.02173
	2			.76067	.75349	.78437	.76511	.63820
	3			.71256	.68903	.71845	.69762	.56070
	4			.70133	.66483	.69812	.67699	.55213
		January						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. viminalis	1	.05187	.02061	.00373	.00008	.00285	.00446	.00318
	2			.59959	.62512	.61862	.58349	.43382
	3			.54851	.54791	.53636	.50857	.36850
	4			.53891	.52538	.51160	.48730	.36275
		February						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. viminalis	1	.21536	.14022	.07765	.03840	.01835	.01543	.02744
	2			.29822	.34764	.34567	.30370	.16203
	3			.24664	.27237	.26691	.24216	.14320
	4			.23563	.25372	.24760	.22539	.14574

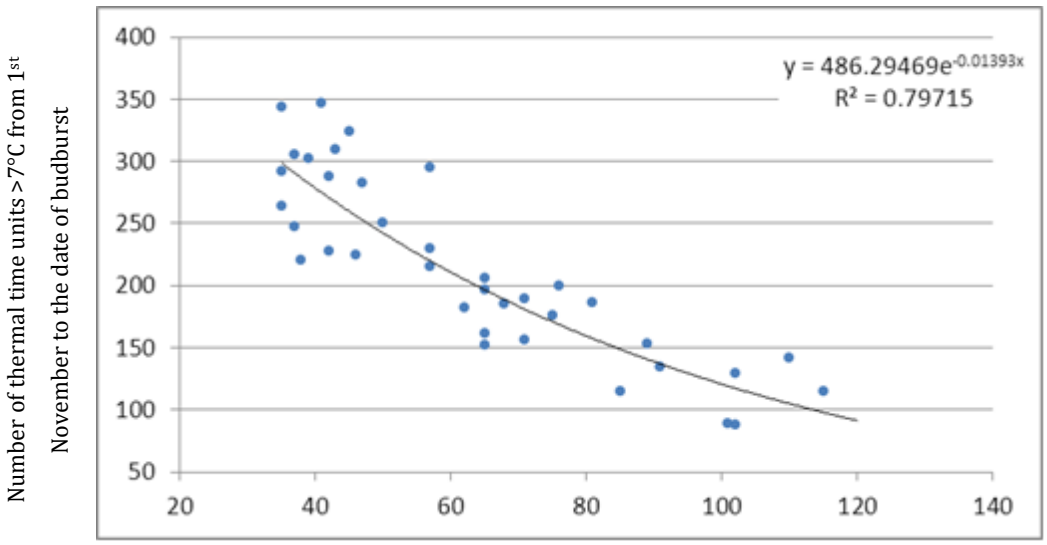


Figure 5.6 Exponential inverse relationship for 37 records of the dates of budburst of *S. viminalis* from three different IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) in Ireland with thermal time units > 7°C from 1st November and chill days ≤ 7°C from 1st November.

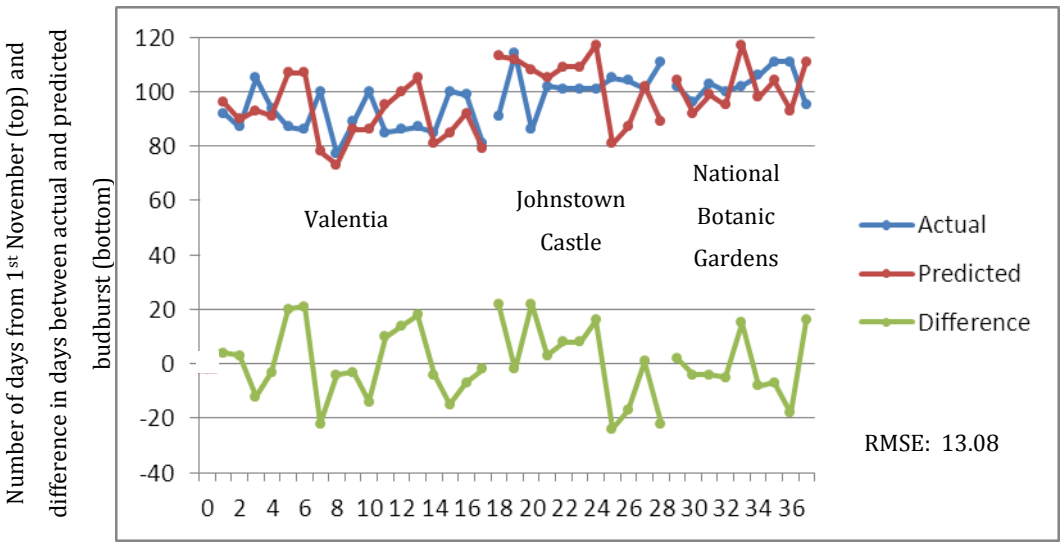


Figure 5.7 Predicted budburst days from 1st November using the Alternating model compared to actual budburst days recorded for *S. viminalis* at three IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) in Ireland.

Table 5.2 Explained variance (R^2) of the exponential relationships between chill days and thermal time units, for *S. smithiana*, *S. acutifolia*, *S. aurita*, *S. glauca* and a combination of all *Salix* species, including *S. viminalis*, with the accumulation of thermal time units, using the Averaging method, and chill days, from arbitrary start dates and base temperatures, using the Alternating model method (not possible to calculate R^2 values denoted by ----)

Species	Method	Base Temperatures						
		November						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. smithiana	2			.73966	.72481	.74564	.70884	.61925
S. acutifolia	2			.62583	.51167	.56228	.46804	.48160
S. aurita	2			.71526	.69577	.68546	.64319	.53656
S. glauca	2			.32307	.25866	.22654	.18030	.10579
S. combination	2			.54300	.53183	.53737	.48198	.35205
		December						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. smithiana	2			.67000	.65510	.69562	.64937	.48095
S. acutifolia	2			.68054	.58360	.68368	.61067	.62391
S. aurita	2			.54716	.52941	.51478	.44600	.24988
S. glauca	2			.34570	.34357	.33495	.24692	.18309
S. combination	2			.43868	.42875	.43633	.36433	.21620
		January						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. smithiana	2			.39818	.42496	.44554	.39728	.23913
S. acutifolia	2			.50571	.50539	.56345	.51401	.49674
S. aurita	2			.22100	.21821	.20513	.15963	.04086
S. glauca	2			.17181	.21896	.21263	.17539	.10456
S. combination	2			.23898	.24752	.24634	.19814	.09366
		February						
		3°C	**4°C**	**5°C**	**6°C**	**7°C**	**8°C**	**9°C**
S. smithiana	2			.06613	.09955	.13114	.11864	.03904
S. acutifolia	2			.27666	.26096	.27696	.22794	----
S. aurita	2			.00335	.00776	.01052	.00487	.00661
S. glauca	2			----	----	----	----	----
S. combination	2			----	----	----	----	----

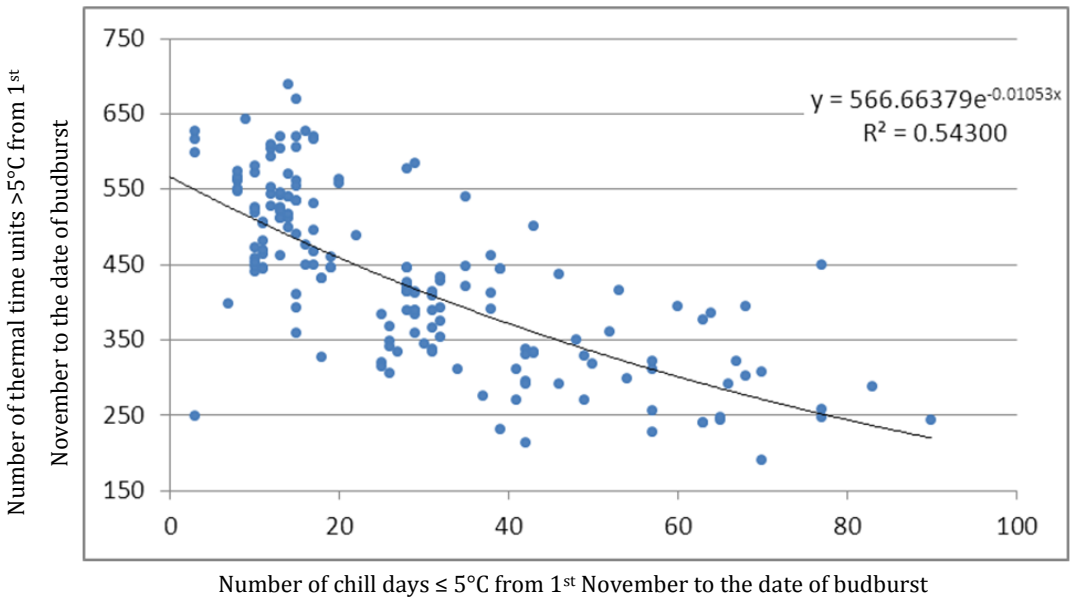


Figure 5.8 Exponential inverse relationship for 184 records of the dates of budburst of *S. viminalis*, *S. smithiana*, *S. acutifolia*, *S. aurita* and *S. glauca* from three different IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) in Ireland with thermal time units > 5°C from 1st November and chilling days ≤ 5°C from 1st November.

When the regression function obtained from the Alternating model method was applied to the ten new observations recorded between 2010 and 2012, the modelled RMSE value increased to 15.48. Additionally, when this data sub-set was combined with the original budburst data-set, and the thermal time units were accrued from 1st November at temperatures greater than 7°C and chill days were collected from the same date at temperatures less than and equal to 7°C, the R^2 value of the regression model dropped from a value of 0.80 to 0.76 (Figure 5.9). Graphical observation showed two data-points were particularly influential – Armagh 2011 and Millstreet 2011. When these were removed, the R^2 value of the regression model rose to 0.86 (Figure 5.10).

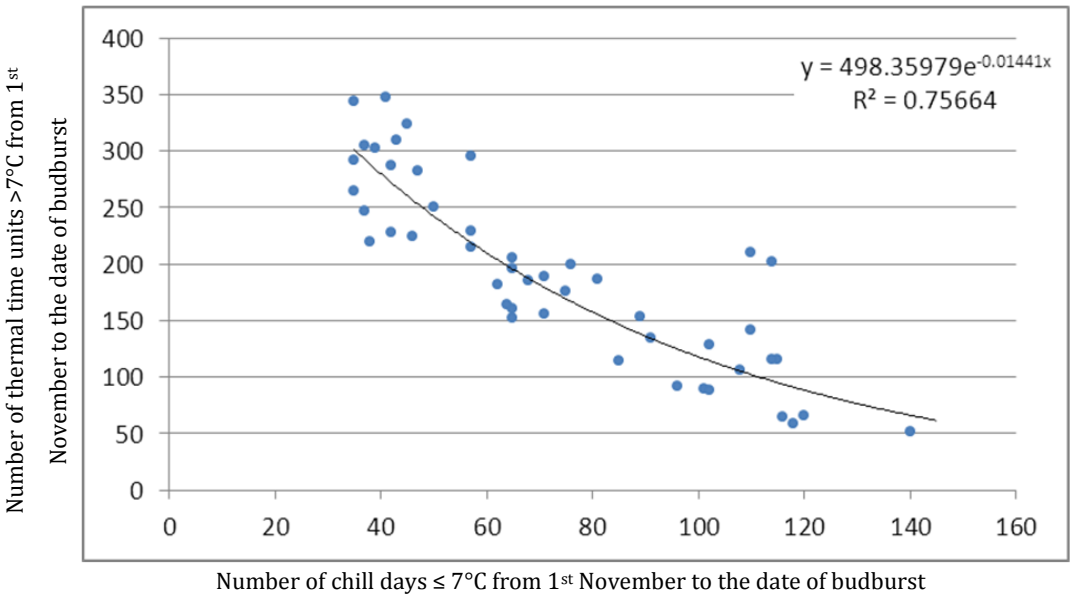


Figure 5.9 Exponential inverse relationship for 37 records of the dates of budburst of *S. viminalis* from three different IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) in Ireland and additional 10 records from four other IPG sites (Carton House, Armagh Observatory, Millstreet County Park and Markree Castle) in Ireland with thermal time units > 7°C from 1st November and chill days ≤ 7°C from 1st November.

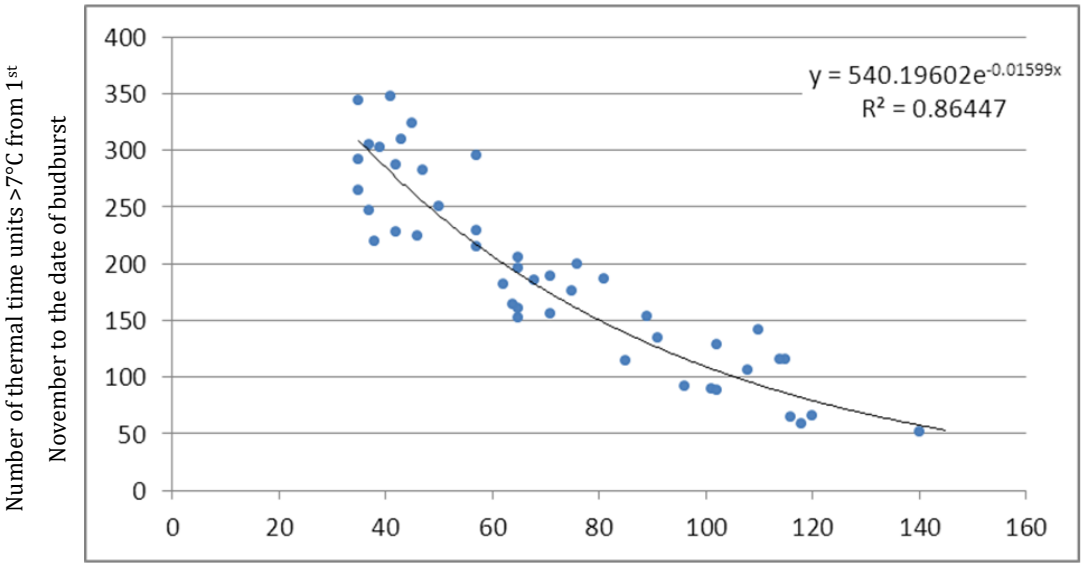


Figure 5.10 Exponential inverse relationship for 37 records of the dates of budburst of *S. viminalis* from three different IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) in Ireland and additional 10 records from four other IPG sites (Carton House, Armagh Observatory, Millstreet County Park and Markree Castle) in Ireland (two outliers Armagh 2011 and Millstreet 2011 removed) with thermal time units > 7°C from 1st November and chill days ≤ 7°C from 1st November.

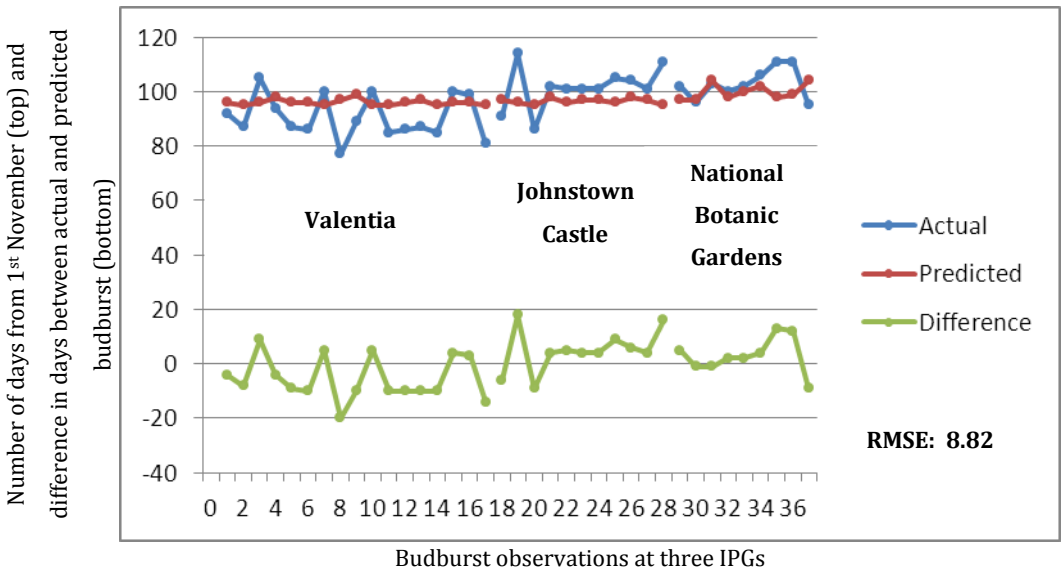


Figure 5.11 Predicted budburst days from 1st November using the Unified model compared to actual budburst days recorded for *S. viminalis* at three IPG sites (Valentia, Johnstown Castle and National Botanic Gardens) in Ireland.

Performing slightly better than the Alternating model, the Unified model yielded a lower value of RMSE of 8.82 when fitted to the observation data-set with best parameter values (Ca = -12.30, Cb = 23.08, Cc = 29.19, Fb = -0.39, Fc = -3.03, C* = -38.36 and F* = 214.2) (Figure 5.11). Applying the empirical rule to the error values representing the difference between observed budburst days and estimated budburst days, 68% of the values lay within 9 days of the mean.

5.5 Discussion

Due to the observed annual synchrony between *P. vulgatissima* (and *G. lineola*) emergence and *S. viminalis* hybrid leaf-unfolding in the field, budburst was chosen as the variable biofix for annual post-diapause development initiation. The construction of models that accurately estimate insect emergence in the field is difficult because many factors affect insect development. Biofix options for emergence include the date of first annual capture in pheromone traps or the first laying of eggs on host plants (Nowatzki *et al*., 2002; Kumral *et al*., 2008). However, pheromone traps were not available for willow beetle species and first egg-laying requires intensive field monitoring. Recent studies have successfully estimated herbivorous insect emergence based on specific host plant phenological stages. For example the onset and proportional emergence of *Diabrotica virgifera virgifera* (western

corn rootworm) adults have been estimated using a thermal unit accumulation model from the date of corn emergence (Stevenson *et al*., 2008). However, the potential for phenological asynchrony that may occur between insect herbivores and their host plants, under future climate change conditions was not accounted for in the study.

Due to the exceptionally cold winter weather of 2009/2010 with mean air temperatures for the season around 2°C lower than average for the 1961-90 period in many places including Cork and Armagh, and the less extreme cold winter of 2010/2011 with mean temperature values for the winter period between 2.5° and 5.8°C amongst the lowest in recent years in southern Ireland and less than 1.5° to 2°C when compared to the mean UK temperature 1971-2000 anomaly, the new *S. viminalis* 2010-2012 data-set was a poor validation option (Met Éireann, 2010; Met Éireann, 2011; Met Office UK, 2011) (Figure 5.8 –Figure 5.9). For Armagh, 75% of the days that occurred from 1st November to 1st April were classified as chill days (when the base temperature was 7°C), decreasing the necessity for excessive thermal units and prompting an earlier estimated budburst on day 156 (from 1st Nov) than observed at the site on day 176 – a difference of 20 days. Similarly, for Cork, 72.5% of the days that occurred from 1st November to 1st April were classified as chill days (when the base temperature was 7°C), decreasing the thermal unit requirement and triggering an earlier predicted budburst on day 157 than observed at the site on day 184 – a difference of 27 days. Furthermore, due to an increase in the number of chill days occurring during these colder seasons, four of the observations from the sub-set would not have been accounted for by the original Alternating model without extrapolation outside the range of the line, which was advised against in other studies (Cannell & Smith, 1983; Harrington *et al*., 2010).

In contrast to similar studies (Doi & Katano, 2008; Linkosalo *et al*., 2008; Fu *et al*, 2012a; 2012c), the limited number of locations from which the observed budburst readings for *S. viminalis* were collected – one site in the East of Ireland, another in the Southeast and the other in the Southwest – presented another limitation to the proposed budburst estimation models. However, when the single budburst observation for Sligo was added to the larger data-set and compared to the predicted budburst date provided by the Alternating model regression function, the difference between the two dates was 5 days, suggesting that such a model may be suitably functional for locations based in northerly or westerly regions. Additionally, although all of the budburst observations for the model development were obtained from locations near Met Éireann synoptic weather stations, temperature data for sites such as Carton House, Millstreet and Markree Castle had to be supplied by synoptic weather stations at Casement Aerodrome, Cork Airport and Knock Airport respectively, due to there being no closer synoptic weather stations or incomplete

temperature data records from a station located near-by. This may have led to less accurate estimations when an attempt was made to cross-validate the Alternating model regression function using the data sub-set. Also, it was recognised that budburst observations are not automated like much of the Met Éireann synoptic station network and although most of the phenological gardens are directly managed by botanical gardens, forest research centres and meteorological services such as Met Éireann (i.e. phenological garden phases were continuously recorded by the same person for more than 20 years at Valentia up until at least 2003), many of the newly established gardens such as those in Millstreet and Carton House are not. Despite the referencing guide distributed by IPG, this may lead to various individuals from diverse backgrounds misinterpreting phenological phases between plants and recording observations differently on an annual basis, leading to inaccurate results.

In a study investigating the regularities and patterns in the spring phenology of different species, results indicated that the geographical pattern of spring advancement was uniform from year to year and between different species, while the mechanisms regulating the timing of phenological events in different species seemed to function in a similar way, suggesting an unanimous optimal response to climatic conditions (Linkosalo, 1999). To investigate if the inclusion of additional species would strengthen the correlation between thermal units and chill day accumulation, budburst observation data was obtained for several other species at locations similar to *S. viminalis* over similar time-frames. With greater percentages of variation being explained when arbitrary base temperatures and start dates were chosen for different species, the development of a *Salix* model based on a combination of species did not warrant further investigation (Figure 5.8).

Towards the end of this research, the fitting of the Unified model proposed by Chuine (2000), to the budburst data, incorporating an optimization algorithm, was assessed. Due to the complexity of the model, only a limited amount of time was dedicated to evaluating its usefulness and a limited number of optimization techniques were reviewed. However, an RMSE value obtained from 5000 different parameter combinations, based on suitable starting point ranges for each parameter obtained from published studies by Fu *et al*. (2012a; 2012b; 2012c), suggested that this model offered an alternative option to the Alternating model. As discussed in Chapter 4 fitting many parameters with relatively few data-points is a difficult process and although model descriptions might be correct, some model parameter values might not be biologically realistic. Additionally, complex phenology models might be over-parameterized. For instance, some parameters of the Unified model can be correlated or not relevant, lowering the quality of the parameterization procedure and perhaps explaining why simpler models are found to have

a better fit than the parameter-rich models (Linkosalo *et al*., 2008; Fu *et al*., 2012a; 2012b; 2012c). Further model evaluation for *S. viminalis* is therefore required.

Results from this study indicated that different model types could be used to reproduce budburst dates based on available phenological data-sets. The Alternating model was ultimately selected for use as biofix for the initiation of post-diapause development in adult beetle populations. It showed that a relationship exists between chilling days and forcing temperatures in releasing winter dormancy and promoting *S. viminalis* budburst respectively when thermal time units were accrued from 1st November at temperatures greater than 7°C and chill days were collected from the same date at temperatures less than and equal to 7°C. Notwithstanding the threshold temperatures and the starting dates for evaluating chilling and thermal time accumulation were arbitrary, this modelling method has been used successfully in many other temperate tree budburst modelling studies with similar statistical results to those obtained in this research (Pop *et al*., 2000; Santini *et al*., 2004; Zhang *et al*., 2007; Vitasse *et al*., 2011; Olsson *et al*., 2013; 2014). In the next chapter, this *Salix* budburst model will be combined with predetermined temperature-dependent insect development models to form a life-cycle phenology/voltinism model for *P. vulgatissima* to be validated and subjected to sensitivity analysis.

6 PHENOLOGY/VOLTINISM MODEL CONSTRUCTION

Insect life-cycle stage development data, obtained over a range of different constant temperatures in artificial environments, can be used to provide estimates for the optimal temperature conditions that insects require for development in their natural environment (see Chapter 3 and Chapter 4). A wide variety of mathematical modelling approaches (Sharpe & DeMichele, 1977; Curry *et al*., 1978; Schoolfield *et al*., 1981; Wermelinger & Seifert, 1999) and model development tools (Wagner *et al*., 1984c; Sporleder *et al*., 2009; Shi *et al*., 2011) have been established. Linear models have been recognised as efficient modelling functions within a restrictive temperature range (Campbell *et al*., 1974, Gilbert *&* Raworth, 1996, Honek, 1999). More realistic and accurate models make use of the non-linear, unimodal nature of physiological responses to temperature using the rate-summation paradigm and account for the intrinsic variation of development rates within populations (Sharpe & DeMichele, 1977; Lactin *et al*., 1995: Briére *et al*., 1999) (see Chapter 4). Based on such techniques, temperature-dependent development for the life-cycles of various pest species have been described, including coleopteran species (Bentz *et al*., 1991; Wermelinger & Seifert, 1998). Phenology models with varying complexity have been developed to gain an understanding of how temperature and additional environmental factors affect insect population development potential in different agroecology zones over entire life-cycles (Logan & Bentz, 1999; Jönsson *et al*., 2007). In the following chapter, examples of such models and generic phenology modelling methods, with particular reference to those specific to coleopterans are discussed. These were subsequently used as templates for the development of a phenology/voltinism model for *P. vulgatissima*, with the

possibility to use the model for other willow beetle species with similiar life-cycles such as *G. lineola*.

6.1 Phenology Models for Coleopteran Species

Schaafsma *et al*. (1991) established a stochastic simulation model that focused on estimating univoltine *Diabrotica virgifera virgifera* (corn rootworm) post-diapause egg hatch in Ontario, Canada. A single biophysical non-linear function (Schoolfield *et al*., 1981) and single cumulative distribution function (Wagner *et al*., 1984c) were incorporated. Soil temperatures model input accounted for the natural environment of the life-cycle stage. Egg hatch was estimated within a number of days of observed occurrence for 5%, 50% and 95% of the populations. In the absence of a biologically meaningful, model initiating biofix, model simulations were set to begin from a fixed calendar date as post-diapause eggs were considered to be in a facultative state of chill-quiescence until soil temperature breached a lower temperature threshold of 11°C. Validation was limited to comparing observed and estimated proportions of larvae emergence over three years and at three locations. The model was considered accurate for estimating egg hatch with negligible differences between observed and estimated values. High egg mortality linked to continuous chilling and harsh temperature conditions experienced prior to diapause and during the overwintering stage were not considered in the development of this model (Meinke *et al*., 2009). The model included the assumption of a constant availability of moisture resulting in undisrupted development over a lower developmental threshold also (Krysan, 1978).

Bentz *et al*. (1991) constructed a model to describe the temperature-dependent temporal distribution of eggs, individual larval instars and pupae of univoltine *Dendroctonus ponderosae* (mountain pine beetle) for mid-western USA. The model employed an algorithm previously used in the development of a pest simulation model called Population Model Design System (PMDS) (Logan, 1988). A selection of development rate and distribution time models (see Sections 4.1 and 4.2) were assessed for optimal fit to data prior to equations chosen for representation of each life-stage based on ecological assumptions and statistical comparison (using R^2_{adj}). The transfer of individuals from one life-stage to the next was based on an advancement of physiological age. In a reformatted version of the model, Logan & Bentz (1999) described the technique as having two steps: the computation of developmental indices for a complete year where proportions of life-cycle stages were completed each day for each life-cycle stage and the cascading from one

stage to the next based on rate summation and calculation of the median day of emergence for each stage, with median day becoming the start day for the next stage. Food availability, moisture and plant resins were all identified by the authors as influential on insect phenology but these factors were not accounted for in the model.

Immature and adult *D. ponderosae* occupy different environments, as do *D. virgifera virgifera*, so model inputs such as temperature need to be appropriate to the life-cycle stage. Phloem temperature measurements were used for *D. ponderosae* model simulation due to the development of all immature life-cycle stages within host trees. Additionally, phenology models for species such as *D. virgifera virgifera* require a starting point such as the breaking of diapause. Some species such as *D. ponderosae* do not exhibit diapause however. Bentz *et al*. (1991) chose to initiate model simulations for *D. ponderosae* on an arbitrary Julian day, when beetles were dispersing to new hosts in the stand, in the absence of a biologically meaningful biofix. Logan & Bentz (1999) corrected for this while accounting for an ovipositing phase – the primary reason for modifying the model – and adjusted the starting point for model simulations to a date when a median value of oviposition was reached. Similar to most phenology models, this model did not commit to recreating events as they occurred in the natural environment as it lacked representation of mortality and mature stage emergence. Information regarding model validation was not provided for both studies.

Ungerer *et al*. (1999) incorporated a similar procedure to those previously discussed, to evaluate the role of temperature in the development of the multivoltine *Dendroctonus frontalis* (southern pine beetle) in USA. The model was created to estimate the number of generations per year. A single biophysical non-linear model was used to explain the developmental process for oviposition and all immature life-cycle stages (egg, larvae and pupae) to adult emergence based on previous work by Gagne *et al*. (1982) and Wagner *et al*. (1984c). Site-specific meteorological records and climate projections (based on a fixed increase and decrease of the average minimum temperatures and corresponding standard deviations of the meteorological data) were used to drive the model. Results included an increase in the estimated number of generations from northern limits in U.S.A to southern states. Validation of the model was confined to comparison with previous studies that estimated similar numbers of generations. Although the model was suitable for purpose based on the author's objectives, it lacked processes contained in previously discussed models such as variation in development among individuals within a population. The model treated mortality as a binomial variable (no mortality or 100% mortality) based on development over a lower lethal temperature. Altitudinal and microclimate variation were also not addressed.

Baier *et al*. (2007) designed a phenology model (PHENIPS) for a spatial and temporal simulation of the seasonal development of *I. typographus* (European spruce beetle) in central Europe (and beyond with model alteration). This species differs to the similarly destructive univoltine non-diapausing *D. ponderosae* as it retains a multivoltine life-cycle, with a photoperiodically controlled reproductive diapause and hibernating adult stage. The model differed to previous coleopteran models as it used topoclimatic corrected air and bark temperatures (reflecting the complex life-cycle), and solar radiation as model inputs to calculate the date of insect infestation and the number of generations. A degree-day method was used to establish the initiation of spring swarming from 1st April – the arbitrary starting point for model simulation. Non-linear functions (see Section 4.1 and 4.2) were fitted to data describing development over a wide temperature range for immature and mature life cycle stages by Wermelinger & Seifert (1998) and used to establish the model. Variability of development time was not accounted for in this model. Heavy storm events and rainfall are understood to trigger insect outbreak and delay insect emergence respectively (Wermelinger, 2004). However, such variables were not regarded during the construction of the model either. Differences in developmental thresholds and thermal requirements between *I. typographus* populations at different altitudes and in different regions were omitted also. Model validation was conducted by comparing the estimated phenological model outputs with microclimate temperatures and developmental progress at different ground levels and altitudes based on trap tree analysis. Further validation was carried out at other Central European sites (Berec *et al*., 2013).

Jönsson *et al.* (2007) developed a process model for large-scale trends of swarming and development of *I. typographus* in southern Sweden. Based on information produced from degree-day (Annila, 1969) and non-linear modelled stage-specific studies (Wermelinger & Seifert, 1998; 1999), the model accounted for hibernation emergence, spring swarming, egg to adult development and summer swarming. The model was subjected to evaluation based on observed beetle activity and additional sensitivity analysis in later studies (Jönsson *et al.,* 2007; 2009). The model was extended to account for reproductive diapause initiated by photoperiod and thermal cues with further assessment of model performance also (Jönsson *et al.,* 2011). Uncertainties related to modelled bark activity and development, due to model parameterisation limitations and population-specific adaptation to location climate, were highlighted by the author (Jönsson *et al.,* 2009).

Along with many of the coleopteran-specific phenology models that have been constructed, a variety of flexible and generic off-the-shelf model building packages have been developed (some available online) that accommodate for commonalities that exist in

the life-cycles of insect pest species, including coleopterans. These enable the modeller with outlets to perform tasks without programming skill requirements. Computer-aided modelling packages include DYMEX (Steinbauer *et al*., 2004; Yonow *et al*., 2004; Nahrung *et al*., 2008), NAPPFAST (Nietschke *et al*., 2007; 2008) and ECAMON (Trnka *et al*., 2007). Another phenology model tool-kit called Insect Life Cycle Modelling (ILCYM) software was developed by the International Potato Centre to estimate temperature-based potato pest population development (particularly for *Phthorimaea operculella* (potato tuber moth)) as well as to determine critical infestation periods for better targeting pests during the cropping season (Sporleder *et al*., 2009). The approach used in ILCYM is to define functions, based on experimental data obtained through constant temperature experiments, describing development rate (such as those described in Section 4.1) variation in development time between individuals in a population (such as those described in Section 4.2), mortality in each immature life-stage of the insect, reproduction frequencies (including changing sex ratio in adults due to temperature, depending on species) and senescence of adults according to temperature.

All models serve a purpose but consequently all have limitations as per the modelling systems discussed. Species-specific models are usually developed with one species in mind making them difficult to adapt for other species. A single modelling approach may not fit to each species of interest due to unique life-cycles and it cannot meet each purpose for which a model is developed. ILCYM is an example as it does not account for insect species seasonality (summer or winter diapause) or life-cycle processes influenced by additional environmental factors (reproductive diapause or host plant dormancy). Components of multi-species modelling packages such as ILCYM can be useful however. The following sections will focus on the development of a full life-cycle phenology/voltinism model for *P. vulgatissima* based on discussed species-specific models and modelling package components. This model was constructed using data obtained from Chapter 3, development rate and time fitted functions from Chapter 4 and the *Salix* budburst model from Chapter 5. The model was subsequently validated and subjected to sensitivity analysis.

6.2 Phenology/Voltinism Model Construction for *Phratora vulgatissima*

A phenology/voltinism simulation model was developed for *P. vulgatissima* using MATLAB™ programming software (Mathworks, Massachusetts, USA) (see Appendix VI). The components for the model were a degree-day based budburst model; temperature-dependent development rate models and temperature-independent distribution time models for each life-cycle stage and an oviposition model (see Figure 6.1). The model was formatted in a manner that allowed for life-stage describing functions and parameters to be adjusted for use with other leaf-feeding beetles such as *G. lineola*.

The data inputs for the model were mean daily temperature and day-length. Mean daily temperatures were calculated from daily minimum and maximum temperature data obtained from Met Éireann for 11 different synoptic stations throughout Ireland (1) Roche's Point, Co. Cork (51°48'N, 08°15'W); (2) Belmullet, Co. Mayo (54°14'N 10°00'W); (3) Clones, Co. Monaghan (54°11'N, 07°14'W); (4) Rosslare, Co. Wexford (52°15'N, 06°20'W); (5) Claremorris, Co. Mayo (53°43'N, 08°59'W); (6) Valentia, Co. Kerry (51°56'N, 10°15'W); (7) Kilkenny, Co. Kilkenny (52°40'N, 07°16'W); (8) Casement Aerodrome, Co. Dublin (53°18'N, 06°26'W); (9) Birr, Co. Offaly (53°05'N, 07°53'W); (10) Shannon, Co. Clare (52°41'N, 08°55'W) and (11) Malin Head, Co. Donegal (55°22'N, 07°20'W) (Figure 6.2). Daily day-length was determined for all synoptic stations, based on latitude and solar declination (SD) – the angle between the equatorial plane and the straight line joining the centres of the earth and the sun, with a maximum declination of 23.45° on 22nd June, a minimum declination of -23.45° on 21st December and equal to 0° on 21st March and 22nd September – according to methods formulated by Supit (1994), Goot (1997) and Supit & Van Kappel (1997):

$$D = 12 + 24 * \operatorname{asin}\left(\frac{\frac{\sin(SD) * \sin(latitude * SD/180)}{\cos(SD) * \cos(latitude * SD/180)}}{\pi}\right) \qquad \textbf{equation 6.1}$$

where SD was determined as:

$$= -\operatorname{asin}\left(\sin\left(\frac{23.45 * \pi}{180}\right) * \cos\left(2\pi \frac{day + 10}{365}\right)\right) \qquad \textbf{equation 6.2}$$

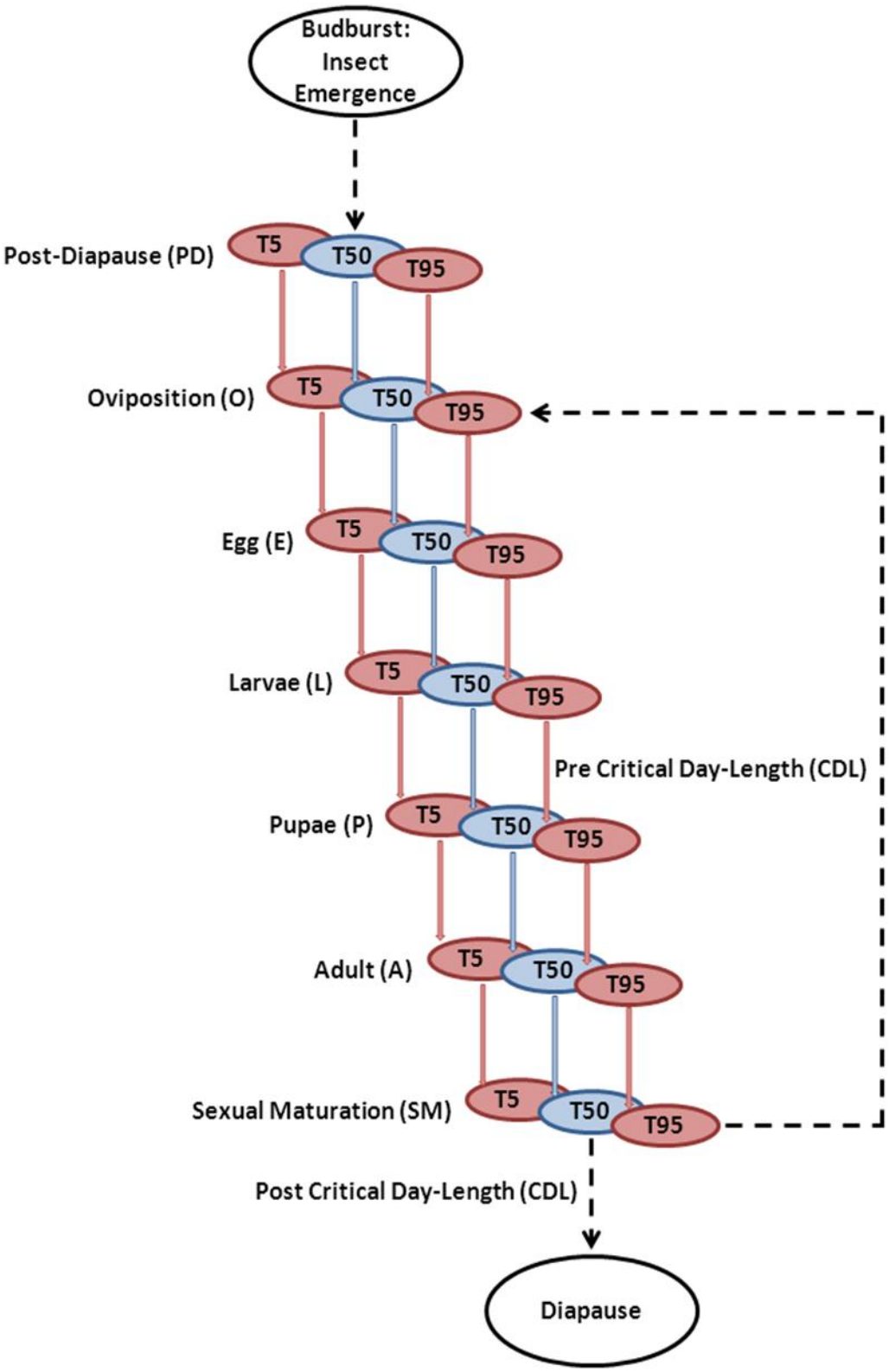


Figure 6.1 Schematic diagram of the life-cycle of *P. vulgatissima* as condensed for use in the phenological model. New generation adults that completed sexual maturation prior to CDL entered diapause, otherwise ovipositing for a second generation occurred. Time (T) in days for percentages of emerging proportions (E.P) (5%, 50% and 95%) that completed development were obtained. T E.P + 1 day for the preceding stage was the starting time for the next stage. Completed life-cycle stages for each percentage cascaded from one stage to the next based on the rate summation paradigm.

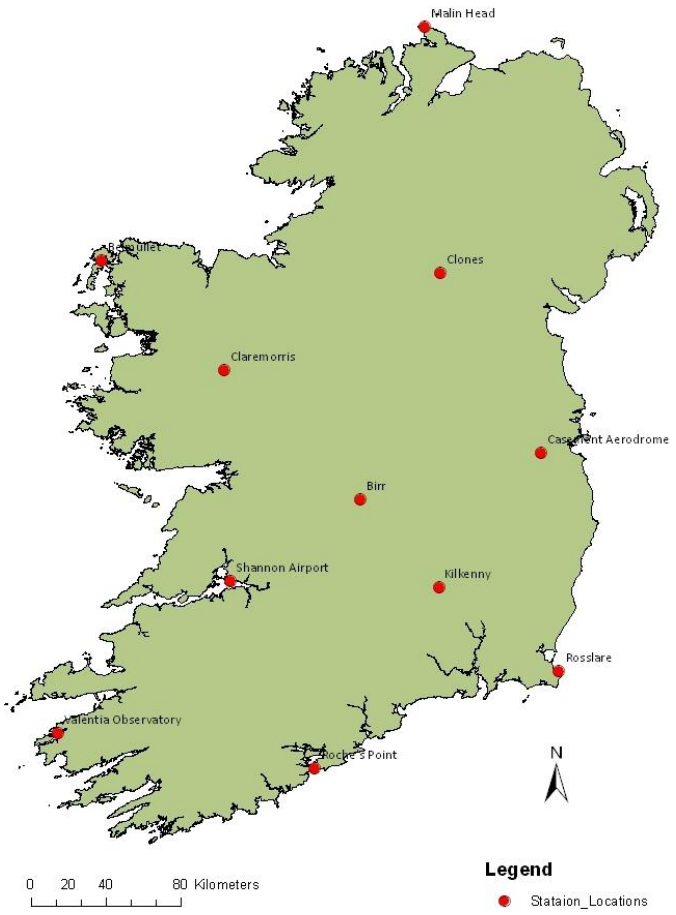


Figure 6.2 Synoptic Station locations throughout Ireland.

The full life-cycle phenology/voltinism model was initiated with the estimation of *S. viminalis* budburst. A sub-function was composed to determine when budburst day had occurred from 1st November (each model run began on 1st November until 31st October the following year). The equation of the line used to predict budburst was set to negative infinity instead of selecting an arbitrary lower bound. Chilling phase and forcing phase temperature data were accumulated on a daily basis consistent with the budburst model (see Section 5.3.3). The sub-function was repeatedly executed while the equation result remained less than zero. Estimated budburst day was deemed to have occurred when the equation result increased to or above zero. The model continued to the next stage when budburst day was estimated.

The post-diapause development sub-function began the day following the estimated budburst day. Using the Lactin equation with four predetermined parameters, the first day of egg-lay was returned for adult females emerging from overwintering through the accumulation of daily instantaneous fractions of development. A sub-function was developed to run synchronously with all *P. vulgatissima* life-cycle stage development

sub-functions (budburst stage not included) and account for the modelled distributions of development time for every insect life-cycle stage using the Weibull (3p) equations. Day of post-diapause life-stage completion differed depending on *P. vulgatissima* E.P been considered. 5%, 50% and 95% were the E.P considered for this study consistent with other research. These proportions were considered to account for earliest E.P times at the median and extreme points along the cumulative distribution curves (Wagner *et al*., 1984c; Knight *et al*., 1991; Schaafsma *et al*., 1991; Logan & Thomson, 2002). These life-cycle stage completion percentages were modifiable within the model set-up. Life-cycle stage progression occurred when days for E.P were estimated for *P. vulgatissima* (or other species with similar life-cycles such as *G. lineola*).

The oviposition period sub-function commenced following post-diapause life-cycle stage completion. Fixed values for the three parameter quadratic polynomial equation, modelling the mean oviposition period and the Weibull (3p) function, describing the time-specific oviposition pattern for *P. vulgatissima*, were used to estimate when the pre-set oviposition period proportions were completed. Starting day varied depending on the E.P for *P. vulgatissima* phenology being examined. When estimating 5% production of eggs by ovipositing females, this sub-function began on the day following post-diapause stage completion for 5% of the population. Similarly, when estimating 50% and 95% production of eggs, this sub-function initiated on the day following post-diapause stage competition for 50% and 95% of the population respectively. Oviposition period stage advancement occurred when the conditions associated with the sub-function used to estimate the proportion(s) of the population completing development had been satisfied.

Following the completion of the oviposition period, the eggs, larval and pupal development sub-functions initiated sequentially. Like the previous life-cycle stage sub-functions, all were dependent on the conclusion of the preceding sub-functions with differing day commencement depending on the proportion of emergence being estimated. Fixed parameters for development rate and development time distribution equations were accessed through model sub-functions corresponding to each life-cycle stage to estimate days for *P. vulgatissima* E.P. At the end of the pupal development stage, the emerging adult beetle proportions entered a sexual maturation period. A sub-function representing this life-cycle stage was included within the combined phenology/voltinism model. Due to limited experimental data obtained for sexual maturation development (see Section 3.2), equations within this sub-function were based on modified versions of equations describing post-diapause development (see Section 4.1.4.1). Additionally, this life-cycle stage was hypothesised to be sensitive to a diapause-inducing stimulus – photoperiod (Tauber *et al*., 1986; Danks, 1987; Hodek 2012). Therefore progression beyond this sub-

function was subjected to constraining photoperiodic conditions. Proportions of new generation adults that finished sexual maturation after CDL – predefined by the model through experimentation (see Section 3.4) – were considered to have entered a state of reproductive diapause and unable to begin ovipositing. The development of further generations was restricted. *P. vulgatissima* adults that completed this stage prior to CDL occurring were permitted to begin ovipositing. An additional beetle generation progressed through the life-cycle stages in the phenology/voltinism model, as previously described, with staggered starting points for emergence proportions defined by the parameterised sub-function equations and further generation occurrence controlled by sexual maturation of adults after CDL.

6.3 **Phenology/Voltinism Model Validation**

Validation of the willow beetle phenology/voltinism model input variables and output values were performed.

Validation of model input occurred in two steps:

- Comparing temperature data obtained from regionally representative synoptic stations (part of Met Éireann network) with local site-specific ambient temperature data and microhabitat temperature data
- Comparing day-length data obtained from an international recognised scientific agency (NOAA) with data calculated by the model's day-length sub-function

Validation of model output occurred in two steps:

- Using constant temperatures to assess for correct initiation, continuation and termination of the model sub-functions
- Using observation data relating to the presence of different life-cycle stages for *P. vulgatissima* in the field

6.3.1 Model Input Validation

6.3.1.1 Temperature Validation

Most insects occupy a variety of different environments throughout their life-cycles. Choice of environment varies depending on the conditions the life-cycle stage needs to avoid – desiccation and saturation during immature stage development, and mortality due to cold winter temperatures and hot summer temperatures during diapausing stages. Soil and vegetation environments have been recognised as providing important microclimates in insect physiological ecology (Willmer, 1982). Temperature in these microclimates can differ significantly from ambient air temperature depending on environmental exposure to sunlight (Régnière & Powell, 2013). These environments can act as temporary or permanent climate refuges from unfavourable conditions.

Leaf beetle species have displayed a preference for different habitats during their life-cycles. Neonate larvae of *G. lineola* commonly feed in the young leaf rolls of their host plant for nutritional benefits, to gain protection against predators and avoid adverse weather conditions (Larsson *et al*., 1997). Adult *G. lineola* are attracted to moist habitats during oviposition as emerging first-instar larvae are vulnerable to desiccation (Sipura *et al*., 2002). Adult *P. vulgatissima* showed a predilection for ovipositing on the underside of host plant foliage, where emerging larvae predominantly feed. Although this is believed to be mainly for obtaining nourishment, this action may provide a safer, possibly quicker development route (under suitable temperature conditions in a less variable crop environment) to future life-cycle development stages.

Data from weather stations is the principle input for phenology models in the absence of locally relevant daily temperature data from strategically placed recording stations relevant to insect ecology and physiology. Although this decision disregards the fluctuation in climatic variables that can occur at a local landscape level, state and semi-state meteorological networks (such as Met Éireann) provide extended and unbroken daily measurements for a range of climatic factors, obtained by well-maintained instruments and based at standard exposure, that allow comparisons to be made between locations and over time (Jarvis *et al*., 2002).

To assess the difference between regionally representative synoptic station data and local site-specific ambient temperature data and microhabitat temperature data, Tinytag Plus Two data-loggers were used to record temperature for an insect development season (May – September 2013). Two sites were chosen (see Figure 2.1):

- Lough Boora Parklands, Kilcormac, Co. Offaly

- Donard, Co. Wicklow c/o Rathcon Farm, Grangecon Co. Wicklow

Two data-loggers were positioned at elevated positions (approximately 2 metres from ground level) in central locations in SRCW at Kilcormac (3 hectares in size) within close proximity of each other (approximately 20 metres apart). Three additional data loggers were placed in two elevated internal (centre of crop) and one external position (edge of crop) at Donard (9.6 hectares in size). Data loggers were checked every two weeks to ensure proper functionality. Daily minimum and maximum temperatures were recorded and a daily mean temperature was calculated.

The two temperature records from the data-loggers placed in SRCW at Kilcormac showed similar fluctuation in daily mean temperatures during the development season from mid-May to the end of August, with a RMSE value of 0.77 when compared (Figure 6.3). These records were pooled and an overall mean was obtained. This data-set was compared to the closest synoptic station temperature data-sets – Mullingar, Co. Westmeath and Oak Park, Co. Carlow – for the same time period (Figure 6.4 and Figure 6.5). The pooled data-set had higher daily mean temperature recordings on a greater number of days than the synoptic data – 112 out of 124 when compared to Mullingar and 74 out of 124 when compared to Oak Park – with RMSE values of 1.79 and 1.69 respectively.

The two temperature records from the data loggers placed in SRCW at Donard showed similar fluctuation in daily mean temperature during the development season from mid-June to the end of September, with a RMSE value of 1.15 when compared (Figure 6.6). These records were pooled and an overall mean was obtained. This in-crop temperature was compared to the edge of crop temperature to investigate the microclimate within the SRCW. An RMSE value of 0.98 suggested that the consideration of a SRCW microclimate might be treated as negligible (Figure 6.7). The three temperature data-sets for Donard were subsequently pooled and compared to closest synoptic station data-sets – Oak Park and Casement Aerodrome – for the same period (Figure 6.8 and Figure 6.9). The pooled data-set had higher mean daily temperatures than the synoptic temperature on a greater number of days – 42 out of 83 when compared to Oak Park and 55 out of 83 when compared to Casement Aerodrome – with RMSE values of 1.22 and 1.09 respectively.

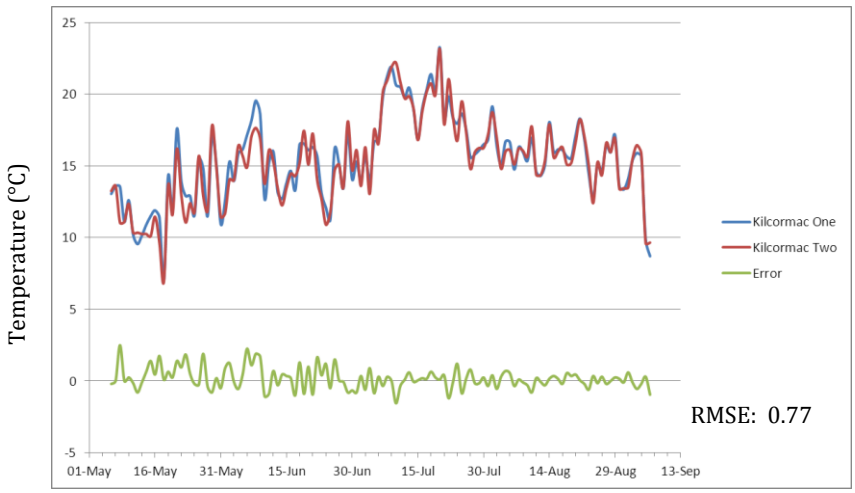


Figure 6.3 Mean daily temperature recordings obtained from data-loggers positioned in SRCW in Kilcormac, Co. Offaly with associated error when compared.

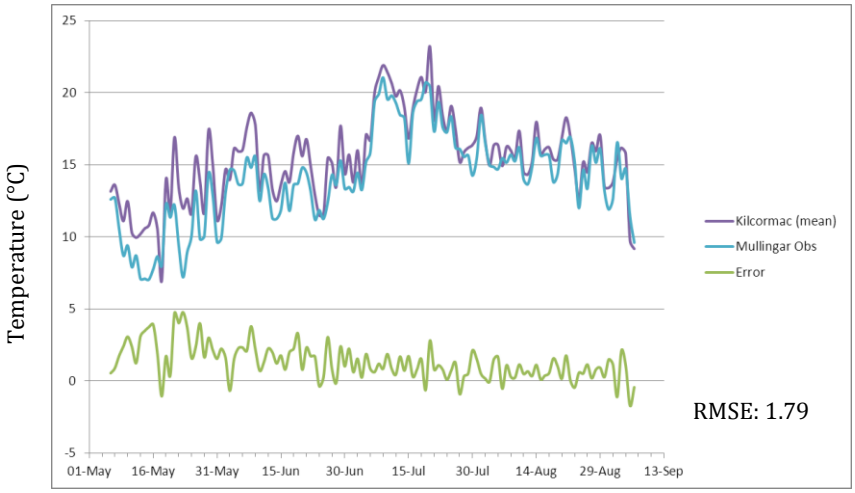


Figure 6.4 Mean of mean daily temperature recordings obtained from data-loggers positioned in SRCW in Kilcormac, Co. Offaly, compared to recorded mean daily temperature at Mullingar synoptic station, Co. Westmeath over the same time period, with associated error when compared.

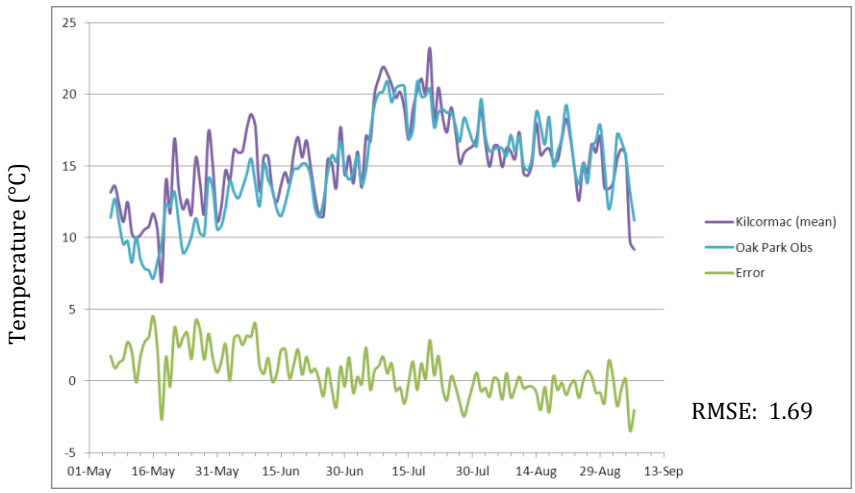


Figure 6.5 Mean of mean daily temperature recordings obtained from data-loggers positioned in SRCW in Kilcormac, Co. Offaly, compared to recorded mean daily temperature at Oak Park synoptic station, Co. Carlow over the same time period, with associated error when compared.

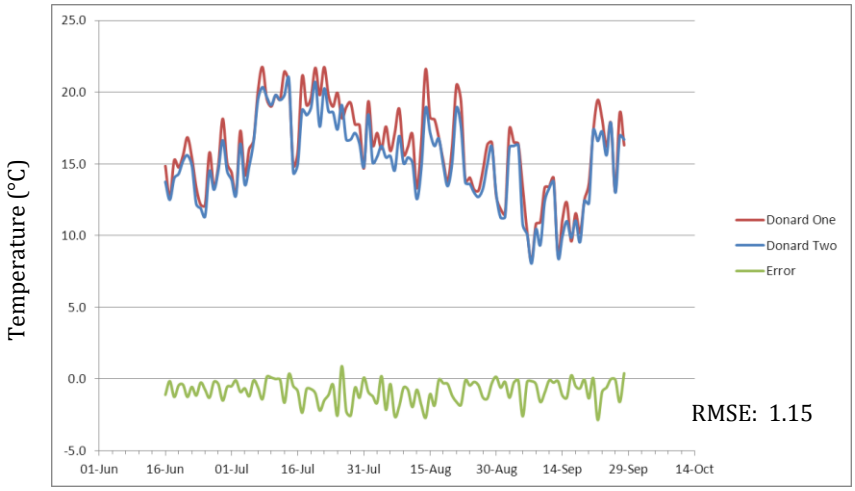


Figure 6.6 Mean daily temperature recordings obtained from data-loggers positioned in SRCW in Donard, Co. Wicklow with associated error when compared.

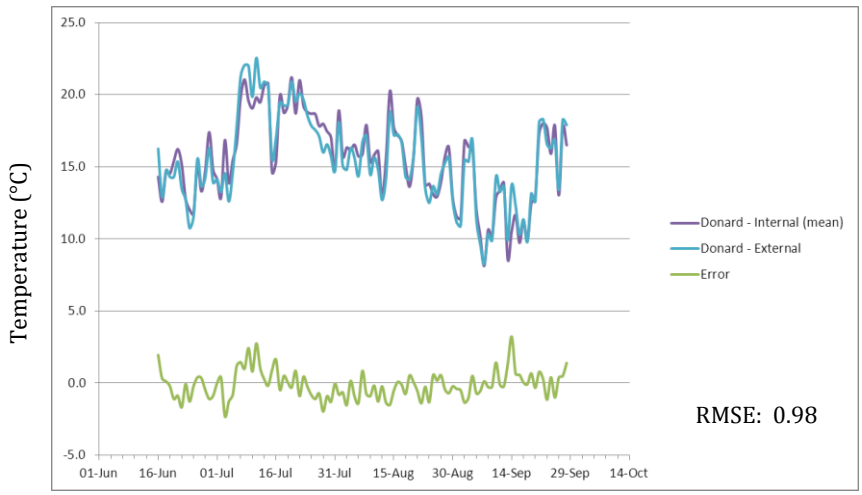


Figure 6.7 Mean of mean temperature recordings obtained from data-loggers positioned in SRCW (internal) and mean temperature recordings obtained from data-loggers positioned at the perimeter of SRCW (external) in Donard, Co. Wicklow, with associated error when compared.

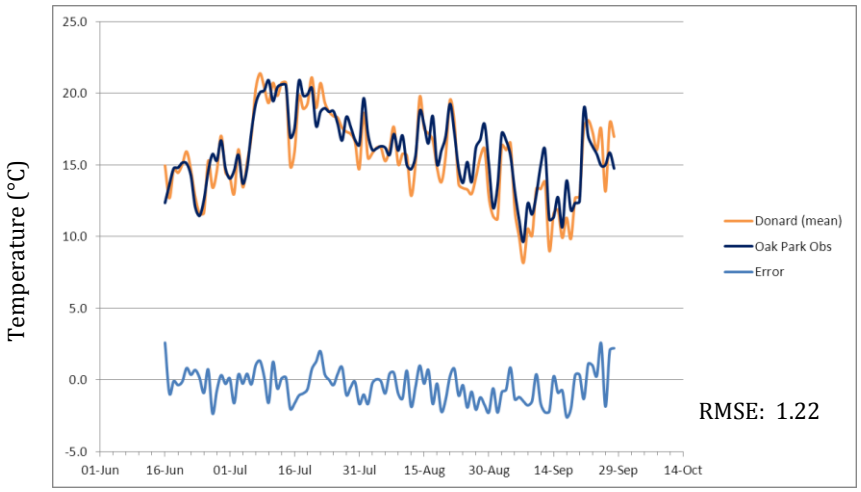


Figure 6.8 Mean of mean temperature recordings obtained from all data-loggers in SRCW in Donard, Co. Wicklow, compared to recorded mean temperatures at Oak Park synoptic station, Co. Carlow over the same time period, with associated error when compared.

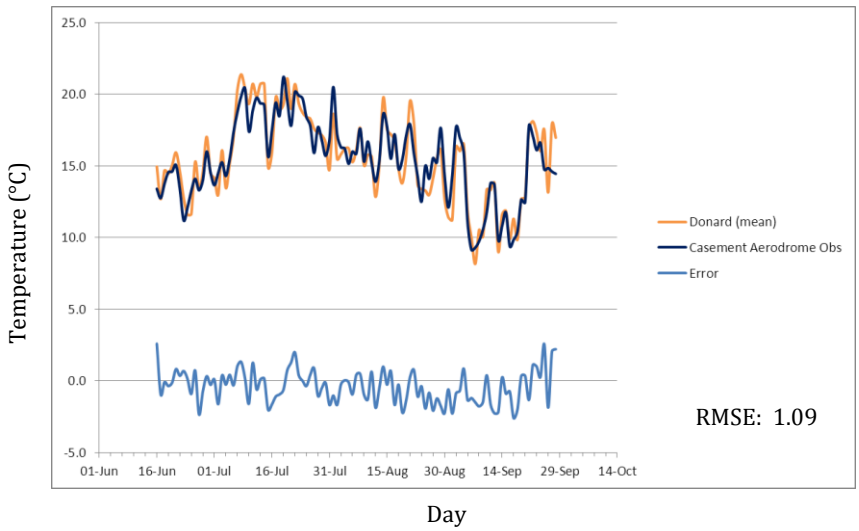


Figure 6.9 Mean of mean temperature recordings obtained from all data-loggers in SRCW in Donard, Co. Wicklow, compared to recorded mean temperatures at Casement Aerodrome synoptic station, Co. Dublin over the same time period, with associated error when compared.

6.3.1.2 Day-length Validation

To determine the accuracy of the day-length sub-function, the method was compared to that used by the NOAA Sunrise/Sunset and Solar Position Calculators (NOAA, 2014). Based on equations from *Astronomical Algorithms* by Jean Meeus (1991), their sunrise and sunset values used for calculating day-length were corrected for atmospheric refraction effects and stated as being theoretically accurate to within a minute for locations between +/- 72° latitude and within 10 minutes outside of those latitudes (with further possible variations in observed values due to variations in atmospheric composition, temperature and pressure conditions).

Day-length variation between the two methods revealed differences of 9-21 minutes when latitudinal (Malin Head (55°22'N, 07°20'W) and Roche's Point (51°48'N, 08°15'W) and longitudinal (Valentia (51°56'N, 10°15'W) and Dublin Airport (53°26'N, 06°14'W)) extremes (relating to synoptic station locations) for Ireland were assessed (Figure 6.10). These differences between methods were more pronounced towards the beginning and the end of the summer season. This equated to a difference for CDL occurrence at assessed synoptic stations of between 4-6 days.

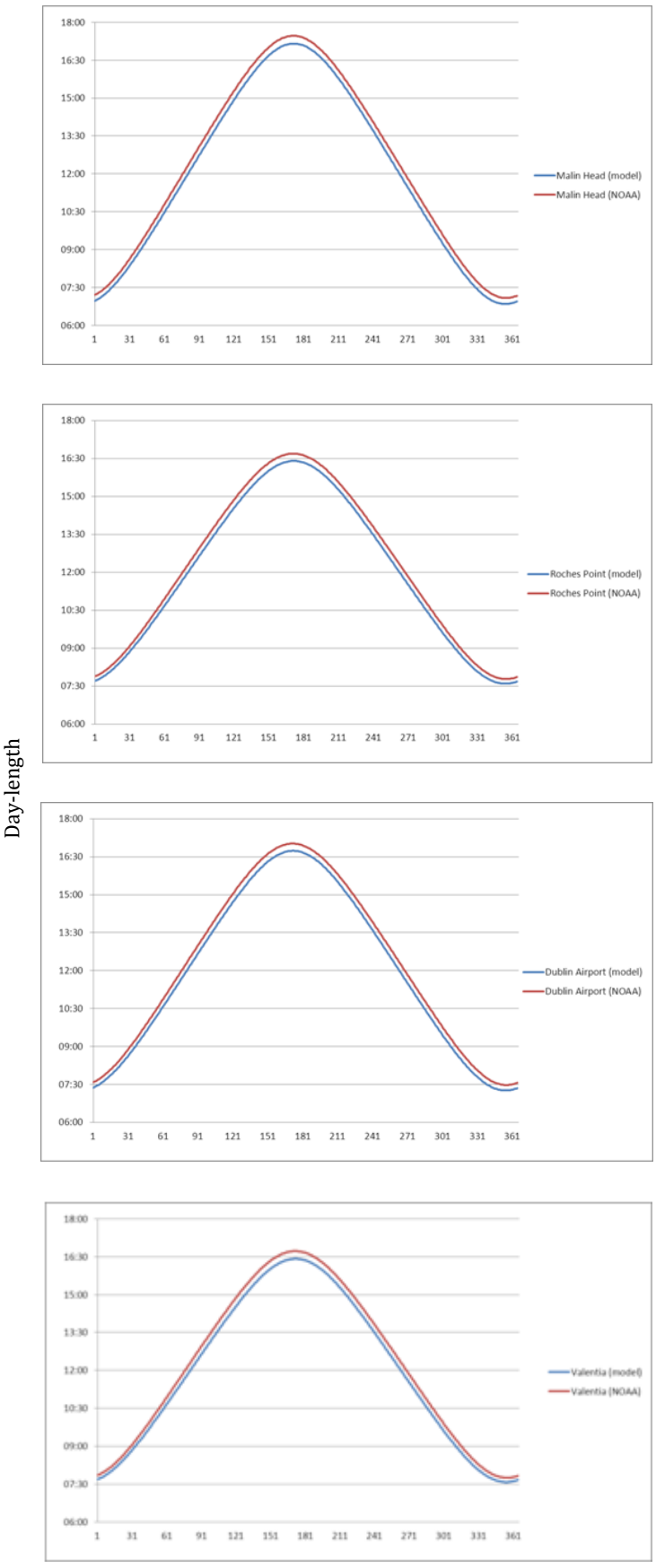


Figure 6.10 Difference between constructed sub-function daily day-length data and NOAA daily day-length data for Malin Head (North), Roche's Point (South), Dublin Airport (East) and Valentia (West).

6.3.2 Model Output Validation

6.3.2.1 Validation Using Constant Temperatures

Model simulations were run with constant temperatures 10°C (Figure 6.11), 15°C (Figure 6.12), 20°C (Figure 6.13), 25°C (Figure 6.14) and 27°C (Figure 6.15). The resulting estimated days by which set proportions of all life-cycle stages were completed were compared to results for development rate and time obtained from the empirical non-linear models describing the completion of life-cycle stages at the same constant temperatures when observed individually. The incorporated budburst model was tested using a lower set of constant temperatures: 8°C and 6°C (Figure 6.11), 9°C and 5°C (Figure 6.12), 10°C and 4°C (Figure 6.13), and 11°C and 3°C (thermal time unit and chill day set temperatures respectively) (Figure 6.14) – and an alternating temperatures regime of 6°C to 8°C with a 1°C daily increase or decrease (Figure 6.15). The simulations confirmed the schematic and cyclical format of the model was maintained, with respect to different proportions completing and entering next stage development on different days, and additional generation occurrence and development restricted by photoperiodic conditions.

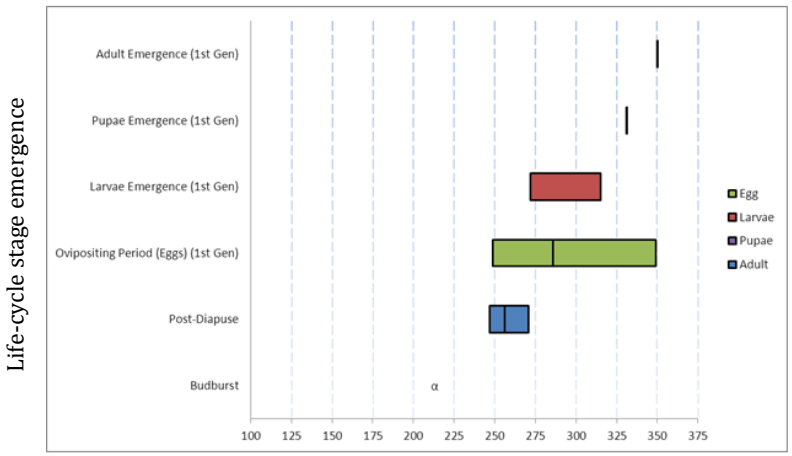


Figure 6.11 Validation of phenology/voltinism model using constant temperatures 8°C and 6°C (thermal time unit and chill day set temperatures respectively) as model inputs for *S. viminalis* budburst prediction (denoted as α) and 10°C as model input for all insect life-cycle stages, with model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion, and α denoting predicted *S. viminalis* budburst.

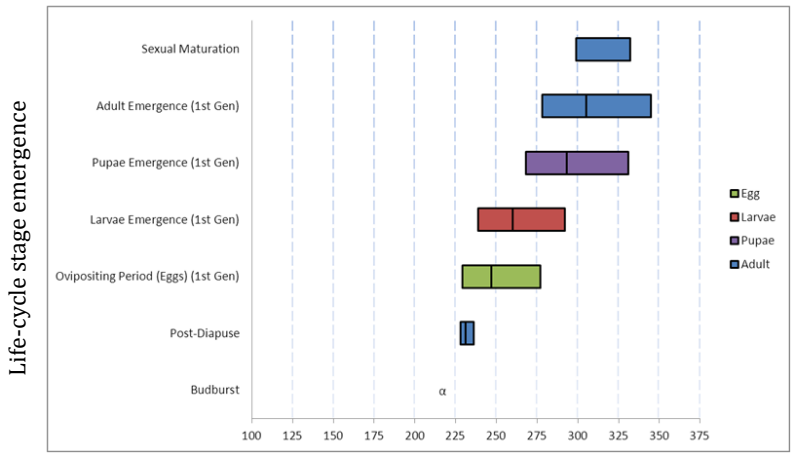


Figure 6.12 Validation of phenology/voltinism model using constant temperatures 9°C and 5°C (thermal time unit and chill day set temperatures respectively) as model inputs for *S. viminalis* budburst prediction (denoted as α) and 15°C as model input for all insect life-cycle stages, with model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion, and α denoting predicted *S. viminalis* budburst.

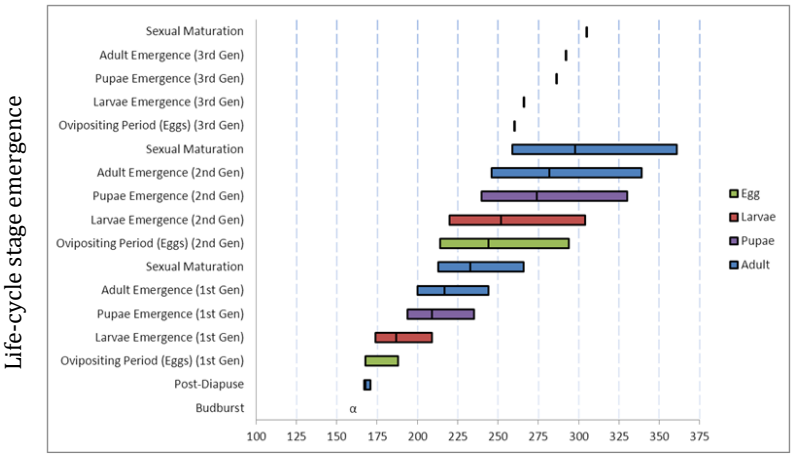
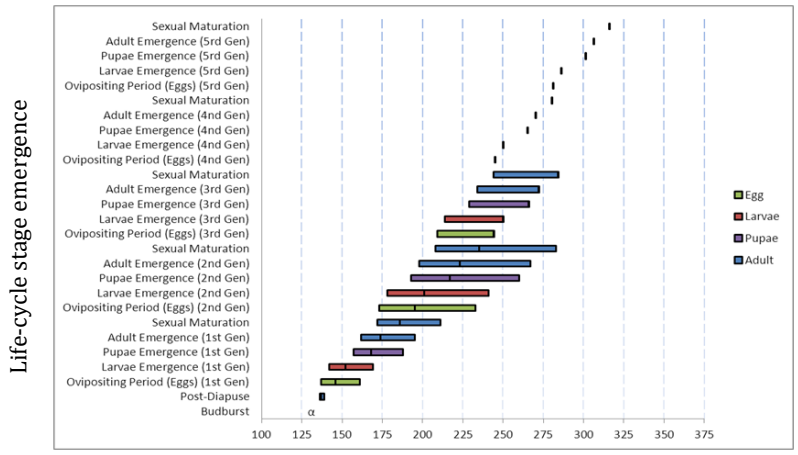
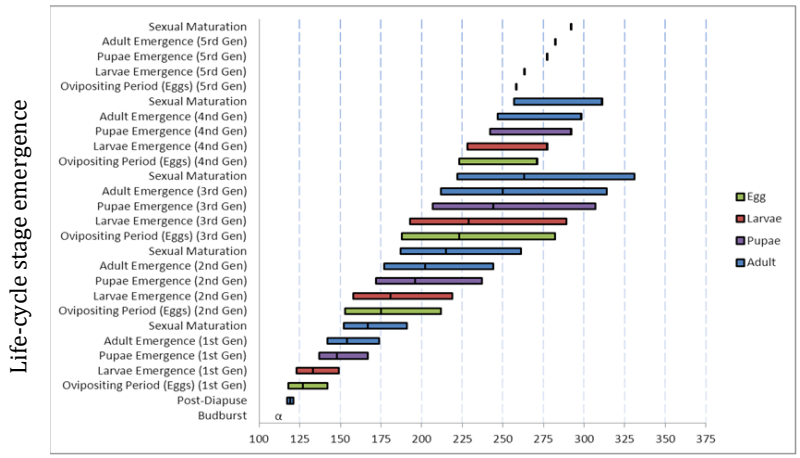


Figure 6.13 Validation of phenology/voltinism model using constant temperatures 10°C and 4°C (thermal time unit and chill day set temperatures respectively) as model inputs for *S. viminalis* budburst prediction (denoted as α) and 20°C as model input for all insect life-cycle stages, with model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion, and α denoting predicted *S. viminalis* budburst.



Number of days from 1st November

Figure 6.14 Validation of phenology/voltinism model using constant temperatures 11°C and 3°C (thermal time unit and chill day set temperatures respectively) as model inputs for *S. viminalis* budburst prediction (denoted as α) and 25°C as model input for all insect life-cycle stages, with model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion, and α denoting predicted *S. viminalis* budburst.



Number of days from 1st November

Figure 6.15 Validation of phenology/voltinism model using a fluctuating temperature regime of 6°C to 8°C for thermal time unit and chill day set temperatures with a 1°C daily increase or decrease as model inputs for *S. viminalis* budburst prediction (denoted as α) and 27°C as model input for all insect life-cycle stages, with model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion, and α denoting predicted *S. viminalis* budburst.

6.3.2.2 Validation Using Observation Data

Observational data relating to the presence of different life-cycle stages for *P. vulgatissima* was obtained during visits to native willow and SRCW sites nationwide between 2009 and

2013 (Figure 6.16, Figure 6.18 and Figure 6.19). The model was further validated by comparing the model outputs with these field observation records and an additional field observation log for *P. vulgatissima* at Long Ashton, Bristol, UK (51°26'N, 2°38'W) during 1995 by Kendall & Wiltshire (1998) (Figure 6.17). No other observation data-sets for this species were available from any Irish or UK agricultural or entomological organisations contacted.

The observation records for Long Ashton (1995) (Figure 6.17) and Donard (2013) (Figure 6.16) were more complete than records for other sites (Figure 6.18 and Figure 6.19), with multiple logs for egg, larvae and adult presence throughout the insect active season. Temperature data from Casement Aerodrome was used as a model input to estimate life-cycle proportion at Donard. Westonbirt, Gloucestershire, UK (51°36'N, 2°13'W) was the closest climate station for Long Ashton. This data-set was obtained from the UK Meteorological Office via the British Atmospheric Data Centre. The ecology and physiology of Irish *P. vulgatissima* populations is similar to UK populations (Sage & Tucker, 1998; Karp & Peacock, 2004). The phenology/voltinism model was therefore considered capable of simulating for *P. vulgatissima* life-cycle proportion development in the UK. However, it was assumed that *P. vulgatissima* populations in the UK adhered to the same critical thresholds as Irish populations for this validation process.

Model estimations for *P. vulgatissima* stage development appeared to correspond with observations in SRCW at Long Ashton (1995) (Figure 6.17), particularly for the 50% emerging proportions. The model estimated budburst to occur on day 146 (25th March) from 1st Nov of the preceding year, 50% adult post-diapause development on day 192 (11th May) and 50% oviposition period development on day 219 (7th June). Emerging adults were first detected in window trap catches after budburst on sample days 164 – 178 (13th – 27th Apr) and they continued to be observed in SRCW until day 242 (30th June). Eggs were present over day range 182 – 242 (1st May – June 30th). Larvae emerged on day 204 (23rd May) and they were present in SRCW until day 249 (7th July). The model estimated 50% larvae emergence by day 236 (24th June). Adult *P. vulgatissima* were recorded again over day range 269 – 321 (27th July – 17th Sept) while the model simulated 50% emergence on day 271 (29th July) and reaching 50% sexual maturation on day 289 (16th Aug). 5% and 95% emerging proportion occurrence for *P. vulgatissima* life-cycle stages such as egg (day 188 (7th May) and day 252 (10th July) respectively) and larvae (day 210 (29th May) and day 263 (21st July) respectively) were estimated marginally outside periods when observed in the field. 95% sexually maturing 1st generation adults continued to complete development further outside the observation window in the field however. A partial second generation was also estimated by the model for 5% emerging which was not detected during sampling.

5% sexually maturing 1st generation adults emerged on day 269 prior to an estimated CDL for further reproduction on day 279. As emergence occurred within the confidence intervals associated with CDL, the occurrence of a partial 2nd generation was ambiguous.

Model estimations for *P. vulgatissima* stage development appeared to agree with observations in SRCW at Donard (2013) (Figure 6.16) also, particularly for the 50% emerging proportions. The model estimated budburst to occur on day 169 (18th April), 50% adult post-diapause development on day 215 (3rd Jun) and 50% oviposition period development on day 233 (21st June). Emerging adults were recorded in SRCW from sample day 185 (4th May) until day 228 (16th June). Eggs were present over day range 199 – 242 (18st May – June 30th). Larvae were observed from day 228 (16th June) and they were present in SRCW until sample day 264 (22nd July). The model estimated 50% larvae emergence by day 247 (5th July). Adult *P. vulgatissima* were recorded again over day range 287 – 333 (14th Aug– 29th Sept) while the model simulated 50% emergence on day 281 (8th Aug) and reaching 50% sexual maturation on day 311 (7th Sept). Predicated development for lower and higher proportions such as 95% oviposition period on day 261 (19th July) and 5% 1st generation adult emergence on day 260 (18th July) did not occur within the field observation window. Greater time differences between observations in this record compared to that for Long Ashton (1995) may reflect badly on the ability of the model however. A partial second generation was also estimated by the model for 5% emerging proportions and this was not detected during sampling. 5% sexually maturing 1st generation adults emerged on day 277 prior to an estimated CDL on day 282. Model outputs were similar to Long Ashton model outputs as emergence occurred within the confidence intervals associated with CDL so the occurrence of a partial second generation was questionable at Donard (2013) also.

Other sporadic observation records were useful for qualitative validation (Figure 6.18 and Figure 6.19). These were collected at Littleton, Co. Tipperary (2009); Kilcormac, Co. Offaly (2009, 2010 and 2013); Donard, Co. Wicklow (2009 and 2012); Grangecon, Co. Wicklow (2009 and 2013); Westport, Co. Mayo (2009) (53°48'N, 9°30'W); Shannon, Co. Clare (2009) (52°44'N, 8°53'W); Slane, Co. Meath (2009) (53°43'N, 6°33'W); and Kildalton, Co. Tipperary (2013). The model was run using temperature data input from synoptic stations Oak Park, Co. Carlow (52°51'N, 6°54'W);; Mullingar, Co. Westmeath; Casement Aerodrome, Co. Dublin; Casement Aerodrome, Co. Dublin; Belmullet, Co. Mayo; Shannon, Co. Clare; Dublin Airport, Co. Dublin and Oak Park, Co. Carlow respectively. These were chosen based on their closest proximity to the observation sites. The majority of recordings were related to adult sightings although there were some observations of larvae made as

well. All observations conformed to model estimations although it was noted that multiple stage recordings would have strengthened these data-points.

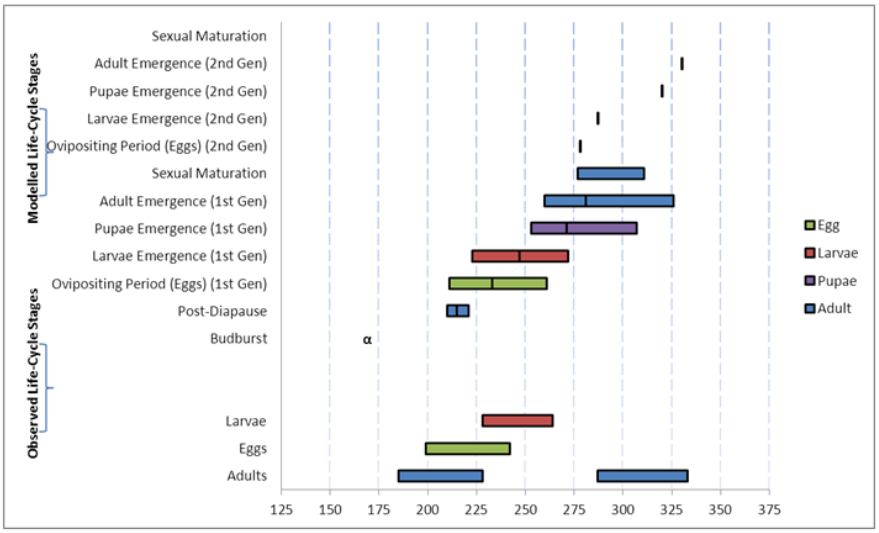


Figure 6.16 Periods of time (in days from 1st Nov previous year) when *P. vulgatissima* eggs, larvae and adults were observed in SRCW at Donard, Co. Wicklow during 2013 (bars at bottom chart), compared to model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion (bars at top of chart), and α denoting estimated *S. viminalis* budburst, using temperature data input from closest synoptic station Casement Aerodrome, Co. Dublin.

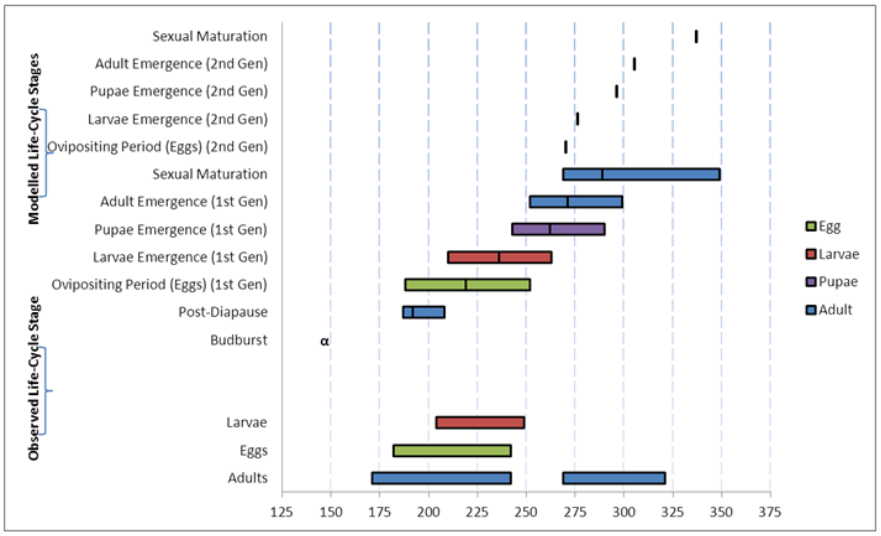


Figure 6.17 Periods of time (in days from 1st Nov previous year) when *P. vulgatissima* eggs, larvae and adults were observed in SRCW at Long Ashton, Bristol, UK during 1995 (bars at bottom chart), compared to model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion (bars at top of chart), and α denoting estimated *S. viminalis* budburst, using temperature data input from closest climate station Westonbirt, Gloucestershire, UK.

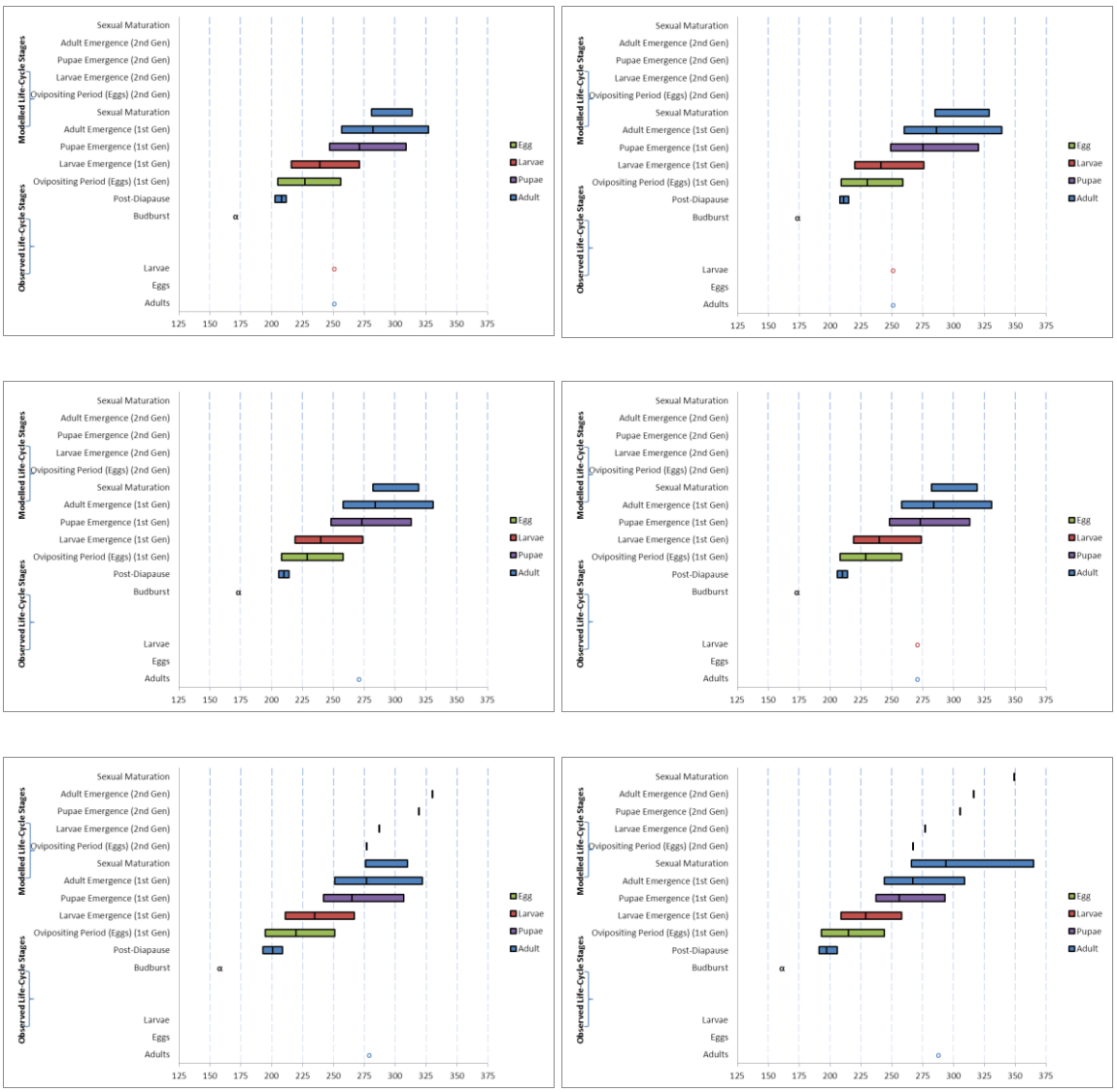
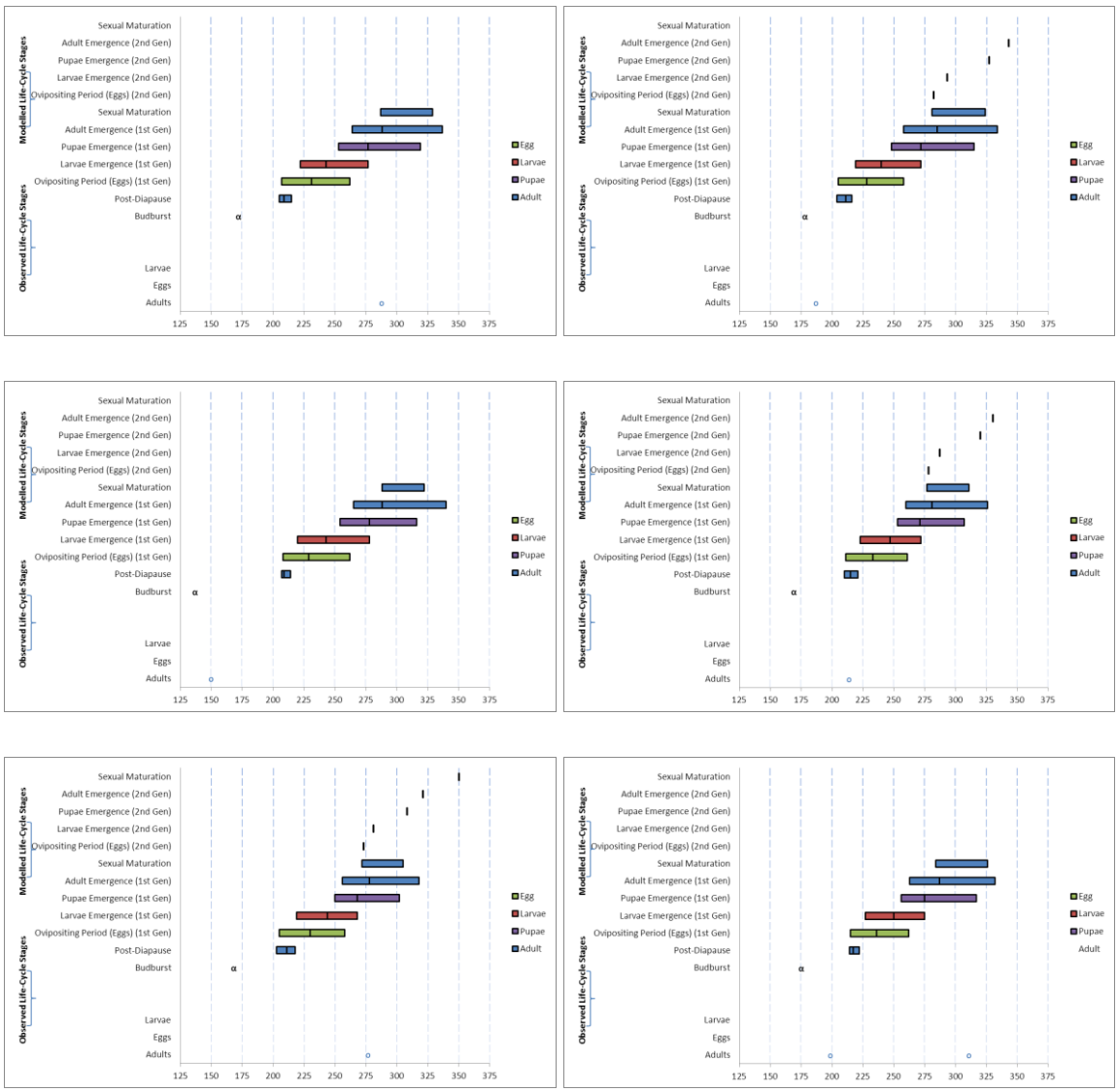


Figure 6.18 *P. vulgatissima* egg, larvae and adult observations (circles) recorded (in days from 1st Nov previous year) in native willow and SRCW at Littleton, Co. Tipperary (2009) (top-left) , Kilcormac, Co. Offaly (2009) (top-right), Donard, Co. Wicklow (2009) (middle-left), Grangecon, Co. Wicklow (2009) (middle-right), Westport, Co. Mayo (2009) (bottom-left) and Shannon, Co. Clare (2009) (bottom-right) (denoted by o at bottom of chart), compared to model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion (bars at top of chart), and α denoting estimated *S. viminalis* budburst, using temperature data input from closest synoptic stations Oak Park, Co. Carlow, Mullingar, Co. Westmeath, Casement Aerodrome, Co. Dublin, Casement Aerodrome, Co. Dublin, Belmullet, Co. Mayo and Shannon, Co. Clare respectively.



Number of days from 1st November

Figure 6.19 P. *vulgatissima* egg, larvae and adult observations (circles) recorded (in days from 1st Nov 1st previous year) in native willow and SRCW at Slane, Co. Meath (2009) (top-left) , Kilcormac, Co. Offaly (2010) (top-right), Donard, Co. Wicklow (2012) (middle-left), Grangecon, Co. Wicklow (2013) (middle-right), Kildalton, Co. Tipperary (2013) (bottom-left) and Kilcormac, Co. Offaly (2013) (bottom-right) (denoted by o at bottom of chart), compared to model outputs estimating 5% (first vertical black line at beginning of stacked bars), 50% (second vertical black line in middle of stacked bars) and 95% (third vertical black line at end of stacked bars) life-cycle stage completion (bars at top of chart), and α denoting estimated *S. viminalis* budburst, using temperature data input from closest synoptic stations Dublin Airport, Co. Dublin, Mullingar, Co. Westmeath, Casement Aerodrome, Co. Dublin, Casement Aerodrome, Co. Dublin, Oak Park, Co. Carlow and Mullingar, Co. Westmeath respectively.

6.4 **Sensitivity Analysis**

When a model has been developed (conceptualized, structured and programmed), verified (programming errors removed), subjected to parameterization (numerical estimation of parameters by some goodness of fit criterion of the model to the data) and validated (confirmed that it conforms satisfactorily with field and/or laboratory data different from the data used for parameterization), sensitivity analysis is the next essential step in mathematical modelling of ecological processes (Park & Lek, 2007). The purpose of sensitivity analysis is to provide an idea of the response of the model properties to variation in the values of some of the parameters or sub-function outputs. One or more outcomes of the model are selected and their behaviour is evaluated by increasing and decreasing corresponding parameters or sub-function outputs over a plausible range. This analysis is usually carried out with respect to the important factors (those suspected of having a strong effect due to conceptual or mathematical relationships with the behaviour of the model) or in relation to those factors that, for some reason, could not be estimated in the field or in the laboratory (cost or time constraints, high mortality in certain later life-cycle stages, difficulties in replicating environmental conditions suitable for life-cycle development in the laboratory) (Park & Lek, 2007).

Sensitivity analysis techniques were based on methods used during the construction of other phenology models and population models (Elliott & Hein; 1991; Mitchell & Riedell, 2001; Wang & Shipp, 2001; Rashleigh & Grossman, 2005; Schaub *et al*., 2005; Fu *et al*., 2012b; Migliavacca *et al*., 2012). The sensitivity of the phenology/voltinism model was assessed by examining the effects of variation in the immature and mature life-cycle stage parameters, and variation in *S. viminalis* budburst occurrence and critical day-length (Figure 6.20 – Figure 6.24). Parameter values for each of the life-cycle stages (post-diapause, oviposition period, larvae emergence, adult emergence and sexual maturation) were increased or decreased, based on ±10% change in the mean development times at different constant temperatures, for each life-cycle stage recorded during experimentation. This arbitrary percentage value was considered suitable as (1) it was supported by the previously cited literature, (2) it accounted for the variation associated with estimated sexual maturation that was partly based on the post-diapause development (see Figure 4.4) and (3) it was more conservative than performing the analysis using standard errors (or using standard deviations, which was not an option as non-linear functions did not always fit to standard deviation adjusted data-sets) associated with the mean development times as these errors were insignificant, particularly for the higher constant temperatures while the arbitrary percentage value captured these errors within the 10% range also. This

technique could not be performed for analysis of pupal emergence however as the fit of the chosen function to the larval life-cycle stage development data-set would not converge to provide unique sets of parameters based on ±10% change in the mean development times. Model sensitivity to budburst and CDL variation was examined by applying ±13 days (one standard deviation based on budburst model estimating capability) to the estimated budburst values and alternating CDL between calculated 95% confidence interval values.

Sensitivity analysis was conducted using daily temperature data for validation sites Donard (2013) and Long Ashton (1995) as model inputs. Temperature data for 1983-2013 was obtained for the closest climatic stations to these sites, Casement Aerodrome and Westonbirt respectively as per validation process. A cold and warm year based on degree-day accumulation (using the averaging method) for temperatures greater than 5°C, 5.5°C, 6°C, 6.5°C and 7°C from 16th March, 1st April and 16th April were selected for both sites to assess model sensitivity under different temperature regimes also. The temperatures and dates to initiate degree-day accumulation were based on early insect life-cycle stage critical thresholds and the majority of budburst days estimated by the model to occur annually around these dates. The years 1986 and 1995 were identified as cold and warm years respectively for Donard with the least and most degree-days accrued from all base temperatures and initiation dates over the thirty-year period respectively. The years 2012 and 1995 (this year already selected for sensitivity analysis) were established as cold and warm years respectively for Long Ashton with the least and most degree-days amassed from all base temperatures and initiation dates over the same time-scale respectively.

The sensitivity of the validated model to changes in the parameter values was evaluated by computing their influence on the day of 50% emergence of sexually mature adults for each year. This stage was chosen against others as it was designated as the final CDL sensitive stage in the insect's life-cycle history with further life-cycle stage development and generation occurrence dependent on changes in parameter values and model inputs up to this point. When sexual maturation was not completed by 50% emergence proportion, the preceding adult emergence stage was utilised for analysis.

Parameter value changes based on ±10% change in the mean development times for immature and mature life-cycle stages had a minor effect on the estimated day for 50% E.P of sexually mature adults at Long Ashton (validation/warm year) (Figure 6.20). The difference in days from a normal model run were no greater than 3 days when changes to parameter values were made consecutively to each assessed life-cycle stage. Similar differences from normal model run outputs of 5 days for Donard (validation year) (Figure 6.22) and 3 days for Donard (warm year) (Figure 6.24) were simulated. Greater differences

from the normal run of 18 days were acquired for Donard (cold year) (Figure 6.23). This was due to the adjustment of sexual maturation parameter values only, as differences from the normal model run were not greater than 3 days when parameters for the other life-cycle stages were modified. 50% E.P of sexually mature adults was not estimated to be reached for Long Ashton (cold year) (Figure 6.21). 50% E.P of adults from pupae development was therefore referred to for analysis purposes with differences of no greater than 2 days from the normal model run for other life-cycle stages.

Increases in the differences in estimated days for 50% E.P of sexually mature adults from the normal model runs, when parameters for all immature and mature life-cycle stages were collectively amended, were more evident for some years such as Donard (validation year) with a difference of 17 days, compared to 6 days for Donard (warm year) and Long Ashton (validation/warm year, and also cold year when sexual maturation was not achieved). Such differences were increased further when budburst variation was also considered, with differences from the normal estimated days rising to 20 days for Donard (validation year), 11 days for Donard (warm year) and 8 days for Long Ashton (validation/warm year). Further analysis involving the introduction of predefined changes to CDL did not have any additional impact on differences described for these years however.

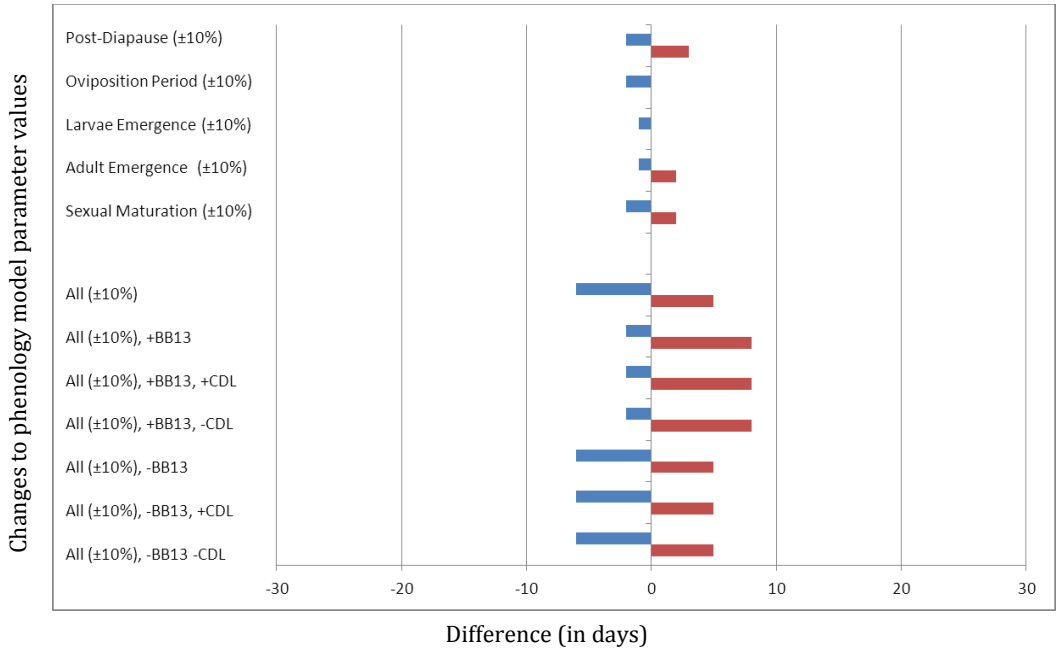


Figure 6.20 The differences (in days) for 50% E.P of sexually mature adults when standard parameter values for life-cycle stages, and standard budburst and CDL were compared with changed parameter values (based on -10% (blue) and +10% (red) changes in mean development times at different constant temperatures for each life-cycle stage), and changed budburst (±BB13) and CDL (CDL±95% C.I) at Long Ashton, Bristol, UK (1995 – validation year and warm insect active season).

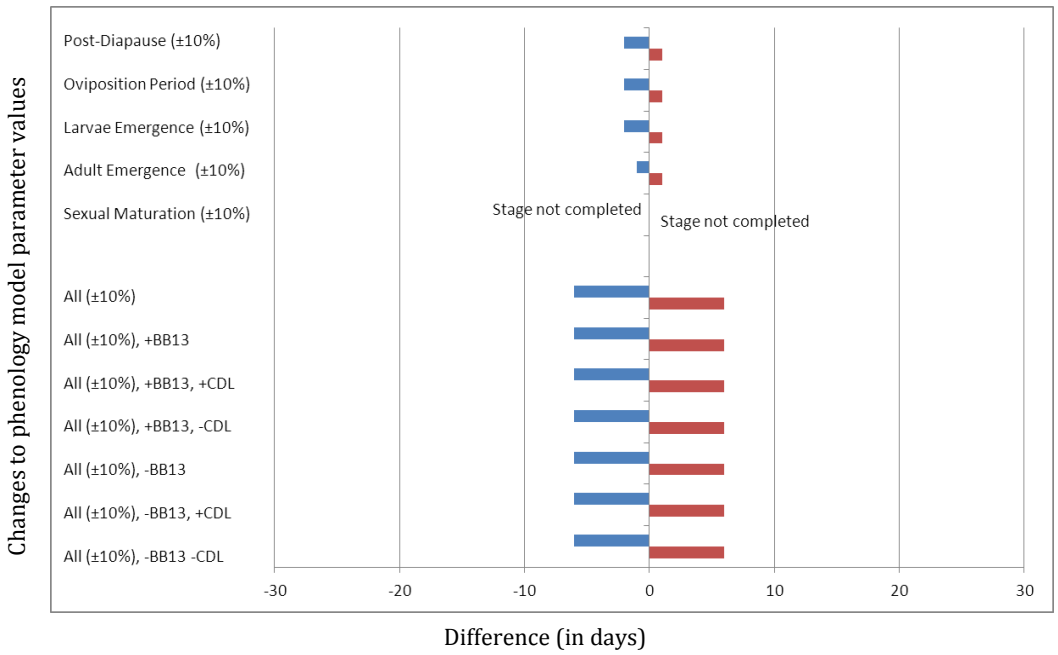


Figure 6.21 The differences (in days) for 50% E.P of adults (pre-sexual maturity) when standard parameter values for life-cycle stages, and standard budburst and CDL were compared with changed parameter values (based on -10% (blue) and +10% (red) changes in mean development times at different constant temperatures for each life-cycle stage), and changed budburst (±BB13) and CDL (CDL±95% C.I) at Long Ashton, Bristol, UK (2012 – cold insect active season).

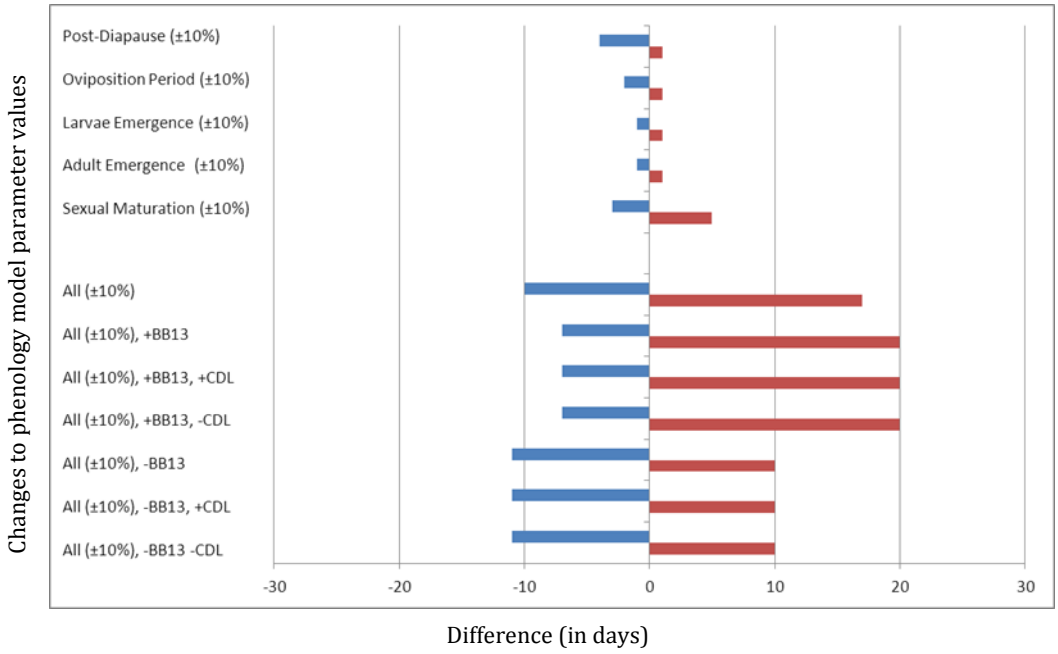


Figure 6.22 The differences (in days) for 50% E.P of sexually mature adults when standard parameter values for life-cycle stages, and standard budburst and CDL were compared with changed parameter values (based on -10% (blue) and +10% (red) changes in mean development times at different constant emperatures for each life-cycle stage), and changed budburst (±BB13) and CDL (CDL±95% C.I) at Donard, Co. Wicklow (2013 – validation year).

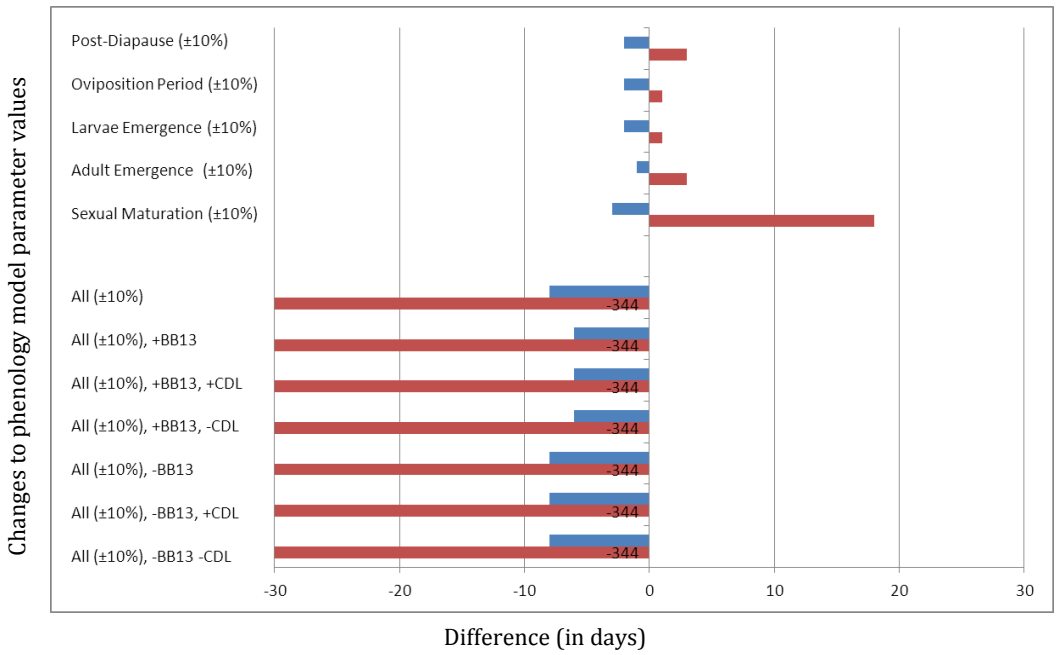


Figure 6.23 The differences (in days) for 50% E.P of sexually mature adults when standard parameter values for life-cycle stages, and standard budburst and CDL were compared with changed parameter values (based on -10% (blue) and +10% (red) changes in mean development times at different constant temperatures for each life-cycle stage), and changed budburst (±BB13) and CDL (CDL±95% C.I) at Donard, Co. Wicklow (1986 – cold insect active season).

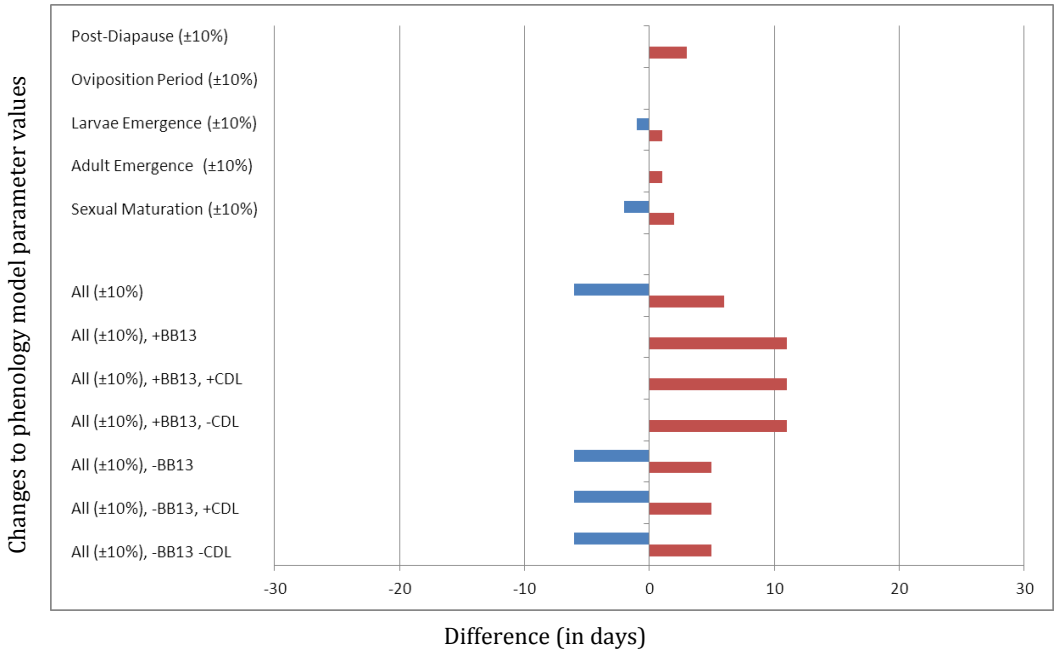


Figure 6.24 The differences (in days) for 50% E.P of sexually mature adults when standard parameter values for life-cycle stages, and standard budburst and CDL were compared with changed parameter values (based on -10% (blue) and +10% (red) changes in mean development times at different constant temperatures for each life-cycle stage), and changed budburst (±BB13) and CDL (CDL±95% C.I) at Donard, Co. Wicklow (1995 – warm insect active season).

The compounding effects of different temperature regimes and parameter value changes for all stages was most apparent for the Long Ashton (cold year) and Donard (cold year). A 10% reduction in mean development times for all stages facilitated for the 50% emergence proportion of sexually mature adults at Long Ashton (cold year) (not shown in graph). This was not estimated to occur under normal model runs. In contrast, a 10% increase in mean development times for all stages impeded the 50% E.P of sexually mature adults at Donard (cold year). This was estimated to occur under a normal model run.

Although model sensitivity was examined by focusing on the estimated days for 50% E.P of sexually mature adults, it is notable that combined changes to life-cycle stage parameters, budburst and CDL values encouraged or prevented second generation development for 5% and 50% E.P. This was observed in particular for both warm years although a second generation for 5% E.P was suggested when parameter values were changed due to the 10% reduction in mean development times and the overwhelming determinant CDL was reduced within the 95% C.I range for Donard (cold year) aswell.

This analysis showed that when parameter variations for life-cycle stages, or budburst or CDL were observed on their own, this had a minor impact on the model outputs. When these variations were observed in combination, it sometimes meant the difference of additional stage development (as observed for Long Ashton (cold year) and Donard (cold year)) or generation development (as observed for other emergence proportions, data not shown). Although such a combination of positive or negative parameter variation was unlikely, the results did reveal modelling limitations when outputs for single years were assessed. Sensitively to CDL parameter variation was of particular importance due to its potential to allow or prevent second generation occurrence. However, this was not recognised to be an issue as model outputs for observed and future time periods incorporating multiple years were assessed in the next chapter.

7 PHENOLOGY/VOLTINISM MODEL RESULTS

This chapter concentrates on the analysis of the results from the combined phenology/voltinism model constructed on the findings from *P. vulgatissima* life-cycle development work and *S. viminalis* budburst work from the preceding Chapters 3-5. Temperature data used as model inputs to represent current and future conditions are initially discussed. The results for selected willow beetle life-cycle stages and synoptic stations representing national temperature variability (north, south, west, east and midlands) are described. Spatial analysis of relative differences between control periods and future time periods including additional synoptic stations, to provide a more comprehensive account of future climate change impacts on beetle emergence and generation occurrence across Ireland, is reviewed also.

7.1 Model Input

Observed daily mean temperature data-sets were acquired for eleven Irish synoptic stations from the Irish national meteorological service, Met Éireann, and used as the phenology/voltinism model inputs for a baseline period (1961-1990). Model outputs (in days from 1st November of the preceding year as this was the date a model runs commenced from) for budburst occurrence and emergence of differing proportions for all *P. vulgatissima* life-cycle stages were collected annually for eleven Irish synoptic stations.

To determine future estimations for budburst occurrence and insect emergence, future temperature projections were required as model inputs. Statistically downscaled climate scenarios derived from Global Climate Models by identifying and establishing mathematical transfer functions or empirical relationships, through multiple linear regression techniques, between observed large-scale atmospheric variables and the surface environmental variable of interest (such as temperature), were employed (Fealy & Sweeney, 2007; 2008; Wilby & Dawson, 2007). Future daily mean temperature projections relating to the eleven stations were obtained from Fealy & Sweeney (2007; 2008) and Sweeney *et al*. (2008). This data consisted of statistically downscaled climate scenarios from three different GCMs, forced with two emissions scenarios (A2 and B2). The GCMs employed were HadCM3 (Hadley Centre for Climate Prediction and Research, UK), CCGCM2 (Canadian Centre for Climate Modelling and Analysis, Canada) and CSIROM2 (Commonwealth Science and Industrial Research Organisation, Australia). The future GHG emissions were taken from the IPCC Special Report on Emission Scenarios where the A2 (medium–high) and B2 (medium–low) emission scenarios project a more regional future development with either a more economical (A2) or environmental (B2) focus (IPCC, 2000). Statistically downscaled temperature data bias correction, as advocated by Karl *et al*. (1990), was applied to both the control period (1961-1990) and all future time periods to remove a systematic bias and improve the correspondence between the statistically downscaled temperature data and observed temperature data (Fealy & Sweeney, 2007; 2008; Fealy, 2010).

Means of the phenology/voltinism model outputs for the baseline period (1961-1990) were calculated to represent baseline period foliage and insect emergence for each location using the observed temperature data-sets. Means of the model outputs for the control period (1961-1990) were also calculated to represent control period foliage and insect emergence (for observation period calibration purposes) for each location using the downscaled temperature data-sets for all climate models. Means of the model outputs during 2010-2039 (2020s), 2040-2069 (2050s), and 2070-2099 (2080s) were calculated to represent future time period foliage and insect emergence for each location using the downscaled temperature data-sets for all climate models. These thirty year periods were selected in order to account for inter-decadal shifts in phenology over the present century.

In recognition of the uncertainty associated with employing a singular GCM or emission scenario, unweighted ensembles based on the mean of the aggregated phenology/voltinism model outputs were produced for baseline, control and future time periods, sampling across all three GCMs and both emission scenarios. Ensembles of the downscaled temperature data initially employed for this analysis were weighted (Fealy &

Sweeney, 2007; 2008; Sweeney *et al*., 2008). The results from the weighted ensembles were based on the Climate Prediction Index (CPI) (Murphy *et al*., 2004). This measure of reliability was used to weight different GCMs based on real world predictive accuracy. This method was further customized by Wilby & Harris (2006) for use with a smaller number of GCM outputs.

Initial analysis indicated that the natural climate variability in the observed and downscaled temperature data-sets was muted for the weighted ensembles. Due to the added complexity of the budburst estimation component within the phenology/voltinism model – a dynamic process responding to chilling days and thermal time units – estimations for this stage were delayed when weighted ensembles were used. This was evident as estimated days for budburst occurrence differed when the model was run with observed temperature data-sets and ensemble control data-sets. Estimated budburst occurrence days were outside the range of individual GCM outputs also. The six individual GCM scenarios were therefore considered as being equally likely and employed as unweighted inputs to the phenology/voltinism model without a subjective attribution of likelihood.

7.2 **Results**

S. viminalis budburst and emergence results for three insect life-cycle stages – eggs development leading to larval emergence, pupal development leading to adult emergence and adult development leading to sexual maturation – and third generation development for any life-cycle stage were chosen for evaluation under observed and future climate scenarios. Budburst occurrence was chosen as it was the precursor stage for the complete phenology/voltinism model and it was necessary for the successive insect development stages to begin. The insect life-cycle stages were selected due to their predatory importance within SRCW. Results for five synoptic stations – Roche's Point, Co. Cork (southerly), Belmullet, Co. Mayo (westerly), Kilkenny, Co. Kilkenny (midlands), Casement Aerodrome, Co. Dublin (easterly) and Malin Head, Co. Donegal (northerly) – were assessed (Figure 6.2). These were chosen to illustrate the spatial variation of model output arising from different temperature regimes. Budburst occurrence and emergence results for all life-cycle stages at the eleven synoptic station locations (including those not reviewed or discussed in depth in this chapter) are provided in the Appendix VII. Relative differences between results for the control periods and future time periods were evaluated for budburst and the three insect

life-cycle stages at all synoptic stations locations also. Relative difference between results for control periods and future time periods was restricted to first generation insect life-cycles during GIS mapping due to limited or no second generation development during the control period to compare to future time periods.

7.2.1 Phenology/Voltinism Estimations for Individual Synoptic Stations

7.2.1.1 Roche's Point (South)

The phenology/voltinism model outputs for predicted mean budburst occurrence and estimated mean emergence days for the assessed life-cycle stages proportions (5%, 50% and 95%) were calculated for the baseline period using the observed daily mean temperature data-set and downscaled daily mean temperature data-sets for the individual GCMs (Table 7.1). The greatest range between the GCM outputs was for the budburst occurrence stage, with differences of up to 24 days. Differences in the estimated mean emergence days for the assessed life-cycle stages were no greater than 5 days when the model was run using the observed and ensemble control data-sets. Ensemble control mean estimations were within the GCM ranges accordingly. All insect E.P recorded an estimated mean value for first generation sexual maturation stage completion employing the observed and ensemble control data-sets. Sexual maturation completion for the 95% E.P was based on calculations for 3% (1 year) of the observed data-set and 5% (8 years) of the ensemble control data-set.

Second generation development for the 5% E.P was estimated to transpire when either observed and ensemble control data-sets were used as model inputs. Estimated mean values for second generation larvae emergence and adult emergence were both based on calculations for 24% (7 years) of the observed data-set and 45% (78 years) of the ensemble control data-set. Sexual maturation stage completion for second generation insects was estimated to occur on day 351 based on calculations for 21% (6 years) of the observed data-set and day 348 based on calculations for 25% (43 years) of the ensemble control data-set. No second generation development was estimated for the 50% or 95% E.Ps when either observed and ensemble control data-sets were used as model inputs.

Table 7.1 Estimated mean for budburst days and emergence days for assessed life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using observed daily mean temperature data and downscaled daily mean temperature data (from 1st Nov – 31st Oct, 1961 – 1990 for both) for individual GCMs (HadCM3, CCGCM2 and CSIROM2) at Roche's Point, Co. Cork. Ranges for emergence days over time period for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for observed and control (GCM ensemble) means are identified when 100% of years from 1961-1990 do not register development. Differences between mean for ensemble control and mean for observed periods are displayed.

Roche's Point Stage	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff
	5% E.P				50% E.P				95% E.P			
Budburst	167	153-177	167	0	167	153-177	167	0	167	153-177	167	0
Larvae Emergence (1st gen)	219	212-219	215	-4	242	234-244	238	-4	276	267-276	271	-5
Adult Emergence (1st gen)	261	253-263	256	-5	287	278-287	282	-5	331	321-331	32	-4
Sexual Maturation (1st gen)	282	273-282	277	-5	315	305-316	311	-4	351 **(3%)**	350-358	355 **(5%)**	+4
Larvae Emergence (2nd gen)	281 **(24%)**	274-284	281 **(45%)**	0								
Adult Emergence (2nd gen)	320 **(24%)**	316-326	323 **(45%)**	+3								
Sexual Maturation (2nd gen)	351 **(21%)**	345-351	348 **(25%)**	-3								

Ensemble mean values for assessed stage emergence for future time periods were compared to those for the control baseline period (Table 7.2). All ensemble estimations across all stages, E.Ps and time-frames were within their respective GCM ranges. The ranges between the individual GCM mean outputs for the budburst occurrence stage were 23 days for the 2020s, 15 days for the 2050s and 28 days for the 2080s. The greatest ranges between the individual GCM mean outputs for the different life-cycle stages were 14 days (1st generation adult emergence 95% E.P) for the 2020s, 16 days (2nd generation adult emergence 50% E.P) for the 2050s and 22 days (2nd generation sexual maturation 50% E.P) for the 2080s. The differences between ensemble control estimations and future time period estimations for all phenology/voltinism model stages became greater for the latter future periods (Table 7.3). A successive advancement of all stages was illustrated across the future time periods (Figure 7.1). These differences ranged from 6-16 days for the 2020s, 13-27 days for the 2050s and 22-40 days for the 2080s.

Table 7.2 Estimated ensemble mean for budburst days and emergence days for assessed life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using downscaled daily mean temperature data (from 1st Nov – 31st Oct) for future time periods (2020s, 2050s and 2080s) at Roche's Point, Co. Cork. Ranges for emergence days over future time periods for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for future means (GCM ensemble) are identified when 100% of years across each future time period do not register development.

Roche's Point Stage	GCM ranges	Ens mean	GCM ranges	Ens mean	GCM ranges	Ens mean
2020	**5% E.P**		**50% E.P**		**95% E.P**	
Budburst	149-172	159	149-172	159	149-172	159
Larvae Emergence (1st gen)	206-210	208	228-232	230	258-264	262
Adult Emergence (1st gen)	245-251	248	268-275	272	304-318	311
Sexual Maturation (1st gen)	263-270	267	291-302	297	339-347	344 **(56%)**
Larvae Emergence (2nd gen)	273-277	275 **(83%)**	296-299	297 **(2%)**		
Adult Emergence (2nd gen)	308-315	311 **(83%)**	340-346	342 **(2%)**		
Sexual Maturation (2nd gen)	332-340	335 **(81%)**				
2050						
Budburst	146-161	149	146-161	149	146-161	149
Larvae Emergence (1st gen)	199-204	202	220-227	224	251-257	255
Adult Emergence (1st gen)	238-244	241	261-266	264	294-305	300
Sexual Maturation (1st gen)	256-261	259	282-290	286	327-335	331 **(86%)**
Larvae Emergence (2nd gen)	266-269	267 **(93%)**	290-302	297 **(18%)**		
Adult Emergence (2nd gen)	298-305	301 **(93%)**	329-345	338 **(18%)**		
Sexual Maturation (2nd gen)	315-327	321 **(93%)**	355-362	357 **(5%)**		
2080						
Budburst	128-156	140	128-156	140	128-156	140
Larvae Emergence (1st gen)	188-198	192	214-221	216	243-250	247
Adult Emergence (1st gen)	232-237	234	251-259	255	283-294	288
Sexual Maturation (1st gen)	247-255	251	270-281	276	312-330	318 **(99%)**
Larvae Emergence (2st gen)	255-264	260	285-299	292 **(53%)**		
Adult Emergence (2st gen)	285-297	291	322-337	330 **(53%)**		
Sexual Maturation (2st gen)	302-318	308	340-362	351 **(31%)**		

A greater percentage of years estimated second generation life-cycle stage completion for the 5% E.P during the future time periods as first generation sexual maturation stage (photosensitive stage) was completed earlier than CDL at this specific station – day-length was estimated to become less than 14.92 hrs on day 279 at Roche's Point. The percentage of years that were used to estimate the ensemble mean for second generation larvae emergence and adult emergence increased across the future time periods

from 45% (78 years) for the control period to 83% (150 years) for the 2020s, 93% (168 years) for the 2050s and 100% (180 years) for the 2080s. The percentage of years that were used to estimate the ensemble mean for second generation sexual maturation stage completion increased across the future time periods from 25% (43 years) for the control period to 81% (146 years) for the 2020s, 93% (167 years) for the 2050s and 100% (180 years) for the 2080s.

Table 7.3 Relative differences between ensemble means for future time periods and control period, for budburst days and emergence days for life-cycle stages and emergence proportions (5% E.P, 50% E.P and 95% E.P) at Roche's Point, Co. Cork.

Roche's Point Stage	2020	2050	2080	2020	2050	2080	2020	2050	2080
	5% E.P			50% E.P			95% E.P		
Budburst	-8	-18	-27	-8	-18	-27	-8	-18	-27
Larvae Emergence (1st gen)	-7	-13	-23	-8	-14	-22	-9	-16	-24
Adult Emergence (1st gen)	-8	-15	-22	-10	-18	-27	-16	-27	-39
Sexual Maturation (1st gen)	-10	-18	-26	-14	-25	-35	-11	-24	-37
Larvae Emergence (2nd gen)	-6	-14	-21						
Adult Emergence (2nd gen)	-12	-22	-32						
Sexual Maturation (2nd gen)	-13	-27	-40						

A greater percentage of years estimated second generation life-cycle stage completion for the 50% E.P during the future time periods. This was despite the ensemble mean values for first generation sexual maturation estimated to occur after CDL for the 2020s and the 2050s. The percentage of years that were used to estimate ensemble means for second generation larvae emergence and adult emergence increased across the future time periods from no development for the control period to 2% (3 years) for the 2020s, 18% (33 years) for the 2050s and 53% (95 years) for the 2080s. Sexual maturation stage completion was estimated for 31% (55 years) by the 2080s also. The percentage of years that were used to estimate the ensemble mean value for first generation sexual maturation stage competition for the 95% emerging insect proportion increased from 5% (8 years) for the control period to 99% (179 years) for the 2080s. No second generation development was estimated to occur for this E.P however.

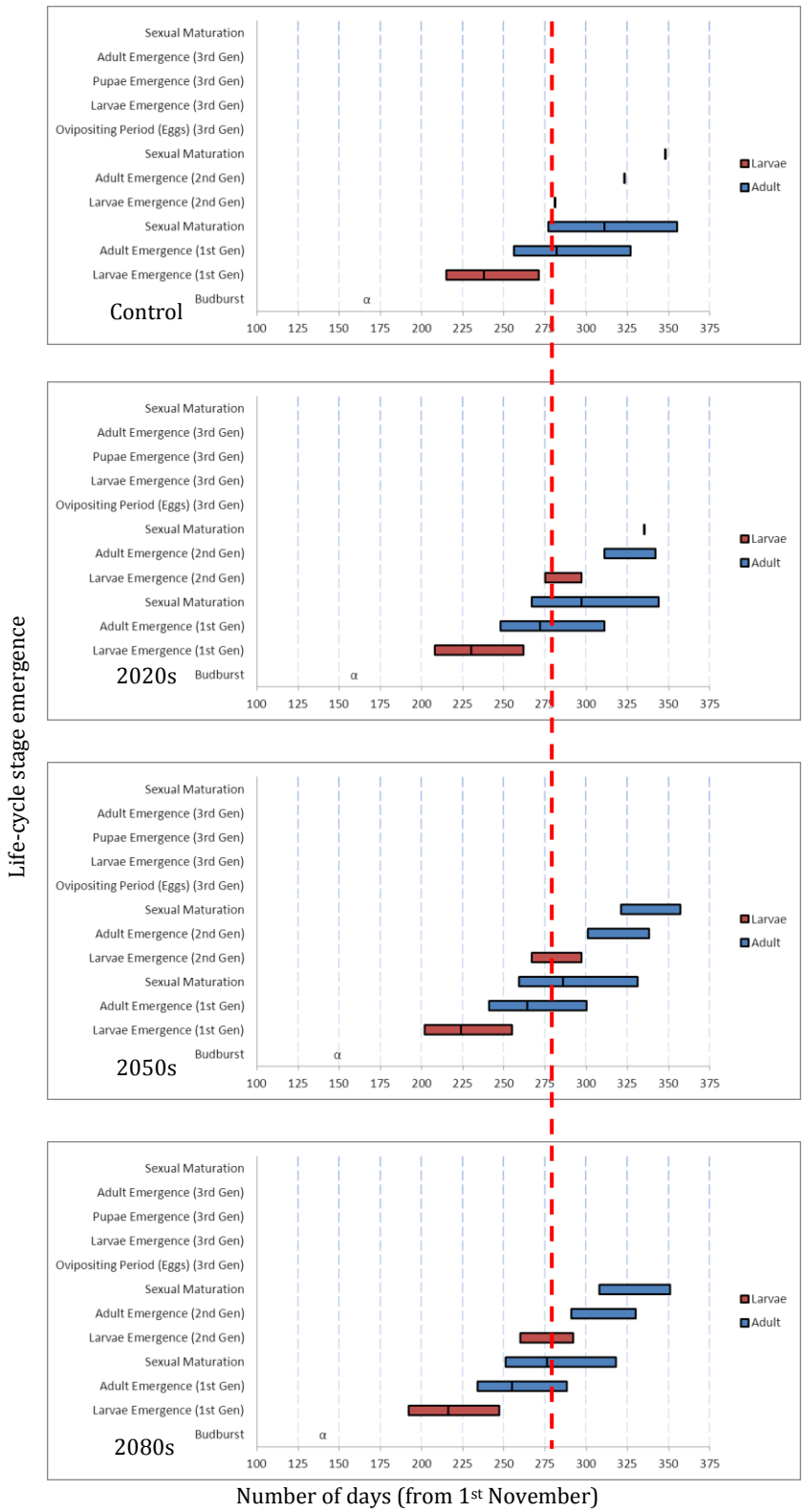


Figure 7.1 Changes in ensemble means for budburst day (denoted as α) and emergence days for life-cycle stage emergence proportions (5% E.P expressed as first vertical black line at beginning of stacked bars, 50% E.P expressed as second vertical black line in middle of stacked bars and 95% E.P expressed as third vertical black line at end of stacked bars) at Roche's Point, Co. Cork across control and future time periods (2020s, 2050s and 2080s) with dashed red line representing CDL occurrence at this specific station.

7.2.1.2 Belmullet (West)

The phenology/voltinism model outputs for predicted mean budburst occurrence and estimated mean emergence days for the assessed life-cycle stages proportions were calculated for the baseline period using the observed mean daily temperature data-set and downscaled mean daily temperature data-sets for the individual GCMs (Table 7.4). The greatest range between the GCM outputs was for the budburst occurrence stage, with differences of up to 19 days. Differences in the estimated mean emergence days for the assessed life-cycle stages were no greater than 6 days when the model was run using the observed and ensemble control data-sets. Ensemble control mean estimations were within the GCM ranges accordingly. The 5% and 50% E.Ps recorded an estimated mean value for first generation sexual maturation completion using the observed and ensemble control data-sets. Sexual maturation stage completion for the 50% E.P was based on calculations for 97% (28 years) of the observed data-set and 98% (170 years) of the ensemble control data-set. No first generation sexual maturation stage completion was estimated to occur for the 95% E.P using either data-set. Adult emergence for the 95% E.P was based on calculations for 83% (24 years) of the observed data-set and 90% (156 years) of the ensemble control data-set.

Second generation development for the 5% E.P was estimated to occur when either observed and ensemble control data-sets were used as model inputs. Estimated mean values for second generation larvae emergence and adult emergence were both based on calculations for 14% (4 years) of the observed data-set and 29% (50 years) of the ensemble control data-set. Sexual maturation stage completion for second generation insects was not estimated to occur for any year within the observed data-set but it was estimated to occur on day 355 based on calculations for 3% (6 years) of the ensemble control data-set.

Table 7.4 Estimated mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using observed daily mean temperature data and downscaled daily mean temperature data (from 1st Nov – 31st Oct, 1961 – 1990 for both) for individual GCMs (HadCM3, CCGCM2 and CSIROM2) at Belmullet, Co. Mayo. Ranges for emergence days over time period for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for observed and control (GCM ensemble) means are identified when 100% of years from 1961-1990 do not register development. Differences between mean for ensemble control and mean for observed periods are displayed.

Belmullet Stage	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff
	5% E.P				50% E.P				95% E.P			
Budburst	171	159-178	170	-1	171	159-178	170	-1	171	159-178	170	-1
Larvae Emergence (1st gen)	222	214-222	218	-4	247	239-249	242	-5	284	274-284	278	-6
Adult Emergence (1st gen)	267	259-268	262	-5	296	285-295	291	-5	344 **(83%)**	337-345	341 **(90%)**	-3
Sexual Maturation (1st gen)	291	281-290	286	-5	329 **(97%)**	319-328	325 **(98%)**	-4				
Larvae Emergence (2nd gen)	289 **(14%)**	283-291	287 **(29%)**	-2								
Adult Emergence (2nd gen)	333 **(14%)**	330-339	335 **(29%)**	+2								
Sexual Maturation (2nd gen)		350-357	355 **(3%)**									

Ensemble mean values for assessed stage emergence for future time periods were compared to ensemble mean values describing the control baseline period (Table 7.5). All ensemble estimations across all stages, E.Ps and time-frames were within their corresponding GCM ranges. The ranges between the individual GCM mean outputs for the budburst occurrence stage were 18 days for the 2020s, 14 days for the 2050s and 20 days for the 2080s. The greatest ranges between the GCM outputs for the different life-cycle stages were 21 days (1st generation adult emergence 95% E.P) for the 2020s, 18 days (1st generation adult emergence 95% E.P) for the 2050s and 24 days (1st generation sexual maturation 95% E.P and 2nd generation sexual maturation 5% E.P) for the 2080s. The differences between ensemble control estimations and future time period estimations for all phenology/voltinism model stages became greater for the latter future periods (Table 7.6). A successive advancement of all stages was illustrated across the future time periods (Figure 7.2). These differences ranged from 5-19 days for the 2020s, 13-32 days for the 2050s and 21-44 days for the 2080s.

Table 7.5 Estimated ensemble mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using downscaled daily mean temperature data (from 1st Nov – 31st Oct 31) for future time periods (2020s, 2050s and 2080s) at Belmullet, Co. Mayo. Ranges for emergence days over future time periods for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for future means (GCM ensemble) are identified when 100% of years across each future time period do not register development.

Belmullet Stage	GCM ranges	Ens mean	GCM ranges	Ens mean	GCM ranges	Ens mean
2020	**5% E.P**		**50% E.P**		**95% E.P**	
Budburst	155-173	164	155-173	164	155-173	164
Larvae Emergence (1st gen)	206-213	210	230-236	234	262-272	268
Adult Emergence (1st gen)	248-254	253	273-283	279	311-332	322
Sexual Maturation (1st gen)	268-279	274	297-315	307	349-357	353 **(19%)**
Larvae Emergence (2nd gen)	277-285	282 **(77%)**	307-310	308 **(2%)**		
Adult Emergence (2nd gen)	315-327	321 **(77%)**	355	355 **(1%)**		
Sexual Maturation (2nd gen)	335-350	346 **(53%)**				
2050						
Budburst	151-165	155	151-165	155	151-165	155
Larvae Emergence (1st gen)	199-207	204	221-230	227	254-263	260
Adult Emergence (1st gen)	240-249	245	264-274	270	299-317	309
Sexual Maturation (1st gen)	259-269	265	286-302	295	338-343	341 **(65%)**
Larvae Emergence (2nd gen)	269-277	274 **(92%)**	300-310	303 **(13%)**		
Adult Emergence (2nd gen)	303-315	310 **(92%)**	342-358	350 **(12%)**		
Sexual Maturation (2nd gen)	324-338	331 **(84%)**	361	361 **(1%)**		
2080						
Budburst	142-162	148	142-162	148	142-162	148
Larvae Emergence (1st gen)	193-200	196	216-224	220	248-257	252
Adult Emergence (1st gen)	235-243	238	257-267	261	290-305	297
Sexual Maturation (1st gen)	253-262	257	278-290	284	319-343	329 **(93%)**
Larvae Emergence (2st gen)	262-272	266	294-306	299 **(43%)**		
Adult Emergence (2st gen)	292-308	300	332-351	342 **(43%)**		
Sexual Maturation (2st gen)	309-333	319 **(99%)**	354-359	356 **(9%)**		

A greater percentage of years estimated second generation life-cycle stage completion for the 5% E.P during the future time periods as first generation sexual maturation stage was completed earlier than CDL at this specific station – day-length was estimated to become less than 14.92 hrs on day 284 at Belmullet. The percentage of years that were used to estimate the ensemble mean for second generation larvae emergence and adult emergence increased across the future time periods from 29% (50 years) for the control period to 77%

(138 years) for the 2020s, 92% (165 years) for the 2050s and 100% (180 years) for the 2080s. The percentage of years that were used to estimate the ensemble mean for second generation sexual maturation stage completion increased across the future time periods from 3% (6 years) for the control period to 53% (96 years) for the 2020s, 84% (151 years) for the 2050s and 99% (179 years) for the 2080s.

Table 7.6 Relative differences between ensemble means for future time periods and control period, for budburst days and emergence days, for life-cycle stages and emergence proportions (5% E.P, 50% E.P and 95% E.P) at Belmullet, Co. Mayo.

Belmullet Stage	2020	2050	2080	2020	2050	2080	2020	2050	2080
		5% E.P			50% E.P			95% E.P	
Budburst	-6	-15	-22	-6	-15	-22	-6	-15	-22
Larvae Emergence (1st gen)	-8	-14	-22	-8	-15	-22	-10	-18	-26
Adult Emergence (1st gen)	-9	-17	-24	-12	-21	-30	-19	-32	-44
Sexual Maturation (1st gen)	-12	-21	-29	-18	-30	-41			
Larvae Emergence (2nd gen)	-5	-13	-21						
Adult Emergence (2nd gen)	-14	-25	-35						
Sexual Maturation (2nd gen)	-9	-24	-36						

A greater percentage of years estimated second generation life-cycle stage completion for the 50% emerging insect proportion during the future time periods. This was despite the ensemble mean values for first generation sexual maturation estimated to occur after CDL for the 2020s, the 2050s and the 2080s. The percentage of years that were used to estimate ensemble means for second generation larvae emergence and adult emergence increased across the future time periods from no development for the control period to 2% (3 years) and 1% (1 years) for the 2020s respectively, 13% (24 years) and 12% (21 years) for the 2050s respectively, and 43% (77 years) for the 2080s. Sexual maturation stage completion was estimated for 9% (13 years) by the 2080s also. The percentage of years that were used to estimate the ensemble mean value for first generation sexual maturation stage competition for the 95% E.P increased from zero for the control period to 93% (167 years) for the 2080s. No second generation development was estimated to occur for this E.P however.

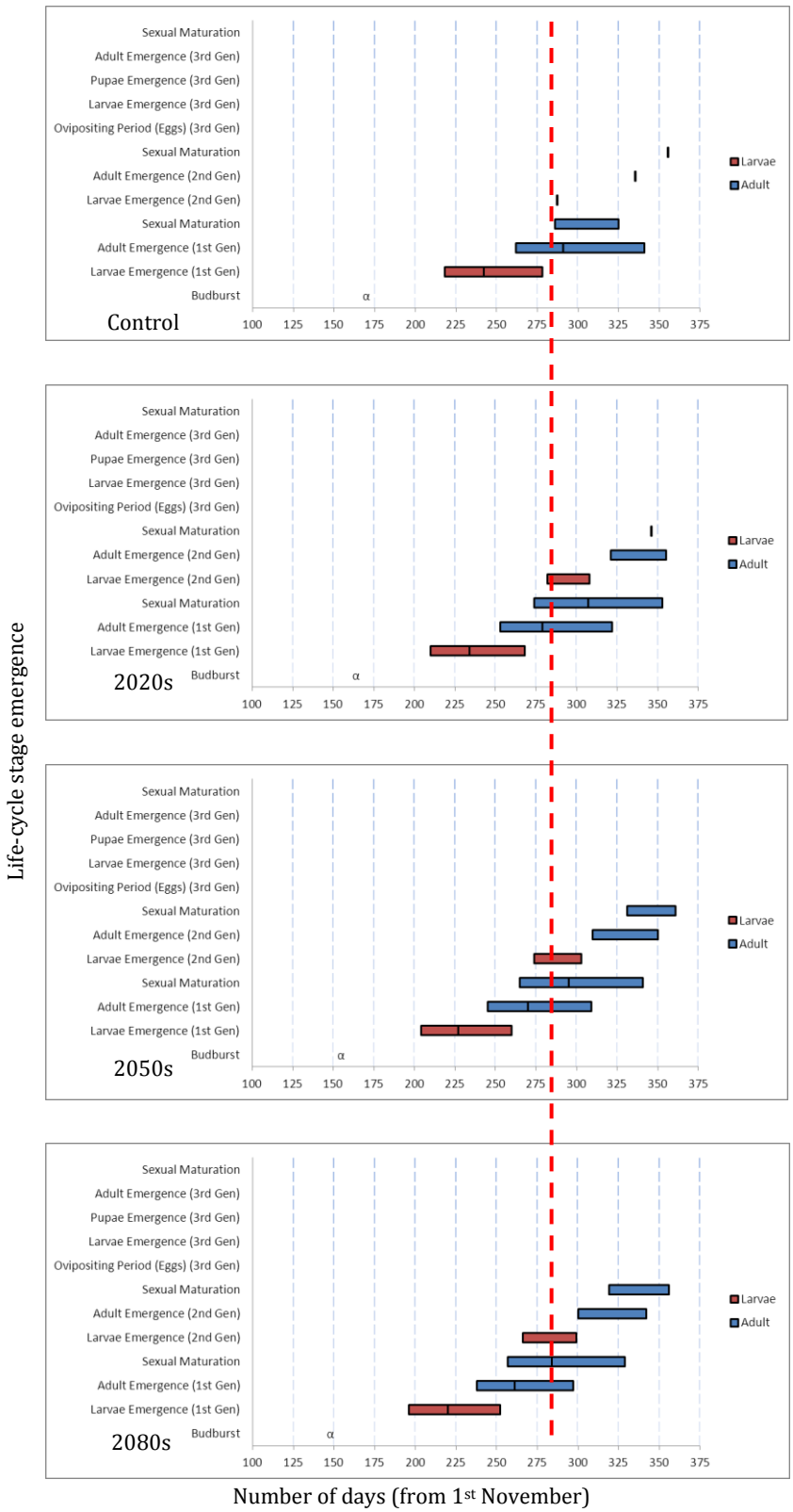


Figure 7.2 Changes in ensemble means for budburst day (denoted as α) and emergence days for life-cycle stage emergence proportions (5% E.P expressed as first vertical black line at beginning of stacked bars, 50% E.P expressed as second vertical black line in middle of stacked bars and 95% E.P expressed as third vertical black line at end of stacked bars) at Belmullet, Co. Mayo across control and future time periods (2020s, 2050s and 2080s) with dashed red line representing CDL occurrence at this specific station.

7.2.1.3 Kilkenny (Midlands)

The phenology/voltinism model outputs for predicted mean budburst occurrence day and estimated mean emergence days for the assessed life-cycle stages proportions were calculated for the baseline period using the observed mean daily temperature data-set and downscaled mean daily temperature data-sets for the individual GCMs (Table 7.7). The greatest range between the GCM outputs was for the budburst occurrence stage and first generation adult emergence 95% E.P, with differences of up to 22 days. Differences in the estimated mean emergence days for the assessed life-cycle stages were no greater than 9 days when the model was run using the observed and ensemble control data-sets. Ensemble control mean estimations were within the GCM ranges accordingly. All E.Ps recorded an estimated mean value for first generation sexual maturation stage completion using the ensemble data-set. Only the 5% and 50% E.Ps recorded an estimated mean value for first generation sexual maturation completion using the observed data-set however. Sexual maturation stage completion for the 50% E.P was based on calculations for 97% (28 years) of the observed data-set and 99% (172 years) of the ensemble control data-set. Adult emergence for the 95% E.P was based on calculations for 90% (26 years) of the observed data-set and 97% (168 years) of the ensemble control data-set. Sexual maturation stage completion for the 95% E.P was not estimated to occur for any year within the observed data-set but it was estimated to occur on day 349 based on calculations for 3% (5 years) of the ensemble control data-set.

Second generation development for the 5% emerging insect proportion was estimated to happen when either observed and ensemble control data-sets were used as model inputs. Estimated mean values for second generation larvae emergence and adult emergence were both based on calculations for 41% (12 years) of the observed data-set and 56% (98 years) of the ensemble control data-set. Sexual maturation stage completion for second generation insects was estimated to occur on day 354 based on calculations for 17% (5 years) of the observed data set and day 345 based on calculations for 18% (32 years) of the ensemble control data-set. Second generation development for the 50% emerging insect proportion was not estimated to occur for any year within the observed data-set but second generation larvae emergence and adult emergence were estimated to occur on day 299 based on calculations for 1% (1 year) and day 357 based on calculations for 1% (1 year) of the ensemble control data-set respectively.

Table 7.7 Estimated mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using observed daily mean temperature data and downscaled daily mean temperature data (from 1st Nov – 31st Oct, 1961 – 1990 for both) for individual GCMs (HadCM3, CCGCM2 and CSIROM2) at Kilkenny, Co. Kilkenny. Ranges for emergence days over time period for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for observed and control (GCM ensemble) means are identified when 100% of years from 1961-1990 do not register development. Differences between mean for ensemble control and mean for observed periods are displayed.

Kilkenny Stage	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff
	5% E.P				50% E.P				95% E.P			
Budburst	165	154-176	167	+2	165	154-176	167	+2	165	154-176	167	+2
Larvae Emergence (1st gen)	219	208-219	215	-4	242	232-246	238	-4	276	263-277	271	-5
Adult Emergence (1st gen)	261	250-264	256	-5	286	273-287	282	-4	331 **(90%)**	311-333	328 **(97%)**	-3
Sexual Maturation (1st gen)	282	268-282	277	-5	317 **(97%)**	297-317	312 **(99%)**	-5		326-361	349 **(3%)**	
Larvae Emergence (2nd gen)	284 **(41%)**	276-285	280 **(56%)**	-4		299	299 **(1%)**					
Adult Emergence (2nd gen)	324 **(41%)**	317-331	323 **(56%)**	-1		357	357 **(1%)**					
Sexual Maturation (2nd gen)	354 **(17%)**	340-351	345 **(18%)**	-9								

Ensemble mean values for assessed stage emergence for future time periods were compared to ensemble mean values describing the control baseline period (Table 7.8). All ensemble estimations across all stages, E.Ps and time-frames were within their respective GCM ranges. The ranges between the individual GCM mean outputs for the budburst occurrence stage were 14 days for the 2020s, 12 days for the 2050s and 22 days for the 2080s. The greatest ranges between the individual GCM mean outputs for the different life-cycle stages were 28 days (1st generation adult emergence 95% E.P and 2nd generation sexual maturation 5% E.P) for the 2020s, 26 days (2nd generation sexual maturation 5% E.P) for the 2050s and 29 days (1st generation sexual maturation 95% E.P) for the 2080s. The differences between the ensemble control estimations and future time period estimations for all phenology/voltinism model stages became greater for the latter future periods (Table 7.9). A successive advancement of all stages was illustrated across the future time periods (Figure 7.3). These differences ranged from 0-20 days for the 2020s, 4-32 days for the 2050s and 11-43 days for the 2080s.

Table 7.8 Estimated ensemble mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using downscaled daily mean temperature data (from 1st Nov – 31st Oct) for future time periods (2020s, 2050s and 2080s) at Kilkenny, Co. Kilkenny. Ranges for emergence days over future time periods for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for future means (GCM ensemble) are identified when 100% of years across each future time period do not register development.

Kilkenny Stage	GCM ranges	Ens mean	GCM ranges	Ens mean	GCM ranges	Ens mean
2020	**5% E.P**		**50% E.P**		**95% E.P**	
Budburst	149-163	157	149-163	157	149-163	157
Larvae Emergence (1st gen)	200-210	207	221-231	229	250-265	260
Adult Emergence (1st gen)	238-249	246	260-275	270	292-320	308
Sexual Maturation (1st gen)	255-271	265	280-303	294	329-347	338 **(57%)**
Larvae Emergence (2nd gen)	264-276	272 **(84%)**	295-309	299 **(12%)**		
Adult Emergence (2nd gen)	295-314	308 **(84%)**	340-354	348 **(11%)**		
Sexual Maturation (2nd gen)	315-343	328 **(73%)**				
2050						
Budburst	143-155	146	143-155	146	143-155	146
Larvae Emergence (1st gen)	193-205	201	213-227	222	243-257	252
Adult Emergence (1st gen)	230-244	240	252-266	261	283-305	296
Sexual Maturation (1st gen)	248-261	257	271-290	283	311-334	324 **(83%)**
Larvae Emergence (2nd gen)	257-268	265 **(94%)**	292-303	295 **(44%)**		
Adult Emergence (2nd gen)	286-305	297 **(94%)**	330-344	336 **(43%)**		
Sexual Maturation (2nd gen)	301-327	316 **(92%)**	350-364	355 **(12%)**		
2080						
Budburst	128-150	137	128-150	137	128-150	137
Larvae Emergence (1st gen)	187-197	192	208-220	215	239-251	245
Adult Emergence (1st gen)	225-238	232	247-260	254	277-293	285
Sexual Maturation (1st gen)	243-256	249	266-281	273	301-330	313 **(99%)**
Larvae Emergence (2st gen)	251-265	257	284-296	288 **(66%)**		
Adult Emergence (2st gen)	279-296	287	320-335	324 **(66%)**		
Sexual Maturation (2st gen)	292-317	303	342-356	347 **(46%)**		
Larvae Emergence (3rd gen)	287	287 **(2%)**				
Adult Emergence (3rd gen)	316	316 **(2%)**				
Sexual Maturation (3rd gen)	335	335 **(2%)**				

A greater percentage of years estimated second generation life-cycle stage completion for the 5% E.P during the future time periods as first generation sexual maturation stage was completed earlier than CDL at this specific station – day-length was

estimated to become less than 14.92 hrs on day 281 at Kilkenny. The percentage of years that were used to estimate the ensemble mean for second generation larvae emergence and adult emergence increased across the future time periods from 56% (98 years) for the control period to 84% (152 years) for the 2020s, 94% (170 years) for the 2050s and 100% (180 years) for the 2080s. The percentage of years that were used to estimate the ensemble mean for second generation sexual maturation stage completion increased across the future time periods from 18% (32 years) for the control period to 73% (131 years) for the 2020s, 92% (165 years) for the 2050s and 100% (180 years) for the 2080s. Third generation life-cycle stage completion for the 5% E.P was estimated for a small percentage of years during the 2080s also – 2% (4 years) estimated larvae emergence, adult emergence and sexual maturation stage completion.

Table 7.9 Relative differences between ensemble means for future time periods and control period, for budburst days and emergence days, for life-cycle stages and emergence proportions (5% E.P, 50% E.P and 95% E.P) at Kilkenny, Co. Kilkenny.

Kilkenny, Co. Kilkenny Stage	2020	2050	2080	2020	2050	2080	2020	2050	2080
	5% E.P			50% E.P			95% E.P		
Budburst	-10	-21	-30	-10	-21	-30	-10	-21	-30
Larvae Emergence (1st gen)	-8	-14	-23	-9	-16	-23	-11	-19	-26
Adult Emergence (1st gen)	-10	-16	-24	-12	-21	-28	-20	-32	-43
Sexual Maturation (1st gen)	-12	-20	-28	-18	-29	-39	-11	-25	-36
Larvae Emergence (2nd gen)	-8	-15	-23	0	-4	-11			
Adult Emergence (2nd gen)	-15	-26	-36	-9	-21	-33			
Sexual Maturation (2nd gen)	-17	-29	-42						

A greater percentage of years estimated second generation life-cycle stage completion for the 50% E.P during the future time periods. This was despite the ensemble mean values for first generation sexual maturation estimated to occur after CDL for the 2020s and the 2050s. The percentage of years that were used to estimate ensemble means for second generation larvae emergence and adult emergence increased across the future time periods from 1% (1 year) for the control period to 12% (22 years) and 11% (19 years) for the 2020s respectively, 44% (79 years) and 43% (78 years) for the 2050s respectively and 66% (119 years) for the 2080s. Sexual maturation stage completion was estimated for 46% (82 years) by the 2080s also. The percentage of years that were used to estimate the ensemble mean value for first generation sexual maturation stage competition for the 95% E.P increased from 3% (5 years) for the control period to 99% (179 years) for the 2080s. No second generation development was estimated to occur for this E.P however.

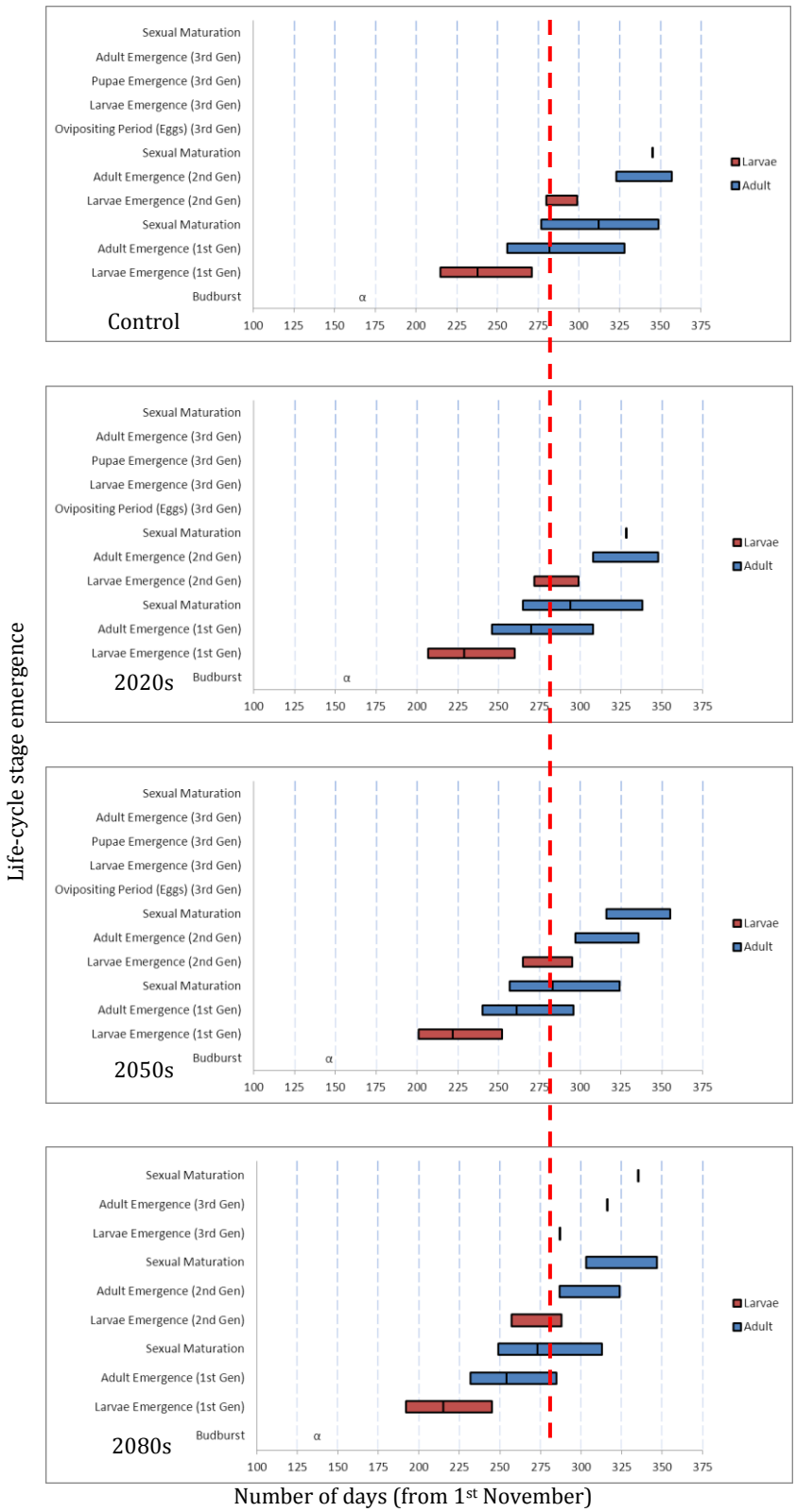


Figure 7.3 Changes in ensemble means for budburst day (denoted as α) and emergence days for life-cycle stage emergence proportions (5% E.P expressed as first vertical black line at beginning of stacked bars, 50% E.P expressed as second vertical black line in middle of stacked bars and 95% E.P expressed as third vertical black line at end of stacked bars) at Kilkenny. Co. Kilkenny across control and future time periods (2020s, 2050s and 2080s) with dashed red line representing CDL occurrence at this specific station.

7.2.1.4 Casement Aerodrome (East)

The phenology/voltinism model outputs for predicted mean budburst occurrence day and estimated mean emergence days for the life-cycle stages proportions were calculated for the baseline period using the observed mean daily temperature data-set and downscaled mean daily temperature data-sets for the individual GCMs (Table 7.10). The greatest range between the GCM outputs was for the budburst occurrence stage, with differences of up to 22 days. Differences in the estimated mean emergence days for the assessed life-cycle stages were no greater than 9 days when the model was run using the observed and ensemble control data-sets. Ensemble control mean estimations were within the GCM ranges accordingly. All E.Ps recorded an estimated mean value for first generation sexual maturation stage completion using the ensemble data-set. Only the 5% and 50% E.Ps recorded an estimated mean value for first generation sexual maturation completion using the observed data-set however. Sexual maturation stage completion for the 50% E.P was based on calculations for 93% (27 years) of the observed data-set and 99% (173 years) of the ensemble control data-set. Adult emergence for the 95% E.P was based on calculations for 86% (25 years) of the observed data-set and 91% (159 years) of the ensemble control data-set. Sexual maturation stage completion for the 95% E.P was not estimated to occur for any year within the observed data-set but it was estimated to occur on day 346 based on calculations for 1% (2 years) of the ensemble control data-set.

Second generation development for the 5% E.P was estimated to occur when both observed and ensemble control data-sets were used as model inputs. Estimated mean values for second generation larvae emergence and adult emergence were both based on calculations for 34% (10 years) of the observed data-set and 45% (79 years) of the ensemble control data-set. Sexual maturation stage completion for second generation insects was estimated to occur on day 358 based on calculations for 7% (2 years) of the observed data set and day 349 based on calculations for 13% (23 years) of the ensemble control data-set.

Table 7.10 Estimated mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using observed daily mean temperature data and downscaled daily mean temperature data (from 1st Nov – 31st Oct, 1961 – 1990 for both) for individual GCMs (HadCM3, CCGCM2 and CSIROM2) at Casement Aerodrome, Co. Dublin. Ranges for emergence days over time period for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for observed and control (GCM ensemble) means are identified when 100% of years from 1961-1990 do not register development. Differences between mean for ensemble control and mean for observed periods are displayed.

Casement Aerodrome Stage	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff
	5% E.P				50% E.P				95% E.P			
Budburst	168	157-179	170	+2	168	157-179	170	+2	168	157-179	170	+2
Larvae Emergence (1st gen)	222	211-222	218	-4	245	236-248	241	-4	279	266-280	274	-5
Adult Emergence (1st gen)	264	253-266	259	-5	289	277-289	285	-4	335 **(86%)**	319-338	332 **(91%)**	-3
Sexual Maturation (1st gen)	285	271-285	280	-5	320 **(93%)**	303-323	317 **(99%)**	-3		344-348	346 **(1%)**	
Larvae Emergence (2nd gen)	287 **(34%)**	277-286	282 **(45%)**	-5								
Adult Emergence (2nd gen)	330 **(34%)**	321-332	326 **(45%)**	-4								
Sexual Maturation (2nd gen)	358 **(7%)**	344-352	349 **(13%)**	-9								

Ensemble mean values for assessed stage emergence for future time periods were compared to ensemble mean values describing the control baseline period (Table 7.11). All ensemble estimations across all stages, E.Ps and time-frames were within their corresponding GCM ranges. The ranges between the individual GCM mean outputs for the budburst occurrence stage were 17 days for the 2020s, 14 days for the 2050s and 22 days for the 2080s. The greatest ranges between the individual GCM mean outputs for the different life-cycle stages were 28 days (1st generation adult emergence 95% E.P) for the 2020s, 22 days (1st generation adult emergence 95% E.P and 2nd generation sexual maturation 5% E.P) for the 2050s and 27 days (1st generation sexual maturation 95% E.P) for the 2080s. The differences between ensemble control estimations and future time period estimations for all phenology/voltinism model stages became greater for the latter future periods (Table 7.12). A successive advancement of all stages was illustrated across the future time periods (Figure 7.4). These differences ranged from 4-19 days for the 2020s, 14-32 days for the 2050s and 21-43 days for the 2080s.

Table 7.11 Estimated ensemble mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using downscaled daily mean temperature data (from 1st Nov – 31st Oct) for future time periods (2020s, 2050s and 2080s) at Casement Aerodrome, Co. Dublin. Ranges for emergence days over future time periods for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for future means (GCM ensemble) are identified when 100% of years across each future time period do not register development.

Casement Aerodrome Stage	GCM ranges	Ens mean	GCM ranges	Ens mean	GCM ranges	Ens mean
2020	**5% E.P**		**50% E.P**		**95% E.P**	
Budburst	151-168	160	151-168	160	151-168	160
Larvae Emergence (1st gen)	203-212	210	225-234	232	254-268	263
Adult Emergence (1st gen)	242-252	249	264-279	273	297-325	313
Sexual Maturation (1st gen)	259-274	268	285-308	299	336-351	342 **(46%)**
Larvae Emergence (2nd gen)	268-280	276 **(82%)**	300-311	302 **(8%)**		
Adult Emergence (2nd gen)	301-320	312 **(82%)**	348-362	354 **(6%)**		
Sexual Maturation (2nd gen)	324-340	334 **(67%)**				
2050						
Budburst	144-158	148	144-158	148	144-158	148
Larvae Emergence (1st gen)	196-207	203	217-230	225	247-260	255
Adult Emergence (1st gen)	234-247	242	256-269	265	287-309	300
Sexual Maturation (1st gen)	251-264	260	276-294	287	318-337	328 **(77%)**
Larvae Emergence (2nd gen)	260-272	268 **(93%)**	294-305	298 **(35%)**		
Adult Emergence (2nd gen)	290-308	301 **(93%)**	333-348	341 **(34%)**		
Sexual Maturation (2nd gen)	307-329	320 **(89%)**	349-362	352 **(4%)**		
2080						
Budburst	131-153	140	131-153	140	131-153	140
Larvae Emergence (1st gen)	192-200	195	212-223	218	242-254	248
Adult Emergence (1st gen)	230-240	235	251-263	258	281-297	289
Sexual Maturation (1st gen)	247-258	252	270-284	277	307-334	318 **(99%)**
Larvae Emergence (2st gen)	255-267	261	287-300	292 **(58%)**		
Adult Emergence (2st gen)	284-300	291	324-340	329 **(58%)**		
Sexual Maturation (2st gen)	298-321	308 **(99%)**	344-356	349 **(30%)**		
Larvae Emergence (3rd gen)	289	289 **(1%)**				
Adult Emergence (3rd gen)	322	322 **(1%)**				
Sexual Maturation (3rd gen)	339	339 **(1%)**				

A greater percentage of years estimated second generation life-cycle stage completion for the 5% E.P during the future time periods as first generation sexual maturation stage was completed earlier than CDL at this specific station – day-length was

estimated to become less than 14.92 hrs on day 282 at Casement Aerodrome. The percentage of years that were used to estimate the ensemble mean for second generation larvae emergence and adult emergence increased across the future time periods from 45% (79 years) for the control period to 82% (148 years) for the 2020s, 93% (167 years) for the 2050s and 100% (180 years) for the 2080s. The percentage of years that were used to estimate the ensemble mean for second generation sexual maturation stage completion increased across the future time periods from 13% (23 years) for the control period to 67% (121 years) for the 2020s, 89% (160 years) for the 2050s and 99% (179 years) for the 2080s. Third generation life-cycle stage completion for the 5% E.P was estimated for a small percentage of years during the 2080s also; 1% (1 year) estimated larvae emergence, adult emergence and sexual maturation stage completion.

A greater percentage of years estimated second generation life-cycle stage completion for the 50% E.P during the future time periods. This was despite the ensemble mean values for first generation sexual maturation estimated to occur after CDL for the 2020s and the 2050s. The percentage of years that were used to estimate ensemble means for second generation larvae emergence and adult emergence increased across the future time periods from no development for the control period to 8% (14 years) and 6% (11 years) for the 2020s respectively, 35% (63 years) and 34% (62 years) for the 2050s respectively, and 58% (105 years) for the 2080s. Sexual maturation stage completion was estimated for 30% (54 years) by the 2080s also. The percentage of years that were used to estimate the ensemble mean value for first generation sexual maturation stage competition for the 95% E.P increased from 1% (2 years) for the control period to 99% (178 years) for the 2080s. No second generation development was estimated to occur for this E.P however.

Table 7.12 Relative differences between ensemble means for future time periods and control period, for budburst days and emergence days, for life-cycle stages and emergence proportions (5% E.P, 50% E.P and 95% E.P) at Casement Aerodrome, Co. Dublin.

Casement Aerodrome Stage	2020	2050	2080	2020	2050	2080	2020	2050	2080
	5% E.P			50% E.P			95% E.P		
Budburst	-10	-22	-30	-10	-22	-30	-10	-22	-30
Larvae Emergence (1st gen)	-8	-15	-23	-9	-16	-23	-11	-19	-26
Adult Emergence (1st gen)	-10	-17	-24	-12	-20	-28	-19	-32	-43
Sexual Maturation (1st gen)	-12	-20	-28	-18	-30	-40	-4	-18	-28
Larvae Emergence (2nd gen)	-6	-14	-21						
Adult Emergence (2nd gen)	-14	-25	-35						
Sexual Maturation (2nd gen)	-15	-29	-41						

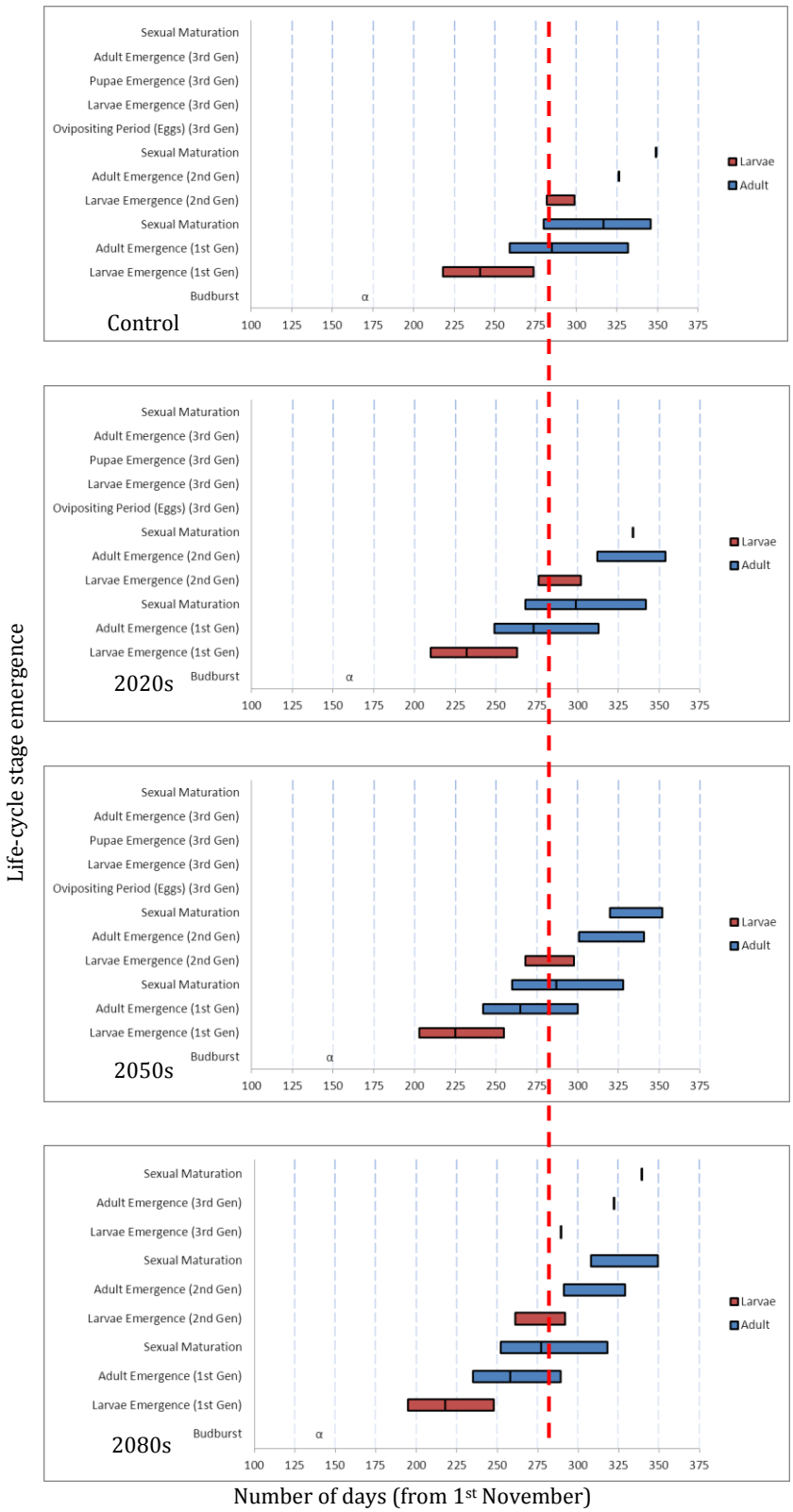


Figure 7.4 Changes in ensemble means for budburst day (denoted as α) and emergence days for life-cycle stage emergence proportions (5% E.P expressed as first vertical black line at beginning of stacked bars, 50% E.P expressed as second vertical black line in middle of stacked bars and 95% E.P expressed as third vertical black line at end of stacked bars) at Casement Aerodrome, Co. Dublin across control and future time periods (2020s, 2050s and 2080s) with dashed red line representing CDL occurrence at this specific station.

7.2.1.5 Malin Head (North)

The phenology/voltinism model outputs for predicted mean budburst occurrence day and estimated mean emergence days for the life-cycle stages proportions were calculated for the baseline period using the observed mean daily temperature data-set and downscaled mean daily temperature data-sets for the individual GCMs (Table 7.13). The greatest range between the GCM outputs was for the budburst occurrence stage and second generation adult emergence 5% E.P, with differences of up to 22 days. Differences in the estimated mean emergence days for the assessed life-cycle stages were no greater than 9 days when the model was run using the observed and ensemble control data-sets. Ensemble control mean estimations were within the GCM ranges accordingly. The 5% and 50% E.Ps recorded an estimated mean value for first generation sexual maturation completion using the observed control and ensemble data-sets. Sexual maturation stage completion for the 50% E.P was based on calculations for 90% (26 years) of the observed data-set and 89% (155 years) of the ensemble control data-set. No first generation sexual maturation stage completion was estimated to occur for the 95% E.P using either data-set. Adult emergence for the 95% E.P was based on calculations for 62% (18 years) of the observed data-set and 63% (109 years) of the ensemble control data-set.

Second generation development for the 5% E.P was estimated to transpire when both observed and ensemble control data-sets were used as model inputs. Estimated mean values for second generation larvae emergence and adult emergence were both based on calculations for 7% (2 years) of the observed data-set, and 15% (26 years) and 14% (25 years) of the ensemble control data-set respectively. Sexual maturation stage completion was not estimated to occur using either data-set.

Table 7.13 Estimated mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using observed daily mean temperature data and downscaled daily mean temperature data (from 1st Nov – 31st Oct, 1961 – 1990 for both) for individual GCMs (HadCM3, CCGCM2 and CSIROM2) at Malin Head, Co. Donegal. Ranges for emergence days over time period for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for observed and control (GCM ensemble) means are identified when 100% of years from 1961-1990 do not register development. Differences between mean for ensemble control and mean for observed periods are displayed.

Malin Head Stage	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff	Obs	GCM ranges	Ens control mean	Ens –v- Obs diff
	5% E.P				50% E.P				95% E.P			
Budburst	176	161-181	175	-1	176	166-181	175	-1	176	166-181	175	-1
Larvae Emergence (1st gen)	227	219-229	223	-4	252	245-255	248	-4	289	280-290	285	-4
Adult Emergence (1st gen)	273	265-274	268	-5	302	292-301	298	-4	350 **(62%)**	345-350	348 **(63%)**	-2
Sexual Maturation (1st gen)	297	287-297	294	-3	338 **(90%)**	332-339	335 **(89%)**	-3				
Larvae Emergence (2nd gen)	296 **(7%)**	280-294	292 **(15%)**	-4								
Adult Emergence (2nd gen)	350 **(7%)**	325-347	341 **(14%)**	-9								

Ensemble mean values for assessed stage emergence for future time periods were compared to ensemble mean values describing the control baseline period (Table 7.14). All ensemble estimations across all stages, E.Ps and time-frames were within their respective GCM ranges. The ranges between the GCM outputs for the budburst occurrence stage were 17 days for the 2020s, 16 days for the 2050s and 23 days for the 2080s. The greatest ranges between the GCM outputs for the different life-cycle stages were 17 days (1st generation sexual maturation 50% E.P) for the 2020s, 18 days (1st generation adult emergence 95% E.P) for the 2050s and 23 days (2nd generation sexual maturation 5% E.P and 2nd generation adult emergence 50% E.P) for the 2080s. The differences between ensemble control estimations and future time period estimations for all phenology/voltinism model stages became greater for the latter future periods (Table 7.15). A successive advancement of all stages was illustrated across the future time periods (Figure 7.5). These differences ranged from 5-18 days for the 2020s, 12-30 days for the 2050s and 17-41 days for the 2080s.

Table 7.14 Estimated ensemble mean for budburst days and emergence days for life-cycle stage emergence proportions (5% E.P, 50% E.P and 95% E.P), using downscaled daily mean temperature data (from 1st Nov – 31st Oct) for future time periods (2020s, 2050s and 2080s) at Malin Head, Co. Donegal. Ranges for emergence days over future time periods for GCMs and SRES are shown. Percentage of years recording complete life-cycle stage development for future means (GCM ensemble) are identified when 100% of years across each future time period do not register development.

Malin Head Stage	GCM ranges	Ens mean	GCM ranges	Ens mean	GCM ranges	Ens mean
2020	**5% E.P**		**50% E.P**		**95% E.P**	
Budburst	161-178	168	161-178	168	161-178	168
Larvae Emergence (1st gen)	213-218	216	236-242	240	269-279	275
Adult Emergence (1st gen)	255-261	259	280-290	286	323-339	332
Sexual Maturation (1st gen)	276-286	282	308-325	317 **(99%)**	355-362	357 **(4%)**
Larvae Emergence (2nd gen)	282-290	287 **(58%)**				
Adult Emergence (2nd gen)	325-334	329 **(58%)**				
Sexual Maturation (2nd gen)	346-358	352 **(21%)**				
2050						
Budburst	155-171	160	155-171	160	155-171	16
Larvae Emergence (1st gen)	206-215	211	228-238	234	261-271	267
Adult Emergence (1st gen)	247-256	252	272-282	278	310-328	319
Sexual Maturation (1st gen)	267-277	273	296-312	305	343-352	349 **(39%)**
Larvae Emergence (2nd gen)	277-284	280 **(79%)**	305-314	307 **(3%)**		
Adult Emergence (2nd gen)	314-323	318 **(79%)**	349	349 **(2%)**		
Sexual Maturation (2nd gen)	337-344	341 **(66%)**				
2080						
Budburst	146-169	155	146-169	155	146-169	155
Larvae Emergence (1st gen)	201-208	205	225-232	228	256-265	260
Adult Emergence (1st gen)	243-251	246	265-276	270	299-316	308
Sexual Maturation (1st gen)	261-271	266	287-302	294	332-349	341 **(75%)**
Larvae Emergence (2st gen)	270-280	275 **(98%)**	296-313	303 **(12%)**		
Adult Emergence (2st gen)	303-318	311 **(98%)**	340-363	347 **(12%)**		
Sexual Maturation (2st gen)	321-344	332 **(94%)**	365	365 **(1%)**		

A greater percentage of years estimated second generation life-cycle stage completion for the 5% E.P during the future time periods as first generation sexual maturation stage was completed earlier than CDL at this specific station – day-length was estimated to become less than 14.92 hrs on day 286 at Malin Head. The percentage of years that were used to estimate the ensemble mean for second generation larvae emergence and adult emergence increased across the future time periods from 15% (26 years) and 14%

(25 years) for the control period respectively to 58% (104 years) for the 2020s, 79% (143 years) for the 2050s and 98% (176 years) for the 2080s. The percentage of years that were used to estimate the ensemble mean for second generation sexual maturation stage completion increased across the future time periods from no development for the control period to 21% (38 years) for the 2020s, 66% (118years) for the 2050s and 94% (170 years) for the 2080s.

A greater percentage of years estimated second generation life-cycle stage completion for the 50% E.P during the future time periods. This was despite the ensemble mean values for first generation sexual maturation estimated to occur after CDL for all future time periods. The percentage of years that were used to estimate ensemble means for second generation larvae emergence and adult emergence increased across the future time periods from no development for the control period to 3% (5 years) and 2% (4 years) for the 2050s respectively, and 12% (22 years) for the 2080s. Sexual maturation stage completion was estimated for 1% (1 year) by the 2080s also. The percentage of years that were used to estimate the ensemble mean value for first generation sexual maturation stage competition for the 95% E.P increased from no development for the control period to 75% (135 years) for the 2080s. No second generation development was estimated to occur for this E.P however.

Table 7.15 Relative differences between ensemble means for future time periods and control period, for budburst days and emergence days, for life-cycle stages and emergence proportions (5% E.P, 50% E.P and 95% E.P) at Malin Head, Co. Donegal.

Malin Head Stage	2020	2050	2080	2020	2050	2080	2020	2050	2080
	5% E.P			50% E.P			95% E.P		
Budburst	-7	-15	-20	-7	-15	-20	-7	-15	-20
Larvae Emergence (1st gen)	-7	-12	-18	-8	-14	-20	-10	-18	-25
Adult Emergence (1st gen)	-9	-16	-22	-12	-20	-28	-16	-29	-40
Sexual Maturation (1st gen)	-12	-21	-28	-18	-30	-41			
Larvae Emergence (2nd gen)	-5	-12	-17						
Adult Emergence (2nd gen)	-12	-23	-30						

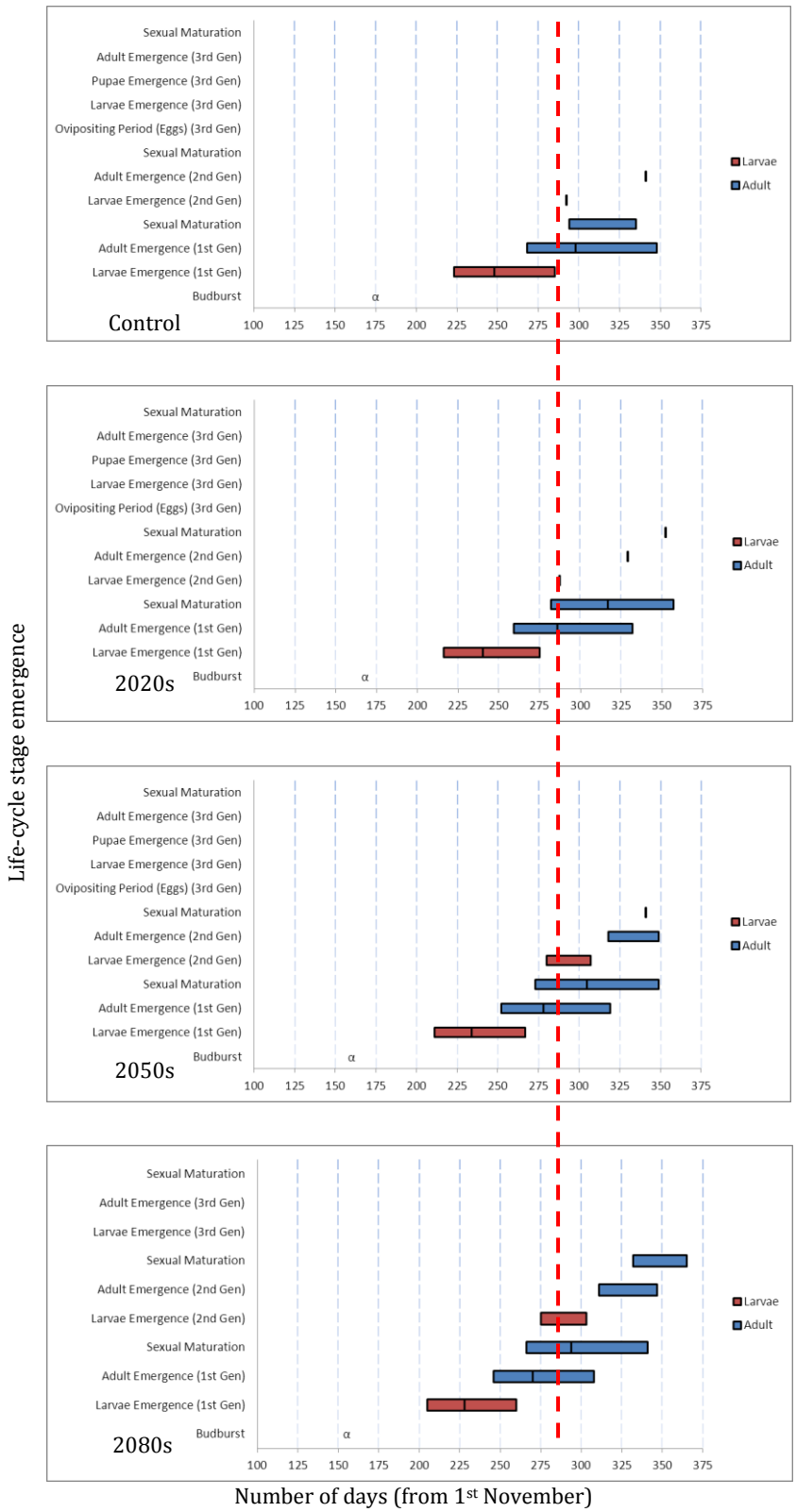


Figure 7.5 Changes in ensemble means for budburst day (denoted as α) and emergence days for life-cycle stage emergence proportions (5% E.P expressed as first vertical black line at beginning of stacked bars, 50% E.P expressed as second vertical black line in middle of stacked bars and 95% E.P expressed as third vertical black line at end of stacked bars) at Malin Head, Co. Donegal across control and future time periods (2020s, 2050s and 2080s) with dashed red line representing CDL occurrence at this specific station.

7.2.2 Spatial Analysis

7.2.2.1 Budburst Occurrence

Model outputs suggested an advancement of budburst at all observed synoptic stations over the three future time periods when compared to budburst day predictions for the control period (Figure 7.6). Overall relative differences from the control period estimations to future time period estimations ranged from 6-30 days. Greater differences were estimated for inland stations Birr and Kilkenny (10 days, 21 days and 30 days for both stations, over 2020s, 2050s and 2080s respectively, and hereafter unless otherwise stated), south-westerly coastal stations Shannon Airport and Valentia Observatory (10 days, 21 days and 30 days for both stations) and the easterly station Casement Aerodrome (10 days, 22 days and 30 days). Predicted differences for budburst occurrence from the control period estimations were smaller for western coastal station Belmullet (6 days, 15 days and 22 days) and northern coastal station Malin Head (7 days, 15 days and 20 days). Smaller differences were estimated for south-easterly coastal station Rosslare and southern coastal station Roche's Point also (7 days, 18 days and 25 days, and 8 days, 18 days and 27 days respectively), particularly for the 2020s and the 2050s.

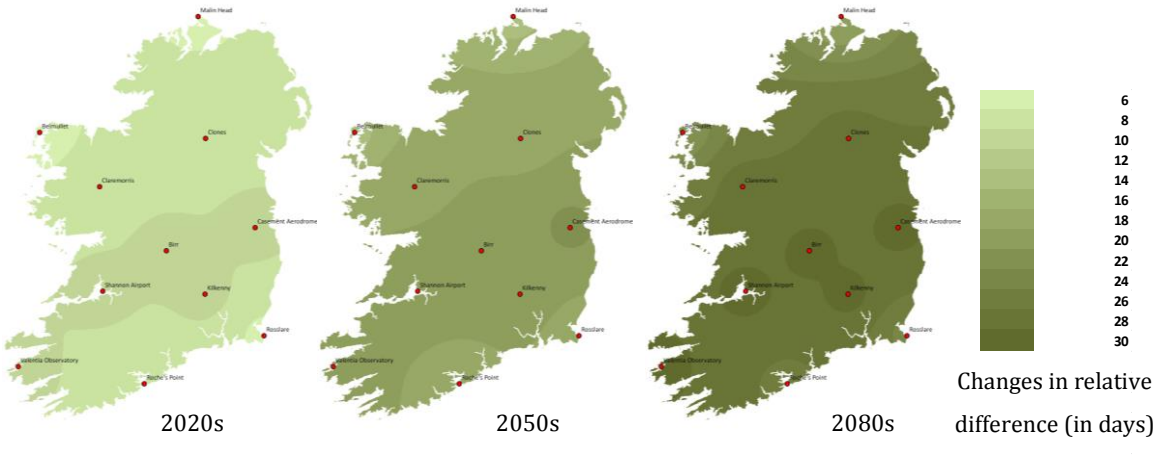


Figure 7.6 Relative differences (in days) between ensemble means for future time periods and control period for budburst at all assessed synoptic stations (red points).

7.2.2.2 Insect Life-Cycle Emergence

Model outputs indicated earlier emergence for all insect life-cycle stages at all observed synoptic stations over the three future time periods when compared to emergence day estimations for the control period (Figure 7.7 – Figure 7.9). Overall relative differences from the control period estimations to future time period estimations ranged from 3-44 days for all E.Ps (7-32 days for 5% E.P, 7-44 days for 50% E.P and 3-44 days for 95% E.P).

7.2.2.3 Larvae Emergence

Model outputs for 5% larvae E.P differed from the control period estimations (7-9 days) for all stations across the 2020s. These differences increased marginally for 50% E.P (7-10 days) and 95% E.P (8-12 days) during the same time period. Differences for coastal stations were slightly lower than inland stations except for Valentia Observatory. Greater increases in the differences from the control period estimations were estimated over the 2050s and 2080s for model outputs relating to 50% larvae E.P and 95% larvae E.P. All coastal stations, expect Valentia Observatory, were estimated to observe marginally less advancement in larvae emergence when compared to centrally located stations.

Estimated differences for the 2050s ranged from 12-18 days for 5% E.P, 12-18 days for 50% E.P and 15-20 days for 95% E.P. Valentia Observatory and Shannon Airport were estimated to experience greater differences for 5% larvae E.P (18 day and 16 days respectively) compared to the smaller differences for Rosslare, Roche's Point and Malin Head (12 days, 13 days and 12 days respectively). Valentia Observatory, Casement Aerodrome and all inland stations were estimated to experience greater differences for 95% larvae E.P (19 days, 19 days and 19-20 days respectively) compared to the smaller difference for Rosslare and Roche's Point (15 days and 16 days respectively).

Estimated differences for the 2080s ranged from 18-28 days for 5% E.P, 19-27 days for 50% E.P and 21-28 days for 95% E.P. Valentia Observatory and Shannon Airport were estimated to experience greater differences for 5% larvae E.P (28 days and 26 days respectively) compared to the smaller differences for Rosslare and Malin Head (20 days and 18 days respectively). Valentia Observatory, Claremorris, Birr and Clones were estimated to experience greater differences for 95% larvae E.P (28 days, 28 days, 27 days and 27 days respectively) compared to the smaller difference for Rosslare and Roche's Point (21 days and 24 days respectively).

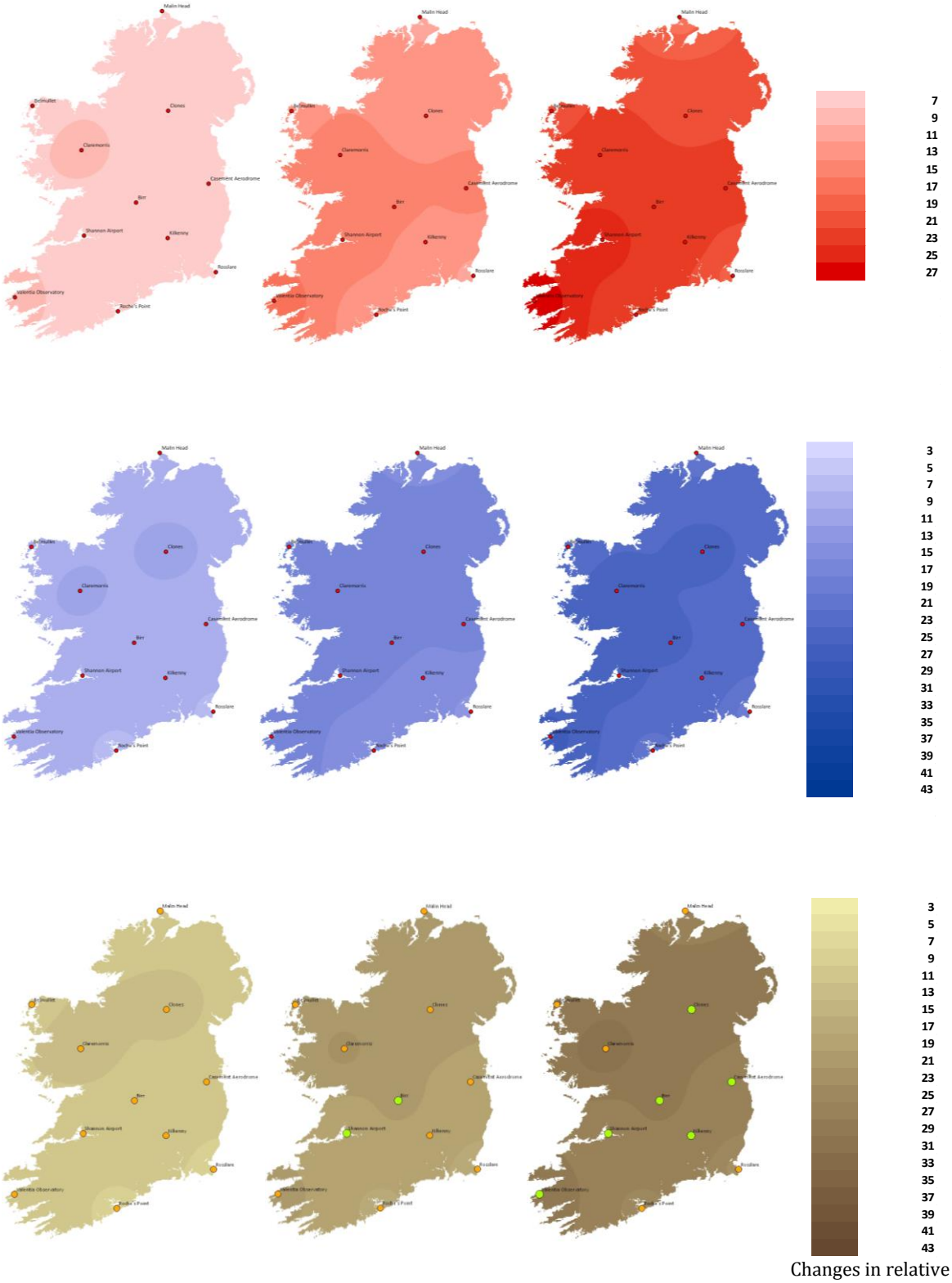


Figure 7.7 Relative differences (in days) between ensemble means for future time periods and control period for emergence days, for 5% larvae E.P (red maps), 5% adult E.P (blue maps) and 5% sexually mature adult E.P (brown maps). Synoptic stations (red points) suggest second generation development (orange points) and third generation development (green points) for a percentage or all years of GCM ensembles relating to future time periods.

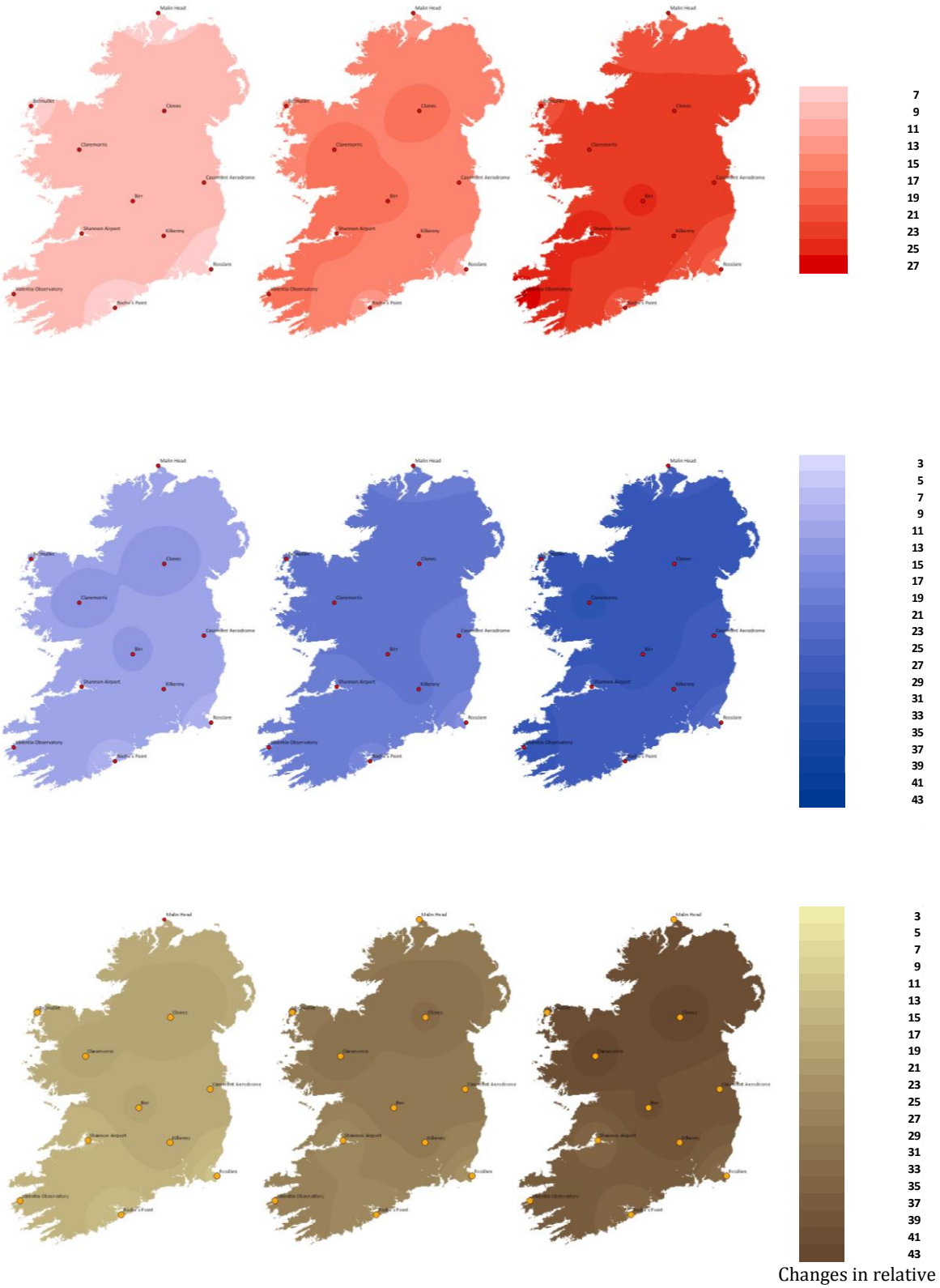


Figure 7.8 Relative differences between ensemble means for future time periods and control period for emergence days, for 50% larvae E.P (red maps), 50% adult E.P (blue maps) and 50% sexually mature adult E.P (brown maps). Synoptic stations (red points) suggest second generation development (orange points) for a percentage or all years of GCM ensembles relating to future time periods.

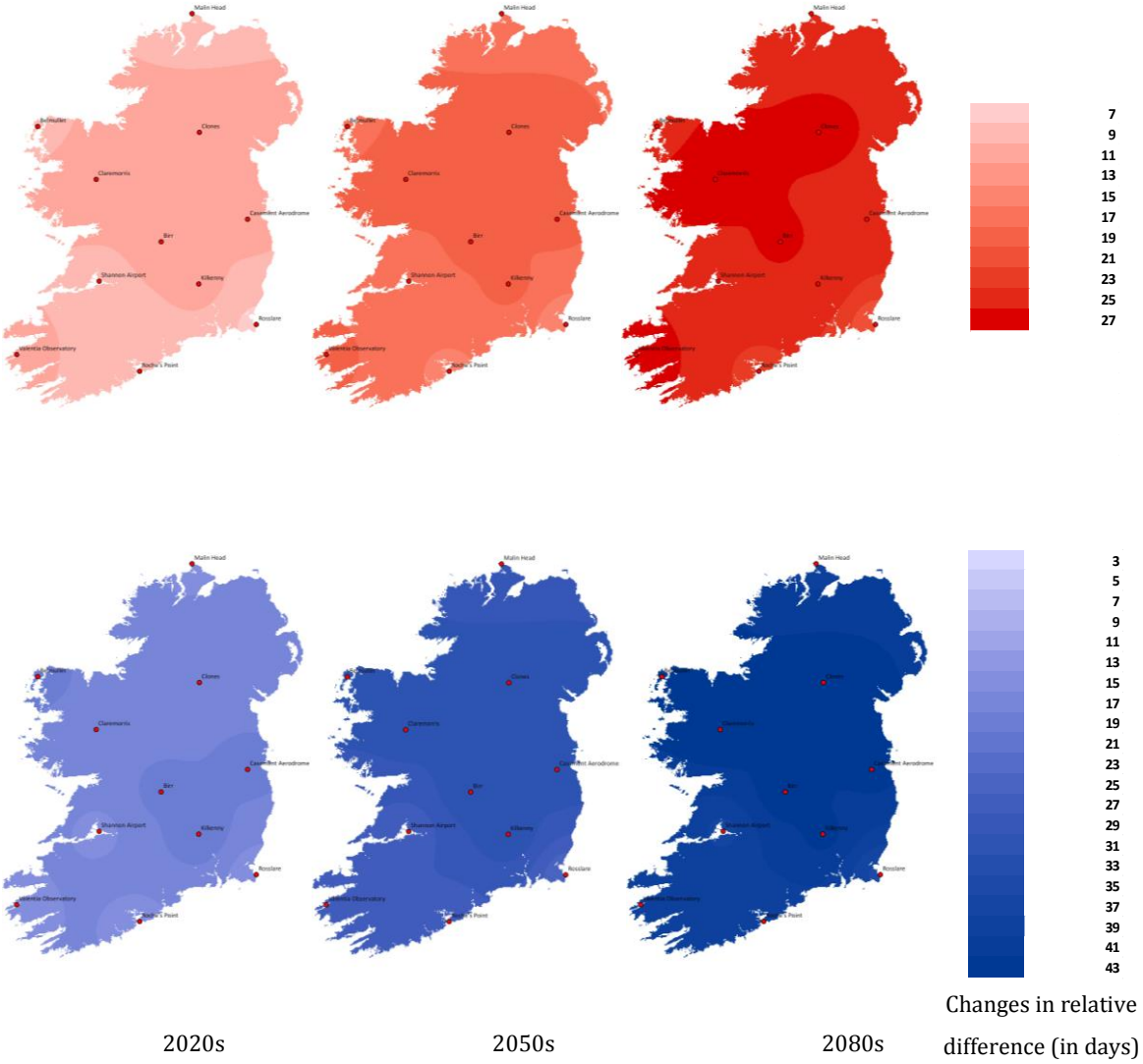


Figure 7.9 Relative differences between ensemble means for future time periods and control period for emergence days, for 95% larvae E.P (red maps) and 95% adult E.P (blue maps) at all assessed synoptic stations (red points).

7.2.2.4 Adult Emergence

Model outputs for 5% adult E.P differed from the control period estimations (8-11 days) for all stations across the 2020s. These differences increased marginally for 50% E.P (9-13 days) and for 95% E.P (15-20 days). A greater advancement for 95% adult E.P was estimated at all inland stations compared to coastal stations, expect Belmullet, during the same period. Greater increases in the differences from the control period estimations were estimated over the 2050s and 2080s for model outputs relating to 50% adult E.P and 95% adult E.P.

Estimated differences for the 2050s E.P ranged from 14-18 days for 5% E.P, 16-22 days for 50% E.P and 25-32 days for 95% E.P. Estimated differences for Rosslare, Roche's Point and Malin Head were smaller compared to other stations for 5% adult E.P (14 days, 15 days and 16 days respectively). Estimated differences for Rosslare and Roche's Point were reduced compared to other stations for 50% adult E.P (16 days and 18 days respectively) also. Greater advancement for 95% adult E.P was estimated for all inland stations (31-32 days) compared to coastal stations (25-29 days), expect Belmullet (32 days).

Estimated differences for the 2080s ranged from 20-27 days for 5% E.P, 23-31 days for 50% E.P and 36-44 days for 95% E.P. Estimated differences for Rosslare, Roche's Point and Malin Head were smaller compared to other stations for 5% E.P (20 days, 22 days and 22 days respectively). Estimated differences for Rosslare and Roche's Point were reduced compared to other stations for 50% E.P (23 days and 27 days respectively) also. Greater advancement for 95% adult E.P was estimated for all inland stations (range: 43-44 days) compared to coastal stations (36-40 days), expect Belmullet (44 days).

7.2.2.5 Sexual Maturation

Model outputs for 5% sexual maturation E.P differed from the control period estimations (9-14 days) for all stations across the 2020s. These differences increased marginally for 50% E.P (13-20 days). Estimated differences for Rosslare and Roche's Point were smaller compared to other stations for 5% E.P (9 days and 10 days respectively). A greater advancement of sexual maturation was estimated for north midland stations Clones and Claremorris (13 and 14 days respectively). Estimated differences for Rosslare and Roche's Point were smaller compared to other stations for 50% E.P (13 days and 14 days respectively) also. Greater advancement of sexual maturation was estimated for inland stations Clones, Claremorris and Birr (20, 19 and 19 days respectively). Greater increases in the differences from the control period estimations were estimated over the 2050s and 2080s for model outputs relating to 50% sexual maturation E.P. North inland stations were estimated to observe marginally greater advancement in sexual maturation stage completion when compared to coastal and other stations for all emerging proportions and future time periods.

Estimated differences ranged from 17-23 days for 5% E.P to 23-33 days for 50% E.P. These differences for Rosslare and Roche's Point were smaller compared to other stations (17 days and 18 days respectively) for 5% E.P. Estimated differences for Rosslare, Roche's Point and Shannon Airport were reduced compared to other stations (23 days, 25

days and 25 days respectively) for 50% E.P also. Greater advancement was suggested for northern inland stations Clones and Claremorris for 5% E.P (22 days and 23 days respectively) and for 50% E.P (33 days and 32 days respectively)

Estimated differences for the 2080s ranged from 24-32days for 5% E.P to 33-44 days for 50% E.P. These differences for Rosslare and Roche's Point were smaller compared to other stations (24 days and 26 days respectively) for 5% E.P. Estimated differences for Rosslare, Roche's Point and Shannon Airport were reduced compared to other stations (33 days, 35 days and 35 days respectively) for 50% E.P also. Greater advancement was suggested for northern inland stations Clones and Claremorris and south-westerly coastal station Valentia Observatory for 5% E.P (30 days, 32 days and 30 days respectively) and Clones and Claremorris for 50% E.P (44 days each).

Model outputs estimated second generation development for 5% E.P for a percentage of the years at all stations during the 2020s – indicated as orange points on the maps (Figure 7.7 – Figure 7.8). Third generation development for 5% E.P was estimated for a percentage of the ensemble years at some stations during the 2050s (Birr and Shannon Airport) – indicated as green points on the maps (Figure 7.7 – Figure 7.8). Valentia Observatory, Shannon Airport, Casement Aerodrome, Birr and Kilkenny were estimated to experience third generation development for 5% E.P for a percentage of the ensemble years during the 2080s. Second generation development was estimated for all stations except Malin Head for 50% E.P for a percentage of the years during the 2020s. Second generation develop was estimated for all stations for the 2050s and 2080s. Second generation development was recorded for a fraction of years by the 2080s at Birr and Shannon Airport for 95% E.P.

7.3 **Discussion**

The minor differences between the observed period mean emergence values and the control period ensemble mean emergence values for all assessed phenological stages and proportions indicated a high level of likeness between the data-sets for the five assessed synoptic stations. These differences were usually no greater between observed period data-sets and control period ensemble data-sets for the other six synoptic stations. Such discrepancies were higher than typically expected for a small number of cases. This was noted for first generation sexual maturation 95% E.P at Valentia Observatory (9 days) and Shannon Airport (8 days), second generation sexual maturation 5% E.P at Kilkenny (9

days), Casement Aerodrome (9 days) and Birr (13 days), and second generation adult emergence 5% E.P at Malin Head (9 days). The number of years used to calculate the control period ensemble mean emergence values and the observed period mean emergence values for these later occurring life-cycle stages were much lower when compared to preceding life-cycle stages. Additionally, the number of years used to calculate the control period ensemble mean emergence values were greater than the number of years used to calculate the observed period mean emergence values in all cases. This facilitated for greater ranges across the annual estimates for stage completion that formed the ensembles. For example, the observed period mean emergence value for first generation sexual maturation 95% E.P at Valentia Observatory was estimated to be 360 days based on a single year (1989) when temperature conditions allowed for life-stage completion to take place. The control period ensemble mean emergence value for the same life-cycle stage, emergence proportion and synoptic station was estimated to be 351 days based on 22 years, therefore providing the difference of 9 days.

Individual GCMs were assessed to establish if specific models were influencing the spread and occurrence of annual estimates for stage completions within the control period ensemble. The CCGCM2 model was perceived to be providing more annual estimates for stage completion to control period ensemble mean emergence value estimations for all of referenced cases. In contrast, the HadCM3 model was recognised to be providing less annual estimates for stage completion to control period ensemble mean emergence value estimations. These observations were deemed to be due to the inherent warming and cooling biases associated with each specific GCM. This phenomenon was detected for later occurring life-cycle stages and second generation life-cycle stages when no annual estimates transpired for observed period mean emergence value calculation and as little as one or two annual estimates (1% of ensemble years) materialised for control period ensemble mean emergence value determination. The CCGCM2 model and CSIRO Mark 2 model were seen to more often overestimate temperature conditions compared to HadCM3 model for the control periods at all locations. This was seen at Belmullet for second generation sexual maturation 5% E.P where 3% (6 years) of ensemble years determined the mean emergence value, none of which originated from HadCM3 model data, 2 years were associated with the CCGCM2 model and 4 years were associated with the CSIROM2 model. Another example included first generation sexual maturation 95% E.P at Kilkenny where 3% (5 years) of ensemble years determined the mean emergence value, again none of which originated from HadCM3 model data, 2 years were associated with the CCGCM2 model and 3 years were associated with the CSIROM2 model. This was observed for other synoptic stations during the control period and future time periods.

Both chilling (cold winter temperatures) and thermal forcing (spring warming) are recognised as important for budburst timing (Sarvas, 1974; Cannell & Smith, 1983; Kramer, 1994). Warmer springs hasten the accumulation of thermal forcing and advance the timing of budburst. Warmer winters may advance budburst occurrence also if they contribute to thermal forcing. Warmer winters may reduce the accumulated chilling however. This might have no effect on budburst if the chilling requirements have already been fulfilled earlier in winter but this could further delay budburst as the chilling requirements are not met in warmer conditions. Climate warming across the future time periods was therefore anticipated to have a contrasting effect on chilling and thermal forcing for this stage in the phenology/voltinism model. Advancement of insect life-cycle stages was also expected to be amplified as they reacted to this preceding stage along with their own accelerated development rates under projected warmer conditions. Increasing advancement in *S viminalis* budburst timing and all subsequent proportions of insect life-cycle stages across the future time periods was one of the most obvious trends to arise from this analysis. This was observed at all synoptic stations. Changes in budburst were slightly greater for Valentia Observatory, Shannon Airport and all inland stations for all future time periods compared to Malin Head, Belmullet and initially Roche's Point (during the 2020s). Hypotheses for these advancements include the chilling requirement of *S. viminalis* was been met even under warmer future period conditions. Alternatively, the delaying effect due to unfulfilled chilling was counterbalanced and overcome by the positive effect of warmer winter conditions.

The advancement of insect life-cycle stage emergence was suggested for all stages and all proportions across all future time periods. It was difficult to determine an overall clear pattern for the advancement at a national level when all was considered. Uniformity in emergence advancement for all life-cycle stages amongst all synoptic stations was suggested for 5% and 50% emerging insect proportions during the 2020s and 2050s as the ranges for relative differences for the future time periods from the control periods were considered low (usually less than or equal to 7 days). The greater relative differences and ranges between synoptic stations were observed during the 2080s. Coastal stations Malin Head, Belmullet, Rosslare and Roche's Point were estimated to experience reduced advancement for stages in comparison to all inland stations, Valentia Observatory and Shannon Airport. Results of a weighted ensemble mean, derived from the same multiple GCMs used in this work, were presented by Fealy & Sweeney (2008) which described the development of a "continental effect" becoming apparent across Ireland during the 2050s and more enhanced by the 2080s. Although an unweighted ensemble mean was used for this analysis, greater warming in the interior of the country may have had an influential

impact on the advancement of insect life-cycle stage emergence inland stations. This does not however explain advancement for Valentia Observatory and Shannon Airport.

The phenology/voltinism model suggested that there was a greater likelihood of changes in voltinism at the different synoptic stations across the successive future time periods based primarily on the condition that the sexual maturation life-cycle stage was increasingly been completed under warmer temperature scenarios for each occurring generation, for a greater number years during the future time periods, prior to CDL occurrence at synoptic stations. The greatest changes in voltinism were suggested to arise for 5% and 50% emerging insect proportions. This was due to an accelerated rate of life-cycle stage completion for the smaller emerging proportions earlier than CDL. Second generation occurrence was estimated at all stations for 5% emerging insect proportion for all future time periods. Third generation occurrence was estimated for Birr and Shannon Airport by the 2050s and Clones, Casement Aerodrome, Birr, Shannon Airport, Kilkenny and Valentia Observatory by the 2080s (albeit the percentage of years exhibiting this at each station was low with the highest been 9% (16 years) of ensemble years and the CCGCM model unsurprisingly contributing the most annual estimates that were used to formulate the ensemble mean emergence values). Second generation occurrence was estimated at all stations except Malin Head for 50% emerging insect proportion for the 2020s and at all stations thereafter. Additionally, second generation occurrence in the form of larvae emergence (adult emergence not reached) was estimated at Birr and Shannon Airport for a small percentage of years (1% (1 year) and 3% (5 years) of ensemble years respectively) for 95% emerging insect proportion by the 2080s (with the CCGCM model again contributing all annual estimates that were used to calculate the ensemble mean emergence values).

The sexual maturation life-cycle stage was hypothesized to be the final photosensitive stage before additional generation development took place. This life-cycle stage was quite often completed shortly before, soon after and sometimes directly on a station specific day related to CDL. This was observed for both the annual estimates that were used to calculate the ensemble mean emergence values for all observed, control and future time periods and for the ensemble mean emergence values themselves. Examples of this for the ensemble mean emergence values included first generation sexual maturation 5% E.P at Valentia Observatory on day 279 (CDL occurring by day 279) for the observed period, first generation sexual maturation 50% E.P at Belmullet on day 284 (CDL occurring by day 284) for the 2080s and first generation sexual maturation 50% E.P at Rosslare on day 280 (CDL occurring by day 280) for the 2080s. This showed how narrow the window of opportunity often was for additional generation development in the context of this model

structure with such a definitive CDL value. This was further emphasised when new generation life-cycle stages were estimated to be completed after the sexual maturation stage for previous generation development. This was due to reduced percentages of years completing sexual maturation stage development ahead of CDL occurrence at synoptic stations and ensemble mean emergence values for new generation stage development been based on these smaller data-sets. Examples of this for the ensemble mean emergence values were numerous for all emergence proportions and all stations across all time periods. It was assumed however that there was a sufficient spread in annual estimates forming the ensemble data-sets for all observed, control and future time periods to capture the representative mean emergence values. It did nonetheless accentuate the necessity to further investigate the possibility of a more climate flexible CDL, as demonstrated by Bean *et al*. (2007) which may have helped to provide better model accuracy and strengthen the knowledge regarding species specific environmental signalling for reproductive diapause.

8 FINAL DISCUSSION

Insect performance is dependent on climate. Temperature increases associated with future projected climate change, coupled with responses to other climatic factors, may affect physiological processes such as development, voltinism and diapause. Potential alterations in the temporal dynamics of insect populations include phenological advances, faster development, increased voltinism and changes in oviposition traits and survival rates. These environmental drivers may also affect species distributions by redefining the spatial dynamics of insect populations. Understanding how these interacting climatic factors impact upon insect life-histories is essential for estimating and managing their occurrence.

The objectives of this research were to account for the impact of abiotic and biotic factors, mainly temperature and photoperiod, but also host plant, on the phenology and voltinism of native leaf-feeding willow beetles, specifically *P. vulgatissima* and *G. lineola*, and link these findings to climate model projections for Ireland in order to inform future policy in this area. The results from this assessment may be considered in determining the potential productivity of SRCW as a biomass option over the course of the present century. Although many studies have described the influences of these factors on different insect species life-histories, no study to the author's knowledge, has attempted to account for the effects of these governing factors on the entire life-cycle of either of these two chrysomelid species simultaneously. The research sought to build upon the existing body of literature on the effects of environmental variables on insect species to derive a unique combined phenology/voltinism model for native willow beetle populations.

The following sections summarise and discuss the findings and contributions of this bipartite (experimentation and modelling) study as well as highlighting limitations of the research and possible avenues that could benefit from future investigation.

8.1 **Summary of Key Research Findings**

The following section provides a summary of the key findings from the experimentation and modelling components of this research.

- *P. vulgatissima* and *G. lineola* development conform to ambient temperature. Days to completion for all life-cycle stages assessed (post-diapause, eggs, larval, pupal and sexual maturation for *P. vulgatissima*, and eggs, larval and pupal for *G. lineola*) decreased as temperatures increased over different ranges of suitable constant temperatures (10°C - 29°C and 10°C - 31°C, with respect to species) until an optimum temperature, after which development time increased at stressfully high temperatures, denoted by decreased percentage survival rates.

- Development was found not to vary considerably when *P. vulgatissima* larvae were reared on different host plants across a range of temperatures (10°C - 27°C). Four host plants varieties (*Tora, Resolution, Tordis* and *Inger*) were selected for the investigation based on their performance in feeding trials (with two seemingly more predated upon than the others (P. Fanning, personal communication)) and inclusion in current Irish genotype yield trials.

- *P. vulgatissima* has a facultative reproductive diapause induced by declining day-length. The CDL for diapause induction was estimated to be 14.92 hrs for Irish populations based on laboratory experiments. This suggested that *P. vulgatissima* could produce a second generation in Ireland if development of the first generation was completed before mid-August.

- Temperature has a profound influence on aspects of *P. vulgatissima* reproduction. Mean oviposition period (number of days from first to last oviposition) decreased as temperature increased over a constant temperature range (10°C - 27°C) until it began to level off at upper temperatures (25°C - 27°C). Total fecundity (total number of eggs laid per female) was greatest at the mid-range temperatures (15°C and 20°C).

- The relationship between temperature and *P. vulgatissima* and *G. lineola* development was represented by applying criteria satisfying non-linear deterministic and stochastic functions to development rates and development

time distributions respectively, for each of the life-cycle stages. The Lactin function was chosen as a suitable option for representation of development rates for all life-cycle stages and for both species, except relative oviposition for which a quadratic polynomial function was used. Biologically important development parameters (T_l, T_{opt} and T_u) were identified for each developmental stage. Models indicated that *P. vulgatissima* develop at lower temperatures compared to *G. lineola* and *G. lineola* develop at higher temperatures compared to *P. vulgatissima*. The Weibull (3P) function was deemed as an appropriate choice for describing development times for all life-cycle stages for both species.

- The relationship between temperature and *S. viminalis* phenological events such as budburst – the acting biofix selected for the commencement of willow chrysomelid post-diapause development – can be explained through the fitting of a plant development function. A mechanistic two-phase Alternating model was employed that considers endodormancy and ecodormancy. It showed that a relationship exists between accumulated chilling days and forcing temperature units in releasing winter dormancy and promoting *S. viminalis* budburst respectively when thermal units were accrued from 1st November at temperatures greater than 7°C and chill days were collected from the same date at temperatures less than and equal to 7°C.

- Emergence patterns for *P. vulgatissima* were accounted for using a multi-component phenological/voltinism model. A model incorporating a *S. viminalis* degree-day budburst model, the temperature-dependent development rate and temperature-independent time distribution functions for each life-cycle stage, the oviposition function and the reproductive diapause inducing CDL was constructed to primarily estimate the number of days, from 1st November, required by proportions of beetle, selected as 5%, 50% and 95% for this study, to complete a full generation of development. The model's secondary function was to estimate the potential for additional generations for each proportion. Validation using constant temperatures and field observation data-sets and sensitivity analysis confirmed the model's usefulness.

- Estimations of future life-cycle stage emergence and occurrence of further generations were made by employing the phenology/voltinism model with observed temperature data-sets and climate projection data-sets as input. The model was run using observed temperature and statistically downscaled climate

scenarios derived from three different GCMs (HadCM3, CCGCM2 and CSIROM2), forced with two emission scenarios (A2 and B2). Ensemble mean outputs for three time periods (2020s, 2050s and 2080s) were compared to those for control period (1961 – 1990), which in turn were compared to those for observed baseline period (1961 – 1990), for five national synoptic stations. Differences between control periods and observed periods were found to be minimal. Advancement of life-cycle stage emergence was suggested for all stations and all proportions across all future time periods, with a second generation estimated to occur for 5% E.P for all stations, and increasingly likely for 50% E.P for all stations by the 2080s. Partial second generation occurrence (larval emergence) was suggested for Birr and Shannon Airport for a percentage of years for 95% E.P also. Greater advancement was suggested for inland locations such as Kilkenny and Casement Aerodrome with development of a third generation for 5% E.P by the 2080s, for a percentage of the ensemble years. When all eleven stations were considered, similar patterns for life-cycle stage advancement were estimated for all stations and all proportions across all future time periods with the occurrence of a third generation for 5% E.P estimated for a percentage of the ensemble years for Clones, Birr, Shannon Airport and Valentia Observatory by the 2080s also.

8.2 Implication of Research Findings

The following sections elaborate on the implications for insect development, regional SRCW production, crop and pest management, and policy based on the findings from this research.

8.2.1 Implications for Insect Development

Climate change may play a pivotal role in future spatial and temporal patterns for willow beetle phenology and voltinism in Ireland. Results from this study indicated advancements in phenology for life-cycle stages, faster development, and increased voltinism for different emerging proportions associated with increasing temperatures. At present, both species of willow beetle are typically univoltine in Ireland (Kelly & Curry, 1991; Kendall & Wiltshire, 1998) although partial generations have been recorded in some years (Hutchinson &

Kearns, 1930). *P. vulgatissima* is suggested to initiate second generation development nationally and even third generation development for some southern and midland stations by the end of the century based on model runs using climate projections. Studies on the phenology and voltinism of other typically univoltine coleopteran pest species in regions across Europe have recorded similar findings. Earlier spring emergence and faster development is expected to increase the probability of additional generations *Ips acuminatus* (pine bark beetle) in Northern Italy (Colombari *et al*., 2012), *I. typographus* (spruce bark beetle) in Southern Sweden (Jönsson *et al*., 2007; 2009) and Norway (Lange *et al*., 2006), and *Leptinotarsa decemlineata* (Colorado potato beetle) in Southern Scandinavia (Jönsson *et al*., 2013). Additional generation development for these species is restricted by diapause inducing photoperiod thresholds (Wilde *et al*., 1958; Gehrken, 1985; Doležal & Sehnal, 2007). *P. vulgatissima* has a facultative reproductive diapause induced by declining day-length also (Dalin, 2011). Photoperiod is therefore suggested to play a defining role regarding the number of generations these species will produce under increased temperatures associated with climate change. Warmer spring and early summer temperatures may have pronounced effects on earlier emergence and faster development, with ovipositing activity for an additional generation(s) more likely to occur prior to CDL at which diapause is induced. However, warmer late summer and early autumn days will have little effect on voltinism in the absence of evolutionary change in species responses to photoperiodic cues that mediate diapause induction if they occur after the trigger for diapause initiation.

Temperature and photoperiod are typically considered the prime factors that influence insect life-histories (Tauber *et al*., 1986 Porter *et al*., 1991; Bale *et al*., 2002). This is mainly due to the fact that most phenology/voltinism studies are associated with insects in the temperate latitudes where large seasonal changes in temperature and photoperiod occur (Tauber *et al*., 1988). Other abiotic factors such as moisture (Tauber *et al*., 1998) and atmospheric GHG concentrations (Zvereva & Kozlov, 2006), and biotic factors such as host plant quality (Hunter, 2001) and natural enemies (Hance *et al*., 2007) may interact with temperature and photoperiod however, to directly and indirectly, influence insect behaviour, ecology and physiology. For example, moisture, in the form of relative humidity, has been shown to affect coleopteran development rates (Howe, 1962; Shires, 1979; Zhou *et al*., 2010) and oviposition (Coombs 1978; Jacob, 1996; Simmons, 2008). Moisture has also been identified as a seasonal cue during various diapause phases also (Hodek, 2003). The effects of moisture, in the form of precipitation, have been less documented, although much can be surmised, particularly of rainfall, as an enhanced mortality factor (Bale *et al*., 2002). Although the combined phenology/voltinism model developed during this research

attended to the roles of temperature and photoperiod, elucidating the roles of other environmental variables in insect seasonal cycles may be crucial to the development of comprehensive combined phenology/voltinism models. This is particularly important as variables will not be invariant in altering thermal regimes and precipitation patterns have been changing on a global scale and are expected to continue doing so (IPCC, 2013: 1076:1079). However, the inclusion of precipitation in this study was explicitly excluded due to the large uncertainties associated with future projections of this variable (only reliable at continental scales and not at regional scales) (IPCC, 2013: 984:986).

8.2.2 Implications for Regional SRCW Production

Spatio-temporal changes in the phenology and voltinism of *P. vulgatissima* for Ireland over the current century due to climate change raise questions about the optimum location(s) for SRCW production in the future. Second generation occurrence was estimated for all synoptic station locations for 5% E.P for all future time periods. Third generation occurrence was suggested for a percentage of years for Birr and Shannon Airport by the 2050s along with Clones, Casement Aerodrome, Kilkenny and Valentia Observatory by the 2080s. Second generation occurrence was estimated for all stations except Malin Head, the most extreme northern station, for 50% E.P by the 2020s and for all stations thereafter. Partial second generation occurrence in the form of larvae was suggested for Birr and Shannon Airport for a percentage of years for 95% E.P by the 2080s. SRCW is not a demanding species but displays a preference for cooler, wetter conditions and largely heavy soils, with a neutral pH at low altitude, conditions widespread throughout Ireland (Dawson, 2007; Wickham *et al*., 2010). Results from this study indicate that future crop production in western regions, north-westerly and south-easterly coastal regions may therefore be beneficial for SRCW establishment and yield due to the less likely or later future time period estimated occurrence of additional beetle generations.

However, crop development, growth and yield is also expected to respond both positively and negatively to climate changes such as higher temperatures, increases in atmospheric CO_2 concentration, altered precipitation and transpiration regimes, and increases in pest and disease pressure (Tubiello *et al*., 2007). A meta-analysis of experiments showed that under optimal conditions that an increase in atmospheric CO_2 concentration increased leaf photosynthesis by 30%–50% and increased crop yields by 10%–20% for C3 plant species (Ainsworth & Long, 2005). Similar results were obtained from experiments involving *Salix*

species (Silvola & Ahlholm, 1992; 1993). Temperature is expected to modify and even counteract the effect of elevated CO_2 in different ways including an increase in crop water demand (Tubiello *et al*., 2007). Additionally, herbivorous insects are expected to react to altered plant metabolism under elevated CO_2 by increasing food consumption, amongst other responses, to compensate for reduced crop nutritional quality (Stiling & Cornelissen, 2007). Similar results were obtained from experiments involving *P. vitellinae* on a variety of *Salix* species (Veteli *et al*., 2002). Therefore, although this research offers information on optimal locations for SRCW for the future based on the effects of climate variables on *P. vulgatissima*, it does not account for the effects of climate change on SRCW and how this will further impact on willow chrysomelids.

8.2.3 Implications for Crop and Pest Management

This study addresses issues directly applicable to renewable energy crop and pest management. The suggested earlier onset of beetle predation and the increasing potential of bivoltinism (and trivoltinism) due to climate change, highlights the need for adaptation of crop management to increased and prolonged windows of pest and disease vulnerability such as screening and selection of varieties for planting as polycultures. Current best practice for SRCW establishment seeks to attain a balance between resistance and biomass yield, using multiple varieties from various breeding programmes such as the UK/Swedish European Willow Breeding Partnership, to ensure maximum genetic diversity (Caslin *et al*., 2010). In general, SRCW resistance and biomass yield trials involving new varieties neglect to account for future climate conditions and potential increased pest predation. Therefore, in the face of increased planting of these species, there is a pressing need for insight into their responses to projected changes in climate to ensure these crops are robust to both changes in climate and pest herbivory in breeding and improvement programmes (Oliver *et al*., 2009).

SRCW is a high volume, low value crop and fungicide and pesticide treatment is economically, environmentally and technically not an option. The development of biocontrol options as substitutes for expensive or phased-out fungicides and pesticides under the European Pesticide Authorisation Directive 91/414/EEC may need to be employed under future climate conditions. These could allow for location-specific and time-specific application to crop for maximum effectiveness. Different native parasitoids (*M. luctuosa*, *C. collaris* and *P. asper*) (see Section 3.2), entomopathogenic fungi (*Metarhizium*

anisopliae and *Beauveria bassiana*) and nematodes (*Heterorhabditis downesi*, *Steinernema carpocapsae* and *Steinernema feltiae*) were identified as potential biocontrol options for *P. vulgatissima* during experimentation (data not shown). Anthocoridae (flower bug) species have been observed feeding on the eggs of *G. lineola* in SRCW (P. Fanning, personal communication). Other natural enemies for willow chrysomelids have been identified in the UK (*D. luctuosa*) and Sweden (*A. nigrisquamata*, *O. marginalis*, *C. fulvomaculatus*, *A. nemorum* and Syrphidae (hoverfly) species) (Kendall & Whitshire, 1998; Björkman *et al*., 2003; Dalin *et al*., 2011; Stenberg, 2012). *P. brevicollis* was shown to reduce herbivory at higher temperatures in Sweden implying that biocontrol may be promoted by a warmer climate (Baffoe *et al*., 2012). However climate change will also impact on such biocontrols in a diverse matter through interactions with pests and crop plant hosts. Although generalisations that include decreased pest size due to poorer host quality will allow for increased predation, and decreased pest density due to increased plant biomass will increase search time, the combined effects of temperature, CO_2 and crop nutrition levels are not easily estimated (Thomson *et al*., 2010).

8.2.4 Implications for Policy

All E.U countries are legally obliged under the European Renewable Energy Directive 2009/28/EC to ensure that a percentage of all energy consumed in the state is from renewable sources by 2020; this is set at 16% for Ireland. Biomass production through the cultivation of willow, eucalyptus, poplar and non-woody perennial grasses such as hemp and miscanthus has been proposed as an option to help meet these energy/environmental targets. These options are susceptible to a number of pests and diseases however: willow and poplar (*P. vulgatissima, G. lineola* and *Phratora vitellinae* (brassy or green willow beetle)); eucalyptus (*Paropsisterna selmani* (eucalyptus leaf beetle)); hemp (*Ostrinia nubilalis* (European corn borer) and *Grapholita delineana* (hemp borer)) and miscanthus (*D. virgifera virgifera*). It has long been recognised that climatic conditions influence the epidemiology and incidence of many pests and diseases. Similar studies to this have estimated earlier insect emergence and increased voltinism due to climate change for some of the aforementioned pests associated with these other energy crops (Trnka *et al*., 2007; Fanning *et al*., 2014).

Such research highlights the need for international policies which mandate levels of renewable energy use to mitigate future climate change, such as Directive 2009/28/EC, to

consider adaptation options in the energy sector under increased levels of pestilence, due to changes in the climate system. The mandatory national targets for renewable energy shares of final energy consumption for 2020 are currently calculated on the basis of the 2005 share of each country plus both a flat-rate increase of 5.5 % per Member State as well as a gross domestic product-weighted additional increase. As climate conditions do not follow national boundaries, policy may need to consider targets that would be more representative of current and projected climate conditions based on environmental zones or climatic stratification such as those defined for Europe by Metzger *et al*. (2005) and Jongman *et al*. (2006). Implementation of policy in such a manner may be of benefit for regions currently suitable for energy crop production but susceptible to increased pestilence due to climate change. Also, such a review in policy application may be of even greater importance for regions in southern Europe such as Spain where the opportunity to meet future targets could be impeded, as the choice of bioenergy crops is expected to be severely reduced in future climates due to increased temperature and drought events (Tuck *et al*., 2006).

8.3 **Research Limitations**

A number of limitations became apparent during the course of conducting this research, the majority of which were methodological in nature. The methodology employed to obtain insect development data and construct a phenology/voltinism model was performed in a manner that, in general, conformed with techniques found within the literature related to the subject area. However, a number of subjective decisions were required to be made at different steps throughout and impacts of these decisions had varying influences on the overall results.

- Insects used for an experiment were usually collected from one source. On occasions when population numbers were low at individual locations, collections from different locations were combined in the laboratory. Intraspecific variation of biologically important development parameters over different altitudes and geographical latitudes has been demonstrated in other studies (Honek, 1996). It was assumed that there was little variation between populations used in experiments due Ireland's small altitudinal and latitudinal ranges and the unsuitability of land for SRCW at higher altitudes; thus all had similar climatic

variable requirements and findings were deemed to be representative for populations at a national level. A diversity study of willow beetle populations in the UK concluded that native species are highly mobile and that the individuals collected from different dispersed sites comprised one large highly polymorphic population of homogeneous allele composition (Karp & Peacock, 2004)

- Populations for *G. lineola* at specific life-cycle stages such as post-diapause were difficult to obtain in the field. Post-diapause temperature-dependent development experimentation was therefore not possible meaning a complete phenology/voltinism model could not be constructed for this species. Adult *G. lineola* overwinter in the same niches as other native chrysomelids within a few hundred metres of SRCW (Sage *et al*., 1999). In this study, *G. lineola* were rarely found in the same overwintering locations as *P. vulgatissima* and never in the same numbers. Overwintering collections did not always account for the dominance of a chrysomelid species subsequently observed in the coppice canopy as overwintering *P. vulgatissima* were predominantly collected at the Donard site but *G. lineola* were the more frequently observed species at the same site during the active season between 2010-2013.

- Reduced percentage survival rates for immature willow beetle life-cycle stages reared in the laboratory, particularly at the lower (<15°C) and upper (>25°C) constant temperatures, along with observed greater deformity for post-eclosion adults, meant that a robust data-set for sexual maturation development time was not obtained for *P. vulgatissima*. A non-linear development rate function could not be fitted to the reciprocals of the data due to very low observations. An observed association between the limited data-set and the related post-diapause development data-set was used to facilitate the inclusion of the life-cycle stage in the comprehensive phenology/voltinism model.

- Willow beetle species complete different life-cycle stage development in different microhabitats and climates where temperature might not be expected to conform with air temperature recorded at near-by meteorological stations (i.e. overwintering in clusters outside of the crop, development of larvae and adults on the foliage at different heights around the perimeter and within the crop, and development of pupae in the ground-cover or upper soil layers). Daily mean temperatures recorded at both internal and external locations of a SRCW were shown to match reasonably well, and corresponded with mean temperatures

recorded at the closest synoptic stations. However, other studies have shown a difference in the amplitude of daily fluctuation between internal and external crop temperature (Peacock, 1975) which could affect development. Additionally, variation in temperature between open and shady habitats has been shown in other chrysomelid studies (Sipura & Tahvanainen, 2000). This could lead to further variation in development, depending on insect location within the crop, whether it is in an exposed or sheltered setting. Soil temperature data-sets for pupal development were also not used for the development of pupae stage.

- The seasonal timing of reproductive diapause in *P. vulgatissima* was predicted based on the response to constant photoperiods in the laboratory. There have been relatively few studies of reproductive diapause induction in the laboratory compared with field-based studies, most likely due to the complex array of environmental and physiological elements (Tauber *et al*., 1986) that may affect the decision to enter diapause under natural circumstances. The use of a constant temperature (20°C) for determining CDL was another limitation. Amongst other factors, CDL for reproductive diapause induction is profoundly influenced by temperature in many species. Interaction between photoperiod and temperature is expressed in thermal alterations of CDL (Bean *et al*., 2007; Doležal & Sehnal, 2007; Xiao *et al*., 2010); a factor which may prove to be of major importance for additional *P. vulgatissima* generation occurrence under future climate conditions. Access to additional incubators and an undefined photosensitive stage were the principal limiting factors here.

- *S. viminalis* budburst was selected as the dynamic biofix for the commencement of willow chrysomelid post-diapause development. Field observations suggested a relatively close synchrony between *Salix* leaf-unfolding and adult beetle emergence from overwintering locations. Vigorous feeding during post-diapause development experimentation further supported the reasoning for this biofix, as the availability of *Salix* foliage as a food source and ovipositioning platform, may be necessary for completion of post-diapause development (Kendall & Wiltshire, 1998; Karp & Peacock; 2004; Dalin, 2011). Additionally, the phenology/voltinism model assumed this close synchrony for future climate conditions (although model allows for budburst to be lag or advance), and this might be considered unlikely based on similar herbivore/host plant synchrony studies (Bale *et al*., 2002, van Asch & Visser, 2007; Robinet & Roques, 2010).

- Calibration and validation of the model used to account for *S. viminalis* budburst was restricted due to the small and fragmented data-set available. It is essential to evaluate plant phenology models with external data as the best fitted models can perform poorly when evaluated against external data (Chuine, 1998). Other plant phenology studies using larger data-sets allow for this (Linkosalo *et al*., 2008; Olsson *et al*., 2013; 2014). However, long time series of phenological data of the same location(s) are rare (Chuine *et al*., 1999). Furthermore, budburst observations were obtained courtesy of the IPG from different phenological gardens nationally. Similar to insect populations, *S. viminalis* was assumed to experience the same chilling and forcing requirements independent of site location. Moreover, observer-based budburst observations are to a certain degree subjective and there are no guarantees that guidelines are being followed despite the existence of a Phenological Observation Guide issued by the IPG.

- The phenology/voltinism model was validated using constant temperatures (as used during experimentation) to assess for correct initiation, continuation and termination of the model sub-functions, and observed temperatures relating to the observed presence of different life-cycle stages for *P. vulgatissima* in the field. Validation based on field observations was restricted to one year of multiple observations at Donard, Co. Wicklow and at Long Ashton, Bristol (the latter data-set obtained from Kendall & Wiltshire (1998)), and irregular observations at other sites around Ireland from 2009 – 2013. Additional surveys of beetle stages and populations in the field could not be obtained from SRCW growers or state bodies in the agriculture and forestry sectors for Ireland or the UK.

- Climate projections were required as input to the phenology/voltinism model to estimate future insect emergence patterns. Another restriction in this study was the availability of statistically downscaled model inputs; data used were derived for three GCMs (HadCM3, CCGCM2, and CSIROM2), forced with two SRES emissions scenarios (A2 and B2) for eleven national synoptic stations (Fealy & Sweeney, 2008). A number of studies have suggested the inappropriate practice of employing a limited number of climate models and emission pathways (Hulme & Carter, 1999, Wilby & Harris, 2006; Tebaldi & Knutti, 2007) as this only amounts to a partial assessment of the total spread of possible climate responses. The combination of outputs from multiple models is regarded as a more pragmatic approach for addressing associated uncertainty and dispelling the over-confidence implicitly associated with using limited realisations of future

climate to produce more reliable results (Weigel *et al*., 2010). Although it was recognised that future application of the model could include a wider range of possible future climate realisations than those currently available in the national scenario database, it was beyond the scope of this thesis to develop additional future climate scenarios that could be employed in this model. However, internationally there are moves towards scenario neutral approaches to developing robust adaptation strategies, which do not require 'accurate' or 'precise' knowledge of the future evolution of the climate system. The approach undertaken within this research was an initial study to assess if climate change would result in a change in vulnerability of future SRCW due to herbivory and therefore the findings represent a first step in the development of robust adaptation strategies for the sector.

8.4 **Suggestions for Future Research**

The limitations discussed in the previous section provide for a number of future areas, among others, of research.

- Further validation is required as per other chrysomelid model studies (Storer, 2003; Baier *et al*., 2007; Berec *et al*., 2013) to strengthen the potential role of this phenology/voltinism model in any future attempt to model dynamics of willow beetle. This could be achieved by conducting more robust field surveys nationwide or by establishing a pest monitoring network, through state and private companies involved in establishing SRCW (examples of which include Biotricity, Bord na Móna and Rural Generation) and through benefiters of grants for SRCW establishment provided by Teagasc's (Irish Agricultural and Food Department Authority) Bioenergy Scheme for Willow, such as networks that exist for agriculture and forestry pests in states across Canada and USA.

- Further calibration and validation of model components such as the *S. viminalis* budburst model is required as more data becomes available. The role of photoperiod and other environmental factors such as moisture and nutrient availability could be investigated to reflect plant physiological realism (Nord & Lynch, 2009; Körner & Basler, 2010).

- More experimentation to investigate the influence of temperature on development for *P. vulgatissima* during sexual maturation, and *G. lineola* during post-diapause, sexual maturation and ovipositioning, to reinforce model output estimates and allow for greater comparison of species life-histories under future climate conditions, particularly as *G. lineola* was found to be the more prevalent leaf beetle at a number of field sites used for collections.

- Although survival data was collected for most life-cycle stages during experimentation, a survival component was not incorporated in the phenology/voltinism model. Future versions of this model could be modified to include for insect mortality responses to temperature, and in doing so, allow for population dynamics analysis instead of proportion based emergence assessment. Research regarding climatic impacts on life-cycles of identified predators (some of which have been referred to in Sections 3.2.4 and 8.2.3) could also be conducted for a better representation of events as they might occur in nature.

- Additional work on the identification of diapause inducing stimuli and sensitive stage(s) for willow beetle species is envisioned. Environmental cues are species-specific and they can be perceived within the parental generation and different stages of embryonal, larval and pupal development through to adulthood (Koštál, 2006). Sensitivity may not be limited to a particular stage, giving the species flexibility in responding to changing environmental cues also (Taylor & Spaulding, 1988). Larvae and adults have been most frequently identified as sensitive stages for different chrysomelid species (Hodek, 2012). *P. vulgatissima* is suggested to remain sensitive to cues such as photoperiod (Dalin, 2011) and host plant quality (Dalin & Nylin, 2012) for diapause induction late in development – possibly to the adult stage (P. Dalin, personal communication). Further examination of interactions between temperature and diapause-inducing interactions should result in improved estimates for future generation development.

8.5 **Final Conclusion**

The principal objectives of this study were to account for the effects of abiotic and biotic factors, on the phenology and voltinism of native leaf-feeding willow beetles, specifically *P. vulgatissima* and *G. lineola*, and link these findings to climate projections for Ireland. The effects of temperature and photoperiod, but also host plant on the chrysomelid's development were assessed during an experimental research phase. The rates of development of all assessed life-cycle stages for both species were influenced by temperature as were fecundity and oviposition period for *P. vulgatissima*. There was negligible difference in *P. vulgatissima* larval development rates when reared on different host plants. Additionally, *P. vulgatissima* had a facultative reproductive diapause induced by declining day-length.

The relationship between temperature and *P. vulgatissima* and *G. lineola* development was described by applying criteria satisfying non-linear functions to development rates and development time distributions calculated for each of the life-cycle stages during the modelling phase. The relationship between temperature and *S. viminalis* budburst events was explained through the fitting of a plant development function. A multi-component phenology/voltinism model for *P. vulgatissima* was constructed. Based on downscaled climate model projections input, it was suggested that a second or third generation would occur due to budburst advancement, earlier emergence of insect proportions and faster development of the first generation prior to a reproductive diapause inducing CDL.

The results from this research emphasise the necessity for further research of this kind, to highlight the impacts of climate change on the development of pests associated with crops proposed as options to meeting energy demands and mitigating GHG emissions. Other woody crops similar to willow such as eucalyptus, and non-woody crops such as hemp and miscanthus that have been proposed as renewable energy options have associated pests and diseases also such as *P. selmani*, *G. delineana* and *D. virgifera virgifera* respectively. Although these crops may appear to be economical and practical solutions in the short-term, without knowledge of insect life-cycles under projected climate change conditions and their impact on these crops, such adaptation measures may falter.

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10 APPENDICES

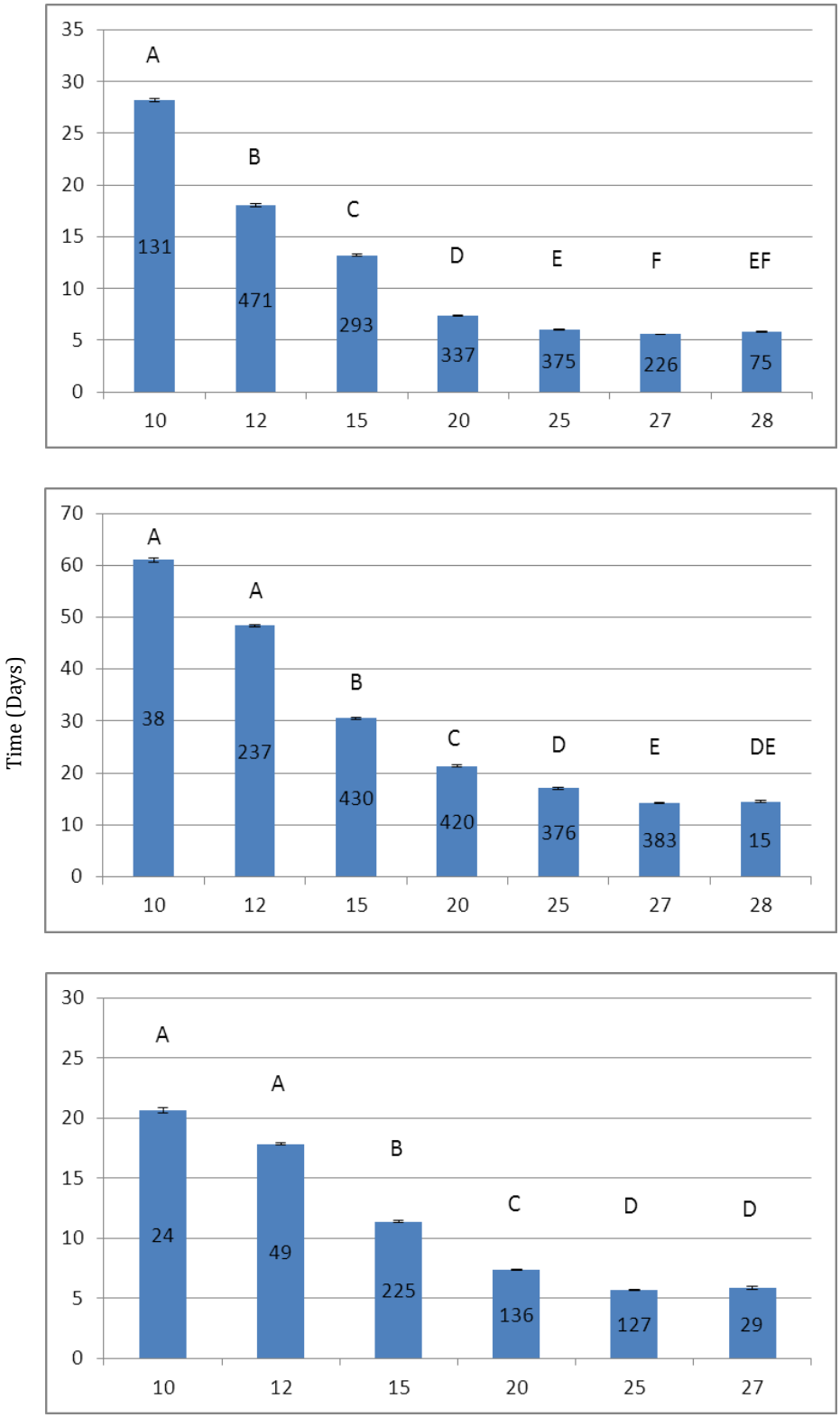

Figure A I-1 Mean (±SE) development times (in days) for *P. vulgatissima* eggs, larval and pupal stages at different constant temperatures. Different letters indicated a significant difference between temperatures (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

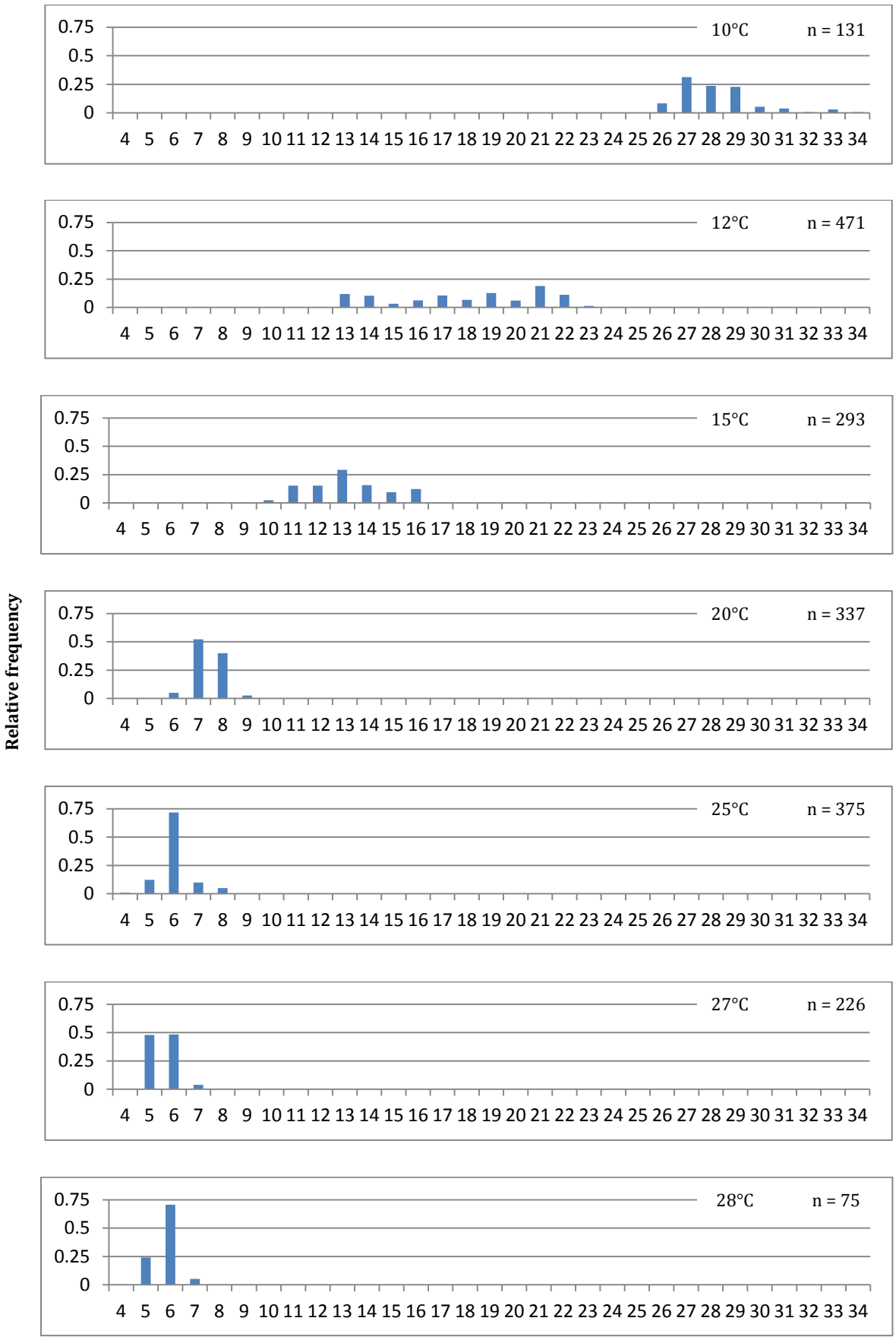

Figure A I-2 Relative frequency distributions of development times (in days) for *P. vulgatissima* eggs at different constant temperatures.

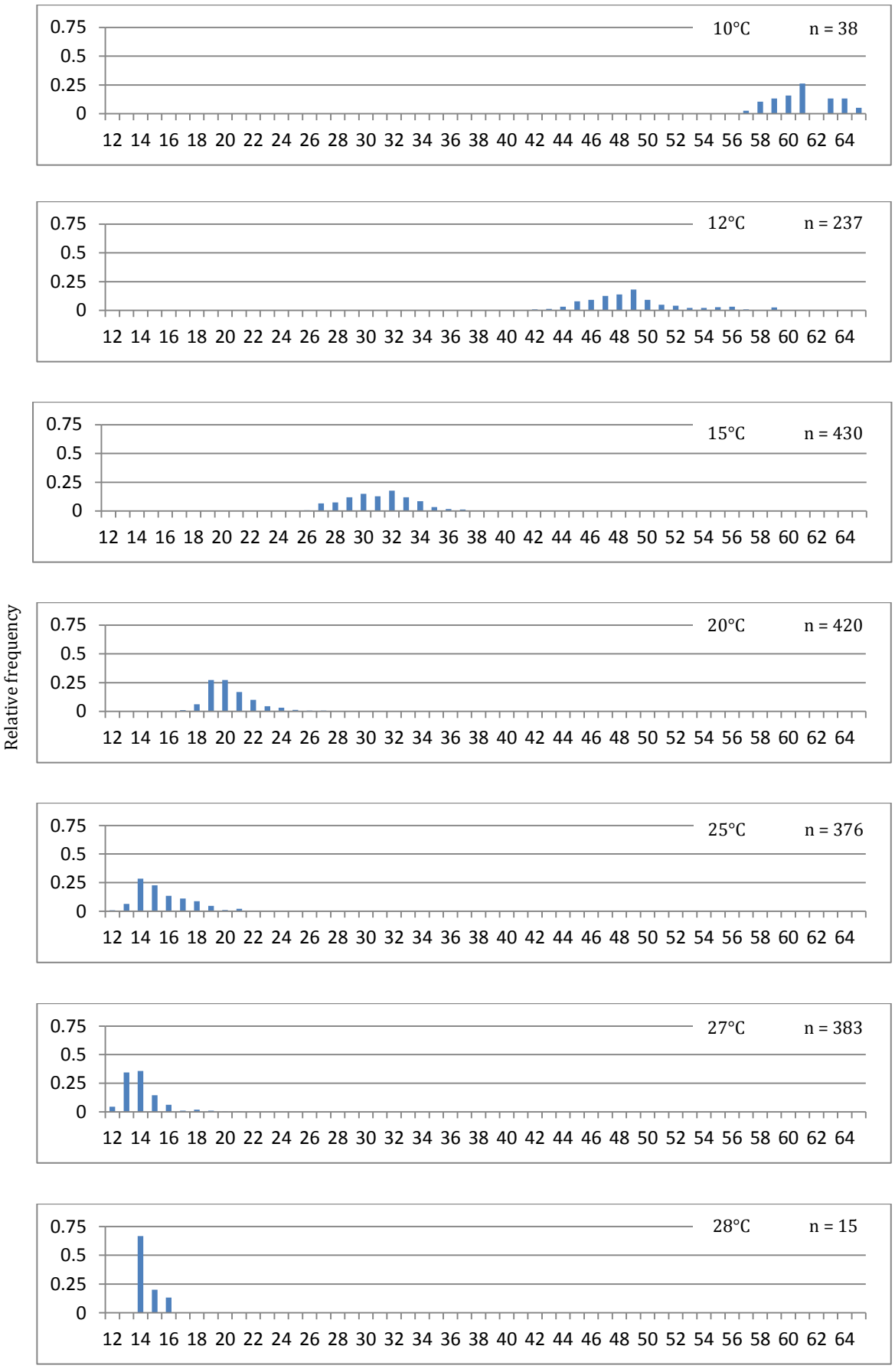

Figure A I-3 Relative frequency distributions of development times (in days) for *P. vulgatissima* larvae at different constant temperatures.

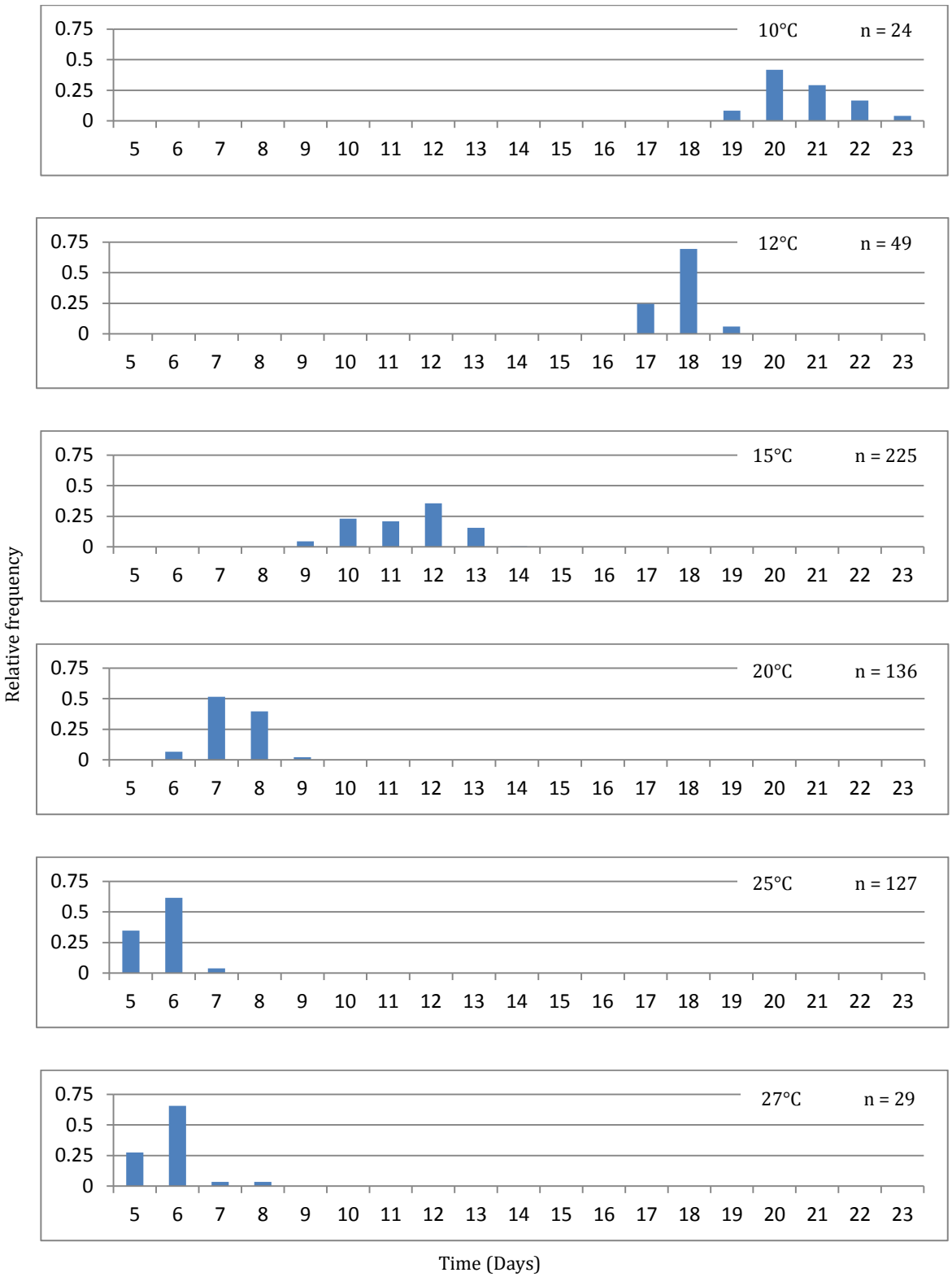

Figure A I-4 Relative frequency distributions of development times (in days) for *P. vulgatissima* pupae at different constant temperatures.

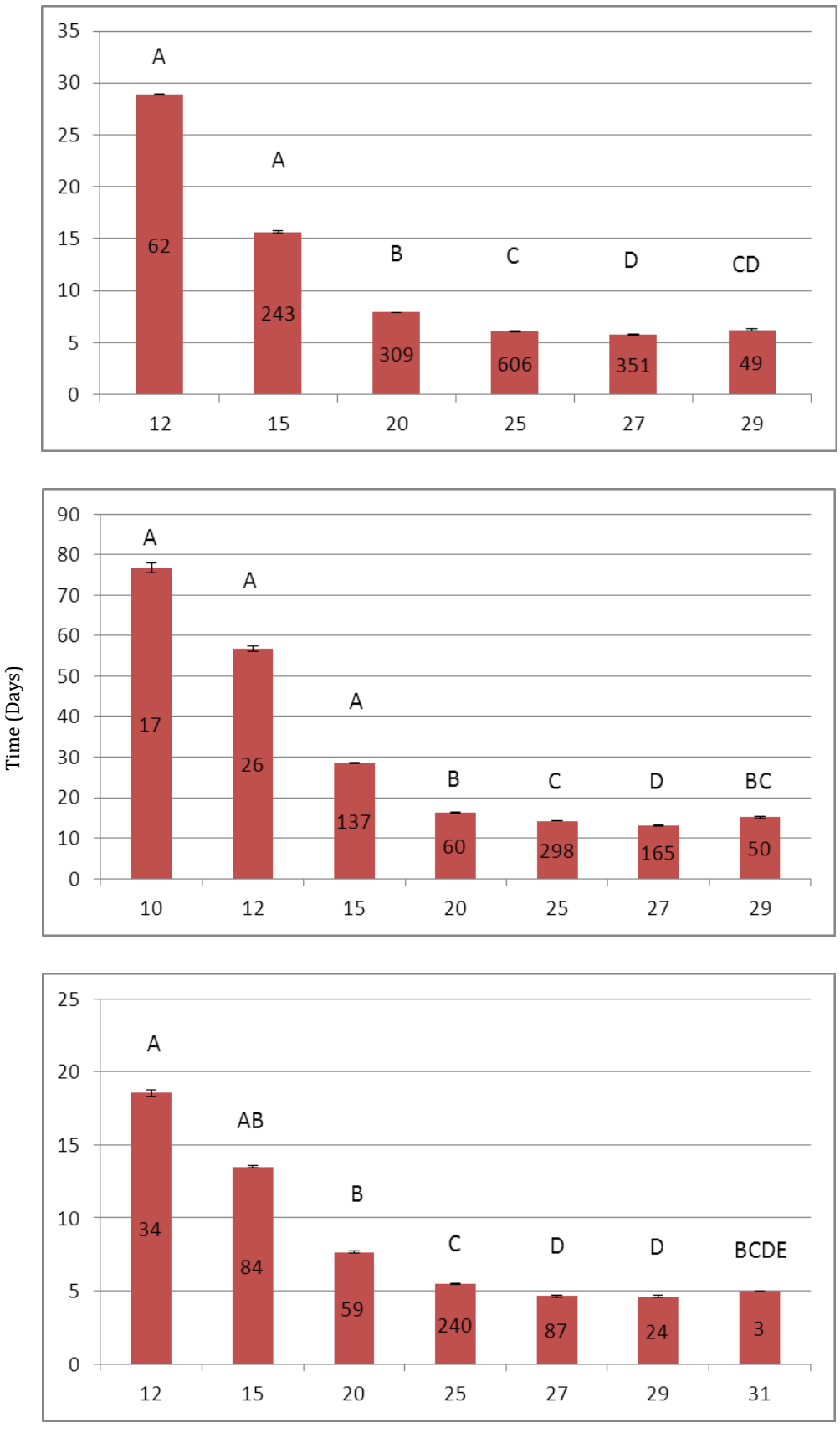

Figure A I-5 Mean (±SE) development times (in days) for *G. lineola* eggs, larval and pupal stages at different constant temperatures. Different letters indicated a significant difference between temperatures (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

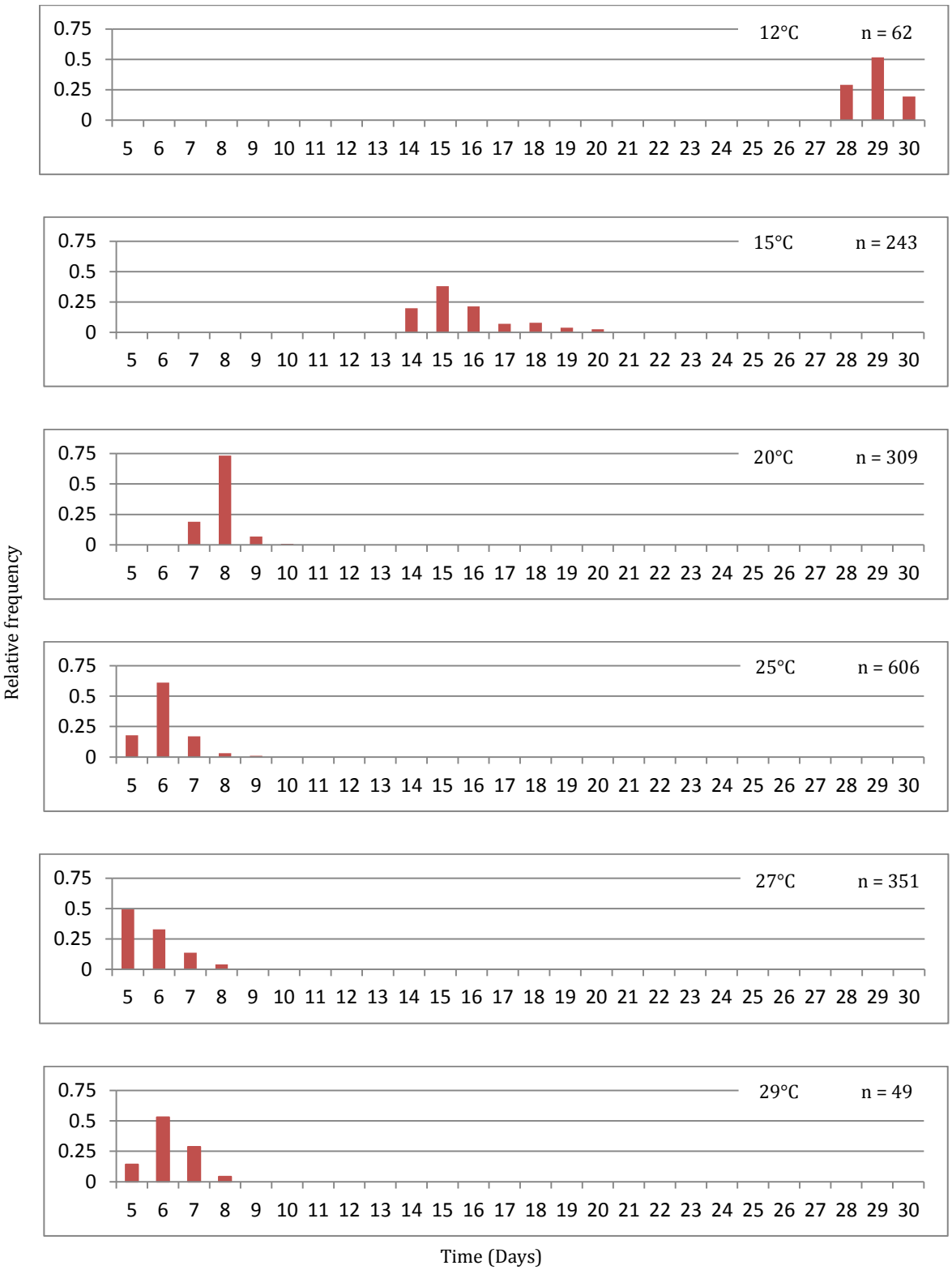

Figure A I-6 Relative frequency distributions (in days) of development times for *G. lineola* eggs at different constant temperatures.

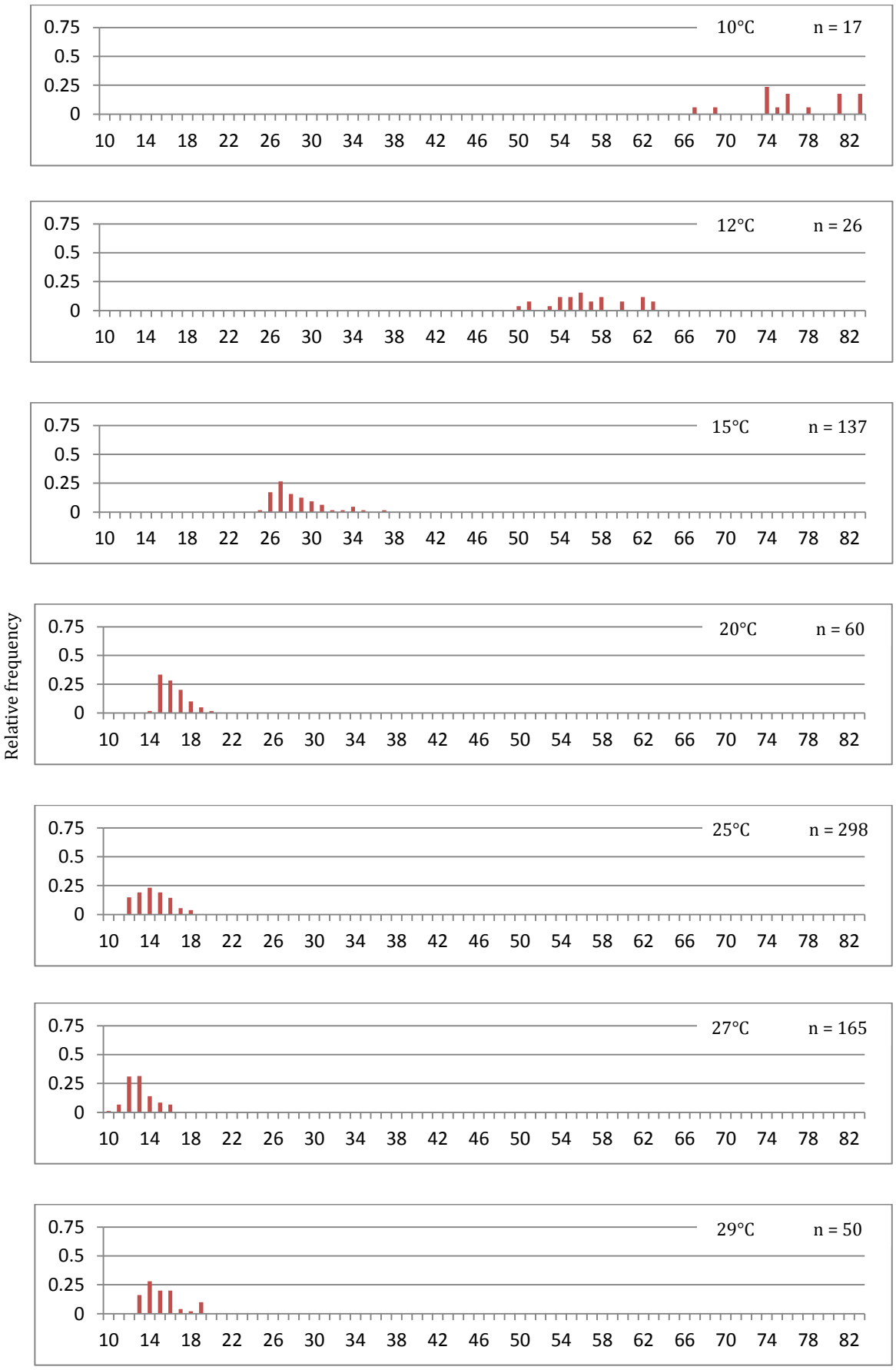

Figure A I-7 Relative frequency distributions (in days) of development times for *G. lineola* larvae at different constant temperatures.

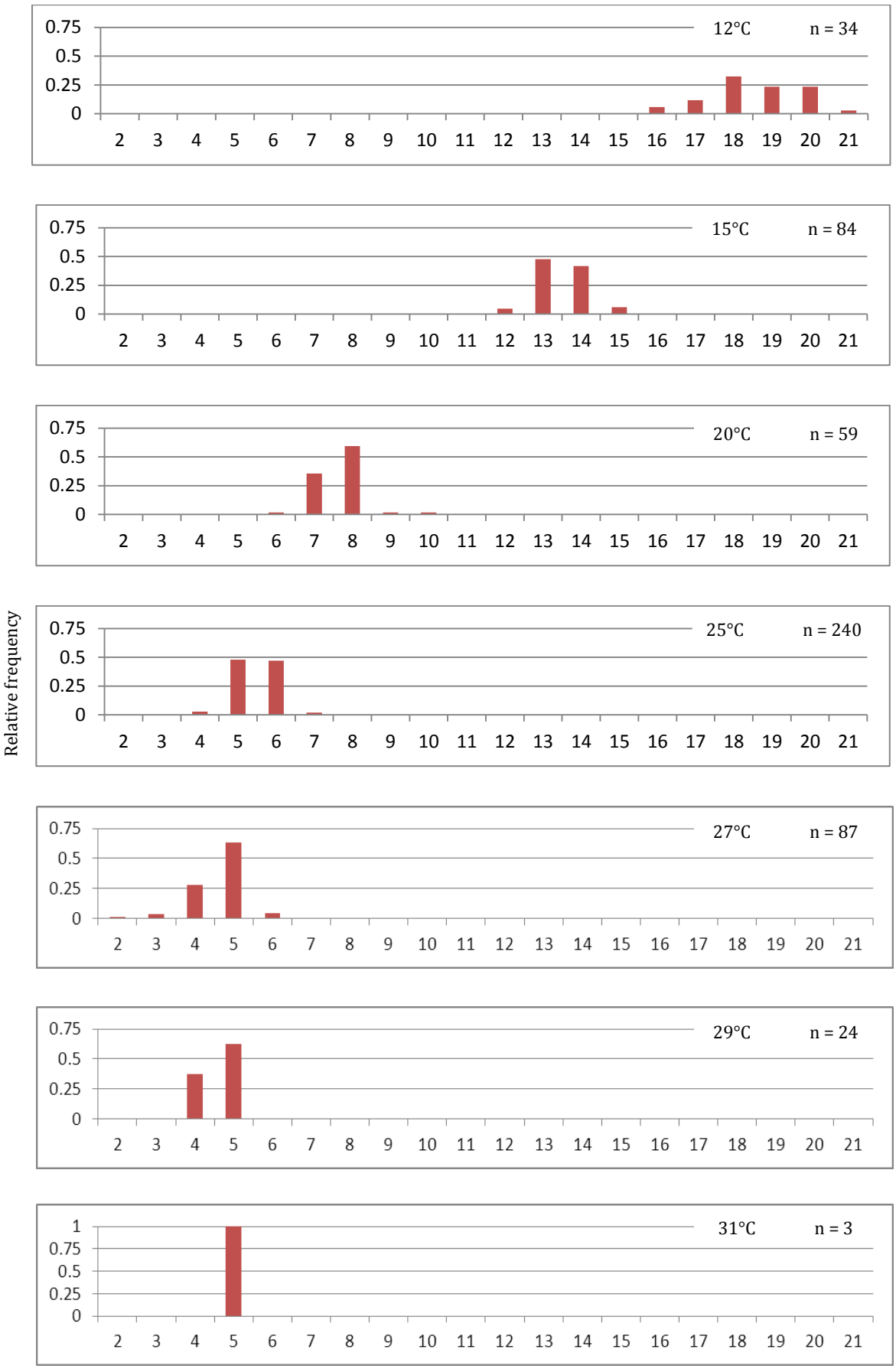

Figure A I-9 Relative frequency distributions (in days) of development times for *G. lineola* pupae at different constant temperatures.

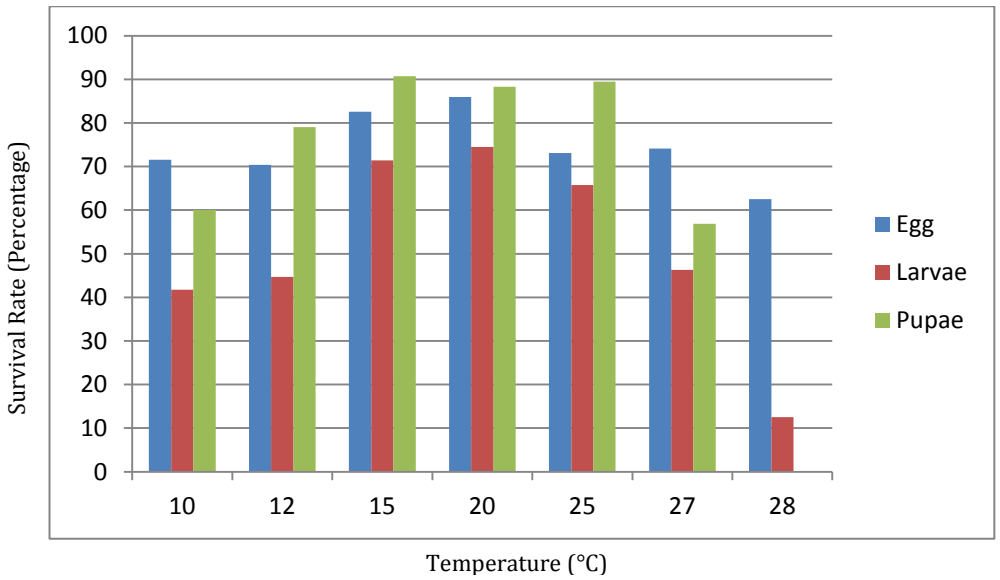

Figure A I-10 Percentage survival rates for *P. vulgatissima* eggs, larval and pupal stages at different constant temperatures.

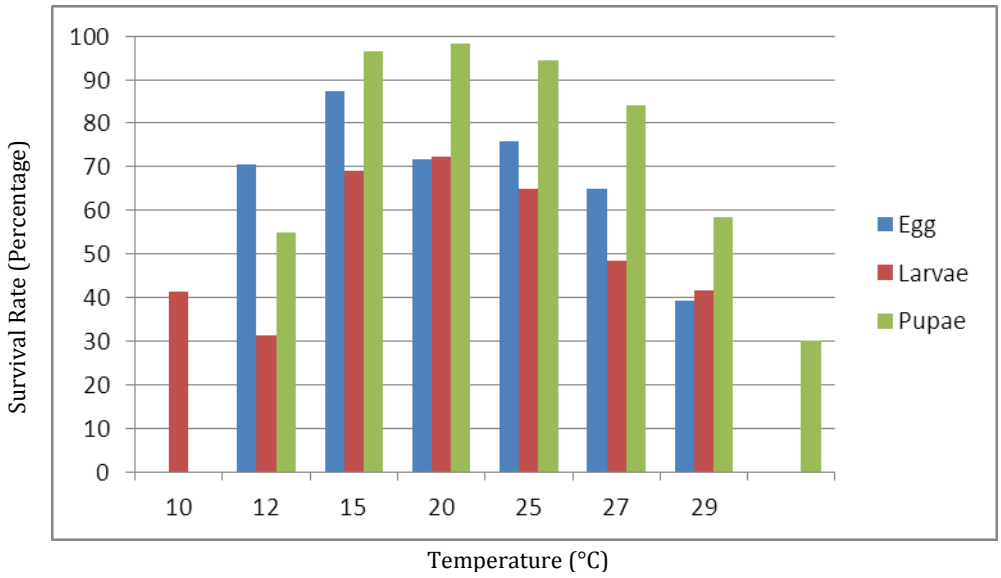

Figure A I-11 Percentage survival rates for *G. lineola* eggs, larval and pupal stages at different constant temperatures.

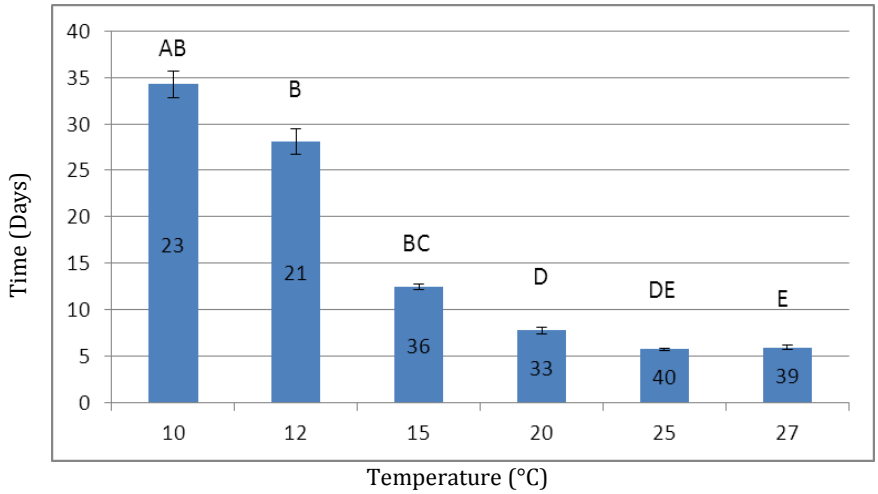

Figure A II-1 Mean (±SE) post-diapause development times in days for *P. vulgatissima* at different constant temperatures. Different letters indicated a significant difference between temperatures (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

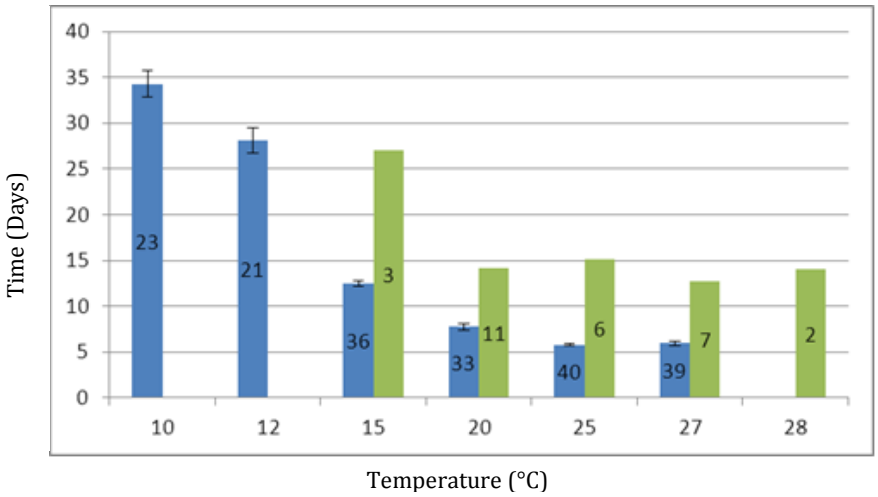

Figure A II-2 Mean (±SE) post-diapause development times (in days) compared to mean post-eclosion development times for *P. vulgatissima* at different constant temperatures.

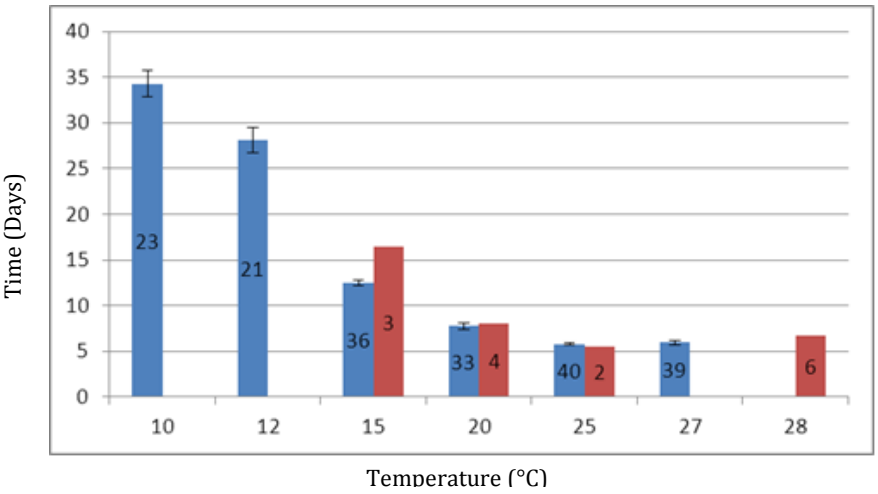

Figure A II-3 Mean (±SE) post-diapause development times (in days) for *P. vulgatissima* compared to mean post-diapause development times for *G. lineola* at different constant temperatures.

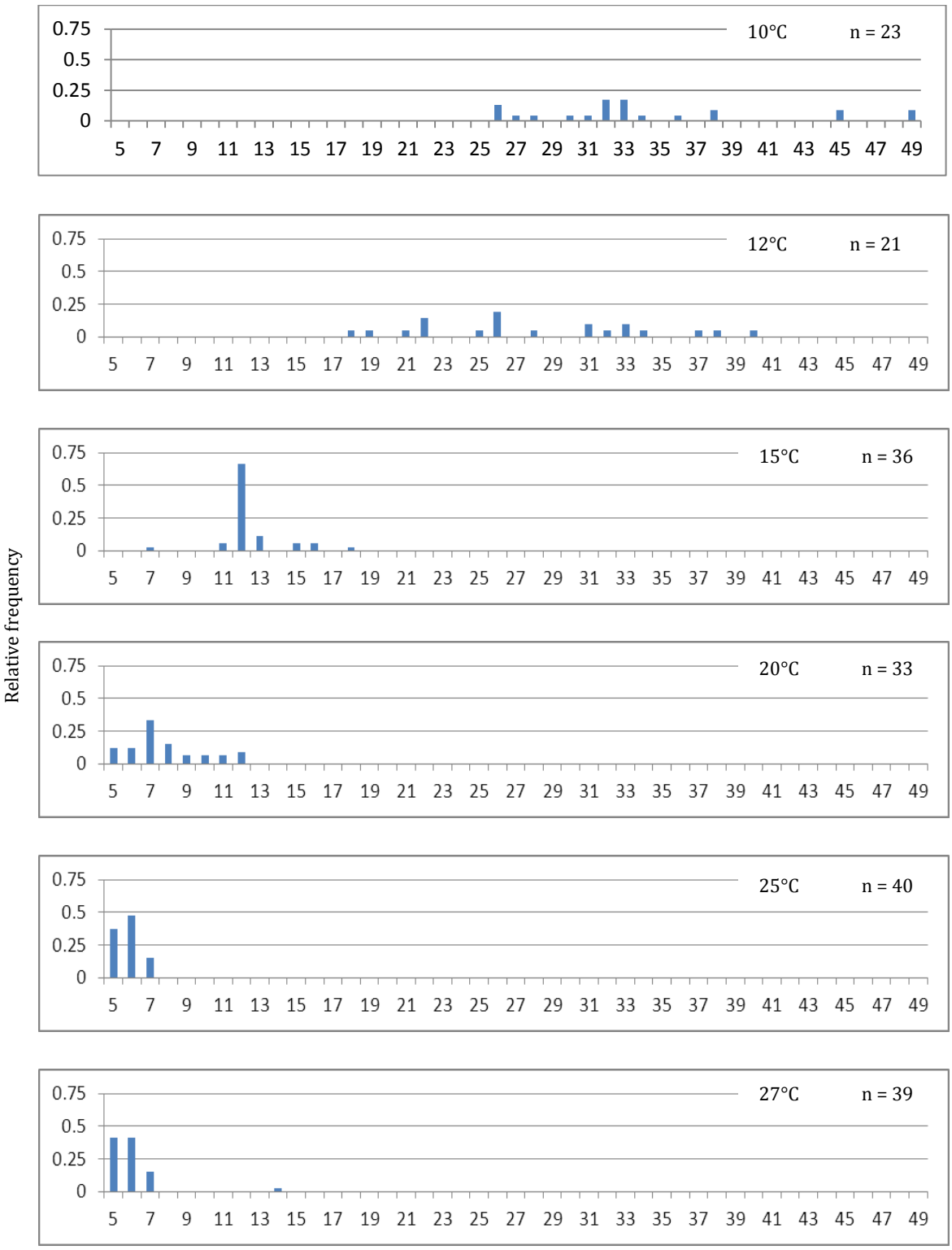

Figure A II-4 Relative frequency distributions (in days) of post-diapause development times for P. vulgatissima eggs at different constant temperatures.

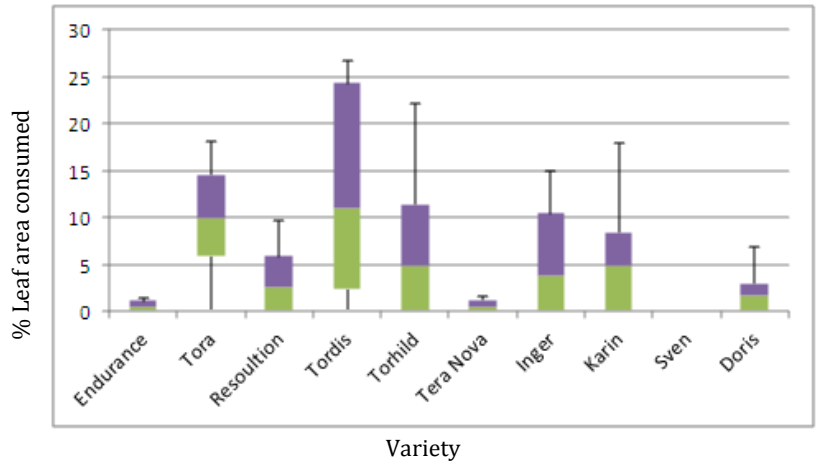

Figure A III-1 Mean percentage leaf disc area consumed (±SE) by P. vulgatissima adults during feeding trials on ten Salix varieties (P. Fanning, personal communication).

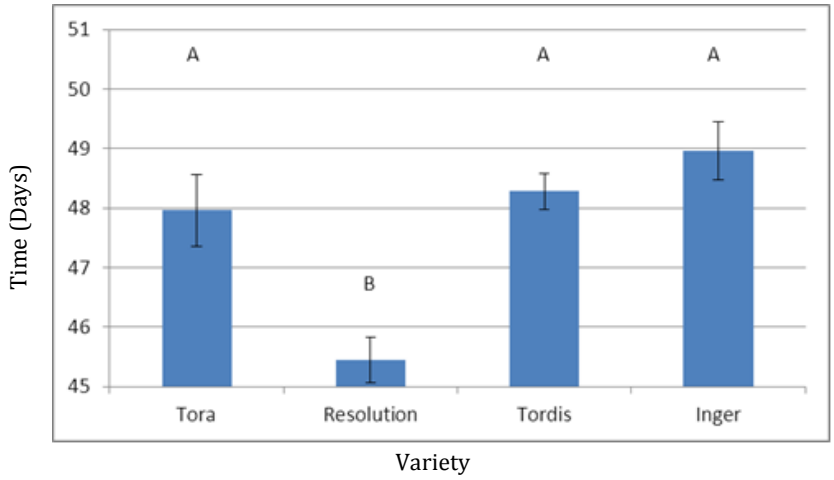

Figure A III-2 Mean (±SE) development times (in days) for *P. vulgatissima* larvae reared on different *Salix* varieties at 12°C. Different letters indicated a significant difference between varieties (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

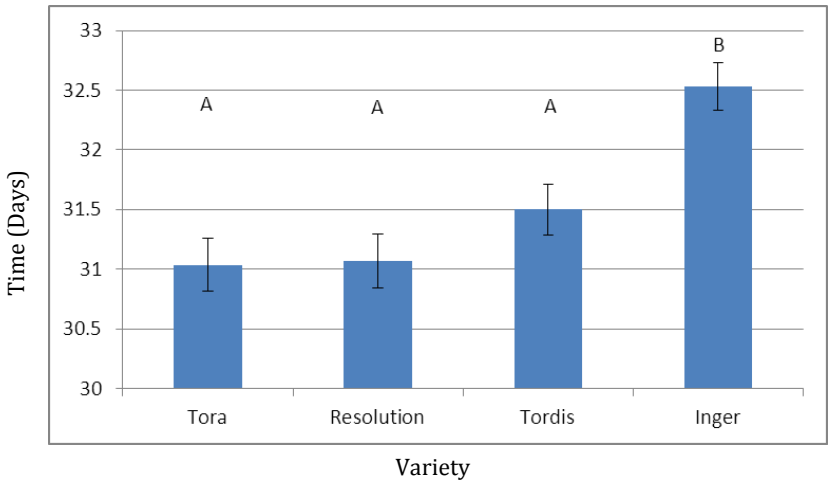

Figure A III-3 Mean (±SE) development times (in days) for P. vulgatissima larvae reared on different Salix varieties at 15°C. Different letters indicated a significant difference between varieties (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

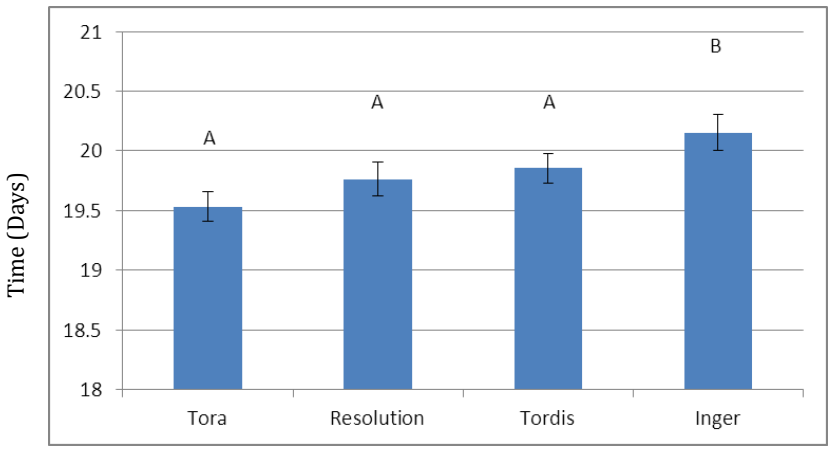

Figure A III-4 Mean (±SE) development times (in days) for *P. vulgatissima* larvae reared on different *Salix* varieties at 20°C. Different letters indicated a significant difference between varieties (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

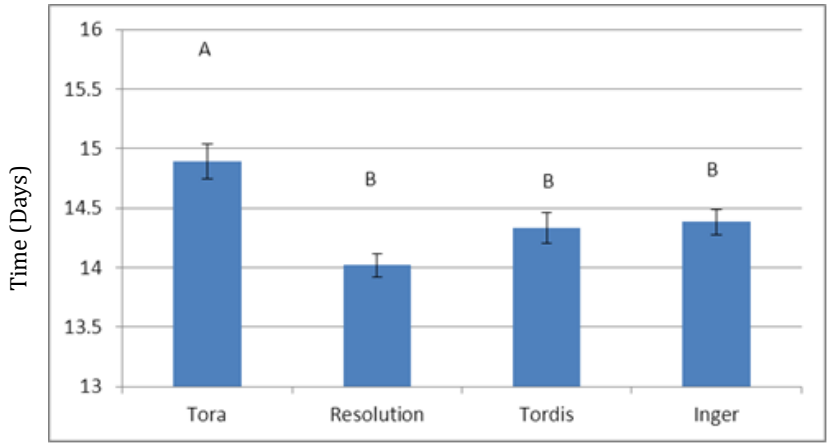

Figure A III-5 Mean (±SE) development times (in days) for *P. vulgatissima* larvae reared on different *Salix* varieties at 25°C. Different letters indicated a significant difference between varieties (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

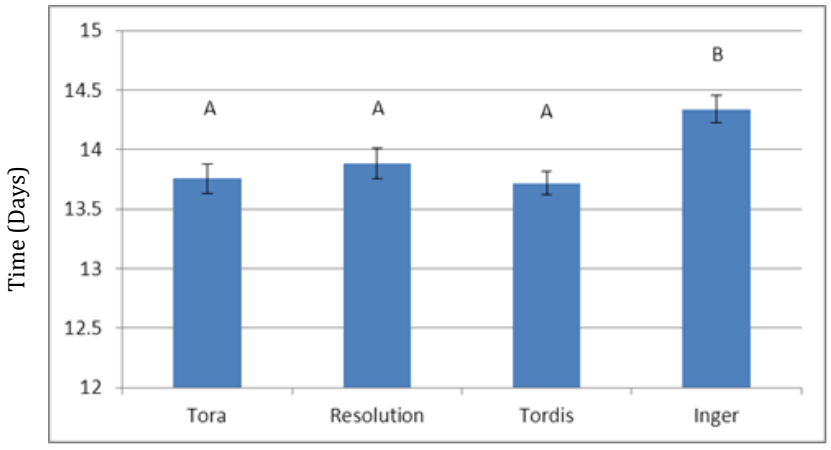

Figure A III-6 Mean (±SE) development times (in days) for *P. vulgatissima* larvae reared on different *Salix* varieties at 27°C. Different letters indicated a significant difference between varieties (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

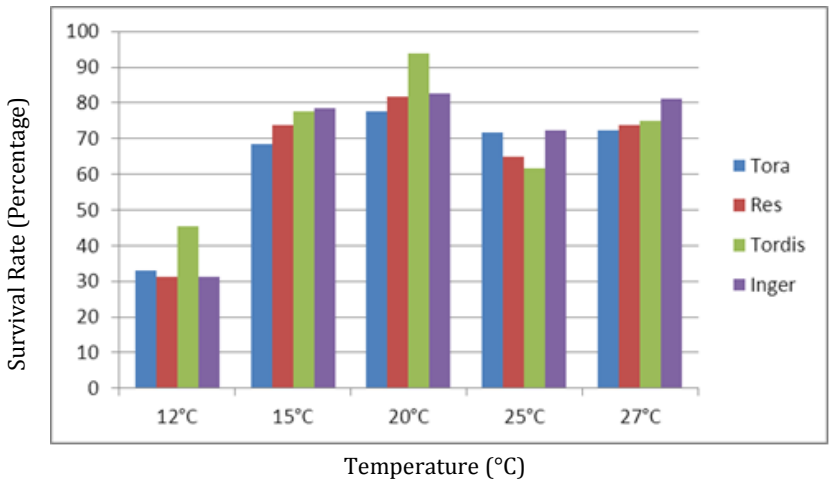

Figure A III-7 Percentage survival rates for P. vulgatissima larvae reared on different willow varieties at different constant temperature

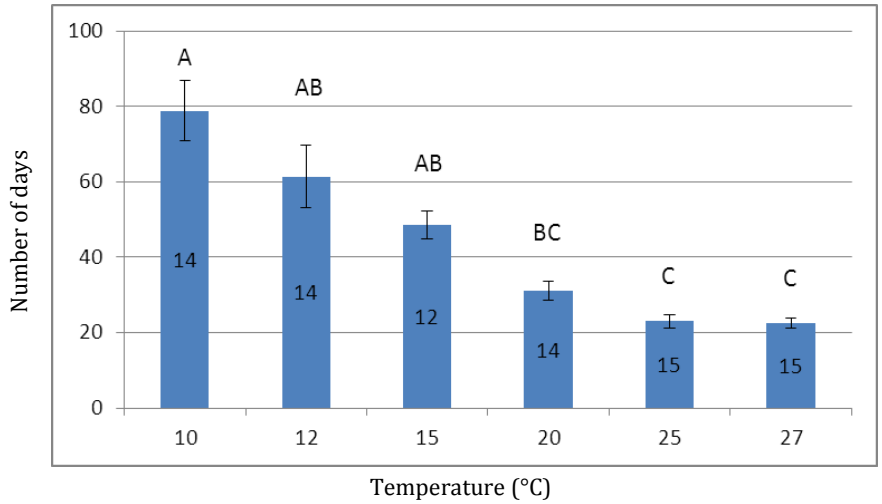

Figure A IV-1 Mean (±SE) oviposition period – the number of days from first to last oviposition – for *P. vulgatissima*. Different letters indicated a significant difference between temperatures (Kruskal-Wallis, P <0.001 and post hoc pairwise comparison, P = 0.05).

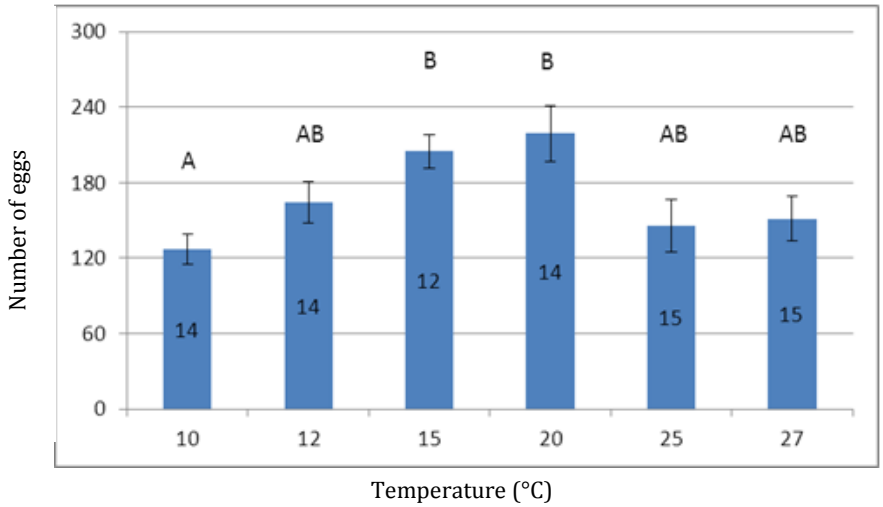

Figure A IV-2 Total fecundity (±SE) – total number of eggs laid per female – for *P. vulgatissima.* Different letters indicated a significant difference between temperatures (One-way ANOVA, P =0.003 and Tukey's post hoc test, P = 0.05).

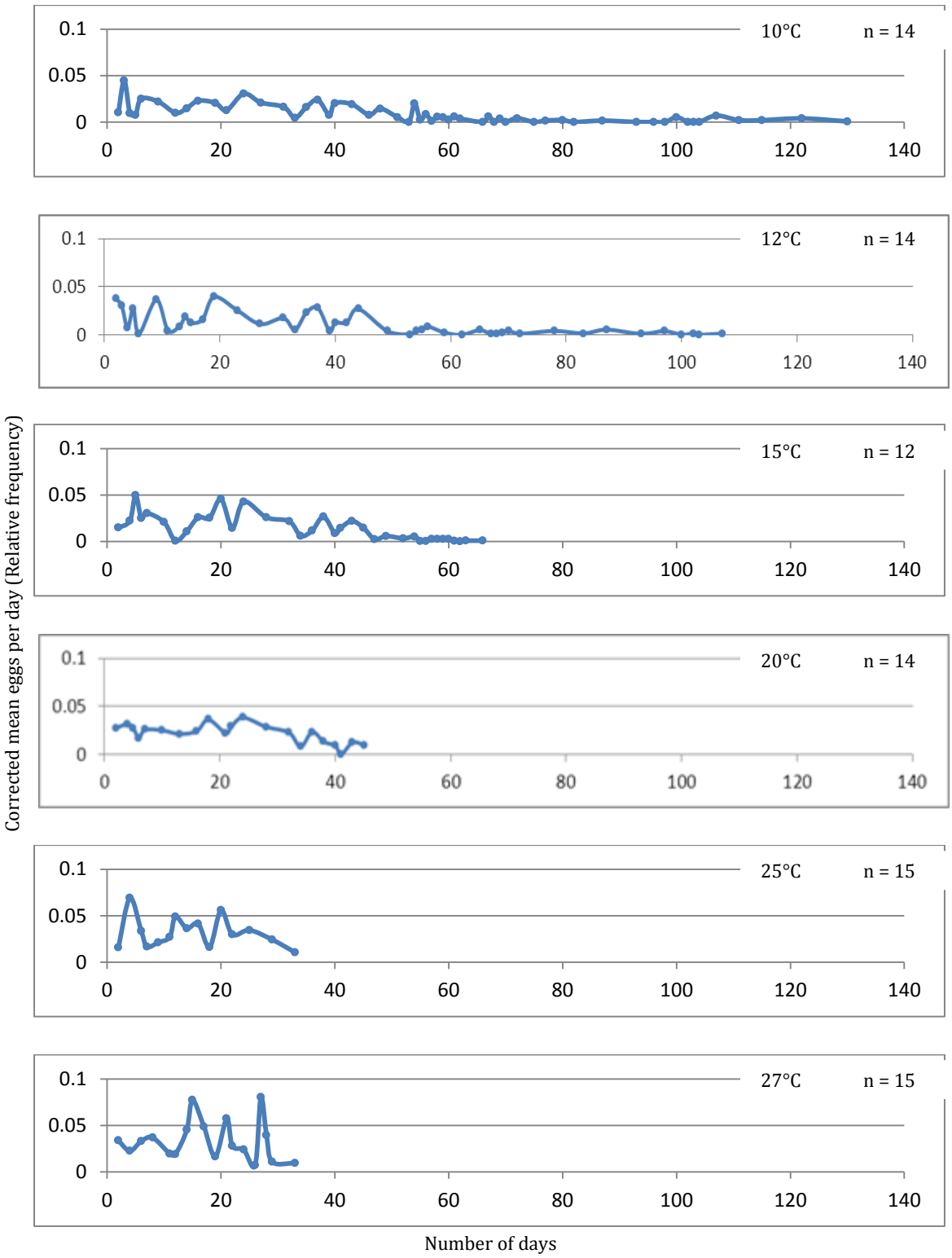

Figure A IV-3 Age-specific fecundity curves for *P. vulgatissima* (number of eggs per female/per day until final egg lay).

this function implements the unified budburst model and returns the starting day for the forcing period, along with the budburst day. Data is supplied to the function in "data" and should be a data frame with one column for each year, temperature data starting on the 1st September.

```
# INPUTS:
# params -> list of all budburst model parameters.
# data -> data frame with one column per year of temperature samples.
# julian -> logical, controls whether the output is in "julian day" or not.
unified_model <- function(params, data, julian=FALSE){
#Set the parameters for the model
Ca <- params["Ca"]
Cb <- params["Cb"]
Cc <- params["Cc"]
Fb <- params["Fb"]
Fc <- params["Fc"]
C_crit <- params["C_crit"]
F_crit <- params["F_crit"]

#first calculate Rc for each day - chilling phase.
Rc <- 1/(1+ exp(Ca*(data-Cc)**2 + Cb*(data -  Cc)))
# Enforcing limits the to Rc value (in case of bad parameter values.)
Rc[data > 10 ] = 0.0
Rc[data < -5 ] = 0.0

#find the onset of quiescence (where cumulative sum of Rc is greater than critical value.)
Rc <- cumsum(Rc)
Rc[Rc < C_crit] <- 1
Rc[Rc > C_crit] <- 0
quiescence <- colSums(Rc)

#calculate the Rf for each day - forcing phase
Rf <- 1/(1+ exp(Fb*(data -  Fc)))
# limit minimum value to 0.0
Rf[data < 0 ] = 0.0

#remove the days before the forcing phase.
for (ii in 1:ncol(data)){
Rf[1:quiescence[ii], ii] = 0.0
}

#find the budburst day.
Rf <- cumsum(Rf)
Rf[Rf < F_crit] <- 1
Rf[Rf > F_crit] <- 0
budburst <- colSums(Rf)

#convert to julian date format if required.
if (julian == FALSE){
budburst <- budburst - 122
quiescence <- quiescence - 122
}
```

```
#form the output data frame with predictions of the budburst for each station/year.
prediction <- as.data.frame(t(rbind(budburst_prediction=budburst,
quiescence_prediction=quiescence)))
prediction$Station_Name_Year <- as.vector(rownames(prediction))
rownames(prediction) <- NULL
prediction
}

# Script to find optimal parameters for budburst model. A parameter search is run using
the "Nelder-Mead" non-linear optimisation technique to minimise errors between
predicted and actual budburst values for each year of data.

# STARTUP
#Run this first section to set everything up

#load the data:
data <- read.csv("temperature_data_all_trees.csv")
budburst <- read.csv("budburst_data_all_trees.csv")

#remove the columns that we don't need
data$Date <- NULL
data$Julian.day <- NULL
data$X <- NULL

# HOW TO RUN THE MODEL FOR ONE SET OF PARAMETER VALUES

#load the model function from the unified model.R file
source("unified_model.r")
source("make_plot.r")

#get the budburst data from the model.
params <- c(Ca=0.2, Cb=9, Cc=9, Fb=-4.19, Fc=3.73, C_crit=35, F_crit=61.7)
#test of prediction model:
prediction <- unified_model(params, data=data)
make_plot(budburst, prediction)

# CODE TO RUN THE OPTIMISATION PROCEDURE

#need to load the function that runs the model for a set of parameters and just returns the
value that we will optimise - i.e. the MSE.

source("get_error.r")

#set the initial parameters:
params <- c(Ca=0.2, Cb=9, Cc=9, Fb=-4.19, Fc=3.73, C_crit=35, F_crit=61.7)

#now run the optimisation, passing in the data and the answer so that we can calculate the
error
# run an optimisation function - minimization using numerical gradient, with original
parameter
# values set as in "params"
result <- optim(p=params, get_error, gr=NULL,
        data=data, measured=budburst$Budburst_Day,
        method="Nelder-Mead", control=list(trace=3))
```

```
#view the data after the optimisation
params <- result$par
make_plot(budburst, unified_model(params, data))

# RUN THE OPTIMISATION OVER A RANGE OF INITIAL VALUES

source("get_error.r")
source("unified_model.R")
source("make_plot.r")
all_results <- data.frame()

#set the number of iterations (5000)
for (i in 1:5000) {

 print (paste(" ----- STARTING ITERATION ", i, " -----"))

 #generate a random set of initial parameters (runif produces a random number):
 #change the ranges here to search a greater range of options in the space:
 params <- c(Ca=runif(1, -5, 5),
          Cb=runif(1, -10, 10),
          Cc=runif(1, -10, 10),
          Fb=runif(1, -10, 10),
          Fc=runif(1, -10, 10),
          C_crit=runif(1, 10, 150),
          F_crit=runif(1, 10, 150) )
 #run the optimisation procedure
 result <- optim(p=params, get_error, gr=NULL,
             data=data, measured=budburst$Budburst_Day,
             method="Nelder-Mead", control=list(trace=2))
 #save the results
 this_result <- cbind(as.data.frame(t(result$par)), as.data.frame(result$value))
 colnames(this_result)[8] <- "MSE"
 all_results <- rbind(all_results, this_result)
}

#save results to a csv file for viewing in Microsoft Excel:
write.csv(all_results, file="optimisation_results_random_values.csv")

#Find best results
minimumIteration <- which.min(all_results$MSE)
bestParams <- as.numeric(all_results[minimumIteration,1:7])
names(bestParams) <- colnames(all_results)[1:7]

#visualise result:
prediction <- unified_model(bestParams, data)
make_plot(budburst, unified_model(bestParams, data))

# Function to calculate Mean Squared Error (MSE) for the budburst model.
# INPUTS:
# params -> parameter values for budburst model
# data -> Input data for model for prediction
# measured -> Actual budburst values for each year.

get_error <- function(params, data, measured){
 #laod the model
```

```
  source("unified_model.r")
  #get the budburst prediction from the model using the current params.
  prediction <- unified_model(params, data=data)
  #calculate the MSE.
  MSE <- sqrt(mean((measured - prediction$budburst_prediction)**2))
}
```

The following m-files are utilities that are used to calculate the number of days required for individuals emerging in proportions of *P. vulgatissima* to complete different life-cycle stages depending on daily day-length and daily mean temperature inputs. The individual m-files are separated by "#####". Although these files are positioned in a way that represents their order of execution, only inputs in the main function m-file are subject to change.

```
#########################################################################

%% script for converting Microsoft Excel files containing temperature
and day-length data to mat-files for use in main function;

directory = 'input';     % input represents folder containing Microsoft
Excel files with temperature data for synoptic stations;

files = ls(directory);   % Gets a list of all the files in the
directory

for i = 3:size(files, 1)
   file = files(i,:);
   data = xlsread([directory, file]);
   name = file(1:strfind(file, '.')-1);
   name = [directory, name];
   save(name, 'data');
   clear data name
end

#########################################################################

%% script for loading mat-files containing station temperature data,
and  chill day and thermal time unit data associated with bud-burst
model;

function [TempData, ThermalUnits, ChillDays] = loadData(year, station)

directory = 'input';          % input represents folder containing
mat-files with  temperature data for synoptic stations;

files = ls(directory);        % gets a list of all the files in the
directory;

for i = 1: size(files,1)      % looks through all the file names and
finds the file whose name contains the year(s) as selected for user
inputs in main function script;
  if strfind(files(i,:), num2str(year))
     break
  end
end

file = files(i,:);
file = [directory, file];     % selects the found file from above
temp = load(file);            % loads the file
data = temp.data;             % extracts the data from the struct
```

```
% function selects requested data - depending on if the year is an even
or odd positive integer, it is positioned differently in the mat-file;
if mod(year, 2) == 1     % odd year selection
  TempData     = data(:,5 + station -1);
  ThermalUnits = data(:,48 + station -1);
  ChillDays    = data(:,79 + station -1);
else                       % even year selection
  TempData     = data(:,99 + station -1);
  ThermalUnits = data(:,142 + station -1);
  ChillDays    = data(:,173 + station -1);
end


######################################################################


%% script for loading mat-files containing station day-length data;

function [Light_Hours] = loadTimeData(station, Temp)

file = 'input';            % selects the day-length data file;

temp = load([pwd file]);   % loads the file;
data = temp.data;          % saves the data;

% Depending on the number of days in the temperature data file (365
days or 360 days), the light hours data below comes from two different
sections of the data, day-length calculated over a normal 365 day year
and day-length calculated over a 360 day year;
if length(Temp) == 365
  Light_Hours = data(:, 3 + 2*station -2);
else
  Light_Hours = data(:, 35 + 2*station -2);
end


######################################################################
%                        This is the main function                   %

close all    % clear workspace, close figures & clear command window;
clc          % clear all input and output from command window;

global oviposition             % Global variable (can be accessed
across functions without being passed in as an input)

%------------------------------
% USER INPUTS
years        = input;          % temperature file corresponding to
year, usually range such as 1961:2099 but input can be single year
also;
stations     = 1:14;           % temperature file corresponding to
climatic station, usually range such as 1:14, input can be single also;
Percentage   = [0.05, 0.5, 0.95];     % percentage emergence being
investigated, usually 0.05(5%), 0.50(50%) and 0.95(95%);
BB_variation = 0;              % Variation of day of budburst in
relation to calculated standard deviations (i.e. +/- 13);
Light_Cutoff = 14.92;          % used to change CDL (input as decimal
place) in relation to calculated confidence intervals (i.e.
14.46/14.92/15.41);

oviposition.newModel = 0;     % Set to 0 to employ the one function
oviposition model, accepted as representative in published material.
```

```
Set to 1 to employ unconfirmed as representative multi-function
oviposition model;

oviposition.numTempDaysAvg  =  0;  % Associated with multi-function
oviposition model. States the number of days the moving average is
calculated over


%------------------------------

% Global variable which can be seen across all functions
global flagCycle                    % Global Flag which is set to 1
whenever sexual maturation has been completed beyond CDL. Ensures model
completion

% Initialise variables
ProportionDay_AllStations   = cell(1, length(years));
S_total_AllStations         = cell(1, length(years));
S_Day_AllStations           = cell(1, length(years));
Weibull_AllStations         = cell(1, length(years));

for i = 1 : length(years)
  ProportionDay_AllStations{i} = zeros(60, 14*3);
end
WeibullMatrix = cell(1,3);
S_totalMatrix = cell(1,3);
S_DayMatrix   = cell(1,3);

Idx = 0;

% Run function over all years specified by user
for year = years
  Idx = Idx + 1;
  % Run function over all stations specified for the given year
   for station = stations

     % load temperature data;
     [TempData, ThermalUnits, ChillDays] = loadData(year, station);
     % load daylight data;
     [Light_Hours] = loadTimeData(station, TempData);

     PropDayMatrix    = zeros(60, 3);
     % matrix that holds the number of days from Nov 1st when each stage
     reaches the specified emergence percentage (i.e. 5%, 50% and 95%);

     WeibullMatrix{1} = zeros(length(TempData), 60);
     WeibullMatrix{2} = zeros(length(TempData), 60);
     WeibullMatrix{3} = zeros(length(TempData), 60);
     % matrixes that save the development time distribution (Weibull
     function) accumulation (per daily time-steps) for proportion
     emergence percentage (i.e. 5%, 50% and 95%) of each occurring life-
     cycle stage from function initiation;

     S_totalMatrix{1} = zeros(length(TempData), 60);
     S_totalMatrix{2} = zeros(length(TempData), 60);
     S_totalMatrix{3} = zeros(length(TempData), 60);
     % matrixes that save the development rate (non-linear function)
     accumulations for each proportion emergence percentage (i.e. 5%,
     50% and 95%) of each occurring life-cycle stage from function
     initiation;

     S_DayMatrix{1}   = zeros(length(TempData), 60);
     S_DayMatrix{2}   = zeros(length(TempData), 60);
```

```
S_DayMatrix{3}   = zeros(length(TempData), 60);
% matrixes that save the development rate (non-linear function)
daily time-steps values for proportion emergence percentage (i.e.
5%, 50% and 95%) of each occurring life-cycle stage from function
initiation;


%% 1) runs budburst model from 1st Nov, calculating budburst day
for a given year
[PropDayMatrix(1,:)] = findBudBurstDay(ThermalUnits, ChillDays);

%% 2) Begin post diapause function (using budburst day +1 day (+/-
13 days)) returning 1st day of egg-lay
[PropDayMatrix(2,:), WeibullMatrix{1}(:,1), S_totalMatrix{1}(:,1),
S_DayMatrix{1}(:,1)] =...
postDiapause(TempData,          PropDayMatrix(1,1)+1+BB_variation,
Percentage);

WeibullMatrix{2}(:,1) = WeibullMatrix{1}(:,1);   % Holds data for
50%
WeibullMatrix{3}(:,1) = WeibullMatrix{1}(:,1);   % Holds data for
95%
S_totalMatrix{2}(:,1) = S_totalMatrix{1}(:,1);
S_totalMatrix{3}(:,1) = S_totalMatrix{1}(:,1);
S_DayMatrix{2}(:,1)   = S_DayMatrix{1}(:,1);
S_DayMatrix{3}(:,1)   = S_DayMatrix{1}(:,1);

for i = 1 : 3       % Looks through all percentages individually -
5% 50% 95%

  stage = 3;        % Used to specify where to place the data in
  the matrices
  flagCycle = 0;    % Used to flag when sexual maturation has
  completed beyond CDL

  while flagCycle == 0

    %% 3) Begin oviposition Period (using egg lay day) returning
    1st day of egg development

    % [OutputDay, Weibull_dev, S_total, S_Day] = postDiapause(Temp,
    StartDay, Percentage)
    [PropDayMatrix(stage,i),WeibullMatrix{i}(:,stage-1),
    S_totalMatrix{i}(:,stage-1), S_DayMatrix{i}(:,stage-1)] = ...
    ovipositionPeriod(TempData,PropDayMatrix(stage-1,i)+1,
    Percentage(i));

    stage = stage + 1;

    %% 4) Begin egg development (using oviposition period day)
    returning 1st day of larvae development
    [PropDayMatrix(stage,i),WeibullMatrix{i}(:,stage-1),
    S_totalMatrix{i}(:,stage-1), S_DayMatrix{i}(:,stage-1)] = ...
    eggDevelopment(TempData,          PropDayMatrix(stage-1,i)+1,
    Percentage(i));

    stage = stage + 1;

    %% 5) Begin larvae development (using egg development day)
    returning 1st day of pupae development
    [PropDayMatrix(stage,     i),     WeibullMatrix{i}(:,stage-1),
    S_totalMatrix{i}(:,stage-1), S_DayMatrix{i}(:,stage-1)] = ...
```

```
            larveDevelopment(TempData,          PropDayMatrix(stage-1,i)+1,
            Percentage(i));

            stage = stage + 1;

            %% 6) Begin pupae development (using larvae development day)
            returning 1st day of sexual maturation development
            [PropDayMatrix(stage,     i),     WeibullMatrix{i}(:,stage-1),
            S_totalMatrix{i}(:,stage-1), S_DayMatrix{i}(:,stage-1)] = ...
            pupaeDevelopment(TempData,          PropDayMatrix(stage-1,i)+1,
            Percentage(i));

            stage = stage + 1;

            %% 7) Begin sexual maturation development (using sexual
            maturation development day)
                            %   - Depending on CDL either
                            %       - Before: Begin oviposition period
                            %       - During: Begin again and give flag?
                            %       - After: Stop
            [PropDayMatrix(stage,     i),     WeibullMatrix{i}(:,stage-1),
            S_totalMatrix{i}(:,stage-1), S_DayMatrix{i}(:,stage-1)] = ...
            sexualMaturation(TempData,          PropDayMatrix(stage-1,i)+1,
            Percentage(i), Light_Hours, Light_Cutoff);

            stage = stage + 1;

          end    % End of while loop
        end      % End of for loop

                % Code used to remove any unused columns in our matrices
            PropDayMatrix(sum(PropDayMatrix,2) == 0,:)          = [];
            WeibullMatrix{1}(:, sum(WeibullMatrix{1},1) == 0)   = [];
                Weibul      lMatrix{2}(:, sum(WeibullMatrix{2},1) == 0) =
[];
            WeibullMatrix{3}(:, sum(WeibullMatrix{3},1) == 0)   = [];
            S_totalMatrix{1}(:, sum(S_totalMatrix{1},1) == 0)   = [];
            S_totalMatrix{2}(:, sum(S_totalMatrix{2},1) == 0)   = [];
            S_totalMatrix{3}(:, sum(S_totalMatrix{3},1) == 0)   = [];
            S_DayMatrix{1}(:, sum(S_DayMatrix{1},1) == 0)       = [];
            S_DayMatrix{2}(:, sum(S_DayMatrix{2},1) == 0)       = [];
            S_DayMatrix{3}(:, sum(S_DayMatrix{3},1) == 0)       = [];

                %% Populate the full PropDayMatrix

            ProportionDay_AllStations{Idx}(1:size(PropDayMatrix,1),
3*station-2:3*station) = PropDayMatrix;
            S_Day_AllStations{Idx}   = S_totalMatrix;
            S_total_AllStations{Idx} = S_DayMatrix;
            Weibull_AllStations{Idx} = WeibullMatrix;


                clear temp stage i t

            end

                % Delete any unused rows from the results matrix

            ProportionDay_AllStations{Idx}(sum(ProportionDay_AllStations{Id
x},2) == 0,:) = [];
end
```

```
#########################################################################

%% function to calculate when budburst day has occurred, using thermal
time unit and chill day accumulations, in temperature data files for
synoptic stations;
function PredBudBurst = findBudBurstDay(ThermalUnits, ChillDays)

c     = -inf;     % Used to step into the while loop below the first
time;
Day   = 0;        % Used to start at day one below;

while c < 0       %  Continues  in  loop  below  until  "c"  becomes
positive;
   Day = Day + 1;                % Increments the day;
   x   = ChillDays(Day);         % Takes the current chill day value;
   y    = ThermalUnits(Day);     % Takes the current thermal time unit
   value;

   c = y - 486.29469 * exp(-0.01393*x);    % Equation of the line to
   calculate c value - if c becomes positive then we have predicted
   budburst;
end

PredBudBurst = Day;          %  Saves  the  day  that  budburst  is
predicted;


#########################################################################

%% function to calculate oviposition period stage completion;
%% Depending on the stage being examined different variables are passed
into the function


%    FUNCTION    [OutputDay,    Weibull_devm    S_total,    S_Day]    =
stageProportions(Temp, PredBudBurst, Percentage, vars, varargin)
%
%   INPUTS:     Temp:          temperature data;
%               PredBudBurst:  day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%               vars:          variables   used   to   calculate   stage
equations
%               varargin:            Additional  variables  required  for
some stages
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function     [OutputDay,     Weibull_dev,     S_total,     S_Day]     =
stageProportions(Temp, PredBudBurst, Percentage, vars, varargin)


%% Set Variables

global flagCycle   % If  we  change  this  here,  will  automatically  be
changed in the main file
global oviposition % Gain access to the global variable
```

```
StartDay        = PredBudBurst -1;              % So that it alligns up.
i.e. StartDay + Day (as Day is indexed from 1)
EndDay          = length(Temp);
NumDays         = EndDay - StartDay;
S_Day           = zeros(NumDays,1);     %creates vector of zeros (number
of days, one column)
S_total         = zeros(NumDays,1);     %creates vector of zeros (number
of days, one column)
OutputDay       = zeros(length(Percentage),1);
Weibull_dev     = zeros(NumDays,1);
Weibull_dev_old = zeros(NumDays,1);
temp_dev        = zeros(NumDays,3);

if StartDay == 0    % Stops the program going in a loop and starting at
day 1 again
  return
end

for Day = 1:NumDays %for - starts loop (day one)

  % If we are at the sexual maturation stage then we need to check if
  % the cycle should stop after this stage or continue for another
loop.
  if nargin > 4                         %   If   the   number   of   input
arguments is greater than 4 (then stage is either oviPos or SexMat)
    if varargin{1} == 5                 % If the current stage is "Sexual
   Maturation" then we need to check whether this should be the last
   cycle through the developmental stages
      Light_Hours  = varargin{2};
      Light_Cutoff = varargin{3};

                        % Check to first ensure we have enough data
      if (StartDay + Day) <= (length(Temp) -1)
                        % If the amount of light per day is decreasing
AND there is less daylight than the predefined cut-off
        if (Light_Hours(StartDay + Day +1) < Light_Hours(StartDay +
      Day)) && (Light_Hours(StartDay + Day) < (Light_Cutoff)) && Day >
      1
                        %  If  the  development  has  not  reached  the
required percentage
          if Weibull_dev(Day-1) < Percentage
                        % Then we set the global flag to 1. This
indicates that the cycle should not start again
            flagCycle = 1;
          end
                        end
                  end
            end
  end

                  % If we are looking at oviposition then we need to
                  compute S_Day using a different equation
       if nargin > 4
    if varargin{1} == 2
                  % Used to calculate oviposition development
                  S_Day(Day)      =  vars.a  +  (vars.b*Temp(StartDay  +
Day)) + (vars.c* exp(Temp(StartDay + Day)));
            else
                  S_Day(Day)     =  exp(vars.p*Temp(StartDay  +  Day))  -
exp((vars.p*vars.tmax)-((vars.tmax  -  Temp(StartDay  +  Day))/vars.d))+
vars.l;
            end
       else
```

```
            % Daily development
            S_Day(Day)       =  exp(vars.p*Temp(StartDay  +  Day))  -
exp((vars.p*vars.tmax)-((vars.tmax  -  Temp(StartDay  +  Day))/vars.d))+
vars.l;
        end

  if S_Day(Day) < 0   % If the daily dev is less than one
     S_Day(Day) = 0;  % Set the value to zero
  end

       %% Updating S_total: Set S_total to the value of S_Day the
first time around

  if (Day == 1)        % If we are on the first day, or if we have gone
into a new stage
     S_total(Day) = S_Day(Day);              % Save the Daily dev value
  else
     S_total(Day) = S_total(Day - 1) + S_Day(Day);
  end

  %% Update Weibulls

  if nargin > 4
     if varargin{1} == 2
       temp_curr = mean(Temp(StartDay + Day - oviposition.numTempDaysAvg
     : StartDay + Day));
       % If oviposition
       % Do combination

       % Calculate the equations for the three different temperatures
       for i = 1 : 3
         temp_dev(Day,i)  =  1-  exp(  -((S_total(Day)  -  vars.Gamma(i))  /
       vars.Eta(i))^vars.Beta(i)); % Calculate the Prob using current
       Weibull data
       end
       % If the current temperature is less than or equal to 12 degrees
     then use
       % the 12 degree line
       if temp_curr <= 12
         Weibull_dev(Day) = temp_dev(Day,1);

         % If the current temperature is greater than or equal to 20
       degrees then use
         % the 20 degree line
       elseif temp_curr >= 20
         Weibull_dev(Day) = temp_dev(Day,3);

         % Otherwise we need to use some combination of the equations
       else
         % If the current temperature is or above 15 degrees (and
         % less than 20 as that was checked above)
         if temp_curr >= 15
           % The gap between the temperatures (20-15)
           tempGap  = 5;
           % The degree difference between the current temperature
           % and the lower level of 15 degrees
           tempStep = temp_curr - 15;
           % Find a linear combination of the equations depending
           % on the current temperature
           Weibull_dev(Day)   =   temp_dev(Day,2)   -   (temp_dev(Day,2)   -
         temp_dev(Day,3))*(tempStep/tempGap);

           % If the current temperature is below 15 degrees (and
```

```
          % greater than 12 as that was checked above)
        else
          % The gap between the temperatures (12-15)
          tempGap  = 3;
          % The degree difference between the current temperature
          % and the lower level of 12 degrees
          tempStep = temp_curr - 12;
          % Find a linear combination of the equations depending
          % on the current temperature
          Weibull_dev(Day)  =  temp_dev(Day,1)  -  (temp_dev(Day,1)  -
        temp_dev(Day,2))*(tempStep/tempGap);
        end
      end
      % Just used as a comparison plot
      Weibull_dev_old(Day)          =  1-  exp(  -((S_total(Day)  -
    vars.GammaOld) / vars.EtaOld)^vars.BetaOld); % Calculate the Prob
    using current Weibull data

    else
      % If not ovipostition : Find Weibull stage as before
                  Weibull_dev(Day)       = 1- exp( -((S_total(Day) -
vars.Gamma) / vars.Eta)^vars.Beta); % Calculate the Prob using current
Weibull data
    end
    else
        Weibull_dev(Day)     = 1- exp( -((S_total(Day) - vars.Gamma) /
vars.Eta)^vars.Beta); % Calculate the Prob using current Weibull data
    end

    % If the Prob value is complex then set it to 0 (values were very
small anyway)
    if ~isreal(Weibull_dev(Day))
        Weibull_dev(Day) = 0;
    end
    % Setting a threshold
    if Weibull_dev(Day) > 0.99995
        Weibull_dev(Day) = 1;
    end

    % Find days which first go above the desired percentage ranges
    for i = 1 : length(Percentage)
        temp  =  find(Weibull_dev  >=  Percentage(i),  1,  'first')  +
StartDay;
        if ~isempty(temp)
            OutputDay(i) = temp;
        end
    end

end


% Added here to allow you to switch back to old model
if nargin > 4
    if varargin{1} == 2 && ~oviposition.newModel
        Weibull_dev = Weibull_dev_old;

        for Day = 1:NumDays
            % If the Prob value is complex then set it to 0 (values
were very small anyway)
            if ~isreal(Weibull_dev(Day))
                Weibull_dev(Day) = 0;
            end
            % Setting a threshold (NEED TO CHECK)
```

```
            if Weibull_dev(Day) > 0.99995
                Weibull_dev(Day) = 1;
            end

            % Find days which first go above the desired percentage
ranges
            for i = 1 : length(Percentage)
                temp = find(Weibull_dev >= Percentage(i), 1, 'first') +
StartDay;
                if ~isempty(temp)
                    OutputDay(i) = temp;
                end
            end
        end
    end
end

% If we have come to the end of the year, set the flag
if sum(OutputDay) == 0
    flagCycle = 1;
end

% Used to align the Weibull day variable in time.
Weibull_dev = [zeros(StartDay, 1); Weibull_dev];
S_total     = [zeros(StartDay, 1); S_total];
S_Day       = [zeros(StartDay, 1); S_Day];


##########################################################################


%% function to calculate post-diapause stage completion;

%    FUNCTION    [OutputDay,    Weibull_devm    S_total,    S_Day]    =
postDiapause(Temp, StartDay, Percentage)
%
%   INPUTS:     Temp:          temperature data;
%               StartDay:      day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function [OutputDay, Weibull_dev, S_total, S_Day] = postDiapause(Temp,
StartDay, Percentage)

vars.Gamma = 0.72073;    % development time function variables;
vars.Eta   = 0.35170;
vars.Beta  = 1.79185;

vars.p     = 0.0091;    % development rate function variables;
vars.tmax  = 32.9460;
vars.d     = 1.6965;
vars.l     = -1.0714;

%% Runs the "stageProportions" function with the variables defined
above
[OutputDay,  Weibull_dev,  S_total,  S_Day]  =  stageProportions(Temp,
StartDay, Percentage, vars);
```

```
##########################################################################

%% function to calculate oviposition period stage completion;

%    FUNCTION    [OutputDay,    Weibull_devm    S_total,    S_Day]    =
ovipositionPeriod(Temp, StartDay, Percentage)
%
%   INPUTS:     Temp:          temperature data;
%               StartDay:      day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function     [OutputDay,     Weibull_dev,     S_total,     S_Day]     =
ovipositionPeriod(Temp, StartDay, Percentage)

vars.GammaOld  = -0.071627382; % development time function variables;
vars.EtaOld    = 0.511696883;
vars.BetaOld   = 1.699719588;

vars.Gamma(1)   =   0.001134224;  % development time function variables
for 12°C
vars.Gamma(2)    =  -0.241143358;  %  15°C  and  20°C  respectively  multi-
function
vars.Gamma(3)  = -0.405202325; % development time model

vars.Eta(1)    = 0.283046113;
vars.Eta(2)    = 0.662214784;
vars.Eta(3)    = 0.965717207;

vars.Beta(1)   = 1.262242895;
vars.Beta(2)   = 2.983019694;
vars.Beta(3)   = 3.376376139;

vars.a      = -0.00897;         % development rate function variables;
vars.b      =  0.00207;
vars.c      = -0.0000000000000049;

%% Main Function
[OutputDay,  Weibull_dev,  S_total,  S_Day]  =  stageProportions(Temp,
StartDay, Percentage, vars, 2);

##########################################################################

%% function to calculate egg stage completion;

%    FUNCTION    [OutputDay,    Weibull_devm    S_total,    S_Day]    =
eggDevelopment(Temp, StartDay, Percentage)
%
%   INPUTS:     Temp:          temperature data;
%               StartDay:      day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
```

```
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function     [OutputDay,     Weibull_dev,     S_total,     S_Day]     =
eggDevelopment(Temp, StartDay, Percentage)

vars.Gamma = 0.57301;    % development time function variables;
vars.Eta   = 0.47056;
vars.Beta  = 3.55922;

vars.p     = 0.0086;     % development rate function variables;
vars.tmax  = 37.7530;
vars.d     = 2.8126;
vars.l     = -1.0549;

%% Main Function
[OutputDay,   Weibull_dev,   S_total,   S_Day]   =   stageProportions(Temp,
StartDay, Percentage, vars);

########################################################################


%% function to calculate larvae stage completion;

% FUNCTION [OutputDay, Weibull_dev] = larvaeDevelopment(Temp, StartDay,
Percentage)
%
%   INPUTS:     Temp:          temperature data;
%               StartDay:      day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function     [OutputDay,     Weibull_dev,     S_total,     S_Day]     =
larvaeDevelopment(Temp, StartDay, Percentage)

vars.Gamma = 0.86520;    % development time function variables;
vars.Eta   = 0.16610;
vars.Beta  = 1.72236;

vars.p     = 0.0030;     % development rate function variables;
vars.tmax  = 30.3760;
vars.d     = 0.4374;
vars.l     = -1.0151;


%% Main Function
[OutputDay,   Weibull_dev,   S_total,   S_Day]   =   stageProportions(Temp,
StartDay, Percentage, vars);


########################################################################


%% function to calculate pupae stage completion;
```

```
%    FUNCTION    [OutputDay,    Weibull_devm    S_total,    S_Day]    =
pupaeDevelopment(Temp, StartDay, Percentage)
%
%   INPUTS:     Temp:          temperature data;
%               StartDay:      day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function     [OutputDay,     Weibull_dev,     S_total,     S_Day]     =
pupaeDevelopment(Temp, StartDay, Percentage)

vars.Gamma = 0.49903;    % development time function variables;
vars.Eta   = 0.53354;
vars.Beta  = 5.35016;

vars.p     = 0.0081;     % development rate function variables;
vars.tmax  = 32.0961;
vars.d     = 1.3694;
vars.l     = -1.0406;


%% Main Function
[OutputDay,  Weibull_dev,  S_total,  S_Day]  =  stageProportions(Temp,
StartDay, Percentage, vars);


########################################################################


%% function to calculate sexual maturation completion;

%    FUNCTION    [OutputDay,    Weibull_devm    S_total,    S_Day]    =
pupaeDevelopment(Temp, StartDay, Percentage, Light_Hours, Light_Cutoff)
%
%   INPUTS:     Temp:          temperature data;
%               StartDay:      day to start stage on;
%               Percentage:    emergence   percentage   to   be   reached
before the next stage begins;
%               Light_Hours:   The daily number of light hours
%               Light_Cutoff:  The cut-off threshold for daily light
%   OUTPUTS:    OutputDay:     day at which the next stage can start;
%               Weibull_dev:   Expected   Weibull   development   during
current stage
%               S_total:       Accumulation of daily developments
%               S_Day:         Daily development

function     [OutputDay,     Weibull_dev,     S_total,     S_Day]     =
sexualMaturation(Temp, StartDay, Percentage, Light_Hours, Light_Cutoff)

vars.Gamma = 0.72073; % development time function variables;

vars.Eta   = 0.3517;
vars.Beta  = 1.79185;

vars.p     = 0.0048; % development rate function variables;
vars.tmax  = 32.6388;
vars.d     = 1.3513;
vars.l     = -1.0370;
```

```
%% Main Function
[OutputDay, Weibull_dev, S_total, S_Day] = stageProportions(Temp,
StartDay, Percentage, vars, 5, Light_Hours, Light_Cutoff);
```

APPENDIX VII

Tables A VII-1 Budburst occurrence and emergence results for all life-cycle stages and emerging proportions (in days from 1st November), for observed and ensemble time periods (control and future time periods (2020s, 2050s and 2080s)) at the eleven synoptic station locations, with percentage of years recording stage completion for observations and ensembles, the minimum and maximum values based on the three GCMs and two emission scenarios to provide a range and the difference between the ensemble and observation values.

Control	Roche's Point						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	167	100	100	153	177	0
5% Post-Diapause	202	199	100	100	195	203	-3
5% Oviposition Period	204	201	100	100	197	204	-3
5% Control Larvae Emergence (1st Gen)	219	215	100	100	212	219	-4
5% Control Pupae Emergence (1st Gen)	251	247	100	100	244	254	-4
5% Control Adult Emergence (1st Gen)	261	256	100	100	253	263	-5
5% Control Sexual Maturation (1st Gen)	282	277	100	100	273	282	-5
5% Control Oviposition Period (2nd Gen)	273	271	24	45	265	275	-2
5% Control Larvae Emergence (2nd Gen)	281	281	24	45	274	284	0
5% Control Pupae Emergence (2nd Gen)	309	311	24	45	305	315	2
5% Control Adult Emergence (2nd Gen)	320	323	24	45	316	326	3
5% Control Sexual Maturation (2nd Gen)	351	348	21	25	345	351	-3
50% Budburst	167	167	100	100	153	177	0
50% Control Post-Diapause (1st Gen)	208	205	100	100	201	208	-3
50% Control Oviposition Period (1st Gen)	228	224	100	100	221	229	-4
50% Control Larvae Emergence (1st Gen)	242	238	100	100	234	244	-4
50% Control Pupae Emergence (1st Gen)	275	270	100	100	267	276	-5
50% Control Adult Emergence (1st Gen)	287	282	100	100	278	287	-5
50% Control Sexual Maturation (1st Gen)	315	311	100	100	305	316	-4
50% Control Oviposition Period (2nd Gen)							
50% Control Larvae Emergence (2nd Gen)							
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	167	167	100	100	153	177	0
95% Control Post-Diapause (1st Gen)	216	212	100	100	209	216	-4
95% Control Oviposition Period (1st Gen)	261	256	100	100	253	263	-5
95% Control Larvae Emergence (1st Gen)	276	271	100	100	267	276	-5
95% Control Pupae Emergence (1st Gen)	315	311	100	100	305	315	-4
95% Control Adult Emergence (1st Gen)	331	327	100	100	321	331	-4
95% Control Sexual Maturation (1st Gen)	351	355	3	5	350	358	4
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Belmullet						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	171	170	100	100	159	178	-1
5% Post-Diapause	205	202	100	100	198	205	-3
5% Oviposition Period	207	203	100	100	200	206	-4
5% Control Larvae Emergence (1st Gen)	222	218	100	100	214	222	-4
5% Control Pupae Emergence (1st Gen)	257	252	100	100	249	259	-5
5% Control Adult Emergence (1st Gen)	267	262	100	100	259	268	-5
5% Control Sexual Maturation (1st Gen)	291	286	100	100	281	290	-5
5% Control Oviposition Period (2nd Gen)	279	277	14	29	271	279	-2
5% Control Larvae Emergence (2nd Gen)	289	287	14	29	283	291	-2
5% Control Pupae Emergence (2nd Gen)	320	322	14	29	318	326	2
5% Control Adult Emergence (2nd Gen)	333	335	14	29	330	339	2
5% Control Sexual Maturation (2nd Gen)		355		3	350	357	
50% Budburst	171	170	100	100	159	178	-1
50% Control Post-Diapause (1st Gen)	211	207	100	100	203	210	-4
50% Control Oviposition Period (1st Gen)	232	227	100	100	224	232	-5
50% Control Larvae Emergence (1st Gen)	247	242	100	100	239	249	-5
50% Control Pupae Emergence (1st Gen)	283	277	100	100	273	283	-6
50% Control Adult Emergence (1st Gen)	296	291	100	100	285	295	-5
50% Control Sexual Maturation (1st Gen)	329	325	97	98	319	328	-4
50% Control Oviposition Period (2nd Gen)							
50% Control Larvae Emergence (2nd Gen)							
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	171	170	100	100	159	178	-1
95% Control Post-Diapause (1st Gen)	219	215	100	100	210	219	-4
95% Control Oviposition Period (1st Gen)	267	262	100	100	258	268	-5
95% Control Larvae Emergence (1st Gen)	284	278	100	100	274	284	-6
95% Control Pupae Emergence (1st Gen)	328	323	100	100	316	327	-5
95% Control Adult Emergence (1st Gen)	344	341	83	90	337	345	-3
95% Control Sexual Maturation (1st Gen)							
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Clones						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	175	176	100	100	167	184	1
5% Post-Diapause	208	205	100	100	199	209	-3
5% Oviposition Period	210	207	100	100	200	211	-3
5% Control Larvae Emergence (1st Gen)	224	220	100	100	212	225	-4
5% Control Pupae Emergence (1st Gen)	257	253	100	100	247	260	-4
5% Control Adult Emergence (1st Gen)	267	263	100	100	256	269	-4
5% Control Sexual Maturation (1st Gen)	290	286	100	100	275	290	-4
5% Control Oviposition Period (2nd Gen)	280	276	31	37	272	279	-4
5% Control Larvae Emergence (2nd Gen)	290	286	31	37	283	288	-4
5% Control Pupae Emergence (2nd Gen)	324	320	31	37	318	322	-4
5% Control Adult Emergence (2nd Gen)	340	334	31	36	329	338	-6
5% Control Sexual Maturation (2nd Gen)		349		2	332	361	
50% Budburst	175	176	100	100	167	184	1
50% Control Post-Diapause (1st Gen)	213	210	100	100	203	214	-3
50% Control Oviposition Period (1st Gen)	233	229	100	100	222	234	-4
50% Control Larvae Emergence (1st Gen)	248	244	100	100	238	251	-4
50% Control Pupae Emergence (1st Gen)	282	278	100	100	269	282	-4
50% Control Adult Emergence (1st Gen)	295	290	100	100	280	294	-5
50% Control Sexual Maturation (1st Gen)	327	325	86	89	309	332	-2
50% Control Oviposition Period (2nd Gen)		296		1	296	296	
50% Control Larvae Emergence (2nd Gen)		310		1	310	310	
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	175	176	100	100	167	184	1
95% Control Post-Diapause (1st Gen)	221	217	100	100	208	221	-4
95% Control Oviposition Period (1st Gen)	267	262	100	100	255	269	-5
95% Control Larvae Emergence (1st Gen)	283	278	100	100	269	283	-5
95% Control Pupae Emergence (1st Gen)	327	324	93	97	307	331	-3
95% Control Adult Emergence (1st Gen)	343	337	72	69	327	344	-6
95% Control Sexual Maturation (1st Gen)		361		1	361	361	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Rosslare						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	168	169	100	100	155	178	1
5% Post-Diapause	204	201	100	100	197	205	-3
5% Oviposition Period	206	203	100	100	199	207	-3
5% Control Larvae Emergence (1st Gen)	221	217	100	100	212	220	-4
5% Control Pupae Emergence (1st Gen)	254	248	100	100	245	254	-6
5% Control Adult Emergence (1st Gen)	263	258	100	100	254	264	-5
5% Control Sexual Maturation (1st Gen)	284	279	100	100	273	283	-5
5% Control Oviposition Period (2nd Gen)	277	273	24	44	268	277	-4
5% Control Larvae Emergence (2nd Gen)	286	282	24	44	278	286	-4
5% Control Pupae Emergence (2nd Gen)	314	313	24	44	309	317	-1
5% Control Adult Emergence (2nd Gen)	325	324	24	44	320	328	-1
5% Control Sexual Maturation (2nd Gen)	351	350	14	23	346	353	-1
50% Budburst	168	169	100	100	155	178	1
50% Control Post-Diapause (1st Gen)	210	206	100	100	202	210	-4
50% Control Oviposition Period (1st Gen)	230	225	100	100	221	230	-5
50% Control Larvae Emergence (1st Gen)	244	239	100	100	235	245	-5
50% Control Pupae Emergence (1st Gen)	277	271	100	100	267	277	-6
50% Control Adult Emergence (1st Gen)	289	283	100	100	278	288	-6
50% Control Sexual Maturation (1st Gen)	317	313	100	100	305	317	-4
50% Control Oviposition Period (2nd Gen)							
50% Control Larvae Emergence (2nd Gen)							
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	168	169	100	100	155	178	1
95% Control Post-Diapause (1st Gen)	218	214	100	100	209	217	-4
95% Control Oviposition Period (1st Gen)	263	257	100	100	253	263	-6
95% Control Larvae Emergence (1st Gen)	278	272	100	100	267	278	-6
95% Control Pupae Emergence (1st Gen)	318	313	100	100	305	317	-5
95% Control Adult Emergence (1st Gen)	334	329	100	100	321	332	-5
95% Control Sexual Maturation (1st Gen)		356		2	344	362	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Claremorris						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	174	173	100	100	163	181	-1
5% Post-Diapause	208	204	100	100	199	208	-4
5% Oviposition Period	209	206	100	100	200	209	-3
5% Control Larvae Emergence (1st Gen)	224	220	100	100	213	225	-4
5% Control Pupae Emergence (1st Gen)	258	253	100	100	248	261	-5
5% Control Adult Emergence (1st Gen)	268	263	100	100	257	270	-5
5% Control Sexual Maturation (1st Gen)	292	287	100	100	277	291	-5
5% Control Oviposition Period (2nd Gen)	279	276	21	29	271	278	-3
5% Control Larvae Emergence (2nd Gen)	290	286	21	29	281	287	-4
5% Control Pupae Emergence (2nd Gen)	324	320	21	29	316	323	-4
5% Control Adult Emergence (2nd Gen)	341	334	21	29	331	336	-7
5% Control Sexual Maturation (2nd Gen)		349		3	328	357	
50% Budburst	174	173	100	100	163	181	-1
50% Control Post-Diapause (1st Gen)	213	209	100	100	203	213	-4
50% Control Oviposition Period (1st Gen)	234	229	100	100	223	235	-5
50% Control Larvae Emergence (1st Gen)	249	244	100	100	239	251	-5
50% Control Pupae Emergence (1st Gen)	284	278	100	100	271	284	-6
50% Control Adult Emergence (1st Gen)	296	291	100	100	282	295	-5
50% Control Sexual Maturation (1st Gen)	326	325	76	89	312	332	-1
50% Control Oviposition Period (2nd Gen)		296		1	296	296	
50% Control Larvae Emergence (2nd Gen)		310		1	310	310	
50% Control Pupae Emergence (2nd Gen)		361		1	361	361	
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	174	173	100	100	163	181	-1
95% Control Post-Diapause (1st Gen)	221	217	100	100	209	222	-4
95% Control Oviposition Period (1st Gen)	268	263	100	100	256	270	-5
95% Control Larvae Emergence (1st Gen)	285	279	100	100	270	285	-6
95% Control Pupae Emergence (1st Gen)	331	325	97	97	310	330	-6
95% Control Adult Emergence (1st Gen)	345	338	69	70	329	346	-7
95% Control Sexual Maturation (1st Gen)		349		1	349	349	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Valentia						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	159	157	100	100	146	167	-2
5% Post-Diapause	195	192	100	100	188	195	-3
5% Oviposition Period	197	194	100	100	190	197	-3
5% Control Larvae Emergence (1st Gen)	213	208	100	100	205	212	-5
5% Control Pupae Emergence (1st Gen)	247	242	100	100	239	249	-5
5% Control Adult Emergence (1st Gen)	257	251	100	100	248	258	-6
5% Control Sexual Maturation (1st Gen)	279	273	100	100	268	278	-6
5% Control Oviposition Period (2nd Gen)	273	270	48	66	264	275	-3
5% Control Larvae Emergence (2nd Gen)	283	280	48	66	274	283	-3
5% Control Pupae Emergence (2nd Gen)	312	310	48	66	306	315	-2
5% Control Adult Emergence (2nd Gen)	323	321	48	66	317	326	-2
5% Control Sexual Maturation (2nd Gen)	352	347	38	44	344	349	-5
50% Budburst	159	157	100	100	146	167	-2
50% Control Post-Diapause (1st Gen)	201	197	100	100	195	200	-4
50% Control Oviposition Period (1st Gen)	222	218	100	100	214	221	-4
50% Control Larvae Emergence (1st Gen)	238	232	100	100	229	239	-6
50% Control Pupae Emergence (1st Gen)	272	265	100	100	262	272	-7
50% Control Adult Emergence (1st Gen)	283	277	100	100	273	283	-6
50% Control Sexual Maturation (1st Gen)	312	307	100	100	299	310	-5
50% Control Oviposition Period (2nd Gen)		291		1	291	291	
50% Control Larvae Emergence (2nd Gen)		303		1	303	303	
50% Control Pupae Emergence (2nd Gen)		340		1	340	340	
50% Control Adult Emergence (2nd Gen)		358		1	358	358	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	159	157	100	100	146	167	-2
95% Control Post-Diapause (1st Gen)	210	206	100	100	202	209	-4
95% Control Oviposition Period (1st Gen)	257	251	100	100	248	258	-6
95% Control Larvae Emergence (1st Gen)	272	266	100	100	262	272	-6
95% Control Pupae Emergence (1st Gen)	312	306	100	100	299	310	-6
95% Control Adult Emergence (1st Gen)	327	321	100	100	313	325	-6
95% Control Sexual Maturation (1st Gen)	360	351	3	13	345	356	-9
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Kilkenny						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	165	167	100	100	154	176	2
5% Post-Diapause	202	200	100	100	195	203	-2
5% Oviposition Period	204	202	100	100	197	205	-2
5% Control Larvae Emergence (1st Gen)	219	215	100	100	208	219	-4
5% Control Pupae Emergence (1st Gen)	252	247	100	100	241	255	-5
5% Control Adult Emergence (1st Gen)	261	256	100	100	250	264	-5
5% Control Sexual Maturation (1st Gen)	282	277	100	100	268	282	-5
5% Control Oviposition Period (2nd Gen)	275	271	41	56	267	277	-4
5% Control Larvae Emergence (2nd Gen)	284	280	41	56	276	285	-4
5% Control Pupae Emergence (2nd Gen)	312	311	41	56	305	318	-1
5% Control Adult Emergence (2nd Gen)	324	323	41	56	317	331	-1
5% Control Sexual Maturation (2nd Gen)	354	345	17	18	340	351	-9
50% Budburst	165	167	100	100	154	176	2
50% Control Post-Diapause (1st Gen)	208	205	100	100	199	208	-3
50% Control Oviposition Period (1st Gen)	228	224	100	100	217	230	-4
50% Control Larvae Emergence (1st Gen)	242	238	100	100	232	246	-4
50% Control Pupae Emergence (1st Gen)	275	270	100	100	263	276	-5
50% Control Adult Emergence (1st Gen)	286	282	100	100	273	287	-4
50% Control Sexual Maturation (1st Gen)	317	312	97	99	297	317	-5
50% Control Oviposition Period (2nd Gen)		288		1	288	288	
50% Control Larvae Emergence (2nd Gen)		299		1	299	299	
50% Control Pupae Emergence (2nd Gen)		336		1	336	336	
50% Control Adult Emergence (2nd Gen)		357		1	357	357	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	165	167	100	100	154	176	2
95% Control Post-Diapause (1st Gen)	217	212	100	100	205	216	-5
95% Control Oviposition Period (1st Gen)	261	256	100	100	249	264	-5
95% Control Larvae Emergence (1st Gen)	276	271	100	100	263	277	-5
95% Control Pupae Emergence (1st Gen)	317	311	100	100	297	316	-6
95% Control Adult Emergence (1st Gen)	331	328	90	97	311	333	-3
95% Control Sexual Maturation (1st Gen)		349		3	326	361	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Casement Aerodrome						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	168	170	100	100	157	179	2
5% Post-Diapause	205	203	100	100	198	206	-2
5% Oviposition Period	207	204	100	100	199	208	-3
5% Control Larvae Emergence (1st Gen)	222	218	100	100	211	222	-4
5% Control Pupae Emergence (1st Gen)	254	250	100	100	245	257	-4
5% Control Adult Emergence (1st Gen)	264	259	100	100	253	266	-5
5% Control Sexual Maturation (1st Gen)	285	280	100	100	271	285	-5
5% Control Oviposition Period (2nd Gen)	278	273	34	45	268	278	-5
5% Control Larvae Emergence (2nd Gen)	287	282	34	45	277	286	-5
5% Control Pupae Emergence (2nd Gen)	317	313	34	45	309	319	-4
5% Control Adult Emergence (2nd Gen)	330	326	34	45	321	332	-4
5% Control Sexual Maturation (2nd Gen)	358	349	7	13	344	352	-9
50% Budburst	168	170	100	100	157	179	2
50% Control Post-Diapause (1st Gen)	211	208	100	100	202	211	-3
50% Control Oviposition Period (1st Gen)	231	227	100	100	221	232	-4
50% Control Larvae Emergence (1st Gen)	245	241	100	100	236	248	-4
50% Control Pupae Emergence (1st Gen)	278	273	100	100	266	279	-5
50% Control Adult Emergence (1st Gen)	289	285	100	100	277	289	-4
50% Control Sexual Maturation (1st Gen)	320	317	93	99	303	323	-3
50% Control Oviposition Period (2nd Gen)							
50% Control Larvae Emergence (2nd Gen)							
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	168	170	100	100	157	179	2
95% Control Post-Diapause (1st Gen)	219	215	100	100	208	219	-4
95% Control Oviposition Period (1st Gen)	264	259	100	100	253	266	-5
95% Control Larvae Emergence (1st Gen)	279	274	100	100	266	280	-5
95% Control Pupae Emergence (1st Gen)	321	316	100	100	302	320	-5
95% Control Adult Emergence (1st Gen)	335	332	86	91	319	338	-3
95% Control Sexual Maturation (1st Gen)		346		1	344	348	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Birr						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	167	100	100	155	176	0
5% Post-Diapause	202	200	100	100	195	203	-2
5% Oviposition Period	204	201	100	100	196	205	-3
5% Control Larvae Emergence (1st Gen)	220	215	100	100	208	219	-5
5% Control Pupae Emergence (1st Gen)	252	248	100	100	242	255	-4
5% Control Adult Emergence (1st Gen)	262	257	100	100	251	264	-5
5% Control Sexual Maturation (1st Gen)	284	278	100	100	270	283	-6
5% Control Oviposition Period (2nd Gen)	276	272	45	59	268	278	-4
5% Control Larvae Emergence (2nd Gen)	286	282	45	59	279	287	-4
5% Control Pupae Emergence (2nd Gen)	315	313	45	59	308	318	-2
5% Control Adult Emergence (2nd Gen)	328	326	45	58	320	332	-2
5% Control Sexual Maturation (2nd Gen)	359	346	14	16	341	352	-13
50% Budburst	167	167	100	100	155	176	0
50% Control Post-Diapause (1st Gen)	208	205	100	100	199	209	-3
50% Control Oviposition Period (1st Gen)	229	224	100	100	217	229	-5
50% Control Larvae Emergence (1st Gen)	243	239	100	100	233	246	-4
50% Control Pupae Emergence (1st Gen)	276	271	100	100	264	277	-5
50% Control Adult Emergence (1st Gen)	288	283	100	100	274	288	-5
50% Control Sexual Maturation (1st Gen)	318	314	93	99	299	320	-4
50% Control Oviposition Period (2nd Gen)		290		1	290	290	
50% Control Larvae Emergence (2nd Gen)		302		1	302	302	
50% Control Pupae Emergence (2nd Gen)		343		1	343	343	
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	167	167	100	100	155	176	0
95% Control Post-Diapause (1st Gen)	217	212	100	100	205	216	-5
95% Control Oviposition Period (1st Gen)	262	257	100	100	250	264	-5
95% Control Larvae Emergence (1st Gen)	277	272	100	100	264	278	-5
95% Control Pupae Emergence (1st Gen)	319	313	100	100	299	317	-6
95% Control Adult Emergence (1st Gen)	332	329	86	95	314	335	-3
95% Control Sexual Maturation (1st Gen)		347		2	330	361	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Shannon Airport						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	163	161	100	100	149	170	-2
5% Post-Diapause	195	193	100	100	189	196	-2
5% Oviposition Period	197	194	100	100	190	198	-3
5% Control Larvae Emergence (1st Gen)	211	208	100	100	203	211	-3
5% Control Pupae Emergence (1st Gen)	244	240	100	100	235	247	-4
5% Control Adult Emergence (1st Gen)	253	249	100	100	245	256	-4
5% Control Sexual Maturation (1st Gen)	273	268	100	100	263	274	-5
5% Control Oviposition Period (2nd Gen)	272	267	86	87	262	274	-5
5% Control Larvae Emergence (2nd Gen)	281	276	86	87	272	282	-5
5% Control Pupae Emergence (2nd Gen)	309	305	86	87	299	310	-4
5% Control Adult Emergence (2nd Gen)	319	315	86	87	308	321	-4
5% Control Sexual Maturation (2nd Gen)	343	340	69	60	337	345	-3
50% Budburst	163	161	100	100	149	170	-2
50% Control Post-Diapause (1st Gen)	201	198	100	100	194	201	-3
50% Control Oviposition Period (1st Gen)	221	217	100	100	211	221	-4
50% Control Larvae Emergence (1st Gen)	235	231	100	100	226	238	-4
50% Control Pupae Emergence (1st Gen)	266	262	100	100	258	269	-4
50% Control Adult Emergence (1st Gen)	277	273	100	100	268	279	-4
50% Control Sexual Maturation (1st Gen)	303	299	100	100	290	303	-4
50% Control Oviposition Period (2nd Gen)		289		2	284	295	
50% Control Larvae Emergence (2nd Gen)		302		2	294	308	
50% Control Pupae Emergence (2nd Gen)		339		2	328	348	
50% Control Adult Emergence (2nd Gen)		351		1	343	358	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	163	161	100	100	149	170	-2
95% Control Post-Diapause (1st Gen)	208	205	100	100	200	208	-3
95% Control Oviposition Period (1st Gen)	253	249	100	100	244	256	-4
95% Control Larvae Emergence (1st Gen)	267	262	100	100	258	269	-5
95% Control Pupae Emergence (1st Gen)	304	299	100	100	291	303	-5
95% Control Adult Emergence (1st Gen)	318	314	100	100	304	318	-4
95% Control Sexual Maturation (1st Gen)	354	346	28	24	344	349	-8
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

Control	Malin Head						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	176	175	100	100	166	181	-1
5% Post-Diapause	210	208	100	100	204	211	-2
5% Oviposition Period	212	209	100	100	205	213	-3
5% Control Larvae Emergence (1st Gen)	227	223	100	100	219	229	-4
5% Control Pupae Emergence (1st Gen)	262	257	100	100	255	265	-5
5% Control Adult Emergence (1st Gen)	273	268	100	100	265	274	-5
5% Control Sexual Maturation (1st Gen)	297	294	100	100	287	297	-3
5% Control Oviposition Period (2nd Gen)	284	281	7	15	269	283	-3
5% Control Larvae Emergence (2nd Gen)	296	292	7	15	280	294	-4
5% Control Pupae Emergence (2nd Gen)	333	328	7	15	312	332	-5
5% Control Adult Emergence (2nd Gen)	350	341	7	14	325	347	-9
5% Control Sexual Maturation (2nd Gen)							
50% Budburst	176	175	100	100	166	181	-1
50% Control Post-Diapause (1st Gen)	216	213	100	100	208	217	-3
50% Control Oviposition Period (1st Gen)	237	233	100	100	229	239	-4
50% Control Larvae Emergence (1st Gen)	252	248	100	100	245	255	-4
50% Control Pupae Emergence (1st Gen)	289	284	100	100	279	289	-5
50% Control Adult Emergence (1st Gen)	302	298	100	100	292	301	-4
50% Control Sexual Maturation (1st Gen)	338	335	90	89	332	339	-3
50% Control Oviposition Period (2nd Gen)							
50% Control Larvae Emergence (2nd Gen)							
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	176	175	100	100	166	181	-1
95% Control Post-Diapause (1st Gen)	224	220	100	100	216	226	-4
95% Control Oviposition Period (1st Gen)	273	267	100	100	264	274	-6
95% Control Larvae Emergence (1st Gen)	289	285	100	100	280	290	-4
95% Control Pupae Emergence (1st Gen)	336	333	100	98	326	336	-3
95% Control Adult Emergence (1st Gen)	350	348	62	63	345	350	-2
95% Control Sexual Maturation (1st Gen)							
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Roche's Point						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	159	100	100	149	172	-8
5% Post-Diapause	199	192	100	100	190	194	-7
5% Oviposition Period	201	194	100	100	191	195	-7
5% Control Larvae Emergence (1st Gen)	215	208	100	100	206	210	-7
5% Control Pupae Emergence (1st Gen)	247	239	100	100	236	242	-8
5% Control Adult Emergence (1st Gen)	256	248	100	100	245	251	-8
5% Control Sexual Maturation (1st Gen)	277	267	100	100	263	270	-10
5% Control Oviposition Period (2nd Gen)	271	266	45	83	264	268	-5
5% Control Larvae Emergence (2nd Gen)	281	275	45	83	273	277	-6
5% Control Pupae Emergence (2nd Gen)	311	302	45	83	298	306	-9
5% Control Adult Emergence (2nd Gen)	323	311	45	83	308	315	-12
5% Control Sexual Maturation (2nd Gen)	348	335	25	81	332	340	-13
50% Budburst	167	159	100	100	149	172	-8
50% Control Post-Diapause (1st Gen)	205	197	100	100	196	199	-8
50% Control Oviposition Period (1st Gen)	224	217	100	100	214	218	-7
50% Control Larvae Emergence (1st Gen)	238	230	100	100	228	232	-8
50% Control Pupae Emergence (1st Gen)	270	261	100	100	258	263	-9
50% Control Adult Emergence (1st Gen)	282	272	100	100	268	275	-10
50% Control Sexual Maturation (1st Gen)	311	297	100	100	291	302	-14
50% Control Oviposition Period (2nd Gen)		287		2	286	289	
50% Control Larvae Emergence (2nd Gen)		297		2	296	299	
50% Control Pupae Emergence (2nd Gen)		329		2	328	331	
50% Control Adult Emergence (2nd Gen)		342		2	340	346	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	167	159	100	100	149	172	-8
95% Control Post-Diapause (1st Gen)	212	205	100	100	202	206	-7
95% Control Oviposition Period (1st Gen)	256	248	100	100	245	251	-8
95% Control Larvae Emergence (1st Gen)	271	262	100	100	258	264	-9
95% Control Pupae Emergence (1st Gen)	311	298	100	100	292	303	-13
95% Control Adult Emergence (1st Gen)	327	311	100	100	304	318	-16
95% Control Sexual Maturation (1st Gen)	355	344	5	56	339	347	-11
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Belmullet						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	170	164	100	100	155	173	-6
5% Post-Diapause	202	194	100	100	193	197	-8
5% Oviposition Period	203	196	100	100	195	199	-7
5% Control Larvae Emergence (1st Gen)	218	210	100	100	206	213	-8
5% Control Pupae Emergence (1st Gen)	252	243	100	100	239	245	-9
5% Control Adult Emergence (1st Gen)	262	253	100	100	248	254	-9
5% Control Sexual Maturation (1st Gen)	286	274	100	100	268	279	-12
5% Control Oviposition Period (2nd Gen)	277	272	29	77	268	275	-5
5% Control Larvae Emergence (2nd Gen)	287	282	29	77	277	285	-5
5% Control Pupae Emergence (2nd Gen)	322	311	29	77	304	316	-11
5% Control Adult Emergence (2nd Gen)	335	321	29	77	315	327	-14
5% Control Sexual Maturation (2nd Gen)	355	346	3	53	335	350	-9
50% Budburst	170	164	100	100	155	173	-6
50% Control Post-Diapause (1st Gen)	207	200	100	100	197	202	-7
50% Control Oviposition Period (1st Gen)	227	219	100	100	215	222	-8
50% Control Larvae Emergence (1st Gen)	242	234	100	100	230	236	-8
50% Control Pupae Emergence (1st Gen)	277	267	100	100	262	270	-10
50% Control Adult Emergence (1st Gen)	291	279	100	100	273	283	-12
50% Control Sexual Maturation (1st Gen)	325	307	98	100	297	315	-18
50% Control Oviposition Period (2nd Gen)		295		2	294	297	
50% Control Larvae Emergence (2nd Gen)		308		2	307	310	
50% Control Pupae Emergence (2nd Gen)		344		2	341	350	
50% Control Adult Emergence (2nd Gen)		355		1	355	355	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	170	164	100	100	155	173	-6
95% Control Post-Diapause (1st Gen)	215	207	100	100	203	210	-8
95% Control Oviposition Period (1st Gen)	262	252	100	100	248	254	-10
95% Control Larvae Emergence (1st Gen)	278	268	100	100	262	272	-10
95% Control Pupae Emergence (1st Gen)	323	307	100	100	297	314	-16
95% Control Adult Emergence (1st Gen)	341	322	90	100	311	332	-19
95% Control Sexual Maturation (1st Gen)		353		19	349	357	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Clones						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	176	167	100	100	161	171	-9
5% Post-Diapause	205	197	100	100	192	200	-8
5% Oviposition Period	207	198	100	100	193	201	-9
5% Control Larvae Emergence (1st Gen)	220	212	100	100	204	215	-8
5% Control Pupae Emergence (1st Gen)	253	243	100	100	236	245	-10
5% Control Adult Emergence (1st Gen)	263	252	100	100	244	255	-11
5% Control Sexual Maturation (1st Gen)	286	273	100	100	262	279	-13
5% Control Oviposition Period (2nd Gen)	276	269	37	75	263	273	-7
5% Control Larvae Emergence (2nd Gen)	286	279	37	75	271	283	-7
5% Control Pupae Emergence (2nd Gen)	320	307	37	75	296	314	-13
5% Control Adult Emergence (2nd Gen)	334	317	36	75	306	325	-17
5% Control Sexual Maturation (2nd Gen)	349	339	2	50	330	348	-10
50% Budburst	176	167	100	100	161	171	-9
50% Control Post-Diapause (1st Gen)	210	202	100	100	195	205	-8
50% Control Oviposition Period (1st Gen)	229	220	100	100	212	223	-9
50% Control Larvae Emergence (1st Gen)	244	234	100	100	227	236	-10
50% Control Pupae Emergence (1st Gen)	278	266	100	100	257	271	-12
50% Control Adult Emergence (1st Gen)	290	277	100	100	267	283	-13
50% Control Sexual Maturation (1st Gen)	325	305	89	100	288	317	-20
50% Control Oviposition Period (2nd Gen)	296	294	1	6	291	295	-2
50% Control Larvae Emergence (2nd Gen)	310	305	1	6	302	306	-5
50% Control Pupae Emergence (2nd Gen)		346		6	338	348	
50% Control Adult Emergence (2nd Gen)		355		2	353	358	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	176	167	100	100	161	171	-9
95% Control Post-Diapause (1st Gen)	217	209	100	100	201	212	-8
95% Control Oviposition Period (1st Gen)	262	252	100	100	244	255	-10
95% Control Larvae Emergence (1st Gen)	278	267	100	100	257	272	-11
95% Control Pupae Emergence (1st Gen)	324	305	97	100	289	315	-19
95% Control Adult Emergence (1st Gen)	337	319	69	96	302	329	-18
95% Control Sexual Maturation (1st Gen)	361	345	1	21	340	356	-16
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Rosslare						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	169	162	100	100	152	174	-7
5% Post-Diapause	201	195	100	100	192	197	-6
5% Oviposition Period	203	196	100	100	194	198	-7
5% Control Larvae Emergence (1st Gen)	217	210	100	100	208	212	-7
5% Control Pupae Emergence (1st Gen)	248	241	100	100	238	244	-7
5% Control Adult Emergence (1st Gen)	258	250	100	100	246	254	-8
5% Control Sexual Maturation (1st Gen)	279	270	100	100	265	272	-9
5% Control Oviposition Period (2nd Gen)	273	268	44	79	265	271	-5
5% Control Larvae Emergence (2nd Gen)	282	277	44	79	274	280	-5
5% Control Pupae Emergence (2nd Gen)	313	305	44	79	301	309	-8
5% Control Adult Emergence (2nd Gen)	324	314	44	79	310	318	-10
5% Control Sexual Maturation (2nd Gen)	350	338	23	77	334	344	-12
50% Budburst	169	162	100	100	152	174	-7
50% Control Post-Diapause (1st Gen)	206	200	100	100	198	202	-6
50% Control Oviposition Period (1st Gen)	225	219	100	100	216	221	-6
50% Control Larvae Emergence (1st Gen)	239	232	100	100	229	235	-7
50% Control Pupae Emergence (1st Gen)	271	264	100	100	259	267	-7
50% Control Adult Emergence (1st Gen)	283	274	100	100	269	277	-9
50% Control Sexual Maturation (1st Gen)	313	300	100	100	293	305	-13
50% Control Oviposition Period (2nd Gen)		290		1	290	290	
50% Control Larvae Emergence (2nd Gen)		300		1	300	300	
50% Control Pupae Emergence (2nd Gen)		332		1	331	332	
50% Control Adult Emergence (2nd Gen)		345		1	343	347	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	169	162	100	100	152	174	-7
95% Control Post-Diapause (1st Gen)	214	208	100	100	204	209	-6
95% Control Oviposition Period (1st Gen)	257	250	100	100	246	254	-7
95% Control Larvae Emergence (1st Gen)	272	264	100	100	260	267	-8
95% Control Pupae Emergence (1st Gen)	313	301	100	100	294	305	-12
95% Control Adult Emergence (1st Gen)	329	314	100	100	306	320	-15
95% Control Sexual Maturation (1st Gen)	356	348	2	50	337	350	-8
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Claremorris						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	173	164	100	100	158	168	-9
5% Post-Diapause	204	196	100	100	190	199	-8
5% Oviposition Period	206	197	100	100	192	200	-9
5% Control Larvae Emergence (1st Gen)	220	211	100	100	203	214	-9
5% Control Pupae Emergence (1st Gen)	253	243	100	100	235	245	-10
5% Control Adult Emergence (1st Gen)	263	252	100	100	244	255	-11
5% Control Sexual Maturation (1st Gen)	287	273	100	100	262	279	-14
5% Control Oviposition Period (2nd Gen)	276	270	29	72	263	274	-6
5% Control Larvae Emergence (2nd Gen)	286	279	29	72	272	284	-7
5% Control Pupae Emergence (2nd Gen)	320	307	29	72	297	315	-13
5% Control Adult Emergence (2nd Gen)	334	318	29	72	306	326	-16
5% Control Sexual Maturation (2nd Gen)	349	340	3	51	330	348	-9
50% Budburst	173	164	100	100	158	168	-9
50% Control Post-Diapause (1st Gen)	209	201	100	100	194	204	-8
50% Control Oviposition Period (1st Gen)	229	220	100	100	212	223	-9
50% Control Larvae Emergence (1st Gen)	244	234	100	100	226	236	-10
50% Control Pupae Emergence (1st Gen)	278	266	100	100	257	271	-12
50% Control Adult Emergence (1st Gen)	291	278	100	100	267	283	-13
50% Control Sexual Maturation (1st Gen)	325	306	89	100	289	318	-19
50% Control Oviposition Period (2nd Gen)	296	294	1	3	293	294	-2
50% Control Larvae Emergence (2nd Gen)	310	304	1	3	303	305	-6
50% Control Pupae Emergence (2nd Gen)	361	343	1	3	339	345	-18
50% Control Adult Emergence (2nd Gen)		359		2	356	360	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	173	164	100	100	158	168	-9
95% Control Post-Diapause (1st Gen)	217	208	100	100	200	211	-9
95% Control Oviposition Period (1st Gen)	263	252	100	100	244	255	-11
95% Control Larvae Emergence (1st Gen)	279	267	100	100	257	272	-12
95% Control Pupae Emergence (1st Gen)	325	306	97	100	290	315	-19
95% Control Adult Emergence (1st Gen)	338	320	70	96	302	330	-18
95% Control Sexual Maturation (1st Gen)	349	346	1	23	344	354	-3
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Valentia						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	157	147	100	100	140	158	-10
5% Post-Diapause	192	182	100	100	179	184	-10
5% Oviposition Period	194	184	100	100	181	186	-10
5% Control Larvae Emergence (1st Gen)	208	199	100	100	196	201	-9
5% Control Pupae Emergence (1st Gen)	242	232	100	100	227	234	-10
5% Control Adult Emergence (1st Gen)	251	241	100	100	236	243	-10
5% Control Sexual Maturation (1st Gen)	273	261	100	100	255	265	-12
5% Control Oviposition Period (2nd Gen)	270	261	66	92	256	262	-9
5% Control Larvae Emergence (2nd Gen)	280	270	66	92	265	272	-10
5% Control Pupae Emergence (2nd Gen)	310	298	66	92	290	302	-12
5% Control Adult Emergence (2nd Gen)	321	307	66	92	298	312	-14
5% Control Sexual Maturation (2nd Gen)	347	329	44	90	319	338	-18
50% Budburst	157	147	100	100	140	158	-10
50% Control Post-Diapause (1st Gen)	197	188	100	100	185	190	-9
50% Control Oviposition Period (1st Gen)	218	208	100	100	204	211	-10
50% Control Larvae Emergence (1st Gen)	232	222	100	100	218	224	-10
50% Control Pupae Emergence (1st Gen)	265	255	100	100	249	257	-10
50% Control Adult Emergence (1st Gen)	277	266	100	100	260	270	-11
50% Control Sexual Maturation (1st Gen)	307	291	100	100	282	297	-16
50% Control Oviposition Period (2nd Gen)	291	287	1	9	285	292	-4
50% Control Larvae Emergence (2nd Gen)	303	298	1	9	295	306	-5
50% Control Pupae Emergence (2nd Gen)	340	329	1	9	325	337	-11
50% Control Adult Emergence (2nd Gen)	358	342	1	9	337	349	-16
50% Control Sexual Maturation (2nd Gen)		363		1	363	363	
95% Budburst	157	147	100	100	140	158	-10
95% Control Post-Diapause (1st Gen)	206	196	100	100	193	199	-10
95% Control Oviposition Period (1st Gen)	251	241	100	100	236	243	-10
95% Control Larvae Emergence (1st Gen)	266	255	100	100	250	259	-11
95% Control Pupae Emergence (1st Gen)	306	292	100	100	283	298	-14
95% Control Adult Emergence (1st Gen)	321	305	100	100	295	312	-16
95% Control Sexual Maturation (1st Gen)	351	339	13	73	331	349	-12
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Kilkenny						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	157	100	100	149	163	-10
5% Post-Diapause	200	191	100	100	187	194	-9
5% Oviposition Period	202	193	100	100	188	196	-9
5% Control Larvae Emergence (1st Gen)	215	207	100	100	200	210	-8
5% Control Pupae Emergence (1st Gen)	247	237	100	100	229	240	-10
5% Control Adult Emergence (1st Gen)	256	246	100	100	238	249	-10
5% Control Sexual Maturation (1st Gen)	277	265	100	100	255	271	-12
5% Control Oviposition Period (2nd Gen)	271	263	56	84	256	266	-8
5% Control Larvae Emergence (2nd Gen)	280	272	56	84	264	276	-8
5% Control Pupae Emergence (2nd Gen)	311	299	56	84	287	305	-12
5% Control Adult Emergence (2nd Gen)	323	308	56	84	295	314	-15
5% Control Sexual Maturation (2nd Gen)	345	328	18	73	315	343	-17
50% Budburst	167	157	100	100	149	163	-10
50% Control Post-Diapause (1st Gen)	205	196	100	100	191	200	-9
50% Control Oviposition Period (1st Gen)	224	215	100	100	208	219	-9
50% Control Larvae Emergence (1st Gen)	238	229	100	100	221	231	-9
50% Control Pupae Emergence (1st Gen)	270	259	100	100	250	264	-11
50% Control Adult Emergence (1st Gen)	282	270	100	100	260	275	-12
50% Control Sexual Maturation (1st Gen)	312	294	99	100	280	303	-18
50% Control Oviposition Period (2nd Gen)	288	288	1	12	285	293	0
50% Control Larvae Emergence (2nd Gen)	299	299	1	12	295	309	0
50% Control Pupae Emergence (2nd Gen)	336	333	1	12	326	345	-3
50% Control Adult Emergence (2nd Gen)	357	348	1	11	340	354	-9
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	167	157	100	100	149	163	-10
95% Control Post-Diapause (1st Gen)	212	204	100	100	197	207	-8
95% Control Oviposition Period (1st Gen)	256	246	100	100	238	249	-10
95% Control Larvae Emergence (1st Gen)	271	260	100	100	250	265	-11
95% Control Pupae Emergence (1st Gen)	311	295	100	100	281	304	-16
95% Control Adult Emergence (1st Gen)	328	308	97	100	292	320	-20
95% Control Sexual Maturation (1st Gen)	349	338	3	57	329	347	-11
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Casement Aerodrome						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	170	160	100	100	151	168	-10
5% Post-Diapause	203	194	100	100	190	197	-9
5% Oviposition Period	204	196	100	100	192	199	-8
5% Control Larvae Emergence (1st Gen)	218	210	100	100	203	212	-8
5% Control Pupae Emergence (1st Gen)	250	240	100	100	233	243	-10
5% Control Adult Emergence (1st Gen)	259	249	100	100	242	252	-10
5% Control Sexual Maturation (1st Gen)	280	268	100	100	259	274	-12
5% Control Oviposition Period (2nd Gen)	273	267	45	82	260	270	-6
5% Control Larvae Emergence (2nd Gen)	282	276	45	82	268	280	-6
5% Control Pupae Emergence (2nd Gen)	313	303	45	82	292	310	-10
5% Control Adult Emergence (2nd Gen)	326	312	45	82	301	320	-14
5% Control Sexual Maturation (2nd Gen)	349	334	13	67	324	340	-15
50% Budburst	170	160	100	100	151	168	-10
50% Control Post-Diapause (1st Gen)	208	199	100	100	194	202	-9
50% Control Oviposition Period (1st Gen)	227	218	100	100	212	221	-9
50% Control Larvae Emergence (1st Gen)	241	232	100	100	225	234	-9
50% Control Pupae Emergence (1st Gen)	273	263	100	100	254	267	-10
50% Control Adult Emergence (1st Gen)	285	273	100	100	264	279	-12
50% Control Sexual Maturation (1st Gen)	317	299	99	100	285	308	-18
50% Control Oviposition Period (2nd Gen)		291		8	289	296	
50% Control Larvae Emergence (2nd Gen)		302		8	300	311	
50% Control Pupae Emergence (2nd Gen)		339		8	334	344	
50% Control Adult Emergence (2nd Gen)		354		6	348	362	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	170	160	100	100	151	168	-10
95% Control Post-Diapause (1st Gen)	215	207	100	100	200	210	-8
95% Control Oviposition Period (1st Gen)	259	249	100	100	242	252	-10
95% Control Larvae Emergence (1st Gen)	274	263	100	100	254	268	-11
95% Control Pupae Emergence (1st Gen)	316	300	100	100	286	308	-16
95% Control Adult Emergence (1st Gen)	332	313	91	100	297	325	-19
95% Control Sexual Maturation (1st Gen)	346	342	1	46	336	351	-4
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Birr						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	157	100	100	150	163	-10
5% Post-Diapause	200	191	100	100	187	194	-9
5% Oviposition Period	201	193	100	100	188	196	-8
5% Control Larvae Emergence (1st Gen)	215	207	100	100	200	210	-8
5% Control Pupae Emergence (1st Gen)	248	238	100	100	230	240	-10
5% Control Adult Emergence (1st Gen)	257	247	100	100	239	250	-10
5% Control Sexual Maturation (1st Gen)	278	266	100	100	256	272	-12
5% Control Oviposition Period (2nd Gen)	272	265	59	88	257	268	-7
5% Control Larvae Emergence (2nd Gen)	282	274	59	88	265	277	-8
5% Control Pupae Emergence (2nd Gen)	313	301	59	88	289	307	-12
5% Control Adult Emergence (2nd Gen)	326	310	58	88	297	317	-16
5% Control Sexual Maturation (2nd Gen)	346	330	16	71	318	338	-16
50% Budburst	167	157	100	100	150	163	-10
50% Control Post-Diapause (1st Gen)	205	196	100	100	191	199	-9
50% Control Oviposition Period (1st Gen)	224	215	100	100	208	219	-9
50% Control Larvae Emergence (1st Gen)	239	229	100	100	221	232	-10
50% Control Pupae Emergence (1st Gen)	271	260	100	100	251	265	-11
50% Control Adult Emergence (1st Gen)	283	270	100	100	261	277	-13
50% Control Sexual Maturation (1st Gen)	314	295	99	100	281	305	-19
50% Control Oviposition Period (2nd Gen)	290	290	1	15	284	295	0
50% Control Larvae Emergence (2nd Gen)	302	301	1	15	294	308	-1
50% Control Pupae Emergence (2nd Gen)	343	337	1	15	325	344	-6
50% Control Adult Emergence (2nd Gen)		350		11	340	360	
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	167	157	100	100	150	163	-10
95% Control Post-Diapause (1st Gen)	212	204	100	100	196	207	-8
95% Control Oviposition Period (1st Gen)	257	247	100	100	238	250	-10
95% Control Larvae Emergence (1st Gen)	272	261	100	100	251	266	-11
95% Control Pupae Emergence (1st Gen)	313	296	100	100	282	305	-17
95% Control Adult Emergence (1st Gen)	329	310	95	100	293	322	-19
95% Control Sexual Maturation (1st Gen)	347	339	2	51	329	348	-8
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Shannon Airport						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	161	151	100	100	145	160	-10
5% Post-Diapause	193	184	100	100	182	187	-9
5% Oviposition Period	194	185	100	100	183	188	-9
5% Control Larvae Emergence (1st Gen)	208	200	100	100	195	202	-8
5% Control Pupae Emergence (1st Gen)	240	230	100	100	224	233	-10
5% Control Adult Emergence (1st Gen)	249	239	100	100	233	241	-10
5% Control Sexual Maturation (1st Gen)	268	257	100	100	251	260	-11
5% Control Oviposition Period (2nd Gen)	267	258	87	97	252	260	-9
5% Control Larvae Emergence (2nd Gen)	276	266	87	97	259	269	-10
5% Control Pupae Emergence (2nd Gen)	305	292	87	97	282	296	-13
5% Control Adult Emergence (2nd Gen)	315	300	87	97	290	306	-15
5% Control Sexual Maturation (2nd Gen)	340	321	60	96	307	331	-19
50% Budburst	161	151	100	100	145	160	-10
50% Control Post-Diapause (1st Gen)	198	189	100	100	186	192	-9
50% Control Oviposition Period (1st Gen)	217	208	100	100	203	211	-9
50% Control Larvae Emergence (1st Gen)	231	222	100	100	215	225	-9
50% Control Pupae Emergence (1st Gen)	262	252	100	100	246	254	-10
50% Control Adult Emergence (1st Gen)	273	262	100	100	255	265	-11
50% Control Sexual Maturation (1st Gen)	299	284	100	100	275	290	-15
50% Control Oviposition Period (2nd Gen)	289	286	2	29	281	289	-3
50% Control Larvae Emergence (2nd Gen)	302	296	2	29	293	300	-6
50% Control Pupae Emergence (2nd Gen)	339	327	2	29	325	332	-12
50% Control Adult Emergence (2nd Gen)	351	340	1	28	339	352	-11
50% Control Sexual Maturation (2nd Gen)		355		2	347	365	
95% Budburst	161	151	100	100	145	160	-10
95% Control Post-Diapause (1st Gen)	205	197	100	100	192	200	-8
95% Control Oviposition Period (1st Gen)	249	239	100	100	233	241	-10
95% Control Larvae Emergence (1st Gen)	262	252	100	100	246	255	-10
95% Control Pupae Emergence (1st Gen)	299	286	100	100	276	291	-13
95% Control Adult Emergence (1st Gen)	314	298	100	100	287	305	-16
95% Control Sexual Maturation (1st Gen)	346	330	24	83	319	342	-16
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2020	Malin Head						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	175	168	100	100	161	178	-7
5% Post-Diapause	208	201	100	100	199	202	-7
5% Oviposition Period	209	203	100	100	200	204	-6
5% Control Larvae Emergence (1st Gen)	223	216	100	100	213	218	-7
5% Control Pupae Emergence (1st Gen)	257	249	100	100	246	251	-8
5% Control Adult Emergence (1st Gen)	268	259	100	100	255	261	-9
5% Control Sexual Maturation (1st Gen)	294	282	100	100	276	286	-12
5% Control Oviposition Period (2nd Gen)	281	277	15	58	272	279	-4
5% Control Larvae Emergence (2nd Gen)	292	287	15	58	282	290	-5
5% Control Pupae Emergence (2nd Gen)	328	318	15	58	315	323	-10
5% Control Adult Emergence (2nd Gen)	341	329	14	58	325	334	-12
5% Control Sexual Maturation (2nd Gen)		352		21	346	358	
50% Budburst	175	168	100	100	161	178	-7
50% Control Post-Diapause (1st Gen)	213	206	100	100	203	208	-7
50% Control Oviposition Period (1st Gen)	233	226	100	100	222	227	-7
50% Control Larvae Emergence (1st Gen)	248	240	100	100	236	242	-8
50% Control Pupae Emergence (1st Gen)	284	274	100	100	269	277	-10
50% Control Adult Emergence (1st Gen)	298	286	100	100	280	290	-12
50% Control Sexual Maturation (1st Gen)	335	317	89	99	308	325	-18
50% Control Oviposition Period (2nd Gen)							
50% Control Larvae Emergence (2nd Gen)							
50% Control Pupae Emergence (2nd Gen)							
50% Control Adult Emergence (2nd Gen)							
50% Control Sexual Maturation (2nd Gen)							
95% Budburst	175	168	100	100	161	178	-7
95% Control Post-Diapause (1st Gen)	220	214	100	100	210	215	-6
95% Control Oviposition Period (1st Gen)	267	259	100	100	255	261	-8
95% Control Larvae Emergence (1st Gen)	285	275	100	100	269	279	-10
95% Control Pupae Emergence (1st Gen)	333	317	98	100	308	323	-16
95% Control Adult Emergence (1st Gen)	348	332	63	95	323	339	-16
95% Control Sexual Maturation (1st Gen)		357		4	355	362	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Roche's Point						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	149	100	100	146	161	-18
5% Post-Diapause	199	185	100	100	183	186	-14
5% Oviposition Period	201	187	100	100	184	188	-14
5% Control Larvae Emergence (1st Gen)	215	202	100	100	199	204	-13
5% Control Pupae Emergence (1st Gen)	247	232	100	100	229	235	-15
5% Control Adult Emergence (1st Gen)	256	241	100	100	238	244	-15
5% Control Sexual Maturation (1st Gen)	277	259	100	100	256	261	-18
5% Control Oviposition Period (2nd Gen)	271	259	45	93	257	260	-12
5% Control Larvae Emergence (2nd Gen)	281	267	45	93	266	269	-14
5% Control Pupae Emergence (2nd Gen)	311	293	45	93	290	295	-18
5% Control Adult Emergence (2nd Gen)	323	301	45	93	298	305	-22
5% Control Sexual Maturation (2nd Gen)	348	321	25	93	315	327	-27
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	167	149	100	100	146	161	-18
50% Control Post-Diapause (1st Gen)	205	191	100	100	189	193	-14
50% Control Oviposition Period (1st Gen)	224	211	100	100	207	214	-13
50% Control Larvae Emergence (1st Gen)	238	224	100	100	220	227	-14
50% Control Pupae Emergence (1st Gen)	270	254	100	100	251	256	-16
50% Control Adult Emergence (1st Gen)	282	264	100	100	261	266	-18
50% Control Sexual Maturation (1st Gen)	311	286	100	100	282	290	-25
50% Control Oviposition Period (2nd Gen)		286		18	279	290	
50% Control Larvae Emergence (2nd Gen)		297		18	290	302	
50% Control Pupae Emergence (2nd Gen)		326		18	317	331	
50% Control Adult Emergence (2nd Gen)		338		18	329	345	
50% Control Sexual Maturation (2nd Gen)		357		5	355	362	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	167	149	100	100	146	161	-18
95% Control Post-Diapause (1st Gen)	212	199	100	100	195	202	-13
95% Control Oviposition Period (1st Gen)	256	241	100	100	238	245	-15
95% Control Larvae Emergence (1st Gen)	271	255	100	100	251	257	-16
95% Control Pupae Emergence (1st Gen)	311	288	100	100	283	291	-23
95% Control Adult Emergence (1st Gen)	327	300	100	100	294	305	-27
95% Control Sexual Maturation (1st Gen)	355	331	5	86	327	335	-24
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Belmullet						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	170	155	100	100	151	165	-15
5% Post-Diapause	202	188	100	100	184	190	-14
5% Oviposition Period	203	189	100	100	185	192	-14
5% Control Larvae Emergence (1st Gen)	218	204	100	100	199	207	-14
5% Control Pupae Emergence (1st Gen)	252	236	100	100	230	240	-16
5% Control Adult Emergence (1st Gen)	262	245	100	100	240	249	-17
5% Control Sexual Maturation (1st Gen)	286	265	100	100	259	269	-21
5% Control Oviposition Period (2nd Gen)	277	265	29	92	260	268	-12
5% Control Larvae Emergence (2nd Gen)	287	274	29	92	269	277	-13
5% Control Pupae Emergence (2nd Gen)	322	301	29	92	294	305	-21
5% Control Adult Emergence (2nd Gen)	335	310	29	92	303	315	-25
5% Control Sexual Maturation (2nd Gen)	355	331	3	84	324	338	-24
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	170	155	100	100	151	165	-15
50% Control Post-Diapause (1st Gen)	207	193	100	100	189	196	-14
50% Control Oviposition Period (1st Gen)	227	213	100	100	208	216	-14
50% Control Larvae Emergence (1st Gen)	242	227	100	100	221	230	-15
50% Control Pupae Emergence (1st Gen)	277	259	100	100	253	262	-18
50% Control Adult Emergence (1st Gen)	291	270	100	100	264	274	-21
50% Control Sexual Maturation (1st Gen)	325	295	98	100	286	302	-30
50% Control Oviposition Period (2nd Gen)		293		13	290	298	
50% Control Larvae Emergence (2nd Gen)		303		13	300	310	
50% Control Pupae Emergence (2nd Gen)		337		13	330	343	
50% Control Adult Emergence (2nd Gen)		350		12	342	358	
50% Control Sexual Maturation (2nd Gen)		361		1	361	361	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	170	155	100	100	151	165	-15
95% Control Post-Diapause (1st Gen)	215	201	100	100	196	205	-14
95% Control Oviposition Period (1st Gen)	262	245	100	100	240	249	-17
95% Control Larvae Emergence (1st Gen)	278	260	100	100	254	263	-18
95% Control Pupae Emergence (1st Gen)	323	296	100	100	287	302	-27
95% Control Adult Emergence (1st Gen)	341	309	90	100	299	317	-32
95% Control Sexual Maturation (1st Gen)		341		65	338	343	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Clones						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	176	157	100	100	153	163	-19
5% Post-Diapause	205	190	100	100	185	194	-15
5% Oviposition Period	207	192	100	100	186	195	-15
5% Control Larvae Emergence (1st Gen)	220	206	100	100	198	210	-14
5% Control Pupae Emergence (1st Gen)	253	236	100	100	227	241	-17
5% Control Adult Emergence (1st Gen)	263	245	100	100	236	250	-18
5% Control Sexual Maturation (1st Gen)	286	264	100	100	254	269	-22
5% Control Oviposition Period (2nd Gen)	276	263	37	91	255	268	-13
5% Control Larvae Emergence (2nd Gen)	286	271	37	91	263	277	-15
5% Control Pupae Emergence (2nd Gen)	320	297	37	91	286	304	-23
5% Control Adult Emergence (2nd Gen)	334	306	36	91	294	315	-28
5% Control Sexual Maturation (2nd Gen)	349	325	2	81	313	334	-24
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	176	157	100	100	153	163	-19
50% Control Post-Diapause (1st Gen)	210	196	100	100	189	199	-14
50% Control Oviposition Period (1st Gen)	229	214	100	100	206	219	-15
50% Control Larvae Emergence (1st Gen)	244	227	100	100	218	232	-17
50% Control Pupae Emergence (1st Gen)	278	258	100	100	249	262	-20
50% Control Adult Emergence (1st Gen)	290	268	100	100	259	274	-22
50% Control Sexual Maturation (1st Gen)	325	292	89	100	279	301	-33
50% Control Oviposition Period (2nd Gen)	296	290	1	29	288	297	-6
50% Control Larvae Emergence (2nd Gen)	310	300	1	29	298	309	-10
50% Control Pupae Emergence (2nd Gen)		334		29	329	337	
50% Control Adult Emergence (2nd Gen)		345		24	336	347	
50% Control Sexual Maturation (2nd Gen)		350		2	350	350	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	176	157	100	100	153	163	-19
95% Control Post-Diapause (1st Gen)	217	203	100	100	195	207	-14
95% Control Oviposition Period (1st Gen)	262	245	100	100	236	250	-17
95% Control Larvae Emergence (1st Gen)	278	259	100	100	249	263	-19
95% Control Pupae Emergence (1st Gen)	324	293	97	100	280	301	-31
95% Control Adult Emergence (1st Gen)	337	305	69	99	290	316	-32
95% Control Sexual Maturation (1st Gen)	361	332	1	62	325	340	-29
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Rosslare						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	169	151	100	100	148	163	-18
5% Post-Diapause	201	188	100	100	186	190	-13
5% Oviposition Period	203	190	100	100	188	192	-13
5% Control Larvae Emergence (1st Gen)	217	205	100	100	201	207	-12
5% Control Pupae Emergence (1st Gen)	248	235	100	100	231	238	-13
5% Control Adult Emergence (1st Gen)	258	244	100	100	240	247	-14
5% Control Sexual Maturation (1st Gen)	279	262	100	100	258	264	-17
5% Control Oviposition Period (2nd Gen)	273	262	44	92	259	264	-11
5% Control Larvae Emergence (2nd Gen)	282	271	44	92	268	273	-11
5% Control Pupae Emergence (2nd Gen)	313	297	44	92	292	300	-16
5% Control Adult Emergence (2nd Gen)	324	305	44	92	301	309	-19
5% Control Sexual Maturation (2nd Gen)	350	325	23	92	321	331	-25
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	169	151	100	100	148	163	-18
50% Control Post-Diapause (1st Gen)	206	194	100	100	191	196	-12
50% Control Oviposition Period (1st Gen)	225	214	100	100	209	216	-11
50% Control Larvae Emergence (1st Gen)	239	227	100	100	222	229	-12
50% Control Pupae Emergence (1st Gen)	271	257	100	100	252	259	-14
50% Control Adult Emergence (1st Gen)	283	267	100	100	263	269	-16
50% Control Sexual Maturation (1st Gen)	313	290	100	100	284	294	-23
50% Control Oviposition Period (2nd Gen)		291		11	289	293	
50% Control Larvae Emergence (2nd Gen)		301		11	398	304	
50% Control Pupae Emergence (2nd Gen)		331		11	326	333	
50% Control Adult Emergence (2nd Gen)		343		11	337	347	
50% Control Sexual Maturation (2nd Gen)		354		1	354	354	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	169	151	100	100	148	163	-18
95% Control Post-Diapause (1st Gen)	214	202	100	100	197	204	-12
95% Control Oviposition Period (1st Gen)	257	244	100	100	239	247	-13
95% Control Larvae Emergence (1st Gen)	272	257	100	100	253	260	-15
95% Control Pupae Emergence (1st Gen)	313	291	100	100	285	295	-22
95% Control Adult Emergence (1st Gen)	329	304	100	100	297	308	-25
95% Control Sexual Maturation (1st Gen)	356	336	2	87	333	340	-20
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Claremorris						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	173	154	100	100	150	160	-19
5% Post-Diapause	204	189	100	100	183	193	-15
5% Oviposition Period	206	191	100	100	185	194	-15
5% Control Larvae Emergence (1st Gen)	220	205	100	100	197	209	-15
5% Control Pupae Emergence (1st Gen)	253	236	100	100	227	240	-17
5% Control Adult Emergence (1st Gen)	263	245	100	100	236	249	-18
5% Control Sexual Maturation (1st Gen)	287	264	100	100	255	269	-23
5% Control Oviposition Period (2nd Gen)	276	263	29	87	256	268	-13
5% Control Larvae Emergence (2nd Gen)	286	271	29	87	264	277	-15
5% Control Pupae Emergence (2nd Gen)	320	297	29	87	287	304	-23
5% Control Adult Emergence (2nd Gen)	334	306	29	87	295	313	-28
5% Control Sexual Maturation (2nd Gen)	349	326	3	81	314	335	-23
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	173	154	100	100	150	160	-19
50% Control Post-Diapause (1st Gen)	209	195	100	100	187	198	-14
50% Control Oviposition Period (1st Gen)	229	214	100	100	205	218	-15
50% Control Larvae Emergence (1st Gen)	244	227	100	100	218	232	-17
50% Control Pupae Emergence (1st Gen)	278	258	100	100	249	262	-20
50% Control Adult Emergence (1st Gen)	291	269	100	100	259	274	-22
50% Control Sexual Maturation (1st Gen)	325	293	89	100	279	302	-32
50% Control Oviposition Period (2nd Gen)	296	289	1	22	287	296	-7
50% Control Larvae Emergence (2nd Gen)	310	299	1	22	297	306	-11
50% Control Pupae Emergence (2nd Gen)	361	331	1	22	326	334	-30
50% Control Adult Emergence (2nd Gen)		344		19	339	348	
50% Control Sexual Maturation (2nd Gen)		351		2	351	351	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	173	154	100	100	150	160	-19
95% Control Post-Diapause (1st Gen)	217	202	100	100	194	207	-15
95% Control Oviposition Period (1st Gen)	263	245	100	100	236	250	-18
95% Control Larvae Emergence (1st Gen)	279	259	100	100	249	264	-20
95% Control Pupae Emergence (1st Gen)	325	294	97	100	281	302	-31
95% Control Adult Emergence (1st Gen)	338	307	70	100	292	318	-31
95% Control Sexual Maturation (1st Gen)	349	333	1	62	327	339	-16
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Valentia						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	157	136	100	100	129	146	-21
5% Post-Diapause	192	173	100	100	161	179	-19
5% Oviposition Period	194	174	100	100	163	181	-20
5% Control Larvae Emergence (1st Gen)	208	190	100	100	181	197	-18
5% Control Pupae Emergence (1st Gen)	242	224	100	100	217	230	-18
5% Control Adult Emergence (1st Gen)	251	233	100	100	226	239	-18
5% Control Sexual Maturation (1st Gen)	273	252	100	100	245	258	-21
5% Control Oviposition Period (2nd Gen)	270	252	66	96	246	257	-18
5% Control Larvae Emergence (2nd Gen)	280	261	66	96	254	266	-19
5% Control Pupae Emergence (2nd Gen)	310	287	66	96	279	294	-23
5% Control Adult Emergence (2nd Gen)	321	295	66	96	286	304	-26
5% Control Sexual Maturation (2nd Gen)	347	314	44	95	302	326	-33
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	157	136	100	100	129	146	-21
50% Control Post-Diapause (1st Gen)	197	179	100	100	168	185	-18
50% Control Oviposition Period (1st Gen)	218	200	100	100	191	206	-18
50% Control Larvae Emergence (1st Gen)	232	214	100	100	207	221	-18
50% Control Pupae Emergence (1st Gen)	265	246	100	100	239	252	-19
50% Control Adult Emergence (1st Gen)	277	257	100	100	249	263	-20
50% Control Sexual Maturation (1st Gen)	307	280	100	100	271	288	-27
50% Control Oviposition Period (2nd Gen)	291	282	1	44	279	287	-9
50% Control Larvae Emergence (2nd Gen)	303	293	1	44	289	299	-10
50% Control Pupae Emergence (2nd Gen)	340	321	1	44	316	327	-19
50% Control Adult Emergence (2nd Gen)	358	333	1	44	326	339	-25
50% Control Sexual Maturation (2nd Gen)		353		18	349	363	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	157	136	100	100	129	146	-21
95% Control Post-Diapause (1st Gen)	206	187	100	100	178	194	-19
95% Control Oviposition Period (1st Gen)	251	233	100	100	226	239	-18
95% Control Larvae Emergence (1st Gen)	266	247	100	100	240	253	-19
95% Control Pupae Emergence (1st Gen)	306	281	100	100	272	289	-25
95% Control Adult Emergence (1st Gen)	321	293	100	100	283	302	-28
95% Control Sexual Maturation (1st Gen)	351	323	13	91	311	335	-28
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Kilkenny						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	146	100	100	143	155	-21
5% Post-Diapause	200	185	100	100	180	188	-15
5% Oviposition Period	202	186	100	100	181	190	-16
5% Control Larvae Emergence (1st Gen)	215	201	100	100	193	205	-14
5% Control Pupae Emergence (1st Gen)	247	231	100	100	222	236	-16
5% Control Adult Emergence (1st Gen)	256	240	100	100	230	244	-16
5% Control Sexual Maturation (1st Gen)	277	257	100	100	248	261	-20
5% Control Oviposition Period (2nd Gen)	271	257	56	94	249	260	-14
5% Control Larvae Emergence (2nd Gen)	280	265	56	94	257	268	-15
5% Control Pupae Emergence (2nd Gen)	311	289	56	94	279	295	-22
5% Control Adult Emergence (2nd Gen)	323	297	56	94	286	305	-26
5% Control Sexual Maturation (2nd Gen)	345	316	18	92	301	327	-29
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	167	146	100	100	143	155	-21
50% Control Post-Diapause (1st Gen)	205	190	100	100	183	194	-15
50% Control Oviposition Period (1st Gen)	224	209	100	100	201	214	-15
50% Control Larvae Emergence (1st Gen)	238	222	100	100	213	227	-16
50% Control Pupae Emergence (1st Gen)	270	252	100	100	243	256	-18
50% Control Adult Emergence (1st Gen)	282	261	100	100	252	266	-21
50% Control Sexual Maturation (1st Gen)	312	283	99	100	271	290	-29
50% Control Oviposition Period (2nd Gen)	288	285	1	44	282	291	-3
50% Control Larvae Emergence (2nd Gen)	299	295	1	44	292	303	-4
50% Control Pupae Emergence (2nd Gen)	336	324	1	44	319	333	-12
50% Control Adult Emergence (2nd Gen)	357	336	1	43	330	344	-21
50% Control Sexual Maturation (2nd Gen)		355		12	350	364	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	167	146	100	100	143	155	-21
95% Control Post-Diapause (1st Gen)	212	198	100	100	190	202	-14
95% Control Oviposition Period (1st Gen)	256	240	100	100	230	245	-16
95% Control Larvae Emergence (1st Gen)	271	252	100	100	243	257	-19
95% Control Pupae Emergence (1st Gen)	311	284	100	100	273	291	-27
95% Control Adult Emergence (1st Gen)	328	296	97	100	283	305	-32
95% Control Sexual Maturation (1st Gen)	349	324	3	83	311	334	-25
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Casement Aerodrome						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	170	148	100	100	144	158	-22
5% Post-Diapause	203	187	100	100	183	191	-16
5% Oviposition Period	204	189	100	100	184	192	-15
5% Control Larvae Emergence (1st Gen)	218	203	100	100	196	207	-15
5% Control Pupae Emergence (1st Gen)	250	234	100	100	225	238	-16
5% Control Adult Emergence (1st Gen)	259	242	100	100	234	247	-17
5% Control Sexual Maturation (1st Gen)	280	260	100	100	251	264	-20
5% Control Oviposition Period (2nd Gen)	273	260	45	93	252	264	-13
5% Control Larvae Emergence (2nd Gen)	282	268	45	93	260	272	-14
5% Control Pupae Emergence (2nd Gen)	313	293	45	93	283	299	-20
5% Control Adult Emergence (2nd Gen)	326	301	45	93	290	308	-25
5% Control Sexual Maturation (2nd Gen)	349	320	13	89	307	329	-29
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	170	148	100	100	144	158	-22
50% Control Post-Diapause (1st Gen)	208	193	100	100	187	197	-15
50% Control Oviposition Period (1st Gen)	227	212	100	100	205	217	-15
50% Control Larvae Emergence (1st Gen)	241	225	100	100	217	230	-16
50% Control Pupae Emergence (1st Gen)	273	255	100	100	246	259	-18
50% Control Adult Emergence (1st Gen)	285	265	100	100	256	269	-20
50% Control Sexual Maturation (1st Gen)	317	287	99	100	276	294	-30
50% Control Oviposition Period (2nd Gen)		288		35	285	293	
50% Control Larvae Emergence (2nd Gen)		298		35	294	305	
50% Control Pupae Emergence (2nd Gen)		328		35	320	335	
50% Control Adult Emergence (2nd Gen)		341		34	333	348	
50% Control Sexual Maturation (2nd Gen)		352		4	349	362	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	170	148	100	100	144	158	-22
95% Control Post-Diapause (1st Gen)	215	201	100	100	193	205	-14
95% Control Oviposition Period (1st Gen)	259	242	100	100	234	247	-17
95% Control Larvae Emergence (1st Gen)	274	255	100	100	247	260	-19
95% Control Pupae Emergence (1st Gen)	316	288	100	100	277	295	-28
95% Control Adult Emergence (1st Gen)	332	300	91	100	287	309	-32
95% Control Sexual Maturation (1st Gen)	346	328	1	72	318	337	-18
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Birr						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	146	100	100	142	156	-21
5% Post-Diapause	200	184	100	100	179	188	-16
5% Oviposition Period	201	186	100	100	180	189	-15
5% Control Larvae Emergence (1st Gen)	215	200	100	100	193	205	-15
5% Control Pupae Emergence (1st Gen)	248	231	100	100	221	236	-17
5% Control Adult Emergence (1st Gen)	257	240	100	100	230	245	-17
5% Control Sexual Maturation (1st Gen)	278	257	100	100	248	262	-21
5% Control Oviposition Period (2nd Gen)	272	257	59	96	249	261	-15
5% Control Larvae Emergence (2nd Gen)	282	266	59	96	257	270	-16
5% Control Pupae Emergence (2nd Gen)	313	290	59	96	279	297	-23
5% Control Adult Emergence (2nd Gen)	326	299	58	96	286	307	-27
5% Control Sexual Maturation (2nd Gen)	346	317	16	92	302	329	-29
5% Control Oviposition Period (3rd Gen)		282		1	282	282	
5% Control Larvae Emergence (3rd Gen)		289		1	289	289	
5% Control Pupae Emergence (3rd Gen)		309		1	309	309	
5% Control Adult Emergence (3rd Gen)		316		1	316	316	
5% Control Sexual Maturation (3rd Gen)		335		1	335	335	
50% Budburst	167	146	100	100	142	156	-21
50% Control Post-Diapause (1st Gen)	205	190	100	100	183	194	-15
50% Control Oviposition Period (1st Gen)	224	209	100	100	200	214	-15
50% Control Larvae Emergence (1st Gen)	239	222	100	100	212	227	-17
50% Control Pupae Emergence (1st Gen)	271	252	100	100	242	257	-19
50% Control Adult Emergence (1st Gen)	283	262	100	100	252	267	-21
50% Control Sexual Maturation (1st Gen)	314	284	99	100	272	291	-30
50% Control Oviposition Period (2nd Gen)	290	286	1	47	283	292	-4
50% Control Larvae Emergence (2nd Gen)	302	296	1	47	292	304	-6
50% Control Pupae Emergence (2nd Gen)	343	325	1	47	320	334	-18
50% Control Adult Emergence (2nd Gen)		338		46	332	346	
50% Control Sexual Maturation (2nd Gen)		352		8	348	357	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	167	146	100	100	142	156	-21
95% Control Post-Diapause (1st Gen)	212	197	100	100	189	203	-15
95% Control Oviposition Period (1st Gen)	257	240	100	100	230	245	-17
95% Control Larvae Emergence (1st Gen)	272	253	100	100	243	258	-19
95% Control Pupae Emergence (1st Gen)	313	285	100	100	273	293	-28
95% Control Adult Emergence (1st Gen)	329	297	95	100	283	306	-32
95% Control Sexual Maturation (1st Gen)	347	325	2	81	312	335	-22
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Shannon Airport						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	161	140	100	100	136	150	-21
5% Post-Diapause	193	176	100	100	169	179	-17
5% Oviposition Period	194	177	100	100	170	181	-17
5% Control Larvae Emergence (1st Gen)	208	192	100	100	187	196	-16
5% Control Pupae Emergence (1st Gen)	240	223	100	100	215	228	-17
5% Control Adult Emergence (1st Gen)	249	232	100	100	224	236	-17
5% Control Sexual Maturation (1st Gen)	268	249	100	100	242	253	-19
5% Control Oviposition Period (2nd Gen)	267	250	87	100	243	254	-17
5% Control Larvae Emergence (2nd Gen)	276	258	87	100	251	263	-18
5% Control Pupae Emergence (2nd Gen)	305	282	87	100	273	288	-23
5% Control Adult Emergence (2nd Gen)	315	290	87	100	280	297	-25
5% Control Sexual Maturation (2nd Gen)	340	307	60	99	295	318	-33
5% Control Oviposition Period (3rd Gen)		279		2	279	279	
5% Control Larvae Emergence (3rd Gen)		286		2	286	286	
5% Control Pupae Emergence (3rd Gen)		308		2	308	308	
5% Control Adult Emergence (3rd Gen)		315		2	315	315	
5% Control Sexual Maturation (3rd Gen)		332		2	332	332	
50% Budburst	161	140	100	100	136	150	-21
50% Control Post-Diapause (1st Gen)	198	181	100	100	175	185	-17
50% Control Oviposition Period (1st Gen)	217	201	100	100	195	205	-16
50% Control Larvae Emergence (1st Gen)	231	214	100	100	207	219	-17
50% Control Pupae Emergence (1st Gen)	262	244	100	100	236	249	-18
50% Control Adult Emergence (1st Gen)	273	253	100	100	246	258	-20
50% Control Sexual Maturation (1st Gen)	299	274	100	100	266	280	-25
50% Control Oviposition Period (2nd Gen)	289	280	2	66	278	284	-9
50% Control Larvae Emergence (2nd Gen)	302	290	2	66	287	295	-12
50% Control Pupae Emergence (2nd Gen)	339	317	2	66	311	323	-22
50% Control Adult Emergence (2nd Gen)	351	328	1	66	322	335	-23
50% Control Sexual Maturation (2nd Gen)		348		33	340	353	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	161	140	100	100	136	150	-21
95% Control Post-Diapause (1st Gen)	205	189	100	100	184	193	-16
95% Control Oviposition Period (1st Gen)	249	232	100	100	223	236	-17
95% Control Larvae Emergence (1st Gen)	262	245	100	100	237	249	-17
95% Control Pupae Emergence (1st Gen)	299	276	100	100	267	282	-23
95% Control Adult Emergence (1st Gen)	314	287	100	100	277	294	-27
95% Control Sexual Maturation (1st Gen)	346	315	24	94	303	327	-31
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2050	Malin Head						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	175	160	100	100	155	171	-15
5% Post-Diapause	208	195	100	100	192	198	-13
5% Oviposition Period	209	197	100	100	193	200	-12
5% Control Larvae Emergence (1st Gen)	223	211	100	100	206	215	-12
5% Control Pupae Emergence (1st Gen)	257	243	100	100	238	246	-14
5% Control Adult Emergence (1st Gen)	268	252	100	100	247	256	-16
5% Control Sexual Maturation (1st Gen)	294	273	100	100	267	277	-21
5% Control Oviposition Period (2nd Gen)	281	271	15	79	268	274	-10
5% Control Larvae Emergence (2nd Gen)	292	280	15	79	277	284	-12
5% Control Pupae Emergence (2nd Gen)	328	308	15	79	305	313	-20
5% Control Adult Emergence (2nd Gen)	341	318	14	79	314	323	-23
5% Control Sexual Maturation (2nd Gen)		341		66	337	344	
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	175	160	100	100	155	171	-15
50% Control Post-Diapause (1st Gen)	213	200	100	100	196	204	-13
50% Control Oviposition Period (1st Gen)	233	220	100	100	214	224	-13
50% Control Larvae Emergence (1st Gen)	248	234	100	100	228	238	-14
50% Control Pupae Emergence (1st Gen)	284	266	100	100	261	270	-18
50% Control Adult Emergence (1st Gen)	298	278	100	100	272	282	-20
50% Control Sexual Maturation (1st Gen)	335	305	89	100	296	312	-30
50% Control Oviposition Period (2nd Gen)		296		3	295	300	
50% Control Larvae Emergence (2nd Gen)		307		3	305	314	
50% Control Pupae Emergence (2nd Gen)		341		3	336	358	
50% Control Adult Emergence (2nd Gen)		349		2	349	349	
50% Control Sexual Maturation (2nd Gen)							
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emegence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	175	160	100	100	155	171	-15
95% Control Post-Diapause (1st Gen)	220	208	100	100	203	212	-12
95% Control Oviposition Period (1st Gen)	267	252	100	100	247	256	-15
95% Control Larvae Emergence (1st Gen)	285	267	100	100	261	271	-18
95% Control Pupae Emergence (1st Gen)	333	305	98	100	297	312	-28
95% Control Adult Emergence (1st Gen)	348	319	63	99	310	328	-29
95% Control Sexual Maturation (1st Gen)		349		39	343	352	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Roche's Point						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	140	100	100	128	156	-27
5% Post-Diapause	199	175	100	100	168	181	-24
5% Oviposition Period	201	177	100	100	170	183	-24
5% Control Larvae Emergence (1st Gen)	215	192	100	100	188	198	-23
5% Control Pupae Emergence (1st Gen)	247	225	100	100	223	229	-22
5% Control Adult Emergence (1st Gen)	256	234	100	100	232	237	-22
5% Control Sexual Maturation (1st Gen)	277	251	100	100	247	255	-26
5% Control Oviposition Period (2nd Gen)	271	252	45	100	248	256	-19
5% Control Larvae Emergence (2nd Gen)	281	260	45	100	255	264	-21
5% Control Pupae Emergence (2nd Gen)	311	283	45	100	278	288	-28
5% Control Adult Emergence (2nd Gen)	323	291	45	100	285	297	-32
5% Control Sexual Maturation (2nd Gen)	348	308	25	100	302	318	-40
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	167	140	100	100	128	156	-27
50% Control Post-Diapause (1st Gen)	205	181	100	100	175	186	-24
50% Control Oviposition Period (1st Gen)	224	202	100	100	198	207	-22
50% Control Larvae Emergence (1st Gen)	238	216	100	100	214	221	-22
50% Control Pupae Emergence (1st Gen)	270	246	100	100	242	249	-24
50% Control Adult Emergence (1st Gen)	282	255	100	100	251	259	-27
50% Control Sexual Maturation (1st Gen)	311	276	100	100	270	281	-35
50% Control Oviposition Period (2nd Gen)		283		53	276	288	
50% Control Larvae Emergence (2nd Gen)		292		53	285	299	
50% Control Pupae Emegence (2nd Gen)		319		53	311	326	
50% Control Adult Emergence (2nd Gen)		330		53	322	337	
50% Control Sexual Maturation (2nd Gen)		351		31	340	362	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	167	140	100	100	128	156	-27
95% Control Post-Diapause (1st Gen)	212	190	100	100	186	194	-22
95% Control Oviposition Period (1st Gen)	256	234	100	100	232	237	-22
95% Control Larvae Emergence (1st Gen)	271	247	100	100	243	250	-24
95% Control Pupae Emergence (1st Gen)	311	277	100	100	273	282	-34
95% Control Adult Emergence (1st Gen)	327	288	100	100	283	294	-39
95% Control Sexual Maturation (1st Gen)	355	318	5	99	312	330	-37
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Belmullet						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	170	148	100	100	142	162	-22
5% Post-Diapause	202	180	100	100	177	183	-22
5% Oviposition Period	203	181	100	100	179	185	-22
5% Control Larvae Emergence (1st Gen)	218	196	100	100	193	200	-22
5% Control Pupae Emergence (1st Gen)	252	229	100	100	226	233	-23
5% Control Adult Emergence (1st Gen)	262	238	100	100	235	243	-24
5% Control Sexual Maturation (1st Gen)	286	257	100	100	253	262	-29
5% Control Oviposition Period (2nd Gen)	277	258	29	100	254	263	-19
5% Control Larvae Emergence (2nd Gen)	287	266	29	100	262	272	-21
5% Control Pupae Emergence (2nd Gen)	322	292	29	100	285	299	-30
5% Control Adult Emergence (2nd Gen)	335	300	29	100	292	308	-35
5% Control Sexual Maturation (2nd Gen)	355	319	3	99	309	333	-36
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	170	148	100	100	142	162	-22
50% Control Post-Diapause (1st Gen)	207	185	100	100	183	188	-22
50% Control Oviposition Period (1st Gen)	227	205	100	100	202	209	-22
50% Control Larvae Emergence (1st Gen)	242	220	100	100	216	224	-22
50% Control Pupae Emergence (1st Gen)	277	251	100	100	247	256	-26
50% Control Adult Emergence (1st Gen)	291	261	100	100	257	267	-30
50% Control Sexual Maturation (1st Gen)	325	284	98	100	278	290	-41
50% Control Oviposition Period (2nd Gen)		289		43	284	295	
50% Control Larvae Emergence (2nd Gen)		299		43	294	306	
50% Control Pupae Emegence (2nd Gen)		329		43	321	336	
50% Control Adult Emergence (2nd Gen)		342		43	332	351	
50% Control Sexual Maturation (2nd Gen)		356		9	354	359	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	170	148	100	100	142	162	-22
95% Control Post-Diapause (1st Gen)	215	193	100	100	191	197	-22
95% Control Oviposition Period (1st Gen)	262	238	100	100	235	243	-24
95% Control Larvae Emergence (1st Gen)	278	252	100	100	248	257	-26
95% Control Pupae Emergence (1st Gen)	323	285	100	100	279	292	-38
95% Control Adult Emergence (1st Gen)	341	297	90	100	290	305	-44
95% Control Sexual Maturation (1st Gen)		329		93	319	343	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Clones						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	176	148	100	100	143	158	-28
5% Post-Diapause	205	183	100	100	179	187	-22
5% Oviposition Period	207	185	100	100	181	189	-22
5% Control Larvae Emergence (1st Gen)	220	198	100	100	193	203	-22
5% Control Pupae Emergence (1st Gen)	253	230	100	100	222	236	-23
5% Control Adult Emergence (1st Gen)	263	238	100	100	231	245	-25
5% Control Sexual Maturation (1st Gen)	286	256	100	100	249	263	-30
5% Control Oviposition Period (2nd Gen)	276	257	37	100	250	264	-19
5% Control Larvae Emergence (2nd Gen)	286	265	37	100	258	273	-21
5% Control Pupae Emergence (2nd Gen)	320	288	37	100	279	298	-32
5% Control Adult Emergence (2nd Gen)	334	296	36	100	287	308	-38
5% Control Sexual Maturation (2nd Gen)	349	315	2	99	302	332	-34
5% Control Oviposition Period (3rd Gen)		284		1	284	284	
5% Control Larvae Emergence (3rd Gen)		290		1	290	290	
5% Control Pupae Emergence (3rd Gen)		312		1	312	312	
5% Control Adult Emergence (3rd Gen)		321		1	321	321	
5% Control Sexual Maturation (3rd Gen)		344		1	344	344	
50% Budburst	176	148	100	100	143	158	-28
50% Control Post-Diapause (1st Gen)	210	188	100	100	184	193	-22
50% Control Oviposition Period (1st Gen)	229	207	100	100	201	212	-22
50% Control Larvae Emergence (1st Gen)	244	221	100	100	213	227	-23
50% Control Pupae Emergence (1st Gen)	278	250	100	100	244	258	-28
50% Control Adult Emergence (1st Gen)	290	260	100	100	254	268	-30
50% Control Sexual Maturation (1st Gen)	325	281	89	100	273	290	-44
50% Control Oviposition Period (2nd Gen)	296	285	1	52	280	294	-11
50% Control Larvae Emergence (2nd Gen)	310	295	1	52	290	305	-15
50% Control Pupae Emegence (2nd Gen)		323		52	316	335	
50% Control Adult Emergence (2nd Gen)		335		52	327	348	
50% Control Sexual Maturation (2nd Gen)		349		13	347	355	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	176	148	100	100	143	158	-28
95% Control Post-Diapause (1st Gen)	217	196	100	100	190	200	-21
95% Control Oviposition Period (1st Gen)	262	238	100	100	231	245	-24
95% Control Larvae Emergence (1st Gen)	278	251	100	100	245	258	-27
95% Control Pupae Emergence (1st Gen)	324	282	97	100	274	291	-42
95% Control Adult Emergence (1st Gen)	337	293	69	100	284	304	-44
95% Control Sexual Maturation (1st Gen)	361	323	1	90	311	339	-38
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Rosslare						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	169	144	100	100	135	159	-25
5% Post-Diapause	201	180	100	100	176	183	-21
5% Oviposition Period	203	182	100	100	178	185	-21
5% Control Larvae Emergence (1st Gen)	217	197	100	100	193	200	-20
5% Control Pupae Emergence (1st Gen)	248	229	100	100	226	231	-19
5% Control Adult Emergence (1st Gen)	258	238	100	100	234	240	-20
5% Control Sexual Maturation (1st Gen)	279	255	100	100	250	259	-24
5% Control Oviposition Period (2nd Gen)	273	256	44	100	251	260	-17
5% Control Larvae Emergence (2nd Gen)	282	264	44	100	259	268	-18
5% Control Pupae Emergence (2nd Gen)	313	288	44	100	283	293	-25
5% Control Adult Emergence (2nd Gen)	324	296	44	100	290	301	-28
5% Control Sexual Maturation (2nd Gen)	350	314	23	100	308	321	-36
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	169	144	100	100	135	159	-25
50% Control Post-Diapause (1st Gen)	206	186	100	100	182	188	-20
50% Control Oviposition Period (1st Gen)	225	206	100	100	203	210	-19
50% Control Larvae Emergence (1st Gen)	239	220	100	100	217	223	-19
50% Control Pupae Emergence (1st Gen)	271	250	100	100	245	253	-21
50% Control Adult Emergence (1st Gen)	283	260	100	100	255	263	-23
50% Control Sexual Maturation (1st Gen)	313	280	100	100	275	285	-33
50% Control Oviposition Period (2nd Gen)		285		34	278	290	
50% Control Larvae Emergence (2nd Gen)		295		34	288	301	
50% Control Pupae Emegence (2nd Gen)		323		34	315	328	
50% Control Adult Emergence (2nd Gen)		333		34	326	340	
50% Control Sexual Maturation (2nd Gen)		354		16	346	361	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	169	144	100	100	135	159	-25
95% Control Post-Diapause (1st Gen)	214	194	100	100	191	197	-20
95% Control Oviposition Period (1st Gen)	257	238	100	100	234	240	-19
95% Control Larvae Emergence (1st Gen)	272	251	100	100	246	254	-21
95% Control Pupae Emergence (1st Gen)	313	282	100	100	277	287	-31
95% Control Adult Emergence (1st Gen)	329	293	100	100	288	299	-36
95% Control Sexual Maturation (1st Gen)	356	324	2	99	318	333	-32
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Claremorris						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	173	145	100	100	139	154	-28
5% Post-Diapause	204	181	100	100	177	186	-23
5% Oviposition Period	206	183	100	100	178	188	-23
5% Control Larvae Emergence (1st Gen)	220	197	100	100	192	203	-23
5% Control Pupae Emergence (1st Gen)	253	229	100	100	221	236	-24
5% Control Adult Emergence (1st Gen)	263	238	100	100	231	245	-25
5% Control Sexual Maturation (1st Gen)	287	255	100	100	249	264	-32
5% Control Oviposition Period (2nd Gen)	276	256	29	100	250	265	-20
5% Control Larvae Emergence (2nd Gen)	286	265	29	100	258	273	-21
5% Control Pupae Emergence (2nd Gen)	320	289	29	100	280	299	-31
5% Control Adult Emergence (2nd Gen)	334	297	29	100	287	309	-37
5% Control Sexual Maturation (2nd Gen)	349	315	3	99	302	333	-34
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	173	145	100	100	139	154	-28
50% Control Post-Diapause (1st Gen)	209	187	100	100	182	191	-22
50% Control Oviposition Period (1st Gen)	229	206	100	100	200	212	-23
50% Control Larvae Emergence (1st Gen)	244	220	100	100	212	227	-24
50% Control Pupae Emergence (1st Gen)	278	250	100	100	243	258	-28
50% Control Adult Emergence (1st Gen)	291	260	100	100	253	268	-31
50% Control Sexual Maturation (1st Gen)	325	281	89	100	273	290	-44
50% Control Oviposition Period (2nd Gen)	296	285	1	48	280	293	-11
50% Control Larvae Emergence (2nd Gen)	310	294	1	48	291	304	-16
50% Control Pupae Emegence (2nd Gen)	361	323	1	48	317	333	-38
50% Control Adult Emergence (2nd Gen)		335		48	328	344	
50% Control Sexual Maturation (2nd Gen)		350		13	347	357	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	173	145	100	100	139	154	-28
95% Control Post-Diapause (1st Gen)	217	194	100	100	189	199	-23
95% Control Oviposition Period (1st Gen)	263	238	100	100	230	245	-25
95% Control Larvae Emergence (1st Gen)	279	251	100	100	244	258	-28
95% Control Pupae Emergence (1st Gen)	325	283	97	100	274	291	-42
95% Control Adult Emergence (1st Gen)	338	294	70	100	284	305	-44
95% Control Sexual Maturation (1st Gen)	349	324	1	90	312	340	-25
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Valentia						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	157	127	100	100	113	140	-30
5% Post-Diapause	192	161	100	100	148	174	-31
5% Oviposition Period	194	163	100	100	150	175	-31
5% Control Larvae Emergence (1st Gen)	208	180	100	100	170	190	-28
5% Control Pupae Emergence (1st Gen)	242	215	100	100	209	224	-27
5% Control Adult Emergence (1st Gen)	251	224	100	100	219	233	-27
5% Control Sexual Maturation (1st Gen)	273	243	100	100	238	250	-30
5% Control Oviposition Period (2nd Gen)	270	244	66	100	239	251	-26
5% Control Larvae Emergence (2nd Gen)	280	253	66	100	247	260	-27
5% Control Pupae Emergence (2nd Gen)	310	277	66	100	269	287	-33
5% Control Adult Emergence (2nd Gen)	321	285	66	100	276	295	-36
5% Control Sexual Maturation (2nd Gen)	347	302	44	100	291	316	-45
5% Control Oviposition Period (3rd Gen)		275		2	275	275	
5% Control Larvae Emergence (3rd Gen)		283		2	283	283	
5% Control Pupae Emergence (3rd Gen)		305		2	305	305	
5% Control Adult Emergence (3rd Gen)		313		2	313	313	
5% Control Sexual Maturation (3rd Gen)		331		2	331	331	
50% Budburst	157	127	100	100	113	140	-30
50% Control Post-Diapause (1st Gen)	197	168	100	100	157	180	-29
50% Control Oviposition Period (1st Gen)	218	190	100	100	182	200	-28
50% Control Larvae Emergence (1st Gen)	232	205	100	100	200	215	-27
50% Control Pupae Emergence (1st Gen)	265	237	100	100	232	245	-28
50% Control Adult Emergence (1st Gen)	277	248	100	100	242	255	-29
50% Control Sexual Maturation (1st Gen)	307	269	100	100	262	278	-38
50% Control Oviposition Period (2nd Gen)	291	277	1	70	274	281	-14
50% Control Larvae Emergence (2nd Gen)	303	287	1	70	283	291	-16
50% Control Pupae Emegence (2nd Gen)	340	314	1	70	308	319	-26
50% Control Adult Emergence (2nd Gen)	358	324	1	70	318	329	-34
50% Control Sexual Maturation (2nd Gen)		346		54	340	353	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	157	127	100	100	113	140	-30
95% Control Post-Diapause (1st Gen)	206	177	100	100	169	188	-29
95% Control Oviposition Period (1st Gen)	251	224	100	100	219	232	-27
95% Control Larvae Emergence (1st Gen)	266	238	100	100	233	245	-28
95% Control Pupae Emergence (1st Gen)	306	271	100	100	264	280	-35
95% Control Adult Emergence (1st Gen)	321	282	100	100	274	292	-39
95% Control Sexual Maturation (1st Gen)	351	311	13	100	299	328	-40
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Kilkenny						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	137	100	100	128	150	-30
5% Post-Diapause	200	175	100	100	173	181	-25
5% Oviposition Period	202	177	100	100	175	183	-25
5% Control Larvae Emergence (1st Gen)	215	192	100	100	187	197	-23
5% Control Pupae Emergence (1st Gen)	247	224	100	100	216	229	-23
5% Control Adult Emergence (1st Gen)	256	232	100	100	225	238	-24
5% Control Sexual Maturation (1st Gen)	277	249	100	100	243	256	-28
5% Control Oviposition Period (2nd Gen)	271	250	56	100	244	257	-21
5% Control Larvae Emergence (2nd Gen)	280	257	56	100	251	265	-23
5% Control Pupae Emergence (2nd Gen)	311	280	56	100	272	288	-31
5% Control Adult Emergence (2nd Gen)	323	287	56	100	279	296	-36
5% Control Sexual Maturation (2nd Gen)	345	303	18	100	292	317	-42
5% Control Oviposition Period (3rd Gen)		280		2	280	280	
5% Control Larvae Emergence (3rd Gen)		287		2	287	287	
5% Control Pupae Emergence (3rd Gen)		308		2	308	308	
5% Control Adult Emergence (3rd Gen)		316		2	316	316	
5% Control Sexual Maturation (3rd Gen)		335		2	335	335	
50% Budburst	167	137	100	100	128	150	-30
50% Control Post-Diapause (1st Gen)	205	181	100	100	178	186	-24
50% Control Oviposition Period (1st Gen)	224	201	100	100	196	207	-23
50% Control Larvae Emergence (1st Gen)	238	215	100	100	208	220	-23
50% Control Pupae Emergence (1st Gen)	270	244	100	100	238	251	-26
50% Control Adult Emergence (1st Gen)	282	254	100	100	247	260	-28
50% Control Sexual Maturation (1st Gen)	312	273	99	100	266	281	-39
50% Control Oviposition Period (2nd Gen)	288	280	1	66	275	286	-8
50% Control Larvae Emergence (2nd Gen)	299	288	1	66	284	296	-11
50% Control Pupae Emegence (2nd Gen)	336	314	1	66	310	323	-22
50% Control Adult Emergence (2nd Gen)	357	324	1	66	320	335	-33
50% Control Sexual Maturation (2nd Gen)		347		46	342	356	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	167	137	100	100	128	150	-30
95% Control Post-Diapause (1st Gen)	212	189	100	100	185	194	-23
95% Control Oviposition Period (1st Gen)	256	232	100	100	225	238	-24
95% Control Larvae Emergence (1st Gen)	271	245	100	100	239	251	-26
95% Control Pupae Emergence (1st Gen)	311	274	100	100	267	282	-37
95% Control Adult Emergence (1st Gen)	328	285	97	100	277	293	-43
95% Control Sexual Maturation (1st Gen)	349	313	3	99	301	330	-36
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Casement Aerodrome						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	170	140	100	100	131	153	-30
5% Post-Diapause	203	179	100	100	176	183	-24
5% Oviposition Period	204	180	100	100	178	185	-24
5% Control Larvae Emergence (1st Gen)	218	195	100	100	192	200	-23
5% Control Pupae Emergence (1st Gen)	250	227	100	100	221	231	-23
5% Control Adult Emergence (1st Gen)	259	235	100	100	230	240	-24
5% Control Sexual Maturation (1st Gen)	280	252	100	100	247	258	-28
5% Control Oviposition Period (2nd Gen)	273	253	45	100	248	259	-20
5% Control Larvae Emergence (2nd Gen)	282	261	45	100	255	267	-21
5% Control Pupae Emergence (2nd Gen)	313	284	45	100	277	291	-29
5% Control Adult Emergence (2nd Gen)	326	291	45	100	284	300	-35
5% Control Sexual Maturation (2nd Gen)	349	308	13	99	298	321	-41
5% Control Oviposition Period (3rd Gen)		282		1	282	282	
5% Control Larvae Emergence (3rd Gen)		289		1	289	289	
5% Control Pupae Emergence (3rd Gen)		312		1	312	312	
5% Control Adult Emergence (3rd Gen)		322		1	322	322	
5% Control Sexual Maturation (3rd Gen)		339		1	339	339	
50% Budburst	170	140	100	100	131	153	-30
50% Control Post-Diapause (1st Gen)	208	184	100	100	182	188	-24
50% Control Oviposition Period (1st Gen)	227	204	100	100	200	209	-23
50% Control Larvae Emergence (1st Gen)	241	218	100	100	212	223	-23
50% Control Pupae Emergence (1st Gen)	273	247	100	100	242	253	-26
50% Control Adult Emergence (1st Gen)	285	257	100	100	251	263	-28
50% Control Sexual Maturation (1st Gen)	317	277	99	100	270	284	-40
50% Control Oviposition Period (2nd Gen)		283		58	277	289	
50% Control Larvae Emergence (2nd Gen)		292		58	287	300	
50% Control Pupae Emegence (2nd Gen)		318		58	314	328	
50% Control Adult Emergence (2nd Gen)		329		58	324	340	
50% Control Sexual Maturation (2nd Gen)		349		30	344	356	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	170	140	100	100	131	153	-30
95% Control Post-Diapause (1st Gen)	215	192	100	100	188	196	-23
95% Control Oviposition Period (1st Gen)	259	235	100	100	230	240	-24
95% Control Larvae Emergence (1st Gen)	274	248	100	100	242	254	-26
95% Control Pupae Emergence (1st Gen)	316	278	100	100	272	286	-38
95% Control Adult Emergence (1st Gen)	332	289	91	100	281	297	-43
95% Control Sexual Maturation (1st Gen)	346	318	1	99	307	334	-28
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Birr						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	167	137	100	100	125	149	-30
5% Post-Diapause	200	175	100	100	170	182	-25
5% Oviposition Period	201	176	100	100	172	183	-25
5% Control Larvae Emergence (1st Gen)	215	191	100	100	187	198	-24
5% Control Pupae Emergence (1st Gen)	248	223	100	100	215	229	-25
5% Control Adult Emergence (1st Gen)	257	232	100	100	224	238	-25
5% Control Sexual Maturation (1st Gen)	278	249	100	100	242	256	-29
5% Control Oviposition Period (2nd Gen)	272	250	59	100	243	257	-22
5% Control Larvae Emergence (2nd Gen)	282	258	59	100	251	265	-24
5% Control Pupae Emergence (2nd Gen)	313	280	59	100	272	289	-33
5% Control Adult Emergence (2nd Gen)	326	288	58	100	279	297	-38
5% Control Sexual Maturation (2nd Gen)	346	304	16	100	293	319	-42
5% Control Oviposition Period (3rd Gen)		279		3	278	283	
5% Control Larvae Emergence (3rd Gen)		286		3	285	290	
5% Control Pupae Emergence (3rd Gen)		307		3	306	311	
5% Control Adult Emergence (3rd Gen)		316		3	315	320	
5% Control Sexual Maturation (3rd Gen)		334		3	333	341	
50% Budburst	167	137	100	100	125	149	-30
50% Control Post-Diapause (1st Gen)	205	180	100	100	177	187	-25
50% Control Oviposition Period (1st Gen)	224	201	100	100	195	207	-23
50% Control Larvae Emergence (1st Gen)	239	214	100	100	207	221	-25
50% Control Pupae Emergence (1st Gen)	271	244	100	100	237	251	-27
50% Control Adult Emergence (1st Gen)	283	253	100	100	247	260	-30
50% Control Sexual Maturation (1st Gen)	314	273	99	100	265	281	-41
50% Control Oviposition Period (2nd Gen)	290	280	1	71	277	288	-10
50% Control Larvae Emergence (2nd Gen)	302	290	1	71	286	299	-12
50% Control Pupae Emegence (2nd Gen)	343	316	1	71	311	326	-27
50% Control Adult Emergence (2nd Gen)		326		71	320	338	
50% Control Sexual Maturation (2nd Gen)		345		39	339	360	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	167	137	100	100	125	149	-30
95% Control Post-Diapause (1st Gen)	212	189	100	100	184	194	-23
95% Control Oviposition Period (1st Gen)	257	232	100	100	224	238	-25
95% Control Larvae Emergence (1st Gen)	272	245	100	100	238	252	-27
95% Control Pupae Emergence (1st Gen)	313	275	100	100	267	283	-38
95% Control Adult Emergence (1st Gen)	329	285	95	100	277	294	-44
95% Control Sexual Maturation (1st Gen)	347	313	2	99	301	331	-34
95% Control Oviposition Period (2nd Gen)		315		1	315	315	
95% Control Larvae Emergence (2nd Gen)		329		1	329	329	
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Shannon Airport						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	161	131	100	100	119	145	-30
5% Post-Diapause	193	165	100	100	158	174	-28
5% Oviposition Period	194	167	100	100	159	176	-27
5% Control Larvae Emergence (1st Gen)	208	182	100	100	177	190	-26
5% Control Pupae Emergence (1st Gen)	240	215	100	100	209	222	-25
5% Control Adult Emergence (1st Gen)	249	224	100	100	218	230	-25
5% Control Sexual Maturation (1st Gen)	268	241	100	100	236	246	-27
5% Control Oviposition Period (2nd Gen)	267	242	87	100	237	247	-25
5% Control Larvae Emergence (2nd Gen)	276	250	87	100	245	255	-26
5% Control Pupae Emergence (2nd Gen)	305	272	87	100	266	279	-33
5% Control Adult Emergence (2nd Gen)	315	279	87	100	273	287	-36
5% Control Sexual Maturation (2nd Gen)	340	294	60	100	286	305	-46
5% Control Oviposition Period (3rd Gen)		277		9	274	280	
5% Control Larvae Emergence (3rd Gen)		283		9	281	288	
5% Control Pupae Emergence (3rd Gen)		305		9	301	312	
5% Control Adult Emergence (3rd Gen)		312		9	308	320	
5% Control Sexual Maturation (3rd Gen)		330		9	324	340	
50% Budburst	161	131	100	100	119	145	-30
50% Control Post-Diapause (1st Gen)	198	171	100	100	165	180	-27
50% Control Oviposition Period (1st Gen)	217	192	100	100	187	199	-25
50% Control Larvae Emergence (1st Gen)	231	206	100	100	202	213	-25
50% Control Pupae Emergence (1st Gen)	262	236	100	100	231	241	-26
50% Control Adult Emergence (1st Gen)	273	245	100	100	241	250	-28
50% Control Sexual Maturation (1st Gen)	299	264	100	100	259	271	-35
50% Control Oviposition Period (2nd Gen)	289	275	2	91	271	281	-14
50% Control Larvae Emergence (2nd Gen)	302	284	2	91	279	291	-18
50% Control Pupae Emegence (2nd Gen)	339	309	2	91	301	321	-30
50% Control Adult Emergence (2nd Gen)	351	319	1	91	310	334	-32
50% Control Sexual Maturation (2nd Gen)		340		74	332	348	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	161	131	100	100	119	145	-30
95% Control Post-Diapause (1st Gen)	205	180	100	100	175	187	-25
95% Control Oviposition Period (1st Gen)	249	224	100	100	218	230	-25
95% Control Larvae Emergence (1st Gen)	262	237	100	100	231	241	-25
95% Control Pupae Emergence (1st Gen)	299	266	100	100	261	273	-33
95% Control Adult Emergence (1st Gen)	314	276	100	100	271	284	-38
95% Control Sexual Maturation (1st Gen)	346	302	24	100	293	316	-44
95% Control Oviposition Period (2nd Gen)		307		3	307	307	
95% Control Larvae Emergence (2nd Gen)		319		3	319	319	
95% Control Pupae Emergence (2nd Gen)		357		3	357	357	
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							

2080	Malin Head						
	Obs emergence	Ens emergence	% years recording completion (Obs)	% years recording completion (Ens)	Min ens value (within agg)	Max ens value (within agg)	Ens - Obs (diff)
5% Budburst	175	155	100	100	149	169	-20
5% Post-Diapause	208	188	100	100	185	190	-20
5% Oviposition Period	209	190	100	100	187	192	-19
5% Control Larvae Emergence (1st Gen)	223	205	100	100	201	208	-18
5% Control Pupae Emergence (1st Gen)	257	237	100	100	234	241	-20
5% Control Adult Emergence (1st Gen)	268	246	100	100	243	251	-22
5% Control Sexual Maturation (1st Gen)	294	266	100	100	261	271	-28
5% Control Oviposition Period (2nd Gen)	281	266	15	98	262	271	-15
5% Control Larvae Emergence (2nd Gen)	292	275	15	98	270	280	-17
5% Control Pupae Emergence (2nd Gen)	328	302	15	98	294	309	-26
5% Control Adult Emergence (2nd Gen)	341	311	14	98	303	318	-30
5% Control Sexual Maturation (2nd Gen)		332		94	321	344	
5% Control Oviposition Period (3rd Gen)							
5% Control Larvae Emergence (3rd Gen)							
5% Control Pupae Emergence (3rd Gen)							
5% Control Adult Emergence (3rd Gen)							
5% Control Sexual Maturation (3rd Gen)							
50% Budburst	175	155	100	100	149	169	-20
50% Control Post-Diapause (1st Gen)	213	194	100	100	191	196	-19
50% Control Oviposition Period (1st Gen)	233	214	100	100	211	217	-19
50% Control Larvae Emergence (1st Gen)	248	228	100	100	225	232	-20
50% Control Pupae Emergence (1st Gen)	284	259	100	100	255	264	-25
50% Control Adult Emergence (1st Gen)	298	270	100	100	265	276	-28
50% Control Sexual Maturation (1st Gen)	335	294	89	100	287	302	-41
50% Control Oviposition Period (2nd Gen)		292		12	285	3021	
50% Control Larvae Emergence (2nd Gen)		303		12	296	313	
50% Control Pupae Emegence (2nd Gen)		333		12	326	347	
50% Control Adult Emergence (2nd Gen)		347		12	340	363	
50% Control Sexual Maturation (2nd Gen)		365		1	365	365	
50% Control Oviposition Period (3rd Gen)							
50% Control Larvae Emergence (3rd Gen)							
50% Control Pupae Emergence (3rd Gen)							
50% Control Adult Emergence (3rd Gen)							
50% Control Sexual Maturation (3rd Gen)							
95% Budburst	175	155	100	100	149	169	-20
95% Control Post-Diapause (1st Gen)	220	202	100	100	199	206	-18
95% Control Oviposition Period (1st Gen)	267	246	100	100	243	251	-21
95% Control Larvae Emergence (1st Gen)	285	260	100	100	256	265	-25
95% Control Pupae Emergence (1st Gen)	333	295	98	100	288	302	-38
95% Control Adult Emergence (1st Gen)	348	308	63	100	299	316	-40
95% Control Sexual Maturation (1st Gen)		341		75	332	349	
95% Control Oviposition Period (2nd Gen)							
95% Control Larvae Emergence (2nd Gen)							
95% Control Pupae Emergence (2nd Gen)							
95% Control Adult Emergence (2nd Gen)							
95% Control Sexual Maturation (2nd Gen)							