Revision of Potato Late Blight Forecasting in the Republic of Ireland

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Dissertation submitted to National University of Ireland Maynooth in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

2020

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Author Note

The research presented in this thesis has been made possible through the financial support by the Department of Agriculture, Food and the Marine STIMULUS project ‘EPIC’ (14/S/879).

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Abstract

Potato late blight (PLB), caused by oomycete *Phytopthora infestans* (Mont) De Bary, is arguably the most important disease of potato in terms of economic losses and environmental and economic impact of the disease management. The Irish Rules model was proposed in the 1950s and is operationally used by the national meteorological agency, Met Éireann, to aid identifying periods of blight conducive weather. Changes in the pathogen population and potato production systems prompted the need to evaluate the model criteria and decision thresholds. The evaluation and subsequent re-calibration of the model using historical disease and weather data led to a significant improvement in diagnostic performance. The modified Irish Rules (MIR) in combination with varietal resistance was further evaluated under field conditions to showcase and empower the use of integrated pest management tools to reliably inform the standard potato late blight management practice under growing conditions and contemporary *Phytophthora infestans* population in the Republic of Ireland. An extensive evaluation has shown that the MIR model represents an optimum modelling compromise due to the uncertainty of the model input variables, which currently demand simpler modelling approaches, such as the MIR. However, constant technological advancements will lead to improvements such as, in numerical weather prediction, and will provide possibilities for more complex risk prediction modelling. Hence, a new model which provides a more realistic interpretation of the *P. infestans* lifecycle is proposed. To facilitate a shorter time-gap between PLB model evaluations, the entire analysis is implemented in a single open source programming environment, completely reproducible and hosted on an open access server. Finally, the recommendations for a modification of the current model, its operational use are proposed, as well as suggestions for further research and improvement of the practical application of decision support in potato late blight forecasting.

Acknowledgements

It seems like it was a few days ago and a few ages ago when I landed in Dublin in February 2016 to start the pursuit of my great aspiration, to work on a decision support in management of plant diseases. A bit more than four years after in time units known and understandable to human and a few lifetimes on a time scale understandable to an early stage researcher, I will probably forget to thank to everyone I should, and I apologise beforehand.

I would like to express my sincere gratitude to my advisors Dr. Rowan Fealy and Dr. Stephen Kildea for the continuous support of my PhD research, for the patience, knowledge and motivation.

My research involved a lot of people "in the house", at Teagasc Oak Park research station. My lab work would go nowhere if it wasn't for help by Dr Sinead Phelan and Dr Helena Mealy and Fiona Hutton. Spraying of crops would be difficult without the help from Deirdre Doyle, Liam Sheppard and Jim Grace. An immense help came from the potato breeding group, Dr Denis Griffin, Colum Kennedy, Andy Bourke, Francesca Mesiti.and Jeanne Moore. Eleanor Butler was great support for administrative and financial business that had to be arranged. I also owe a great deal of gratitude to a number of interns who worked with me over these four years.

I need to give my sincere thanks to several international collaborators. EuroBlight – where special thanks go to Jens Hansen, Dr Adam Sparks University of Southern Queensland, Dr Peter Skelsey from James Hutton Institute and Prof. Neil McRoberts from UC Davis.

Last but not the least, I would like to mention all students with whom I hope, I made a long lasting friendships and who helped through some tough times, Tara, Michele, Diana, Evelin, Elena, Ashok, Katie, Niamh, Jeroen, and one of a young spirit – Sean.

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Glossary

Abbreviation	**Full Form**
AHDB	UK Agriculture and Horticulture Development Board
AUC	Area under the curve
AUROC	Area under receiver operating curve
BIC	Bayesian information criterion
BM	Danish potato late blight risk prediction model Blight Management
BQ	British Queen (potato variety)
CCC	Concordance correlation coefficient
Co.	County
DAFM	Department of Agriculture, Food & the Marine
DAPC	Discriminant Analysis of Principal Components
DSS	Decision Support Systems
EBH	Effective blight hours
ECMWF	European Centre for Medium-range Weather Forecasts
FP	False positive
FN	False negative
GLMM	Generalized linear mixed model
HRES	High-resolution forecast atmospheric model operationally run by the European Centre for Medium-Range Weather Forecasts
IR	The Irish Rules model
CL	Clone T5821/11 form Teagasc breeding programme
GLMM	Generalized linear mixed model
IPM	Integrated pest management
KE	King Edward (potato variety)
LOESS	Locally estimated scatterplot smoothing
LW	Leaf wetness
MIR	Modified Irish Rules
MLG	Multilocus genotypes
MSN	Minimum spanning networks
NWP	Numerical weather prediction
PCR	Polymerase chain reaction
PPP	Plant protection products
PLB	Potato late blight
rAUDPC	Relative area under the disease progress curve
RH	Relative humidity
R^2	Coefficient of determination
R^2 *adjusted*	Adjusted coefficient of determination
RMSE	Root mean square error
RO	Roster (potato variety)
ROC	Receiver operating curve

SD	Sporulation duration
SE	Setanta (potato variety)
SSR	Polymorphic simple sequence repeat markers or microsatellites
SM	Sarpo Mira (potato variety)
TP	True positive
TPR	True positive rate
TN	True negative
TRR	Treatment reduction rate

1. General Introduction

1.1. Introduction

Globally, it is expected that the demand for agricultural production will increase between 60 and 110% by 2050 (Tilman *et al.*, 2011) due to increasing human population, expected to reach 9 billion by 2050. However, the production of food is strongly threatened by diseases and pests, particularly in recent decades, due to an increase in epidemic invasions linked to globalization (Crowl *et al.*, 2008). Fungi and oomycetes causing crop diseases, have been at the centre of global food crises historically and continue to represent a serious threat to global food security (Savary *et al.*, 2017). Crop losses, caused by fungal diseases, exceed 200 billion euros annually, which would be enough to feed 8.5% of the world's current population (Fisher *et al.*, 2012). Therefore, in order to sustainably intensify agricultural production to meet growing demands, within environmental constraints, will require significant and ongoing management of these parasites.

While the potato remains one of the most important food crops grown globally, *Phytophthora infestans*, the causal agent of the late blight disease (PLB), continues to be the primary biotic constraint of potato production. High humidity and mild temperatures are essential for the development of epidemics, and, under optimal conditions, the disease can destroy an entire crop in a couple of weeks (Fry *et al.*, 2013). The pathogen population is also changing, continuously evolving through recombination and migration between geographical regions (Fry, 2008). While the frequent use of fungicides remains the most common tactic for the management of the disease (Fry, 2016), environmental considerations have led to the increasing use of integrated control measures such as resistant varieties, sanitation, decision support tools, in-field inoculum/disease detection and molecular characterisation (Schepers *et al.*, 2009). In this chapter, the host-pathogen-environment complex (plant disease triangle, (Scholthof, 2007)) and the disease management practices of the potato late blight disease are presented, with a focus on north-western European and specifically, the Irish perspective.

1.2. Potato

1.2.1. *The taxonomy and biology*

Potato (*Solanum tuberosum L.*) is a herbaceous perennial which belongs to the family *Solanaceae*. Amongst over 1000 other members of the genus *Solanum*, are food crops of high economic importance and include tomato (*S. lycopersicum*), eggplant (*S. melongena*) and agricultural weeds such as black nightshade (*S. nigrum*) and bittersweet (*S. duclamara*). The centre of origin of cultivated potato is the Andean region of South America where the wild relatives of the plant were domesticated at least 7000 years ago. The first record of potato cultivation in Europe dates from 1565 in Spain's Canary Islands (Hawkes *et al.*, 1993).

The potato plant has a cycle of development which includes three main stages: growth, tuberization and vegetative rest. The first stage includes the breaking of dormancy and growth of sprouts (present in the soil) which are transformed into leafy stems in the aerial part, or in stolons in the underground part. The elongation of stolons leads to the tuberization phase. The tubers are then formed in stolon tip swellings, by storing reserve substances produced from the metabolites synthesized by the plant at the foliage level (Gregory, 1965). The initiation of marketable tubers lasts approximately two weeks, while the entire tuberization stage can last up to three months.

1.2.2. *Potato as a staple crop*

Globally, potato is one of the most important food crops grown: with 378 million tons produced on an estimated 19 million hectares of farmland (FAOSTAT, 2017). It is the world's third most important food crop in terms of human consumption, after wheat and rice (FAOSTAT, 2013). The mean worldwide potato intake is equivalent to 93 g per person per day. However there is considerable variation in consumption; varying from 50 to 150 g per adult per day in developed countries to 300 – 800 g per day per adult in some rural areas of Africa and in the highlands of Latin America (FAO/OMS/UNU, 2005).

The long-term trend analysis of the area cultivated under potato shows a trend of a low-rate decline in the developed world (EUROSTAT 2008), whilst the production and demand are rapidly increasing in the developing world (Hijmans, 2001). However, the trend in the achieved yields is in marked contrast, primarily associated with more advanced agricultural practices in developed countries. For example, while farmers in the Netherlands harvest an average of over 50 t/ha; yields in China are seldom more than 20 t/ha (FAOSTAT, 2008). In the northern hemisphere, the highest concentration of potato production is found in the temperate zone, where it is grown as a cash crop in summer, during the frost-free period (Devaux *et al.*, 2020).

1.2.3. *Potato production in Ireland*

Over time, increasing economic, biological and environmental constraints on potato production in the Republic of Ireland have led to a marked decrease in the area planted. During the period from 1955 to 2015, the area cultivated decreased from 115,000 hectares to only 8,800 hectares, or approximately 1% of the available arable land (EUROSTAT) (Figure 1.1). This is in marked contrast to 1841, just prior to the Irish famine, when over 1 million hectares were under potato crops; although this had decreased to 475,000 hectares by 1859 (Bourke, 1993). The contemporary change in land area under potato production has also been accompanied with a decrease in the number of growers, decreasing from 1,741 in 1993 to 592 in 2001 (Leonard, 2003).

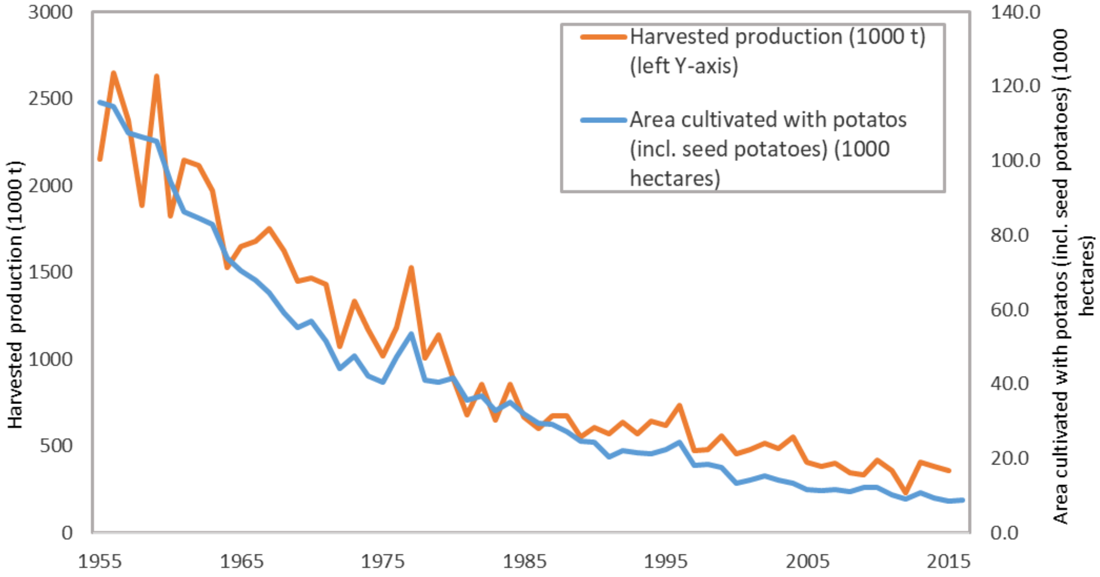


Figure 1.1 Potato production in the Republic of Ireland from 1955 to 2015. Yield (orange line) is presented on primary axis and cultivated area (blue line) on secondary (Data source: EUROSTAT).

Table 1.1. The structure of potato production in 2011 in the Republic of Ireland (Anonymous, 2011).

Rooster	**Kerrs Pink**	**British Queens**	**Golden Wonder**	**Record**	**Earlies**	**Other Reds**	**Processing**	**Salads**	**Whites**
55.60%	9.80%	7.80%	3.10%	1.90%	3.10%	0.20%	10.00%	1.20%	7.20%

Geographically, the main potato producing areas are now concentrated along the east and south coasts of Ireland (Figure 1.2), with the exception of Donegal, largely reflecting the influence of market location and proximity to the large population of the capital city, Dublin. In terms of varieties, Rooster remains the most popular variety grown, followed by Kerrs Pink and British Queens (Anonymous, 2011) (Table 1.1).

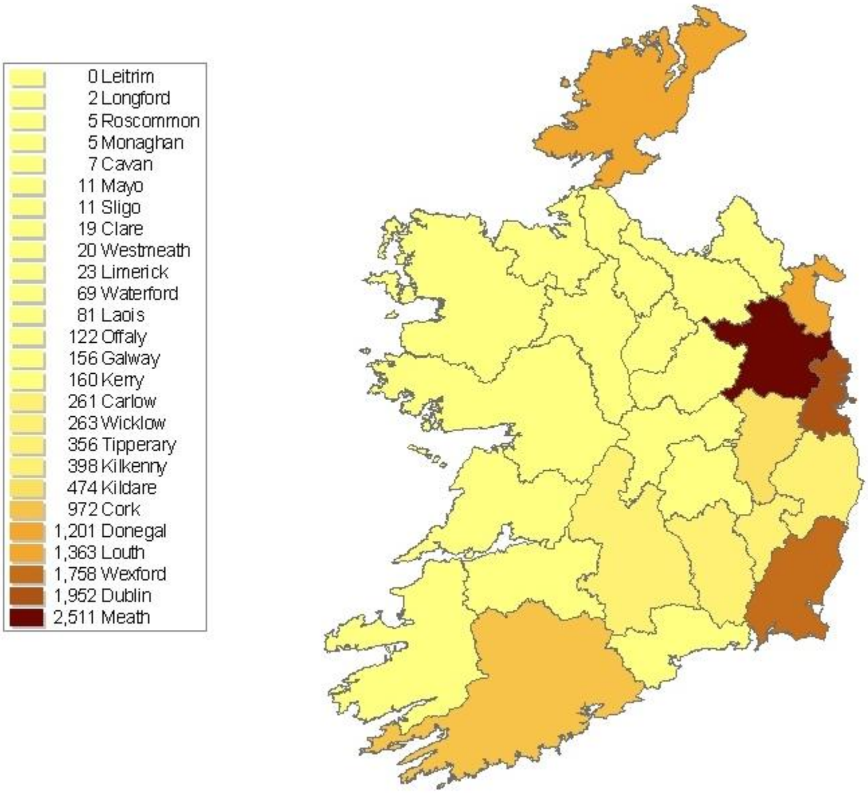


Figure 1.2 Distribution of potato production (in hectares) per county in 2011 (Irish sub-national division units in IE) (Anonymous, 2012)

1.3. The potato late blight disease

While potato crop is a host to numerous pests and pathogens, such as Common Scab (*Streptomyces* spp.), Early blight (*Alternaria solani*), Potato Virus Y and several parasitic nematodes (e.g. *Globodera rostochiensis* and *G. pallida*, *Meloidogyne* spp. and *Pratylenchus* spp.), potato late blight (PLB) caused by the *Phytophthora infestans* is one of the world’s most devastating diseases of potato and tomato crops (Fry, 2008). The re-occurring problem of PLB, due to its explosive asexual cycle and recent diversification of *P. infestans* population, demands continuous attention and the use of integrated management tools in sustainable food production systems. The biology and life cycle of *P. infestans,* and PLB disease management are presented in this section.

1.3.1. *Taxonomy and biology*

Phytophthora infestans was previously classified as a fungus due to a resemblance to filamentous fungi but is now classified as oomycete in the kingdom of Stramenopiles

(Kamoun *et al.* 2014). It belongs to the family *Peronosporaceae*, a family which contains numerous plant pathogens (Agrios, 2006). The approximately 60 species of *Phytophthora* arguably constitute the most devastating single genus of pathogens of dicotyledonous plants (Erwin *et al.*, 1996). The genus name, *Phytopthora,* comes from the Greek φυτό–(phyto) and φθορά (phthora), meaning "plant" and "decay, ruin, perish", respectively. The species name, *infestans*, originates from the Latin verb *infestare*, which means "attacking, destroying". The "water moulds" belonging to genus *Phytopthora* spp. result in enormous economic losses on crops worldwide, such as *P. capsici* which infects the fruits of *Cucurbitaceae* plants or the soya bean root and stem rot agent *P. sojae* (Agrios, 2006). *Phytophthora* spp. are mostly pathogens of dicotyledons, and many are relatively host-specific. Amongst cultivated crops, *P. infestans* can infect only two agricultural crops, potato (*Solanum tuberosum*) and tomato (*S. lycopersicum*), and several weeds from the genus *Solanum,* such as bittersweet nightshade (*S. dulcamara*) (Lima *et al.*, 2009).

Phytophthora infestans is a heterothallic species, a near-obligate hemibiotrophic pathogen under natural and agricultural conditions, with two mating types, A1 and A2. Production of gametangia (antheridia, oogonia) is stimulated by the proximity of the two mating types and once sexually combined they form oospores, which can survive adverse conditions in a dormant state for a period of several years (Smoot, 1958).

1.3.2. *Symptoms of potato late blight*

Symptoms appear first as water-soaked spots on leaves and stems, light to dark brown in colour. In moist weather, the spots enlarge rapidly and form irregularly shaped lesions when not limited by leaf veins. The lesions can be surrounded by a yellow halo or a zone of white growth 3 to 5 mm wide which appears at the border of the lesions on the undersides of the leaves. The entire plant can be destroyed in a matter of days giving off a characteristic odour under wet conditions. The pathogen is inactive during dry weather conditions, existing lesions stop growing, curl and wither, and no mycelial growth occurs on the underside of the leaves. The pathogen then reactivates when the weather becomes moist again. Symptoms on tubers present as areas comprised of slight depressions which are brown in colour. As symptoms develop, the affected areas become firm and dry and somewhat sunken. The rot continues to develop after harvest and in storage. Pathogen mycelium can develop on the surface of affected tubers, or it can be affected by secondary fungi and bacteria, causing soft rots and giving the rotting potatoes a putrid, offensive odour (Agrios, 2006).

1.3.3. *Origins and migrations*

Many consider that Central Mexico is the centre of origin for *P. infestans* (Grünwald *et al.*, 2005). *Phytophthora infestans* was first introduced in Europe and North America in the early-nineteenth century, followed by several waves of migration (Spielman *et al.*, 1991). Potato late blight epidemics in the 19th century were caused by genotype HERB-1, which persisted for over 50 years but was ultimately replaced by the US-1 (Yoshida *et al.*, 2013).

Smoot *et al.* (1958) reported that all isolates from the United States, Canada, western Europe, South Africa, the West Indies (105 isolates) and Mexico (4 isolates) were of the A1 mating type, except for some isolates from Mexico, which were of the A2 mating type. More recently, it was determined that most of the populations worldwide were dominated by a single clonal lineage referred to as US-1 (Fry, 2016). The first reported occurrence of the A2 mating type in Europe was in Switzerland during 1980 (Hohl *et al.*, 1984). Further studies indicated that A2 not only became widespread in Europe, but worldwide (Fry *et al.*, 2015). It is hypothesised that the migration of A2 at this time was caused by the shipping of large quantities of potato in the mid-1970s to Europe from regions in Mexico where the A2 mating type is common (Niederhauser, 1991). Since then, increasing globalization has resulted in further worldwide migration of the pathogen, leading to the rise and spread of new lineages, some of which demonstrate increased aggressiveness (Fry *et al.*, 2015). This has resulted in the displacement of the old clonal population (Day *et al.*, 2004).

Despite having relatively low genetic diversity, European populations of *P. infestans* undergo frequent and important changes (Cooke *et al.*, 2012; Fry, 2008). Until recently these populations were dominated by clonal lineages such as EU_2_A1, EU_8_A1 or EU_5_A1, but in 2003, the first occurrence of EU_13_A2 (hereafter 13A2) was recorded (Cooke *et al.*, 2012). This clonal lineage, commonly called "Blue_13", became dominant within two to three years (Cooke *et al.*, 2012; Li *et al.*, 2012). Subsequently, another clonal line, EU_6_A1 (hereafter 6A1), commonly called "Pink_6", also experienced strong population growth, although not quite as rapidly as 13A2. First observed in 2004, the frequency of 6A1 remained low, before progressing rapidly in 2010 (Cooke *et al.*, 2012; Stroud *et al.*, 2016). Since then, 13A2 and 6A1 have continued to dominate *P. infestans* populations in Western Europe. However, the population is continuously changing with new clonal lineages emerging, with EU_36_A2, EU_37_A2 and EU_41_A2 representing the new emerging threats (Cooke et al. 2019). As part of a European-wide monitoring programme, EuroBlight continuously monitors the ongoing evolution of the European *P. infestans* population and reports are regularly presented at meetings organised by the society and through their website (https://agro.au.dk/forskning/internationale-platforme/euroblight/).

The first recording of the A2 mating type on the island of Ireland was in Northern Ireland (NI) in 1987, with an overall frequency of 3% in 1992; it subsequently appeared in the Republic of Ireland (ROI) where 9-10% of isolates typed were of the A2 type between

1993 and 1994 (Cooke *et al.*, 1995). It is hypothesized that the major pathway of introduction of genetically different *P. infestans* was via infected seed tubers (Carlisle *et al.*, 2001; Griffin *et al.*, 2002); however, the transfer of air-borne inoculum from the south-east of England and continental Europe has also been identified as a potential pathway (Bourke, 1964; Griffin *et al.*, 2002). Between 1998 and 2002, none of 204 isolates recovered in Northern Ireland were of the A2 mating type; the population consisted of a limited number of clones related to, but in a different form, populations in the rest of the UK and Europe (Cooke *et al.*, 2006).

The occurrence of the A2 mating type in the UK and Ireland remained largely undetected until 2007 (Cooke *et al.*, 2014); between 2008 and 2010, the 13A2 type became the dominant genotype (Kildea *et al.*, 2010), declining markedly in 2011, only to resurge once again in 2012, with 37% of samples analysed belonging to this lineage (Cooke *et al.*, 2014). The sudden increase in the frequency of the A2 type in the UK and Ireland was associated with the increase in this single genotype, following a similar trajectory to that experienced in France and the UK between 2004 and 2005 (Cooke *et al.*, 2011). A similar trend was not evident with the 6A1 strain, which was established and become dominant in the UK, but was rarely detected in Ireland until 2014 (Cooke *et al.*, 2014; Stellingwerf *et al.*, 2018). The number of miscellaneous strains (i.e. strains not belonging to established pathogen strains) in the ROI is very low, suggesting that even though the potential for sexual reproduction exists (both 13A2 and 6A1 can be found in Irish potato crops), its occurrence or survival of sexually produced oospores and progeny is low. One possible reason is that mild winters may allow oospore germination, during periods when there is an absence or lack of host tissue availability.

The factors that led to the recent changes in the western European populations of *P. infestans* remain a topic of discussion. Undoubtedly, one of the main factors determining the long-term survival and success of individual clonal lineages depend on its level of aggressiveness (Day *et al.*, 1997; Cooke *et al.*, 2012). Clonal lines that exhibit most aggressiveness during the infectious cycle (e.g. short latency period, high level of sporulation) are likely to be more competitive and, therefore, have better evolutionary success. However, the overall fitness of a clone is also determined by its ability to survive between epidemics. Recent work shows the existence of a trade-off between aggressiveness and the inter-epidemic transmission of isolates in *P. infestans* (Pasco *et al.*, 2016). Therefore, it is important to understand how the fitness of clonal lines is impacted by the interepidemic phase of the pathogen life cycle.

1.4. The life cycle of *Phytophthora infestans*

The life cycle of the *P. infestans* (Figure 1.3) can be broadly separated into an epidemic phase, fuelled by the succession of numerous production cycles of asexual spores, and a survival phase, whether on the host or as sexual oospores. The epidemic phase of the life cycle of *P. infestans* is initiated by multi-nucleated sporangia produced by the pathogen, that germinate when in contact with the host plant and infect the host, either directly or indirectly, through the formation of between 6 and 10 uni-nucleated biflagellate zoospores per sporangium which individually infect (Judelson *et al.*, 2005). The infection mechanism depends on the climatic conditions, with indirect infection by the zoospores occurring at lower temperatures (10 - 15 °C) and direct infection at higher temperatures (15 - 20 °C), although at these higher temperatures the germination rate is reduced (<30%) (Crosier, 1934). Sporangia and zoospores (after encystment for the latter) produce a germ tube allowing them to penetrate the host plant, either through natural openings such as stomata and lenticels, or through the plant walls by the formation of an appressorium (Coffey *et al.*, 1991). If the host is compatible, a haustorium is formed, and a network of intra- and intercellular hyphae invade the host tissues (Coffey *et al.*, 1991).

Suitable environmental factors, such as a period of three days with temperatures between 17 and 25 °C and high relative humidity, are required for sporangiophores to grow through stomata. These branched sporangiophores produce lemon-shaped sporangia at their tips (Judelson *et al.*, 2005; Fry, 2008). The sporangia growing on the underside of the leaf can present as the first macroscopic symptom, and the entire cycle can be completed within 96 hours on a susceptible host and under optimal environmental conditions (Fry *et al.*, 2013). The sporangia then become the secondary inoculum, which can then be dispersed over longer distances by wind or locally by rain splash to the same or nearby host plant, initiating a new infection cycle.

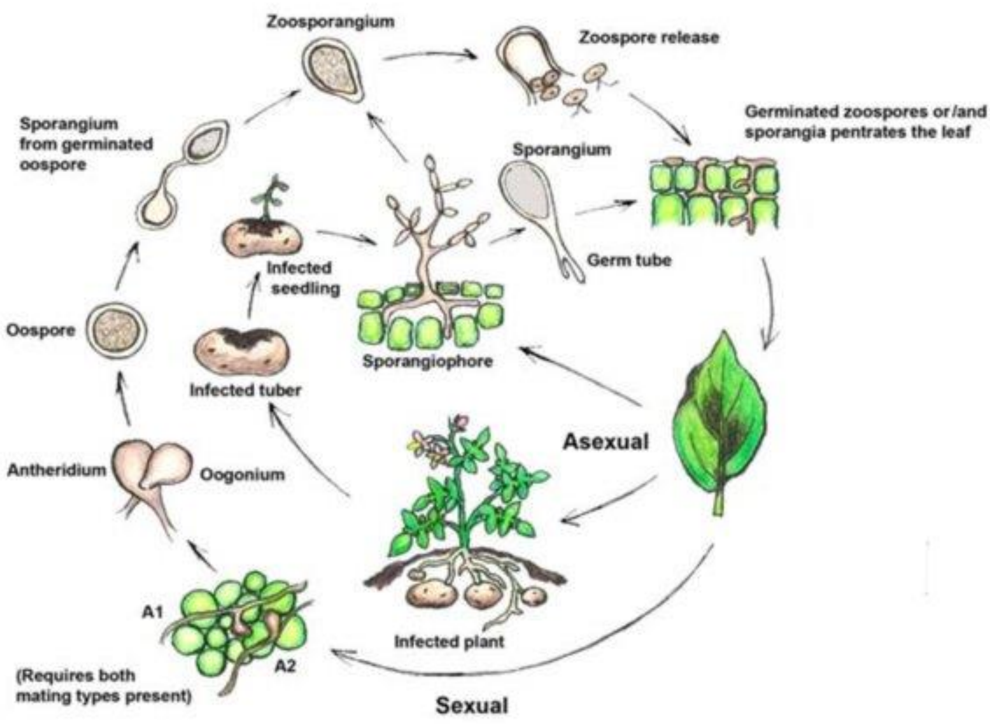


Figure 1.3 The life cycle of *Phytophthora infestans* (source: Bengtsson, 2013)

The brevity of the asexual cycle of *P. infestans* and formation of a large number of sporangia, estimated in the region of 300,000 per lesion over its lifetime (Fry, 2008) and facilitating the aerial dispersal of the disease (Aylor *et al.*, 2001), are the main factors explaining the rapid development of the disease. While detached sporangia can survive for weeks in soil, the survival time of sporangia in the air is reduced to hours or minutes, limiting the dispersal of *P. infestans* sporangia over longer distances. If exposed to sunlight, sporangia die in under an hour; under cloudy conditions, sporangia can survive for several hours in the air (Rotem *et al.*, 1985; Mizubuti *et al.*, 2000; Weille, 1961). Skelsey *et al.* (2009) estimate that the likely dispersal range of *P. infestans* sporangia is between 5-20 km.

Phytophthora infestans can survive between the potato growing seasons as resilient sexually produced oospores or as mycelium surviving on either dormant tubers or actively growing plants (Andrivon, 1994) (Figure 1.3). The former sexually produced oospores have a thick wall (0.7-1 μm) (Drenth *et al.*, 1995), allowing them to survive for several years in the soil in the absence of a host, even under unfavourable weather conditions (Andersson *et al.*, 1998). Oospores then germinate, producing a sporangium initiating the asexual cycle. Alternatively, asexual sporangia produced on the foliage during an epidemic fall or are washed to the ground and subsequently the developing tubers during rain. Once there, they can infect the tubers directly or germinate releasing zoospores which infect through the lenticels or wounds. Depending on infection levels, environmental conditions, and the specific aggressiveness of the *P. infestans* strain, tuber infections can stay dormant for several months. Infected tubers can be left in the soil after harvest, discarded on cull piles or potentially used as seed in the subsequent season. Epidemics are initiated when conditions are favourable for the development of *P. infestans* sporangiophores and sporangia and if available host tissue is in proximity.

In geographical regions where climatic conditions limit the survival of infected tubers left in the soil after harvest or in cull piles, epidemics are mainly initiated via oospores or from infected seed tubers (Yuen *et al.*, 2013). In these regions, populations of *P. infestans* have higher levels of genetic diversity due to sexual reproduction (Sjöholm *et al.*, 2013).

Conversely, in milder regions, such as in western Europe, epidemics are initiated by sporangia surviving in overwintering tubers or waste piles (Pasco *et al.*, 2015). As such, *P. infestans* populations in these regions are characterized by clonal structures, and consequently, low levels of genetic diversity (Montarry *et al.*, 2010; Cooke *et al.*, 2012).

1.5. Effects of the environmental factors on potato late blight epidemics

While the impact of the environmental conditions will be treated in more detail in the following chapter, as a part of the modelling process, the most important aspects regarding the impact of weather conditions on the life cycle are presented here in a general context.

The association between severe PLB epidemics and mild, wet weather has been observed since PLB was first observed in Europe (Large, 1959). If moisture is not limiting, foliar diseases induced by pathogenic fungi and oomycetes during the growing season are dependent on optimal temperatures for their growth (Fry, 1975). Although potato late blight mainly occurs under conditions of mild temperatures (12 - 24 °C) and moist conditions (Wallin, 1962), the speed of development depends on specific sequences of suitable conditions (Fry *et al.*, 2013). Sequences of the secondary cycles of the disease require suitable environmental conditions, with diverse optimum ranges, for their completion; i.e. a temperature of 20 °C is optimum for sporulation; zoospore release and infection occur at lower temperatures in the range of 12 - 15 °C; direct sporangial germination and infection are promoted by higher temperatures with optimum at 24 °C, and; incubation at 23 °C (Crosier, 1934).

Leaf wetness is critical for driving PLB epidemics, although it is only necessary for the infection stage (Crosier, 1934); while sporangia of *P. infestans* are produced only if the air around the infected surface where the pathogen is actively spreading is saturated

(Harrison *et al.*, 1989). It has been reported that the formation of sporangia of *P. infestans* is inhibited during hours of high light intensity (Cohen *et al.*, 1975; Xiang *et al.*, 2014). Sporangia of *P. infestans* are actively released and dispersed in the morning, due to a drop in relative humidity, and breaking of sporangiophores and their survival depends on solar radiation, temperature and relative humidity (Fry *et al.*, 2013).

1.5.1. *Irish weather and PLB*

The climate in Ireland is characterized as being mild, maritime, largely reflecting its proximity to the moderating effects of the Atlantic Ocean. The climatological mean annual temperature range is between 9-11 °C. At inland locations, summer temperatures typically reach between 18 – 20 °C and about 8 °C in winter (Met Éireann). Consequently, the temperature range in Ireland lies within the biological range for PLB throughout the potato growing season. As the dominant airflow direction is from the west and south-west, the maritime influence on rainfall is most apparent along the Atlantic coast; precipitation is generally higher on the west coast due to the presence of natural mountain barriers interacting with the airflow and decreases with distance inland (Figure 1.4). Mean annual rainfall in the west of the country ranges between 1000 and 1400 mm, with receipts in excess of 2000 mm in upland locations; in the eastern half, receipts of between 750-1000 mm are more typical. The annual average rainfall over the entire country is approximately 1200 mm (Walsh, 2012). For these reasons, the weather conditions experienced during the growing season in the Republic of Ireland are considered conducive for blight development (Dowley *et al.*, 2008).

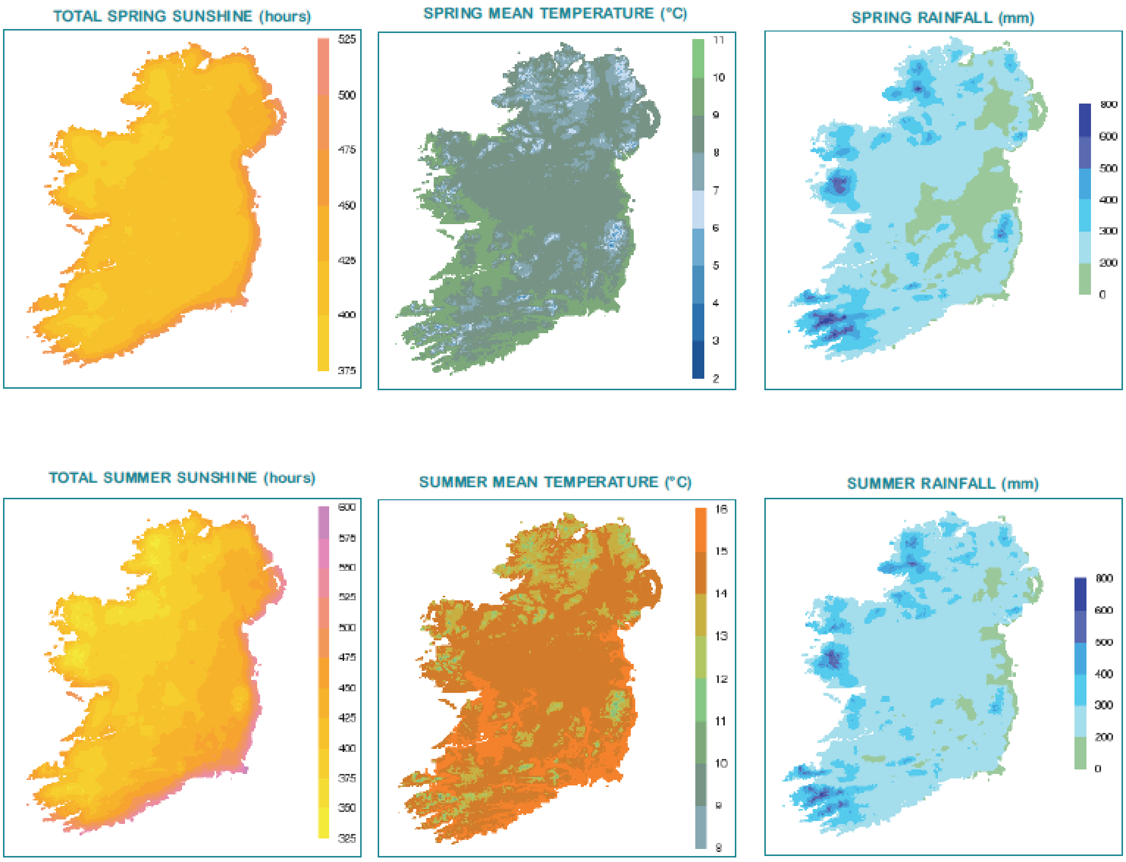


Figure 1.4 Spring (upper row) and summer (lower row) sunshine (left), temperature (middle) and rainfall (right) meteograms of long term average (1981 – 2010) for Ireland (Walsh, 2012).

1.6. Disease management

The continual displacement of *P. infestans* populations by increasingly aggressive lineages, the predominant cultivation of susceptible varieties and intensification of potato production makes the management of PLB an increasingly challenging task. It is therefore of the utmost importance that the risk of the disease outbreak is managed through the use of integrated pest management (IPM) approaches, such as sanitary measures and resistant varieties (Fry *et al.*, 2015; Schepers *et al.*, 2009). Sanitary measures include the use of healthy seed, removing or destruction of cull piles and volunteer plants (Schepers *et al.*, 2009). Strict crop rotation can help to reduce the potential of early disease outbreaks, especially in areas where the oospore infections are confirmed (Bødker *et al.*, 2006). Desiccation or removal of the haulm before harvest by thermal, mechanical or chemical means, reduce the potential risk of tuber infection (Fry, 1982); while burial by ploughing leads to increased risk of latently infected potato plants (volunteers) which could act as a primary infection source (Cooke *et al.*, 2011).

Another major way to manage PLB is through planting varieties with increased levels of resistance. Two main types of resistance have been described in plants: qualitative resistance and quantitative resistance. The first, also called specific resistance (van der Plank, 1968), is based on gene-for-gene interactions between the host plant and the pathogen after the host recognises the parasite (Flor, 1971) and is associated with a hypersensitivity reaction that can also be linked to dying of the plant cells located near the pathogen penetration point (Agrios, 2006). Quantitative resistance is generally governed by several genes or genomic regions called Quantitative Trait Loci (QTLs) that lead to a reduction in the severity of disease symptoms. The remarkable pathogenic potential of *P. infestans* has stimulated many attempts to breed resistant cultivars (Fry, 2008). Initial efforts, dating from the mid-19th century, resulted in partially successful quantitative or 'field resistance' (Wastie, 1991). However, the discovery of the first resistance genes (R-genes), which conferred qualitative resistance shifted the attention of breeders towards the introduction of such R-genes from the wild species *S. demissum*. These R-genes were quickly circumvented by *P. infestans*, which led to rapid selection of the pathogen strains compatible with the specific R-gene, rendering them ineffective and failing to provide durable disease control (Malcolmson, 1969; Wastie, 1991). Currently, attention is shifting towards stacking R-genes by conventional resistance breeding or genetic engineering techniques (Leesutthiphonchai et al., 2019). Other strategies are based on the pyramid of major genes, with or without the use of genetic engineering techniques (Haverkort *et al.*, 2009). Most of the current commercially available cultivars are blight susceptible due to market demand for traditional varieties (Agrios, 2006) and deploying stacked R genes through genetic modification of old, known varieties which are in demand by the market could provide a sustainable long term solution for the PLB management problem (Kessel *et al.*, 2018)

The combination of partial resistance developed using conventional resistance breeding or genetic engineering techniques and fungicides can slow down the development of the late blight epidemic and help preserve the genetic potential of resistant varieties. Trials have been conducted in several European countries to investigate the possibilities for reduced fungicide usage in resistant cultivars (Fry, 1975; Nærstad *et al.*, 2007; Spits *et al.*, 2007).

Fungicides still have a key role in the integrated control of PLB due to a zero blight-tolerance requirement and the economic risks associated (Schepers *et al.*, 2009). This intensive and primarily preventive control strategy has led to an excessive reliance on the prophylactic use of fungicides, with 5- to 7-day treatment frequency and up to 20 applications in a single season to control the potato late blight disease (Cooke *et al.*, 2011). However, the frequent use of targeted selective oomycete fungicides has led to the development and rapid selection for fungicide resistance populations of *P. infestans*, e.g. the widespread development of resistance to the phenylamide group of fungicides, which has rendered these fungicide ineffective (Childers *et al.*, 2015; Gisi *et al.*, 1996; Matson *et al.*, 2015). Additionally, it has been shown that fungicides have adverse effects on the health of users as well as on the environment (Savary *et al.*, 1994). This problem has been recognised in the European Union (EU), and the European Community Directive 128/2009 on the Sustainable Use of Pesticides (European Commission, 2009) establishes a strategy for the use of plant protection products (PPPs). Additionally, food chains are imposing increasing restrictions regarding pesticide residues on producers to meet consumer demands (Hardwick, 2006). To achieve these demands, decision-makers in conventional agricultural systems need to transition to IPM based systems, which require increased knowledge as they must deal with greater complexity (Rossi *et al.*, 2012). This knowledge, often not available or easily accessible, can potentially be streamlined through the use of a decision support system (DSS), which could aid timing of the treatment, as well as the selection and dose of the active ingredient, to achieve the maximum efficacy with the minimum use of PPPs (Rossi *et al.*, 2012). Such systems do not only serve for the purpose of reducing impact of chemical crop protection, but also to justify its use (Hardwick, 2006).

1.7. Problem statement and research objective

Potato production in the Republic of Ireland is decreasing due to an increase in associated risks involved. Potato late blight is one of the leading financial and time inputs associated with potato production while remaining the main limiting factor of production. The potato late blight decision support system devised to assist in the disease management decision making process in the Republic of Ireland is based on the Irish Rules model (Bourke, 1953a). The algorithm, its calibration and the decision strategy of the decision support tool operated by Met Éireann was devised in the 1950s. The system has not been systematically evaluated since it was originally devised. Significant changes in the population of *P. infestans*, potato production systems and technological advancements with regards to weather observation and forecasting demand to be incorporated into a new, improved understanding of the opportunities, and limitations, of employing decision support in potato late blight management under Irish conditions.

The aim of the present work is to integrate alternative, environmentally friendly and economically viable options to assist in the control of the primary disease of an important agricultural crop, potato, under Irish conditions. A key challenge is to apply a methodologically sound research approach to a practical problem that requires immediate attention and to apply these findings in an operational capacity. To achieve this, an interdisciplinary approach is taken, integrating data analysis methods with both field and laboratory-based evaluations.

Research Objectives:

- Review the history and current state of the decision support in potato late blight disease management and assess possibilities for its integration in the Irish context (2nd chapter)
- Evaluate and re-calibrate the IR model and decision thresholds (Paper 1)
- Undertake field-based evaluations of approaches for optimising current grower's practice using environmental risk estimation, varietal resistance and molecular tools (Paper 2)
- Enhance the modelling framework to ensure that research findings can be readily integrated into the continued development of a DSS suitable for use in decision support (Paper 3)

An additional objective of the thesis was to develop a robust model evaluation and calibration methodology, in a well-documented and reproducible manner, using a single accessible programming environment to facilitate future work on the development of potato late blight forecasting, and crop disease forecasting more generally, in Ireland. Additionally, such scientific contribution is not only valuable for the target ecosystem but should be transferable to other parts of the world with the potential to be used in practice, research and education.

The collection of papers included in this thesis are contextualised in the 1st, 2nd and 6th chapters. Having defined the primary rationale and research aims; the principles, examples and history of potato late blight modelling for the use in practical disease management are presented in the 2nd chapter. The experimental work on the model re-calibration, evaluation and future-proofing is presented in the 3rd, 4th and 5th chapters, respectively, and the general discussion and conclusions are presented in the 6th chapter. A more detailed description of each chapter of this thesis is as follows:

1. Initially, an overview of the potato late blight disease triangle is presented, including information regarding the pathogen, host, environment and human intervention to control the disease globally and from the Irish perspective. An overview of the work to be carried out is presented, as well as an outline of how this research will be implemented.
2. Chapter 2 describes the historic development and the current state of potato late blight forecasting is reviewed, focusing on the development of models, the issues of model complexity and limitations, including their practical application. Chapter 2 also outlines the model currently used to forecast PLB in the Republic of Ireland, its current operational application and information delivery mechanism.
3. Chapter 3 undertakes a systematic evaluation of the Irish Rules model. Following this evaluation, the model is re-parameterised to reflect the changes in the potato late blight pathosystem since the IR model was originally proposed.
4. Chapter 4 seeks to assess the available options for optimising current standard potato late management growers' practice using integrated pest management tools. The modified IR model and varietal resistance were employed in order to assess if prophylactic fungicide inputs could be reduced. To complete the disease triangle, the response of the pathogen population to applied factors was also monitored.
5. Chapter 5 presents a new modelling framework, which incorporates a suite of sub-models to facilitate the incorporation of improving meteorological

forecasting capabilities and increasing differentiation of the pathogen population. Additionally, the existing and newly proposed models are evaluated for suitability in relation to the uncertainty introduced by the weather forecast.

6. Chapter 6 discusses the results from the work and develops recommendations for implementing measures regarding the optimisation of potato late blight control in Ireland. The limitations of the current research are identified and future avenues for research and development are highlighted.

2. Overview of potato late blight forecasting

2.1. Introduction

Potato late blight disease forecasting has been employed for informing the disease management for almost a century. There is a wide array of models and DSSs, which differ in their complexity, structure, purpose and user experience. Finding a compromise between the ability of the meteorological network and reasonable simplification of the pathogen biology, and providing it in a user-friendly, regularly updated, economically and environmentally beneficial system has proven challenging. However, the development and accessibility of technology and high-speed computing is having a positive impact on the revival of integrated pest management aided by a knowledge base stored on the computer. Whilst the overall complexity of the models used in PLB DSSs have increased over time, most of the systems are still based on the simple estimation of the duration of wet conditions within a certain temperature range, reflecting conditions conducive to sporulation and infection.

In Ireland, PLB has a long history, as well as the attempt to forecast it. The risk prediction model used since the 1950s is in need of revision, as well as its decision thresholds and information delivery. To provide the background for the experimental work, an overview of biological and meteorological aspects, modelling frameworks, as well as their development globally and in the Republic of Ireland is presented. While the main focus is on the empirical (territorial) models, some relevant examples from simulation modelling are presented, in the context of the current research.

2.2. Decision support systems in crop protection

A decision-support system (DSS) is an interactive software-based system that helps decision makers obtain useful information from raw data, documents, personal knowledge, or models in order to identify and solve problems and make informed decisions (Power, 2007). DSSs in crop production collect and organise, analyse and interpret the information to recommend the most appropriate action or action choices to overcome a problem (Rossi *et al.*, 2012). In specific relation to plant disease control, DSSs utilise the available information (weather, crop growth stage and susceptibility, etc.) to provide users with an estimated level of risk their crop may be exposed to due to a particular disease (Figure 2.1) (Gent *et al.*, 2010). They range from simple data processing tools, including rules, schedules of management, equations, combinations of decision aids, to expert systems, with a level of complexity determined by human resources (knowledge specialists), available technical and financial resources, the degree of industry organization and support, and the expectations of end users (Magarey *et al.*, 2002).

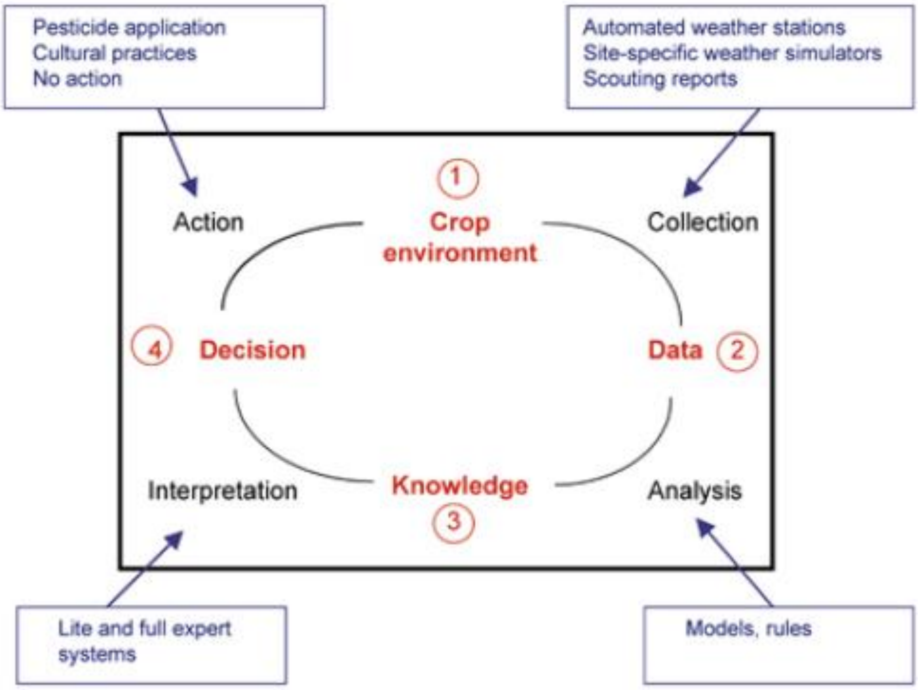


Figure 2.1 DSS scheme showing components (red font), methodology (black font), and tools (blue font). (Source: Magarey *et al.*, 2002).

Numerous DSSs have been developed which have contributed little to practical agriculture (Gent *et al.*, 2010). Widespread adoption of DSSs in most cropping systems is low, with a number of users ranging between a few enthusiasts and up to just 3% of the number of professional farmers; and their main use is through advisors who serve as an "information filter" (Rossi *et al.*, 2012). Reasons for their poor up-take range from a lack of comprehensive information regarding all management aspects (i.e. not a single disease), low quality (especially the commercial products); lack of a user friendly information delivery and presentation (Magarey *et al.*, 2002); time required to operate; lack of maintenance and update (i.e. weather and PPPs) (Rossi *et al.*, 2012). Magarey *et al.* (2002) suggested that the ideal, 21st century DSS was a 'super consultant', which incorporates total management solutions for growers, but that the user remains responsible for the choice and implementation of subsequent actions.

2.2.1. *Disease risk models employed in crop disease DSSs*

A need for knowledge and understanding of climate in the environment where the pest/host interaction develops has long being recognised. However, this interaction was adequately quantified only after simulating these relationships using mathematical models (Magarey *et al.*, 2006). The use of mathematical models to understand and control plant disease epidemics has a relatively long history (Kranz, 1974; Pietravalle *et al.*, 2003). Computing power has enabled plant pathologists to create, evaluate and use these models more effectively. Modelling a phenomenon, such as disease development, consists of integrating the knowledge acquired through experimentation, experience and theory in the form of mathematical equations (Madden *et al.*, 2007).

By including meteorological data into these models, the potential risk of outbreaks and their frequency and severity under favourable weather conditions can be estimated (Gommes *et al.*, 2008). This is currently an irreplaceable segment of research in plant disease epidemiology, resulting in two main groups of models used to forecast plant disease (after Gommes *et al.*, 2010):

- Mechanistic (field) models intended for use at the microscale (field/canopy layer);
- Empirical (territorial) models intended for use at the mesoscale.

However, such divisions are arbitrary, since most models contain components from both (Madden *et al.*, 1988a). Empirical models have been developed using observed historical data on the disease and weather data (most often temperature, relative humidity, rain, and in some studies solar radiation) to derive 'rules' from the associations identified. Such models provide qualitative information regarding the risk status and are typically limited to the specific geographical region and ecosystem in which they were developed. Empirical models are employed with macroscale weather conditions, providing limited opportunities for point predictions, and are subject to the accuracy of the weather forecast (Gommes *et al.*, 2010). Whilst empirical models have the advantage of being less laborious to produce and simpler to implement and calibrate, developing accurate models has proven difficult. More complex mechanistic type models are assumed to be more reliable but require increased information and development (Rossi *et al.*, 2010a). However, Madden and Ellis (1988a) argue that to develop an accurate and usable disease forecast model, it has to be as simple as possible. In relation to potato late blight, complex models based on a number of questionable assumptions often based on experiments where the environment is not controlled, are only slightly more reliable than the simple ones (Harrison, 1995b).

2.3. Potato late blight risk prediction DSSs

It is often considered that the risk prediction model is a DSS, and vice versa, while in fact, it is only a part of a DSS platform. The risk estimation segment of DSSs typically includes several of the components shown in Table 2.1. Outputs of those components could be estimated using models or measured and/or observed. For example, leaf wetness could be measured using sensors or estimated with the aid of models (Gleason *et al.*, 2008). The applicability and usefulness of the elements outlined in Table 2.1 depend on the type and purpose of the DSS and its scale of application. While a brief history of PLB DSSs and approach to modelling will be presented below, the main focus of this section is to review the possibilities of, and obstacles to, risk estimation modelling on a territorial level, in order to evaluate possibilities for improvement of the current PLB DSS in Ireland.

Table 2.1 Components utilized in various PLB DSSs.

Weather	**Crop**	**Pathogen**	**Life cycle**
Temperature	Blight resistance (foliar and tuber)	Primary inoculum (asexual/oospores)	Overwintering survival
Leaf wetness	Phenological stage	Population size	Sporulation
Relative humidity	New growth	Population structure	Spore release
Solar radiation	Fertilization	Fungicide resistance	Spore survival
Wind	General health status		Infection
Weather forecast	Fungicide protections status		

2.3.1. *Development of PLB DSS*

Plant disease risk prediction models are a backbone of DSSs in crop protection. An inherited trade-off between model framework uncertainty and data uncertainty requires finding an optimal level of model complexity to fit the purpose (Pascual *et al.*, 2003), as shown in Figure 2.2. The complexity of models depends on resources available during development; their intended scale of application; contemporary knowledge regarding pathogen epidemiology; and, available data inputs (Magarey *et al.*, 2002; Shtienberg, 2013). However, the decision regarding the model complexity, or the point of minimum uncertainty, remains a subjective decision by the model developer. Hence, in this section, a brief overview of modelling approaches and uncertainty introduced by the input data, as well as the practical application of risk estimation information, is described.

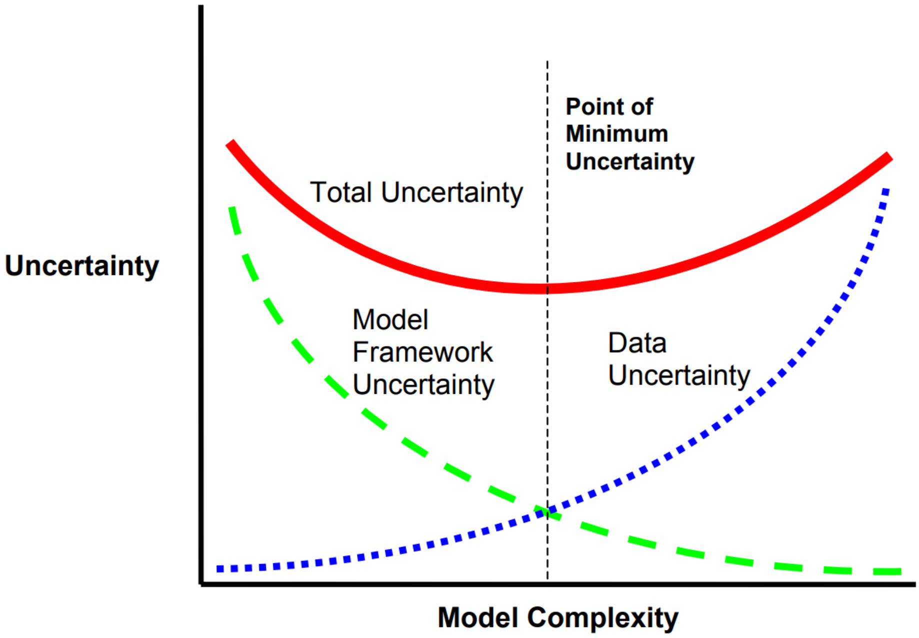


Figure 2.2 Conceptual relationship between model uncertainty and uncertainty of the knowledge and data used to build the model, and their interaction (source: Pascual *et al.*, 2003).

2.3.2. *Modelling the life cycle of the P. infestans*

Risk estimated by plant disease risk model is typically based on one or more life stages of the pathogen (Madden *et al.*, 1988a; Magarey *et al.*, 2007). Relevant modelling examples are shown as segments of the life cycle of the pathogen in this subsection.

Initial inoculum and infection pressure

Empirical models are usually based on later stages of the life cycle, and the risk is estimated mainly on conditions for the infection; while dynamic models, due to their quantitative nature, make assumptions on the size of the initial inoculum to quantify the population growth (Rossi *et al.*, 2010a). Initial inoculum depends on several factors including, levels of seed infection, hygiene of the waste piles and storage plants and the intensity of potato production in the surrounding region. Traditionally, empirical models consider that the inoculum originates from within the crop, rather than from external sources (e.g. Gutsche *et al.*, 1996; Michaelides, 1991; Schrödter *et al.*, 1967; Skelsey *et al.*, 2009). This may be an acceptable assumption for regions in which potato production is limited. However, in regions where intensive potato cultivation occurs, affected tubers in storage or in plots that are latently infected with *P. infestans* are an important factor. Only a few models include the influence of disease pressure from the surroundings, such as volunteer plants or infections in nearby crops. In Symphyt I, the model used in Germany (Kluge et al., 1990), initial inoculum is calculated to reflect the physiological state of the crop, PLB resistance of the varieties planted and a measure of infection pressure in the region. To develop a model that estimates disease pressure during the growing season, Forrer and Gujer (1991) monitored PLB disease progress in 100 small plots with an untreated susceptible variety (Bintje) across Switzerland. In their modelling approach, Krause *et al.* (1975) indicate that Blitecast should not be used for scheduling treatments if there is blight in the plot itself, while Fry (1977) advises against the use of warning systems, if abundant inoculum sources have been observed in the vicinity of the production field.

Sporulation

PLB lesions require extended humid periods for the production of sporangia, which are subsequently dispersed by rain and wind (Crosier, 1934; Harrison *et al.*, 1989). Although sporulation has traditionally been included in some PLB disease prediction models, it has often only been in a qualitative manner signifying the minimum time duration needed for the production of sporangia, disregarding the lower rate of development that may occur at sub-optimal temperatures (e.g. Bourke, 1953a). Schrödter and Ullrich (1967) developed a model based on the temperature-dependent equilibrium of sporulation (at relative humidity > 90%), where a minimum of 10 hours with relative air humidity > 90% is required to initiate the risk accumulation. This function is employed in the Negative Prognosis (Schrödter *et al.*, 1967) model as 6 temperature ranges with different weighting factors; the epidemic-free period ends when the threshold of 150 disease units is reached.

In his dynamic model, Michaelides (1985) implemented equations based on data from Crosier (1934) on the influence of temperatures between 3 and 26 °C (optimum at 18 °C) on the production of spores. He considered that spore production is only possible in saturated air and which linearly increases if the relative humidity is higher than 95%.

Infection

Crosier (1934) and Schrödter and Ullrich (1967) have shown that the plant is predominantly infected by the indirect, zoospore, infection pathway. At an optimum temperature of 12-13 °C, 60-80% of the zoospores germinated indirectly after 3 hours; at an optimum for direct germination (24 °C), only 20% of sporangia germinated after 20 hours (Crosier, 1934). For this reason, indirect infection is assumed more important by a number of modelling groups (See Hartill *et al.*, 1990; Michaelides, 1991; Schrödter and Ullrich, 1967). Although several modellers used the data from Crosier (1934), their lateral temperature limits for pathogen development differ; for example, Duvauchelle (1993) employed the range from 5 to 33 °C (Duvauchelle, 1993) while Schrödter and Ullrich (1967) employed the range from 10 to 24 °C (Schrödter *et al.*, 1967).

Infections occur only if the leaf surface is wet (Crosier, 1934). Schrödter and Ullrich (1967) consider that germination and penetration occur after a minimum of four hours at relative air humidity > 90%. Bourke (1953a) considers that the infection period is initiated immediately after the sporulation period, but it is reduced by four hours if the rain was < 0.1 mm at the beginning of that period.

Incubation time

The incubation period is the only stage of the disease cycle that does not depend on relative humidity or leaf wetness. It is, however, temperature dependent. Hartill and Young (1990) report that incubation is optimised at 23 °C and the latent period for *P.*

infestans is 60 hours at this temperature, while it could take up to 160 hours at 10 °C. Incubation, however, is not included in disease prediction models used in practice, but is typically incorporated in simulation models used for research purposes, as it is necessary for the estimation of the time lag between reproduction cycles.

Survival

Rotem *et al.* (1978) argue that the survival of spores in Israel during the period from 3 hours after sunrise to sunset is determined by the temperature, relative humidity and radiation. According to Rotem *et al.* (1970), the survival of spores on the leaf depends more on solar radiation than on air temperature and a formula defining this relationship can serve as an indicator of the sporangia survival. Similar work was later implemented in the US (Mizubuti *et al.*, 2000) and more recently in the UK (Skelsey *et al.*, 2017). Although all authors agree on the negative impact of radiation on sporulation, the estimated rate of survival varies, with a steeper exponential decrease in viability with cumulative solar radiation dose observed in the US study. Such differences could arise from differences in the diffusion of solar radiation in two different climatic zones (New York State, USA, and Scotland, UK) and pathogen lineages. Although the effect of radiation on spore survival is acknowledged by many authors, and simple equations are available (e.g. Mizubuti *et al.*, 2000; Rotem *et al.*, 1985; Skelsey *et al.*, 2017; Sunseri *et al.*, 2002), to the best of our knowledge it is yet to be included in disease prediction models used in practice. This could be explained by the fact that solar radiation data was not easily obtainable in the past (Gleason *et al.*, 2008) or widely measured.

According to Schroetter and Ullrich (1967), the number of hours per week with relative humidity < 70% is a measure of the negative influence of drought on *P. infestans.* Michaelides (1985) developed formulas based on data from Crosier (1934), which quantify spore survival based on temperature and relative humidity; he considered the necessary temperature range to be 3-30 °C (optimum between 12.5-22.5 °C) and employed six categories of relative humidity above 45% (Figure 2.3).

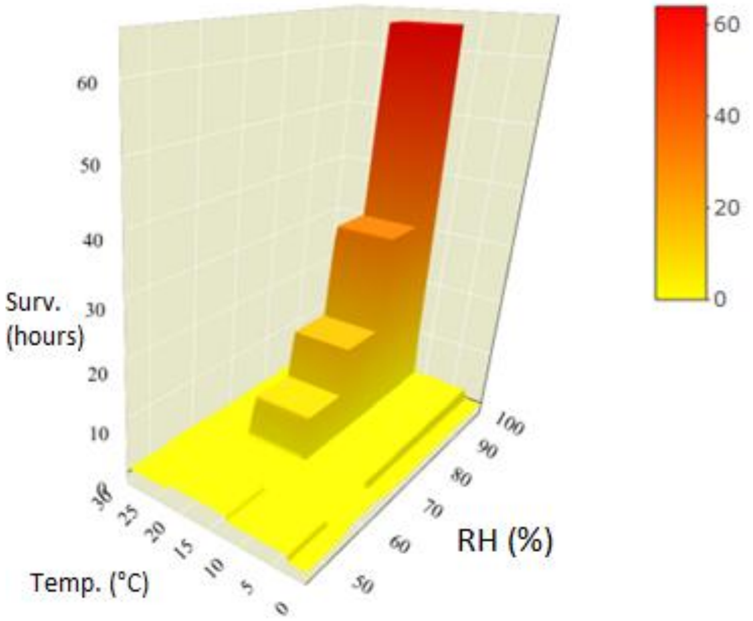


Figure 2.3 The probability of *P. infestans* sporangia survival based on the relationship between temperature and relative humidity (Michaelides, 1991).

Whole infection cycle

Most of the assumptions regarding the entire infection cycle in both empirical and semi-empirical models employ a temperature-dependent period with relative humidity (most often > 90%) as a condition for PLB development (e.g. Bruhn, 1981; Duvauchelle, 1993; Krause *et al.*, 1975; Wallin, 1962; Winstel, 1993). For example, in the model by Bruhn and Fry (1981), blight units are assigned according to temperature ranges of 3-7 °C; 8-12 °C; 13-22 °C and 23-27 °C when the relative humidity > 90%. The accumulation of risk is highest in the 13-22 °C temperature range. Exceptions to the 90% relative humidity minimum threshold include some quantitative models, such as Simphyt I (Kluge *et al.*, 1990), where risk hours are accumulated according to hours with a temperature greater than 8 °C and relative humidity > 75%. Kluge and Gutsche (1990) summed the influence of the temperature for germination, penetration, incubation time and sporulation. Duvauchelle (1993), in the Guntz Divoux model, considers that there is no risk of infection under 7 °C and depending on the temperature and number of hours with relative humidity > 90%, the model outputs three levels of risk for infection.

2.3.3. *Turning risk estimation into decision support*

The ultimate goal of PLB forecasting is to aid decision making regarding control programmes, for instance, the initiation of fungicide control programmes and subsequent treatments (Bourke, 1955a). In general, territorial models are mainly limited to indications of the risk or warnings of blight conducive weather; the more localised, micro-scale models and DSSs attempt to translate the information into advice. Examples of DSSs offering advice on the initial and subsequent fungicide treatments are presented below.

The initial treatment

Several models provide an estimate of the initial fungicide treatment date based on an accumulation of incubation units (e.g. Kluge *et al.*, 1990; Schrödter *et al.*, 1967; Wallin, 1962). In practice, fungicide protection is often initiated after a ‘zero date’ or a certain phenological stage (Cooke *et al.*, 2011). While zero dates differ regionally, applications are not typically initiated until the plants meet in the row (Cooke *et al.*, 2006). At that point, plants start forming their own microclimate with less turbulence resulting in an increase in humidity compared to the ambient or surrounding conditions (Jacobs *et al.*, 2009). Although this is not always acknowledged, in practice, applications can be initiated earlier due to perceived risk because of higher susceptibility of plants at earlier phenological stages (Fry *et al.*, 1986). In Simphyt I, Kluge and Gutsene (1990) predict the start of an epidemic using empirically determined regional risk factors, based on historical disease observations, in combination with the varietal resistance. Krause *et al.* (1975) proposed different thresholds for the initial fungicide application based on varietal resistance suggested in Blitecast. However, Doster *et al.* (1989) reported that disease occurred before these thresholds were reached, and advised against the use of Blitecast for the initiation of fungicide protection. Conversely, the recommendation to initiate fungicide protection by Prophy, a more personalised DSS, is related to the phenological stage of the plant. Prophy recommends initiation of fungicide programme when the crop reaches an average height of 15 cm (Nugteren, 2004).

Spray intervals

Spray intervals depend on the fungicide degradation rate, which is determined by exposure to ultra-violet light, temperature and rain (Caffi *et al.*, 2018), the varietal resistance and the morphology of the potato variety (Fry *et al.*, 1983). Whilst none of these specific aspects are considered in the older DSS based on simpler territorial risk estimation, they are often included in newer DSS platforms (e.g. Small *et al.*, 2015a) and personalised commercial PLB DSS (e.g. Nugteren, 2004). However, in practice, there is a need for constant re-evaluation due to the dynamic nature of the pathosystem and changes of fungicide efficacy and varietal resistance levels (e.g. Fry *et al.*, 1983; Grünwald *et al.*, 2002). Bruhn and Fry (1981) proposed a spray interval correction in Simcast, based on varying the “blight unit” accumulation according to the varietal resistance, temperature and the duration leaf wetness. Simcast has three levels of varietal resistance (very sensitive; sensitive; moderately resistant) with different assumptions regarding the number of hours with relative air humidity > 90% needed to reach the decision threshold risk accumulation. Grünwald *et al.* (2002) reported that the system was advising too many spray warnings for cultivars with increased levels of blight resistance and they further modified the system to reduce the fungicide usage on such varieties.

Similar to Blitecast, Symphyt (Kluge *et al.*, 1990) considers the varietal resistance based on the calculation of the new infections and three risk groups, to estimate fungicide treatment intervals. PhytoPRE (Forrer *et al.*, 1993) and Blight Management (DK) (Hansen *et al.*, 2017) also account for the high, intermediate and low-level resistance levels when advising different decision-making rules for spray intervals.

2.3.4. *Challenges*

Translating biological knowledge, usually derived from experiments implemented in controlled environments, into a modelling framework comes with uncertainty which impacts the subsequent estimation of risk (Madden *et al.*, 1988a). A key challenge in developing DSS is to determine an optimum compromise between the current scientific knowledge regarding the biology of the pathogen that can be incorporated into a model, the level of the risk associated with the disease outbreak, ability of the weather network and numerical weather prediction models to provide reliable information at plot scale, and accessible computing resources. The following sections outline some of these challenges in more detail.

Underlying Biology

The algorithm of the model intended for practical use needs to be based on sound scientific knowledge (Pascual *et al.*, 2003). However, several pathogen epidemiology *in vitro* experiments are reported with different equations quantifying the impact of an environmental variable on a certain stage(s) of the pathogen life cycle. Such quantitative differences arise mainly due to different experimental conditions, different pathogen strains used and their vitality, as well as the number of biological and environmental interactions included in the experimental design (Hartill *et al.*, 1990; Madden *et al.*, 1988a; Rotem, 1971; Rotem *et al.*, 1978). For example, while all researchers agree that solar radiation has an inhibitory effect on sporangia, reports on the lethal doses vary (e.g. Mizubuti *et al.*, 2000; Rotem *et al.*, 1985; Skelsey *et al.*, 2017; Weille, 1961).

Host phenology

It is important to differentiate genetic, physiological and crop ecological aspects, as well as their interaction, when discussing the relation of host phenology and PLB management.

The critical stages of the potato crop phenology in relation to PLB management, are periods of intensive growth, stable canopy and tuberization. Fry and Apple (1986) found that the age of the plants affected the sensitivity to *P. infestans*, with epidemics developing faster on older plants (>90 days post-emergence) compared to those of intermediate age (60 days); while emerging crops will be very susceptible to infection but the rapid drying of the young and unformed canopy compensates by reducing the epidemic progression. Equally, it has been shown that the potato plant becomes more susceptible to PLB if excessive nitrogen fertilization is applied due to an increase in crop biomass, which in combination with the phenological stage and morphological characteristics of the potato variety, determines the microclimate of the crop (Harrison, 1992a). Resistance levels increase for plant parts that are formed later in time, and late maturing varieties have higher levels of PLB resistance to early ones (Struik, 2010).

However, such differences are hard to estimate with territorial models since the standard weather measurements come from 2 m height outside of the crop microclimate. Hence, synoptic risk models are regularly calibrated to minimise the risk and the level of assumption susceptible host with fully developed haulm is implied.

Temperature

The temperature in the crop is strongly related to the development of crop. A closed crop develops its own (micro) climate. In an open, developing crop the temperature is also determined by the radiation from the ground. The temperature in an open crop is highest at 10 cm (2-4 °C warmer than at the official measuring height and in a closed crop about 30 cm (Broadbent, 1950)). The lowest temperature of a crop in dry soil occurs at about 60 cm, whilst in wet soil is at 10 cm. Variation is also due to the density of the crop, variety, etc. However, this difference is insignificant during rainy, low-radiation days and occasionally the crop minimum temperature can be higher than the screen minimum. Van Eimern (1964) found that during rainy weather, the temperature in the crop at the height of 15 cm was up to 0-1 °C lower than the temperature at 2 m, and at 45 and 60 cm height, it was 0.5-1 °C and 1 °C higher, respectively. Because the greatest risk of *P. infestans* occurs on such low-radiation days, temperature measurement at official measuring height (2m) may suffice (Hansen, 1993). However, deviations in meteorological conditions do not stop there. The radiation absorbed by leaves is not fully compensated by the cooling effect of transpiration, which leads to higher leaf temperatures than the surrounding air temperature. These differences are potentially important for the calculation of risk, such as incubation time, or for specific components of a DSS, such as, spray intervals reflecting fungicide degradation.

Air moisture and surface wetness

Two important environmental variables in the epidemiology of *P. infestans* are moisture in the air and on the plant surface. Moisture in the air can be expressed in different ways, with the relative humidity being the most widely used measurement in plant pathology, but is also the most troublesome (Rowlandson *et al.*, 2014), often leading to inaccuracies in the risk estimation due to inaccurate representation of the crop microclimate conditions

(Hansen *et al.*, 2017). Relative humidity indicates the relative amount of water vapour in the air and is expressed as a percentage of the amount needed for saturation at the same temperature; with the maximum saturation pressure increasing with temperature (Monteith *et al.*, 2007). It is almost always higher in the crop than at the standard meteorological measurement height (van Eimern, 1964).

Due to high spatial variability, leaf wetness estimation is even more problematic (Gillespie *et al.*, 2008). Precipitation and dew are the main processes responsible for the establishment of wetness on leaf surfaces. It can be also be caused by deposition associated with fog and mist. Under rainy conditions, leaves intercept precipitation, leading to the formation of surface leaf wetness. Dew occurs mainly during the night when water is extracted from the atmospheric water reservoir; dew rise, a process which occurs when soil water evaporated during the night is intercepted by the canopy, and by guttation, a process where excess plant water is released (Beysens, 1995; Rowlandson *et al.*, 2014). Whilst leaf wetness usually starts on the upper canopy levels, the longest wetness periods occur on the lower canopy layers (Jacobs *et al.*, 2005). The duration of leaf wetness can also vary spatially in the crop due to leaf area index, shading, solar declination and soil structure (Gleason *et al.*, 2008). Wind can equally influence leaf wetness formation and duration, but its effects vary depending on the phenology of the crop, having less impact on closed canopies (Anderson, 1936; Monteith, 1957). Leaf wetness is not a standard observed meteorological parameter because it is a property of surfaces as well as the atmosphere (Gleason *et al.*, 2008). However, there is a long history of theoretical research on surface wetness formation (e.g. Anderson, 1936; Beysens, 1995; Monteith, 1957). A number of leaf wetness models has been developed to estimate leaf wetness duration, ranging from simple empirical threshold based estimation techniques using a single minimum value of relative humidity (Rowlandson *et al.*, 2014);

empirical models based on a set of simple if/else rules (e.g. Gleason, 1994), to complex physical models requiring a number of inputs, including those that are not available as standard measurements on simpler farm weather stations, such as net radiation (e.g. Sentelhas *et al.*, 2006). Rowlandson *et al.* (2014) suggest that, considering the uncertainty behind each approach and the ease of calculation, the best compromise is using a minimum relative humidity threshold. However, they also warn about the need for calibration of this threshold for each agroecosystem and individual crop type. Magarey *et al.* (2005a) also warn that the leaf wetness duration resulting from rainfall could persist for several days in certain crop types, even after the relative humidity values are below the indicated threshold.

Uncertainty in forecasted weather data

Given the predominance of protective fungicides for PLB control with short (5-7 day) intervals which results in several applications per year and the low availability of curative fungicides and their limited effect (24-48 hours)(Cooke *et al.*, 2011), models require the use of weather forecast data due to time constraints (Magarey *et al.*, 2002). While DSSs based on extended weather forecast data have been on the market since the 1990s (Magarey *et al.*, 2002), there is a shortage of information regarding the accuracy of these products (Baker *et al.*, 2007; Firanj Sremac *et al.*, 2018).

Over the last decade, numerical weather prediction (NWP) forecasts have become more skilful largely due to significant advances in computational resources and parameterization schemes. However, model skill varies depending on the meteorological variable and the forecast lead time (McDonnell *et al.*, 2017). For example, the high-resolution (HRES) atmospheric model developed by the European Centre for Medium-Range Weather Forecasts (ECMWF), operationally employed in the current Irish PLB risk forecasting system, has been reported to have a significant loss in accuracy of forecasted temperature values after the 5-day lead time (Firanj Sremac *et al.*, 2018). Although numerical models employed to derive forecasts of the weather with lead times out to 10 days are improving, predicting the weather over even these short timescales entails an additional error factor beyond those inherent in making weather measurements and model-based estimates; necessitating a trade-off between timeliness and accuracy (Gleason *et al.*, 2008).

2.4. Model evaluation

As described in the previous section, the development of risk prediction models is often subjective, reflecting a compromise between scientific knowledge and available data. Translation of the risk estimation into decision thresholds is an integral part of the model application in decision support; both the model and its decision thresholds require continuous re-evaluation (Magarey *et al.*, 2007). The reasons for this are twofold. Firstly, the quality of the input data is constantly improving (Gleason *et al.*, 2008) as well as our knowledge regarding the PLB disease cycle, offering opportunities for improving the models. Secondly, one that is more dangerous and urgent, is that the evolving pathogen population and intensification of the potato production (Fry, 2016) could lead to an increased ability of the pathogen to operate beyond model assumptions (Shtienberg, 2013).

Validation of the IR model

The IR model was extensively validated in the 1950s, during the period when it was proposed (Bourke, 1953b, 1953c). A humid period of 12 hours was considered as a requirement for the occurrence of sporangia (Bourke, 1955a). Humid spells of 16 hours were found to be the minimum requirement for blight spread. Risk accumulations occurring early in the season were noted as less effective because of the low inoculum pool. Conversely, shorter humid spells later in the season were identified as possible triggers for epidemics (Bourke, 1959). Initial blight infections were usually found in the West, South and South-West. The first half of June was identified as a period of high risk, with the highest number of blight weather spells occurring in this month during ‘bad blight years’: 1924, 1931, 1936, and 1943. The disease outbreaks and their subsequent development was monitored by 32 inspectors in 26 counties; the focus of monitoring efforts was mainly on fields with certified potato seed (Bourke, 1953c); blight scouting and reporting continued throughout the second half of the last century (Keane, 1982). Bourke (1953b, 1953a, 1953c) concluded that the first outbreaks of the disease, as well as being a period of major spread, were in agreement with model outputs, although no quantitative analysis or methods were reported.

The first evaluation of the IR model was undertaken by agricultural scientists in the 1970s, when Frost (1976) evaluated the model at the Oak Park agricultural research station, located in County (Co.) Carlow. Frost (1976) did not find any significant correlation between disease outbreaks and the accumulation of Effective Blight Hours (EBH) based on weather data from Mullingar (Co. Westmeath) and Kilkenny (Co. Kilkenny), the two closest synoptic weather stations. This analysis was re-evaluated by Keane (1982), who included two additional weather stations (Casement Aerodrome, Co. Dublin and Birr, Co. Offaly) and examined ten-day periods during the growing season. Keane (1982) found that at least two stations had accumulations of EBH ten days prior to primary disease outbreak at Oak Park; and that high accumulation of 25 EBH or more during a ten-day period would give rise to 1 to 5 % of disease in plots according to the PLB measuring scale. These high accumulations were found to occur more frequently in the regions of the South and South West, and temporally, during the months of July and August (Figure 2.4).

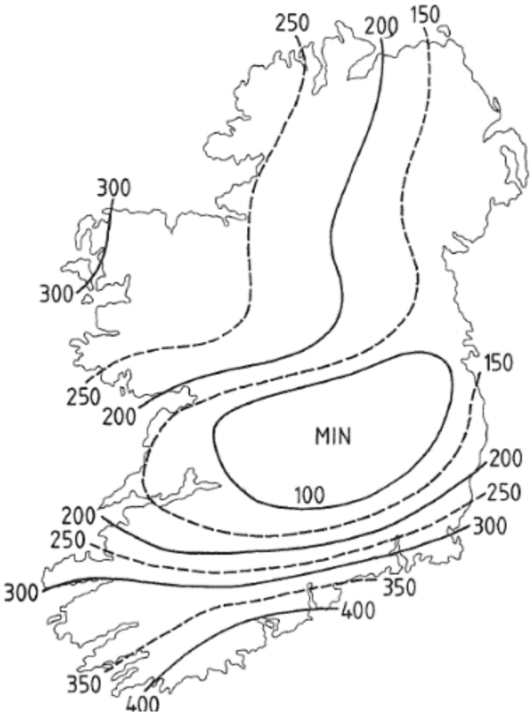


Figure 2.4 Average accumulations of effective blight hours (EBH) from May to September for the period 1957-1981 (after Keane, 1982).

The development of technology and increased awareness of environmental damage caused by the conventional approach to pest management led to an increased effort to use DSSs to support IPM approaches. Changes in the pathogen population (Cooke *et al.*, 1995), fungicide resistance (Dowley *et al.*, 2002; Griffin *et al.*, 2002), agricultural practices, and feedback from producers, have resulted in the value of existing forecasting schemes being questioned both in Ireland and internationally (Taylor *et al.*, 2003). During that period, Leonard (2001) reported results of field trials, implemented at Oak Park, comparing routine fungicide protection, with Met Éireann warnings using the IR model and the Negfry DSS (Hansen, 1995) for the years 1996, 1997 and 1998. The variety used in the experiments was the Rooster, which at the time had the resistance rating of 4 (on a scale of 1-9, with 9 being highest resistance level) for the foliage and 6 for the tuber blight resistance, according to the EuroBlight scale (Hansen *et al.*, 2005). Both DSSs resulted in a significant reduction in treatments. However, only the Negfry DSS was able to provide an acceptable level of blight protection. Although it is suggested that the warnings from Met Éireann were used, the exact decision thresholds remain unclear.

2.5. History of PLB models

The initial models used to estimate the risk of PLB were proposed in the early 20th century and are still being developed. Some of the important references and models are presented below, starting with early qualitative models, initial quantitative models and finishing with examples of modern web-based DSS platforms which include several elements from Table 2.1. Further details regarding these models and DSSs, their components and use have been reviewed elsewhere (e.g. Bourke, 1959; Large, 1959; Schepers *et al.*, 1995; Schepers, 2004; Mizubuti *et al.*, 2006) and presented on the following web pages:

- The web page of the Integrated Pest Management Program of University of California Davis (http://ipm.ucanr.edu/DISEASE/DATABASE/potatolateblight.html)
- The EuroBlight webpage: (https://agro.au.dk/forskning/internationale-platforme/euroblight/control-strategies/dss-overview/
- Models included in IPMBlight2.0 project (Andrivon *et al.*, 2017) https://agro.au.dk/forskning/internationale-platforme/euroblight/research-projects/ipmblight20/decision-support-systems-overview/)

However, it is worth noting that the only reported model in 2000s, which is also being used in practical PLB risk forecasting, is Simblight (Kleinhenz *et al.*, 2007).

The initial models: Qualitative empirical models

Empirical models are normally associated with the simple qualitative rule-based criteria, indicating a risk period (one or more days) without quantifying the risk. Although such models were predominantly 'legacy' models developed in the past, they remain in active use. An example of such model is Hutton criteria (Dancey *et al.*, 2017) from the UK, previously known as the Smith Period (Smith, 1956). The Smith Period aimed to help identify critical periods for PLB development to aid timing of the fungicide applications; it constitutes two consecutive days where the minimum temperature ≥ 10 °C and on each day there are at least 11 hours where the relative humidity is ≥ 90% (Smith, 1956). The validity of the environmental parameters was brought to question due to reports of an increasing number of missed events (Taylor *et al.*, 2003) and the changes of the *P. infestans* population (Cooke *et al.*, 2012). This led to the revision of the Smith Period, resulting in a new model named the Hutton Criteria, which kept the same requirement in terms of the length and temperature threshold (two days where each day has a minimum temperature of 10 °C). However, the Hutton Criteria has a reduced requirement for the duration of humid periods, from at least 11 to at least six hours with relative humidity ≥ 90%, to reflect changes in the ‘new’ pathosystem (Dancey *et al.*, 2017). Similar models have been reported from Norway (Försund and Flaatten, 1958), The Netherlands (Van Everdingen, 1926), and the USA (Hyre *et al.*, 1955).

Further development: Quantitative empirical models

While quantitative empirical models are often classified as empirical models, they differ from simple yes/no criteria (described in the previous section), in their ability to quantify the risk. The risk is usually estimated as matrix based system where a risk value is assigned to the period fulfilling certain criteria. Models started gaining such quantitative features in the 1950s. The IR model (Bourke, 1953a) was the first model of this kind; it sought to include knowledge of the disease life cycle as opposed to being entirely an empirical approach linking weather conditions to blight outbreaks (Bourke, 1953a). The selection of suitable weather criteria was determined from previously published *in vitro* experiments by Crosier (1934).

Additional examples of such models used for predicting the initiation of the epidemics are the Wallin Period (Wallin, 1962), from the USA, and Negative Prognosis (Schrödter *et al.*, 1967), from Germany. Both models estimate the epidemic initiation by accumulating the risk values according to temperature ranges during periods with high relative humidity > 90%. Similarly, the Guntz Divoux model (Duvauchelle *et al.*, 1997) from France estimates risk, classified into three categories, within the temperature range 7 - 27 °C and relative humidity > 90%.

The access to automated weather data and the use of computers to automate the algorithm calculations have led to further evolution of models. To compensate for some of the limitations associated with earlier models and to provide more comprehensive advice, new quantitative empirical models have been developed on the basis of these earlier models. For example, NegFry (Hansen, 1995) is a combination of the Negative Prognosis model (Schrödter *et al.*, 1967), used for the scheduling of initial treatments, and the model by Fry (Fry *et al.*, 1983), incorporating the scheduling for subsequent treatments. Following the same principle, BliteCast (Krause *et al.*, 1975) combines elements of the Wallin Period (Wallin, 1962) criteria, and the Hyre model (Hyre *et al.*, 1955), to time the initial and subsequent treatments, respectively.

An example of a model integrating even more elements, moving towards a mechanistic approach, is the French model Milsol proposed in 1985 (after Ladeveze, 1988). It was built from elements of the Guntz-Divoux model, the Wallin model, Blitecast and the

English model Blight developed by Sparks (1983). The quantification of the epidemic in Milsol is comprised of 4 compartments depending on the epidemic cycle of *P. infestans*: infection, inoculum pressure, survival and sporulation capacity.

Disease Simulators

One of the first plant disease simulators was developed by Waggoner (1968), followed by a number of other models simulating temporal (e.g. Andrade-Piedra *et al.*, 2005a; Michaelides, 1991; Shtienberg *et al.*, 1989), as well as spatial disease development (Firester *et al.*, 2018; Skelsey *et al.*, 2009). Although complex disease forecasting models, such as Milsol (after Ladeveze, 1988) or Symblight 3 (Kleinhenz *et al.*, 2007), incorporate some elements of dynamic models, their level of detail is not as high as in simulation models. Due to their complexity and high level of assumption, simulation models are not often employed in practical disease forecasting, but serve as a base for each new generation of models used in practice through the incorporation of new elements (Harrison, 1995a). They are mainly used as a tool in basic research (Van Oijen, 1991) and education (Small *et al.*, 2015a).

2.5.1. *Current PLB DSS platforms*

While the weather is the primary driver of PLB epidemics, the correction of the disease risk estimation is necessary by means of integration of the other parts of the disease triangle, including human intervention. Hence, contemporary DSSs employ a variety of segments and are based on models of different complexity, subject to availability of resources and predominant research tendencies. Examples of commercial and non-commercial DSSs employed in neighbouring geographical areas and worldwide reflecting this diversity are presented below.

International PLB DSSs

In the UK, the newly proposed Hutton Criteria are employed in the DSS system called Blightwatch. Alerts are provided free-of-charge by the AHDB Potatoes (Agricultural and Horticultural Development Board, Potato Division) throughout Great Britain; e-mail or text message alerts are sent to the grower if a Hutton Period occurs in their specified postcode district. Another free-of-charge tool is provided by Syngenta, BlightWatch (www.syngenta.co.uk/blightcast), which employs both Smith Periods and Hutton Criteria for the strains of blight capable of developing at shorter humid periods. The risk is calculated for a lead time of five days based on weather forecast data.

The German PLB DSS, operated by ISIP (Information System for Integrated Plant Production), is based on two components: monitoring and prognosis. The initial treatment is calculated based on model SYMPHYT2 (Gutsche *et al.*, 1996). The 14-day disease pressure is calculated based on SIMBLIGHT3 (SYMBLIGHT1 is described by Kleinhenz *et al.*, 2007). The risk is calculated for 570 weather stations based on observed weather and three days of weather forecast data interpolated to 1 km^2 grid; outputs are presented using a 'traffic light' warning system. An example output of both models is available in Figure 2.5. The system was recently supplemented with field-specific individual forecasts. The monitoring system is based on the actual disease observations in more than 250 monitoring fields and validated regularly. SYMPHYT2 model correctly predicted 81% of disease outbreaks in 2010 using the closest weather station data and 78% using the interpolated weather data (www.imisp.de).

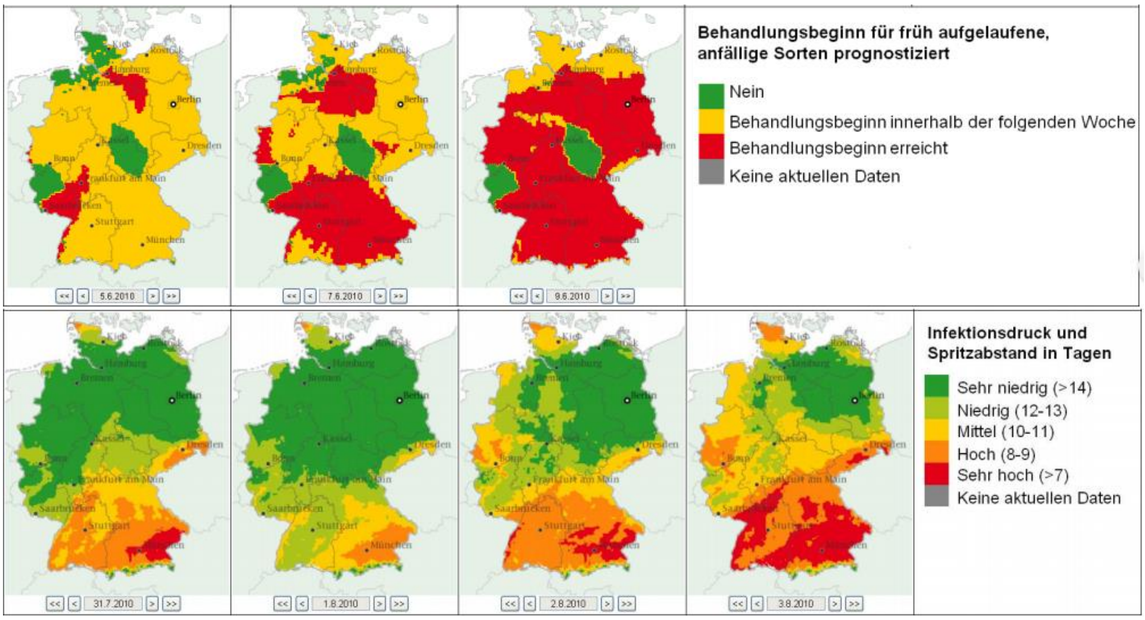


Figure 2.5 SIMPHYT1 (upper) and SYMBLGHT3 (lower) risk maps from 2010 (source www.isp.de)

BlightPro (US) is an integrated web platform which provides outputs of three models (Small *et al.*, 2015a):

- Blitecast, used to predict the initial occurrence of late blight in northern temperate climates, as well as the subsequent spread of late blight (Krause *et al.*, 1975),
- Simcast, the model that integrates host resistance into subsequent treatments with varietal resistance correction, and
- LB2004 (Andrade-Piedra *et al.*, 2005a) simulations used to predict disease dynamics and fungicide weathering and loss.

BlightPro (Small *et al.*, 2015a) was developed not only in order to improve in-season disease management, but also as a research tool which could be used with historical weather data to explore disease management scenarios, or function as a teaching aid. It is a personalised information system, where a user defines the location of the crop. Outputs of models are then calculated using the nearest weather station as a source of observed weather data and corresponding 2.5 square km grid resolution weather forecast. A cultivar resistance database was created from published plant disease management reports and field experiments. The system generates reports for observed and forecasted weather and all three models for the period of +/- 7 days. Users can sign up for automated alerts about upcoming critical thresholds, distributed via SMS or e-mail.

An example of a successful commercially available PLB DSS is ProPhy (Netherlands), marketed by Opticrop (now Agrovision). ProPhy was initially developed in 1988 (Nugteren, 1997; 2004). The system is built on several elements derived from empirical data and practical knowledge. Country specific versions were developed to accommodate differences in varieties, chemicals, application laws etc. Risk is calculated based on observed and forecasted weather data. The duration of the protection is calculated based on the active ingredient, the dose, variety, resistance, rain fastness of the fungicide, disease pressure and crop growth. The system provides advice on the timing of fungicide treatments, product choice and dose.

PLB DSS in the Republic of Ireland

The IR model (based on the Irish Rules as described briefly above) is operationally deployed by Met Éireann (Ireland National Meteorological Service). They currently employ forecasts from two NWPs as input to the model in order to generate the blight warning forecasts. The NWP forecasts employed are:

- Numerical weather forecasts from European Centre for Medium-range Weather Forecasts (ECMWF) which are updated daily at 7 and 19h. The NWP model, referred to as *ECMWF-fine,* has a 12.5 km horizontal resolution and 3-hourly temporal resolution, for the first 6 days of the forecast, decreasing to 6-hourly resolution out to 10-day lead time.

- Numerical weather forecasts from HIRLAM, updated every 6 hours starting from 4 hours after midnight. The HIRLAM model has a 10 km horizontal resolution and a 3-hourly temporal resolution for 48 hours.

The decision to issue a blight warning is made based on the following outputs:

- **Meteogram** with plots of relative humidity, temperature, EBH accumulation and precipitation (Figure 2.6). Accumulations on EBH plot are yellow until reaching 12 hours of a single spell when they turn red. Meteograms are produced for the point-based locations of meteorological stations, selected as representative for the most important potato growing areas (the distribution of potato production in the Republic of Ireland is presented in Figure 1.2): East Cork (Fermoy - Moorepark), Wexford (Johnstown Castle), Dublin (Dunsany), Carlow (Oak Park) and Donegal (Malin Head).
- **Animated Blight maps** showing the spatial distribution of accumulated effective blight hours based on HIRLAM model (Figure 2.7) is produced for ten-day lead time in the form of single ‘quick glance’ map as well as animations.

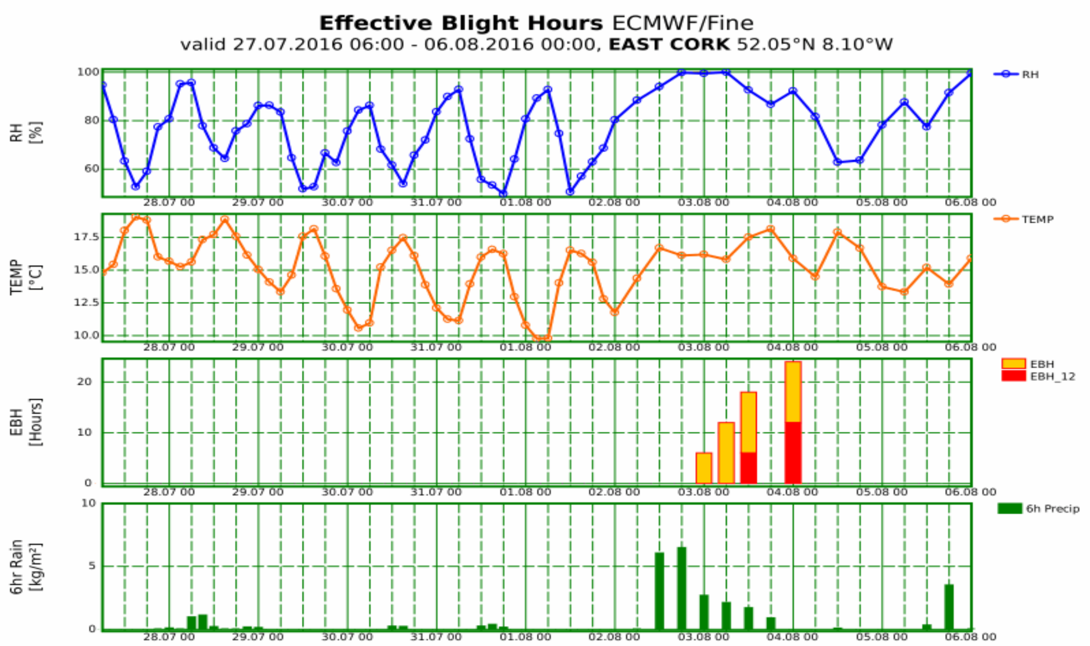


Figure 2.6 Meteogram showing the forecasted weather conditions and the model outputs for the ten-day lead time.

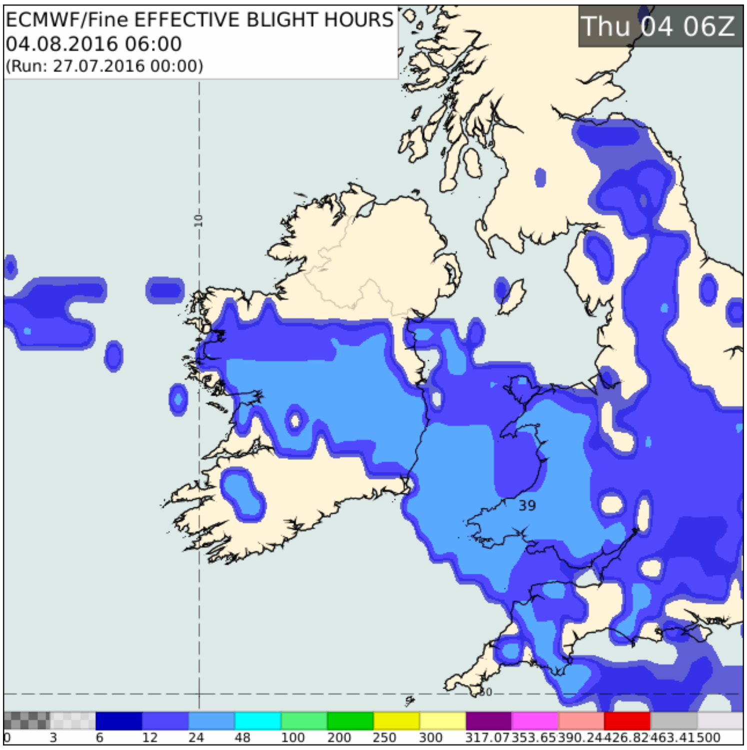


Figure 2.7 Animated maps showing accumulation of EBH for the ten-day lead time.

Currently, the decision to issue a blight warning and its termination is a human decision, made by the meteorologist on duty. Blight warnings include information about areas affected, duration of the spell, and opportunities for spraying, where possible. Optimal spraying conditions considered by Met Éireann are winds of force 3 or less (< 11 knots, or 5.66 m^{-s}) according to Beaufort scale (Mather, 2005), with little or no precipitation and trafficable soils. A blight warning is cancelled when the blight conditions cease. If blight conditions are expected to cease sooner than it is indicated in an existing blight warning, then a cancellation is issued. The warnings are cancelled/prolonged if the meteorological situation changes during the time before the blight spell. An example content of a warning message:

"Weather conditions favouring the spread of potato blight will develop through the midweek period. There will be opportunities for spraying and these should be optimal on Tuesday."

"Weather favourable for the spread of Potato Blight in Connacht, Ulster and north Leinster on Wednesday, Thursday and Friday. There will be opportunities for spraying this afternoon and evening."

Currently, the 'zero date' for the initiation of the blight warning service is 1st May, and warnings issued during May include the specification 'for early planted crops'.

2.6. Summary and conclusions

DSSs in crop protection typically have low uptake (Gent *et al.*, 2013; Shtienberg, 2013). To propose a successful DSS, one must keep in mind the numerous components of plant disease pathosystem, the human factor, technological opportunities and limitations. Setting over-enthusiastic and over-ambitious goals could lead to not only failure of the system but could also potentially endanger the livelihood of producers in such high-risk pathosystem. Ultimately, even if a proposed complex system and proven as a useful disease management tool, there is a constant need for its validation due to the nature of the dynamic pathosystem. Hence, the territorial models employed in practical disease forecasting remain simpler compared to those used for studying dynamic processes due to a lower level of required assumptions and input variables. The century-long development of modelling approaches applied to PLB DSSs was condensed in this chapter, to present the opportunities and challenges in developing one.

Due to the complexity of the system, DSSs in crop protection are based on the integration of knowledge from different fields, such as agronomy, agrometeorology, plant pathology, but also information technology. To develop a DSS, the modeller(s) acquires the knowledge regarding these segments and decides on the point of minimum uncertainty introduced by each component of pathosystem based on available technology and knowledge, as well as personal opinions and risk adversity. Examples of different DSS have been shown depicting a variety of approaches employed over time. While some DSSs have increased in their complexity, there are examples of those which have remained relatively simple, possibly for subjective reasons based on an awareness of high risk associated with the uncertainty of complex assumptions. The approach taken in this thesis is to find an optimum compromise between these uncertainties under Irish conditions, with the consideration of current knowledge of pathosystem as well as the ability of the weather measuring network and numerical weather prediction models.

Despite the great diversity, all models are based on the PLB lifecycle - epidemics are initiated and heavily dependent on the environment, most importantly, availability of moisture and mild temperatures. Although simple, the IR model goes beyond the simple empirical qualitative risk estimation and incorporates additional information, expressed as the duration of weather conditions suitable for PLB development. It is a well-known and established tool in the Republic of Ireland but is in need of evaluation due to changes in *P. infestans* population and production conditions in the Republic of Ireland (Chapter 1). However, as indicated in Section 2.4, our knowledge of the pathosystem is increasing, as well as the quality of model inputs, which presents an opportunity for seeking an increase in accuracy of the PLB risk estimation, providing an opportunity to overcome some of the oversimplifications heretofore required to develop these models.

In conclusion, while the complexity of the model and demands from the input variables should be kept to a minimum due to the potential risks, there is a need to attempt to push the model boundaries forward to achieve more accurate and more precise risk estimates. If these goals can be achieved, the potential exists to increase the security, and lead to more sustainable food production – the one certainly needed in case of potato late blight. Hence, the current operational model employed in Ireland, the IR, is evaluated and re-calibrated as an immediate solution in Chapters 3 and 4; a new risk prediction framework and model approach, which seeks to improve the risk estimation, is presented Chapter 5.

3. Evaluation of Irish Rues, the Potato Late Blight Forecasting Model and its Operational use in the Republic of Ireland

3.1. Preface

This Chapter is published as:

Cucak, M., Sparks, A. H., Moral, R., Kildea, S., Lambkin, K., Fealy, R. (2018) Evaluation of Irish Rules, the Potato Late Blight Forecasting Model and its Operational use in Republic of Ireland. *Agronomy,* 9(9): 515

This paper is positioned at the beginning of the present collection as this work was necessary to lay the groundwork for the rest of the research. The main assumptions of the IR model, related to environmental conditions for the disease outbreak under changing PLB pathosystem were evaluated using mathematical methods, while keeping in sight the biology of the pathogen. Also, it was considered necessary to confirm that the new proposed calibration is still an economically viable alternative and/or supplement to the standard growers' practice in the Republic of Ireland.

While the methodology for the evaluation of risk prediction models for the diseases of medium risk has been in use since the 1990s (Yuen *et al.*, 1996; Hughes *et al.*, 1999), such methods were not directly applicable to zero-tolerance disease. Hence, the method was adapted to fit the purpose of the re-calibration of the IR model. Additionally, being aware of the lack of coherent methodology and systemic evaluation of the model over time, the entire analysis is provided as a fully reproducible open-source compendium to facilitate the ongoing evaluation of the model.

3.2. Abstract

Potato late blight caused by *Phytophthora infestans* is one of the most important plant diseases known, requiring high pesticide inputs to prevent disease occurrence. The disease development is highly dependent on weather conditions and as such several forecasting schemes have been developed worldwide, which seek to reduce the inputs required to control the disease. The Irish Rules, developed in the 1950s and calibrated to accommodate the meteorological network, the characteristics of potato production and the *P. infestans* population at the time, is still operationally utilised by the national meteorological agency, Met Éireann. However, numerous changes in the composition and dynamics of the pathosystem and the risks of production/economic consequences associated with potato late blight outbreaks have occurred since the inception of the Irish Rules model. Additionally, model and decision thresholds appear to have been selected ad hoc and without an explicit criterion. We developed a systematic methodology to evaluate the model using the empirical receiver operating curve (ROC) analysis and the response surface methodology for the interpretation of the results. The methodology, written in the R language, is provided as an open, accessible and reproducible platform to facilitate the ongoing seasonal re-evaluation of the Irish Rules and corresponding decision thresholds. Following this initial analysis, based on the available data, we recommend the reduction of the thresholds for relative humidity and initial period duration from 90% and 12 hours to 88% and 10 hours, respectively. Contrary to recent reports, we found that the risk of blight epidemics remains low at temperatures below 12 °C. With the availability of more comprehensive outbreak data and with greater insight into the founder population to confirm our findings as robust, the temperature threshold in the model could potentially be increased from 10 °C to 12 °C, providing more opportunities for reductions of pesticide usage. We propose a dynamic operational decision threshold between 4 and 11 EBH set according to frequency of the disease

outbreaks in the region of interest. Although the risk estimation according to the new model calibrations is higher, estimated chemical inputs, on average, are lower than the usual grower’s practice. Importantly, the research outlined here provides a robust and reproducible methodological approach to evaluate a semi-empirical plant disease forecasting model.

3.3. Introduction

Potato late blight (PLB) caused by *Phytophthora infestans* (Mont.) de Bary (De Bary, 1876) is amongst the most destructive diseases of potato crops (Mizubuti *et al.*, 2006); due to its fast reproductive cycle and aggressiveness, if left untreated it can rapidly lead to the total destruction of the crop, either in the field or in storage, following harvest (Hardwick, 2006). In Ireland, historical outbreaks of potato blight have had a significant cultural and economic impact and are partly attributed to mass starvation and the subsequent migration of large portions of the population fleeing from famine during the 1840s (Bourke, 1993). In Ireland alone an estimated €5 million is spent annually on fungicides to control PLB, whilst globally the cost of control and losses are estimated to exceed €1 billion annually (Haverkort *et al.*, 2008a). Although *P. infestans* can form overwinter oospores, under Irish conditions these are not believed to occur (Louise Cooke, *personal communication*) and typically the pathogen overwinters in infected tubers (in dumps, volunteers or infected seed) (Hirst *et al.*, 1960). The rate of late blight epidemic progression is highly dependent on the weather; with temperature, relative humidity and precipitation being the most important variables, with the latter two closely related (Harrison, 1992b). Prolonged periods of humid and cool weather provide conditions favourable for pathogen sporulation (Crosier, 1934); short-lived sporangia subsequently spread through a mixture of rain splash and wind dispersal (Wallin, 1962). The disease impacts yield both indirectly and directly, indirectly, by reducing photosynthetic surface, and directly, when sporangia washed from foliage infect tubers in the ground (Hirst *et al.*, 1960).

Since the late 1970s, increasing globalization has resulted in the worldwide migrations of pathogen genotypes of both mating types, leading to the displacement of dominant older clonal lineages or genotypes commonly referred to as US-1 (Goodwin *et al.*, 1994); this has facilitated the development and spread of new lineages, some of which demonstrate an increased aggressiveness (Fry, 2016). This rise of new genotypes has introduced changes in the ecology of *P. infestans* (Mizubuti *et al.*, 1998, 2000; Fry, 2008; Mariette *et al.*, 2016a). The increasing genetic variability of *P. infestans* is likely reducing the durability of late blight resistance based on R gene stacks (Li *et al.*, 2012). Although the structure of the Irish *P. infestans* population shows little genetic variation, it is dominated by a few clonal genotypes comprised of more aggressive EU_13_A2 and EU_6_A1 strains (Cooke *et al.*, 2006; Griffin *et al.*, 2002). New genotypes have established in Ireland and have been reported in higher frequencies in recent years (Kildea *et al.*, 2010; Cooke, 2015; Stellingwerf *et al.*, 2018). In addition, the majority of potato production in Ireland is based on more susceptible potato cultivars, guided by market demand (Anonymous, 2011). Population diversification coupled with the influence of climate change (Haverkort *et al.*, 2008b) has led to increased difficulty in controlling PLB (Baker *et al.*, 2005; Chowdappa *et al.*, 2015). Presently, due to the high risk of PLB epidemics in high-input agriculture, associated with increased aggressiveness of the pathogen, intensive fungicide regimes are routinely used; in Western Europe this equates to more than 10 applications per season (Haverkort *et al.*, 2008a; Dowley *et al.*, 2008), while in some countries crops can receive as many as 20 fungicide applications (Cooke *et al.*, 2011). The need to develop late blight forecasting models for use as decision support tools has been long acknowledged as one of few integrated pest management (IPM) approaches available for PLB management, motivated by both environmental and economic factors

(Bourke, 1970; Fry, 1982; Shtienberg, 2013). In response to the environmental challenges posed from increased pesticide usage, the European Community Directive 128/2009 on the Sustainable Use of Pesticides provides strict guidelines for the sustainable use of plant protection products in order to reduce risks to human health and the environment (Rossi *et al.*, 2012). Reliable disease forecasting offers the potential to reduce yield losses and crop inputs during unfavourable blight weather conditions, while also supporting an *ex post facto* justification for the use of plant protection products (Hardwick, 2006; Shtienberg, 2013) in compliance with national and international regulations. Kessel *et al.* (2018) have shown the necessity for environmental risk prediction to guide low input chemical protection to prevent the resistance breakdown of currently resistant potato cultivars. Forecasting systems that involve numerous alerts have been shown to be useful in this regards when applied on a pathosystem involving a valuable crop and rapid disease (Madden *et al.*, 1988b).

At their core, crop disease forecasting systems employ algorithms, either mechanistic (fundamental) or empirically based, to predict disease cycle. Mechanistic based models are developed from laboratory experiments in controlled environment chambers, greenhouse or field and describe one or more segments of the host-parasite relationship as influenced by the environment (Madden *et al.*, 1988b). Initially, the development of such models centred around the use of weather events to predict the development and onset of epidemics and were mainly empirical in nature (Pavan *et al.*, 2011), based on the duration of weather events beyond a crude weather threshold (e.g. (Van Everdingen, 1926; Smith, 1956)) and phenological stage (Baldacci, 1947). More recently, the use of mechanistic approaches has been increasingly employed in an effort to encompass more complex components of PLB epidemics, as well as crop growth, chemical protection and cultural practices (Fry, 2016; Kessel *et al.*, 2018). Due to its historical and relative economic importance, Ireland has a long history in the development of forecasting systems for use in PLB management.

Austin Bourke, one of potato late blight forecasting pioneers, developed the PLB model referred to as the 'Irish Rules' (IR). This model sought to include knowledge of the disease life cycle as opposed to being an entirely empirical approach (Bourke, 1953a). For example, the selection of suitable weather criteria was determined from previously published laboratory experiments (Crosier, 1934), rather than a retrospective analysis of historical weather during blight outbreaks such as in the development of the 'Dutch rules' (Van Everdingen, 1926) and 'English rules' (Beaumont, 1947). Bourke (Bourke, 1953b) found that the frequency of warnings produced by these latter models was too high under Irish conditions and consequently the IR model was devised as an intermediate solution between empirical and process based approaches (Harrison, 1992b; Madden *et al.*, 2007) , to aim of which was to increase the accuracy of disease life cycle interpretation.

The first attempt to undertake an evaluation of the IR model dates back to the 1970s, when Frost (1976) found no significant relationship between disease outbreaks at a site located in the south east of the country, Oak Park, Co. Carlow (now a Teagasc research centre) and risk accumulation derived from weather data from two nearest synoptic weather stations, Mullingar and Kilkenny. Following re-analysis of this work, Keane (Keane, 1982), who included two additional surrounding weather stations, reported that IR were able to predict those outbreaks, although the exact evaluation methodology is not well documented. Reported field evaluations of the IR model performance have shown that the control according to the model outputs results in a significant reduction in fungicide usage, but with unsatisfactory disease control compared to the Negfry Decision Support System (DSS) (Hansen, 1995) or routine fungicide protection (Dowley *et al.*, 2004). More recently, as part of a pan-European initiative, a theoretical comparison of the risk accumulation between several European PLB risk prediction models has shown that the IR model simulates the lowest estimate of risk due to its strict criteria (Hansen, 2017).

The uptake and use of DSS in blight forecasting worldwide is limited largely due to the level of risk associated with a costly disease outbreak (Gent *et al.*, 2013; Magarey *et al.*, 2017; Shtienberg, 2013). Risk-averse farmers use DSS to support an increased number of chemical treatments (Madden *et al.*, 1988b), which is often the case in Ireland. The main incentive for producers to use plant disease risk prediction in recent times is to increase economic benefit through cost reduction, and to comply with pesticide use policies required by supermarket chains (Gent *et al.*, 2013; Hardwick, 2006). Irish producers use, but do not necessarily rely on, operational blight warnings, hence it is now timely to review the IR and undertake an evaluation with a view to refining the rules in light of recent changes in disease and plant ecology.

The aim of this study was therefore to provide a comprehensive, systematic and transparent method to facilitate an ongoing evaluation of the IR model, and its operational application, in the context of changes in the disease epidemiology and increasing regulation (market/policy). The impact of the proposed modifications on the potential number of treatments and fungicide usage is also determined and presented. Additionally, this research provides the first completely reproducible report in the area of plant disease forecasting, with a view to inspire and enable researchers elsewhere to modify, adapt and use the proposed methods and the code outlined here.

3.4. Data and Methods

The paper is structured as follows, initially, an overview of the site and available biological and weather data is presented. The Irish Rules model is described after which the evaluation of the model parameter thresholds, currently employed operationally is presented. Proposed model modifications and identified decision thresholds are further assessed by comparison of treatment frequency and dose reduction. A schematic of the workflow is outlined in Figure 3.1.

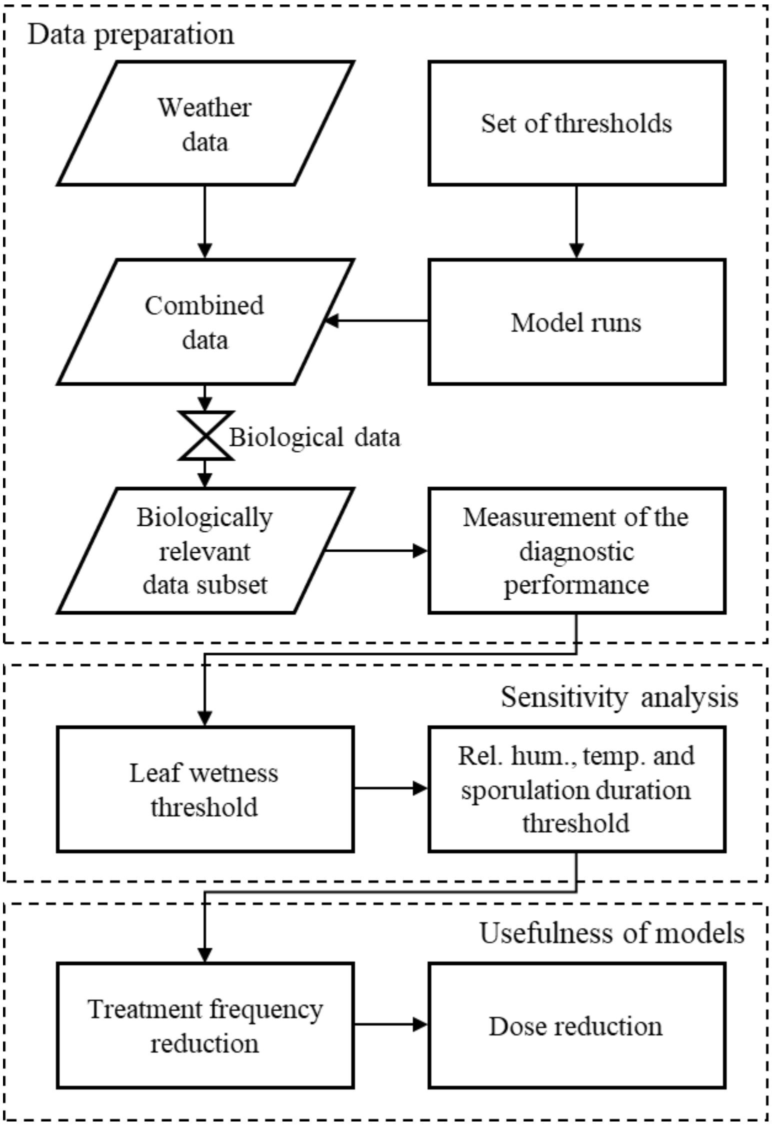


Figure 3.1 Simplified flowchart of the steps taken in IR model evaluation.

Table 3.1. List of frequently used abbreviations in the manuscript along with their full forms.

Abbreviations	Full form
IPM	Integrated Pest Management
DSS	Decision Support System
PLB	Potato late blight
IR	Irish Rules
RHt	Relative humidity threshold
Tt	Temperature threshold
SDt	Sporulation duration threshold
LWt	Leaf wetness threshold
EBH	Effective blight hours
ROC	Receiver operating characteristic
AUROC	Area under the ROC curve
FP	False positive
TP	True positive
FN	False negative
TN	True negative

3.4.1. *Site description*

Oak Park, Co. Carlow, Ireland (latitude: 52.8560 and longitude: -6.9121), a Teagasc (Irish agricultural advisory body) research centre, is located in the south-east of Ireland. Soils are composed of light limestone gravelly soils and heavy textured soils derived from limestone till.

Typical weather conditions calculated over the growing period (April to October) for the period 2007 to 2016 indicate that average daily relative humidity values were typically high throughout the potato growing season, which is a characteristic of Irish conditions more generally. The mean temperature over the period was 13 °C, relative humidity 80.2 % and the average sum of precipitation 398.31 mm. The nighttime temperatures during the early part of the potato growing season are low, with averages of 6.6 °C in April and 9.2 °C May.

3.4.2. *Data*

Biological data

Planting dates and primary disease outbreak data were acquired from the Teagasc breeding program field trial records for the period 2007 to 2016. The breeding program trials consisted of 25-60 potato varieties in all years, representing all levels of susceptibility to potato late blight. Trials were laid out in randomised complete block design, with six blocks and plots of 20 plants. The seeds were propagated in accordance with the seed certification scheme of the Irish Department of Agriculture, Food and the Marine (DAFM) to ensure no latently infected tubers; the *P. infestans* inoculum originated from natural sources. Crop rotation was undertaken on a five-year cycle. Plots did not receive any fungicide treatments. All plots were visually inspected for disease occurrence on a weekly basis, from crop emergence, and generally more frequently during periods of humid weather. This data provided information about the disease outbreaks used in the model analysis and evaluation outlined here.

Planting dates in the biological data are somewhat later compared to the usual agricultural practice in Ireland, which is suitable for the analysis because the healthy green tissue is present throughout summer. Outbreak dates vary from 26th of June to 23rd of August.

Weather data

Hourly weather data for the historical period under investigation, was acquired from the Met Éireann synoptic weather station at Oak Park. The weather variables obtained include the hourly air temperature (°C) and relative humidity (%) at 2m, and the total hourly precipitation (mm). The trial sites were within a radius of 500 m of the weather station in all years and are located on flat ground with no physical barriers in between.

Availability of good quality weather and biological data is crucial for successful calibration and evaluation of plant disease forecasting models (Gleason *et al.*, 2008).

Quality control of the available weather data and appropriate imputation of missing values is often disregarded in agriculture, which could lead to imprecise or wrong results (Hansen, 2017; Magarey *et al.*, 2002). Post-processing of the weather data undertaken as part of this study included checking for duplicate entries and recorded values outside of 'expected' ranges, determined using histograms. The data had only six missing values for both precipitation and temperature and seven missing values for relative humidity, over the period of interest. These short intervals of consecutive hours of missing data for temperature and relative humidity were imputed by spline interpolation using the Forsythe, Malcolm and Moler method (Forsythe *et al.*, 1977), as suggested by Shah *et al.* (Shah *et al.*, 2013).

The IR model and its operational use

According to original Irish Rules (Bourke, 1953b), illustrated in Figure 3.2, periods with temperatures ≥ 10 °C and relative humidity ≥ 90 % provide the necessary environmental conditions considered conducive for potato late blight. These periods are further split into:

- Sporulation period - the initial stage considered necessary for the formation of sporangia is set to a minimum of 12 consecutive hours; and,
- Infection period - starts after the 12-hour sporulation period is completed. If the surface of the plant is not wet at the beginning of the infection period, effective blight hours (EBH) begin accumulating from the 16th hour (12 hours sporulation period + 4 hours = 16 hours); where the surface of the plant is wet at the beginning of the infection period, the EBH accumulation is reduced by a period of 4 hours (16 hours – 4 hours = 12 hours). The leaf (surface) wetness (LWt) is considered present if there was a considerable amount of precipitation (≥ 0.1 mm) during the time window of 3 hours before and 3 hours after the 12th consecutive hour of sporulation. The infection

period lasts until conditions (temperatures ≥ 10 °C and relative humidity ≥ 90 %) are not broken for more than 5 consecutive hours, required for spore survival.

Hours fulfilling these criteria are termed effective blight hours (EBH). The risk of potato late blight outbreak estimation is based on the longevity of the infection period, expressed as a sum of the EBH.

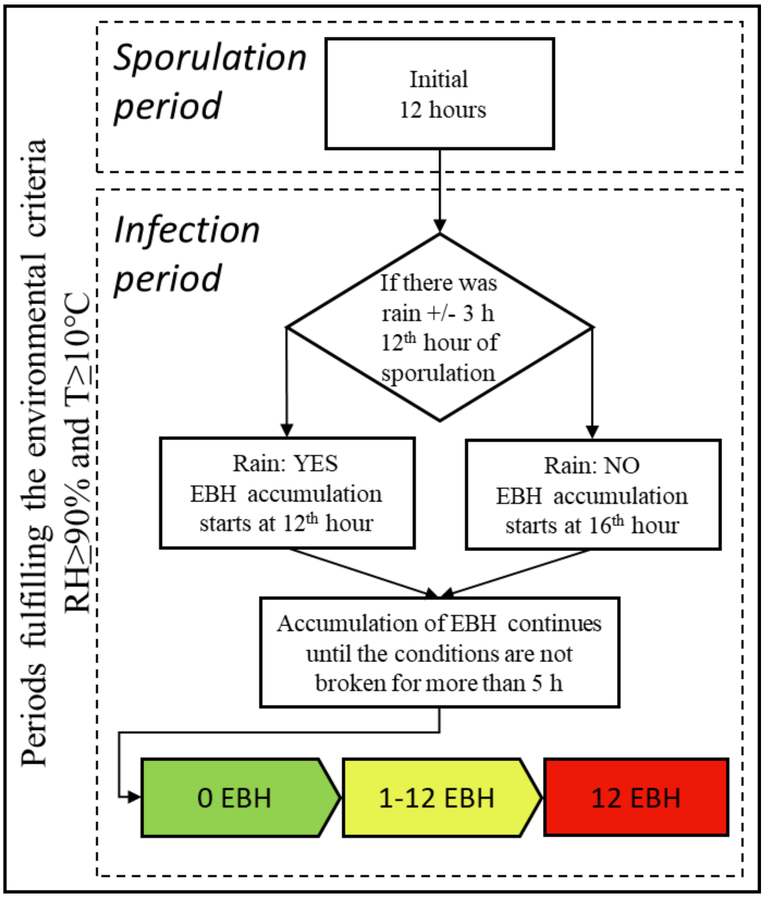


Figure 3.2. Simplified presentation of Irish Rules algorithm. The operational warning threshold scale is presented as the "traffic light" scheme, ranging from green (no warning), yellow when the warning considered and red when the warnings are issued without delay.

Currently, the warning system is used operationally by the national meteorological service, Met Éireann. The IR model is utilised in their original form to support the blight warning service issuing spray advice (Dowley *et al.*, 2004; Keane, 1982). The decision on issuing a blight warning and its termination is determined by the meteorological officer on duty after visual inspection of the IR model outputs based on a 10-day numerical weather prediction (NWP) model forecast from the European Centre for Medium-range

Weather Forecasts (ECMWF). Warnings are disseminated through the Met Éireann web portal, radio and television weather broadcasts and mobile application. Operationally, a decision threshold to issue a blight warning is considered for an accumulation of 12 EBH. Additionally, if a continuous spell of mild, humid and damp weather lasting 24 hours or more is expected, a blight warning may be considered even if it does not explicitly meet the warning criteria. Blight warnings are typically issued 2 to 6 days in advance and include information about areas likely affected, duration of spell and opportunities for spraying, where possible. The decision threshold of 12 EBH is established from operational experience since the 1950's (for example, between 1950 and 2000, a network of blight scouts reported on regional blight outbreaks and the progress of epidemics) although it was not systemically documented. Currently, the 1 May is the 'Zero date', a date threshold after which warnings are considered valid.

3.4.3. *Evaluation procedure*

Model thresholds under evaluation.

The IR model is a set of algorithms mimicking the processes contained in mechanistic models. The transition between these processes is determined by an empirically derived set of thresholds, which ultimately influences the risk estimation expressed as the duration of an infection period. Four of these primary thresholds were subjected to a sensitivity analysis. The environmental thresholds for relative humidity (RHt), temperature (Tt) and the duration of period considered as necessary for the inoculum production - the sporulation duration threshold (SDt), were varied from -3 to +3 units of their respective default values (Table 3.2). To assess the leaf surface wetness indicator, the default estimation using rain (≥ 0.1 mm) was compared to using the combined rain and relative humidity thresholds as an indicator (Rain ≥ 0.1 mm and RH ≥ 90). The model was run using all combinations of model variable thresholds. Outputs were then combined with the hourly weather data for further analysis.

Table 3.2 Model variable threshold variations evaluated in the analysis.

Range	Relative humidity (%) (RHt)	Temperature (°C) (Tt)	Sporulation duration (hours) (SDt)
+3	93	13	15
+2	92	12	14
+1	91	11	13
Existing	90	10	12
-1	89	9	11
-2	88	8	10
-3	87	7	9

Analysis of diagnostic performance

The period considered in the sensitivity analysis was from planting date to the recorded disease outbreak in each season, which was further split in two segments (Figure 3.3):

- **No infection period:** considered as the period when the healthy (susceptible) host is present, but no infections were observed. This period lasts from emergence, which is estimated to start three weeks after planting, to 14 days prior to the first observation of the disease in the field. Specificity or true negative rate was measured during this period. It was considered that each warning during this period activates a chemical treatment which provides protection for the subsequent period of 7 days and is considered as a false positive (FP). True negatives (TN) were calculated as a proportion of the remaining period, when fungicide protection was not recommended.
- **Warning period:** considered as a period when infections occurred and was assigned a 10-day time window, starting 14 days and ending 4 days prior to the disease being observed in the field. A risk warning of disease outbreak 10 days ahead has been reported as an optimum warning time (Taylor *et al.*, 2003), and a period of four days was considered to be a minimum incubation period. Sensitivity or true positive rate was assessed during ‘warning period’. Warning periods where the value of the warning threshold was reached and would trigger a fungicide treatment, is considered as a true positive (TP) and if the warning was not issued false negatives (FN).

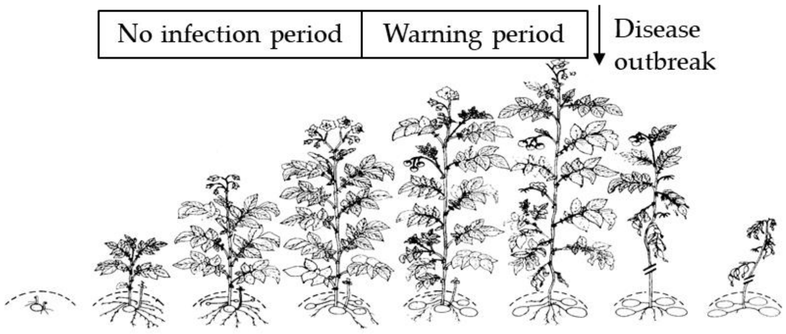


Figure 3.3. Simplified schematics illustrating the temporal split of the data for the diagnostic performance calculation (source (Bleiholder *et al.*, 2001)).

Contingency tables were created with sensitivity and specificity values from a confusion matrix (as shown in Table 3.3) for each evaluated disease warning decision threshold for all model outputs. The range of decision thresholds used as cut-off points, or the level of risk leading to treatment, was from 1-18 EBH.

Table 3.3. Confusion matrix used for calculating the cutoff points for contingency tables.

Disease Forecast	Disease Observed	
	Yes	No
Yes	TP Warning period	FP No infection period
No	FN Warning period	TN No infection period
Measures of the performance	Sensitivity TP/(TP + FN)	Specificity TN/(TN + FP)

Receiver Operating Characteristic (ROC) curves

The performance of each model was assessed using receiver operating characteristic curves (ROC). An ROC curve is a graphical technique for assessing model predictive ability through the relationship of specificity and sensitivity (Skelsey *et al.*, 2017; Yuen *et al.*, 2002). Empirical ROC curves were constructed with cut-off points for different thresholds on a discrete scale. Specificity (i.e. 1-specificity) on the x-axis and the sensitivity on the y-axis was plotted for each cut-off point. The accuracy of the model was evaluated based on the area under the ROC curve (AUROC), serving as a single measure of the discriminatory ability of the model (Hanley *et al.*, 1982; Rosner, 2015). The area under the curve (AUROC) was calculated for model outputs using the trapezoidal rule (Rosner, 2015). In general, an AUROC of 0.5 suggests no discrimination (i.e. the model is no better than a random predictor); as the value of AUROC approaches 1, the better the predictive value of the model (Hosmer Jr *et al.*, 2013).

3.4.4. *Statistical analysis*

Evaluation of leaf wetness estimation

In order to evaluate the LWt estimation, two indicators are evaluated; values of hourly rain (rain ≥ 0.1 mm) and rain and humidity (rain ≥ 0.1 mm and RH ≥ 90 %). The model runs were split in two groups with each run having a measure of the LWt indicator in each group. The difference between paired samples was calculated and normality of the sample distribution was visualised using a histogram and density plot and assessed with the Shapiro–Wilk test. Where samples did not conform to a normal distribution, a non-parametric paired two-samples Wilcoxon rank sum test was carried out to assess the difference between groups. Model outputs with a higher performing LWt indicator were kept for further analysis.

Evaluation of main variable thresholds

Boxplots were used for the initial visualisation of change in model accuracy with change in each factor level of a single variable. A polynomial surface, using locally estimated scatterplot smoothing (LOESS), was fitted to the AUROC data using each variable as a predictor and all possible interactions, to model the trend of AUROC response with change for each variable threshold individually.

An orthogonal polynomial regression model was used to study the sensitivity of the AUROC with the change in the model variable thresholds and their interaction. Polynomial response models have shown to be useful for summarizing relationships

(Rawlings *et al.*, 1998). The response surface methodology (Box *et al.*, 1951) consists of a group of mathematical and statistical procedures used for approximating the functional relationship between a selection of control variables which have an influence on the response variable (Khuri, 2017). The polynomial models were fitted sequentially, starting from first order and adding higher degree terms up to the fourth order. Model fits were assessed with R^2 *-value* and an R^2 *adjusted-value,* Shapiro-Wilks test of residuals and examination of the fitted surface, until overfitting was indicated on the response surface plane. Additionally, the non-parametric local regression (loess) was used to obtain predicted values for the 4- dimensional response surface, using RHt, Tt, and, SDt and all 3- and 2- way interactions as the predictors. The extent of agreement was then compared between polynomial regressions and the loess regression to aid in choosing the degree of the polynomial regression, measured using the concordance correlation coefficient (Lin, 1989). The lowest-degree polynomial that accomplished the required degree of approximation was subsequently adopted. The higher degree polynomial models offer increased flexibility in the response surface, but they need to be fitted with caution due to the potential to 'overfit' these models (Rawlings *et al.*, 1998).

The fitted polynomial equation was then expressed in the form of three-dimensional (3D) surface plots, in order to visualise the interaction between the changes in thresholds (Table 2) and the response variable. The graphical representation provides a method to visualize the relationship between the response and experimental levels of each variable, and the type of interactions between the test variables.

Due to awareness of constraints of the limited data set, current knowledge of PLB disease epidemiology is used as a guide for interpretation of the results. Hence, a suite of model versions was selected based on the results of the sensitivity analysis which were subjected to further examination based on the position and grouping of the cut-off points in the

ROC space. Defining an optimal decision threshold is not a trivial task (Skelsey *et al.*, 2017). The high cost of false negatives (FN) associated with potential onset of PLB epidemics (Fry, 2008; Large, 1959) predetermines that the decision threshold lie closer to the upper right-hand corner of the ROC curve in order to minimise the associated risk of the disease development (Madden, 2006).

Treatment frequency and dose reduction

The crop risk prediction model is useful only if it provides the same level of protection as the standard practice, while reducing necessary costs and labour (Madden *et al.*, 1988b; Rossi *et al.*, 2012). In this theoretical study, the differences in the active ingredient or the type of the fungicide are not taken into account, but merely try to associate a reasonable estimation of possible reductions in the number of treatments or/and dose reduction with predictive power at predefined decision thresholds. After defining the 'optimum' sets of model thresholds, it was necessary to compare the number of treatments and the pesticide usage recommended by the model versions compared to standard growers’ practice. This was done in order to determine if the recommended model parametrisations are economically and environmentally viable. Currently, spray intervals range from 5-7 days under Irish conditions, which are the intervals accounted for in this study. Three model parametrizations are evaluated, the IR with the default parameters (Section 2.1.3, The IR model and its operational use), and two improved parametrisations as identified in the subsequent analysis.

We assume that planting starts the day after the daily average soil temperature is greater than 8 °C for three consecutive days after the 1 April. This is a common practice in Ireland in line with recommendations from the national advisory body, Teagasc. Farmers typically start fungicide treatments as soon as the emergence progresses over 50% and continue until the potato above-ground potato haulm completely dies off, typically three weeks after desiccation. It is assumed here that the growing season lasts 120 days. However, the pesticide protection continues during these three weeks, until the above-ground potato haulm is desiccated.

The difference between standard growers' practice and model versions is evaluated in two ways:

1. Reduction in the number of treatments, split into:

- Model guided: A fungicide treatment is applied every time the warning threshold is reached with a minimum period of 5 days prior to following treatment; and,
- Model and calendar guided: a minimum of 5 and maximum of 10 days between treatments.

The sum of recommended treatments is calculated for all decision thresholds and seasons. The resulting summaries are presented visually as point graphs. A LOESS curve was fitted to estimate the minimum decision threshold where the protection according to the model is for fewer treatments then the usual 5- or 7-day practice.

2. Dose reduction based on 7-day calendar treatment. Currently, Irish growers do not rely on the operational warnings issued by the Met Éireann, but do increase the dose or use stronger, often less environmentally friendly, formulations during those periods identified as *at risk*. Possible dose reductions are calculated for the usual 7-day calendar treatment. The dose reductions are based on the maximum risk calculated by the model during the 7-day period between treatments. The maximum dose is applied if the risk is over 12 EBH, which is the current warning decision threshold in Ireland.

Software used for the analysis and the reproducibility

This analysis has been implemented in R, a freely available statistical programing language (R Core Team, 2018). A portion of the data was imported using readxl

(Wickham *et al.*, 2016). Packages used for data munging: tidyverse (Wickham, 2017), zoo (Zeileis *et al.*, 2005), data.table (Dowle *et al.*, 2019) and pracma (Borchers, 2018). Packages used for visualisations: ggplot2 (Wickham, 2016), cowplot (Wilke, 2018), ggrepel (Slowikowski, 2018) and rsm (Lenth, 2009), ggthemes (Arnold *et al.*, 2019). Univariate series imputation was implemented using functions from package imputeTS (Moritz *et al.*, 2017). Package zoo (Zeileis *et al.*, 2005) was used for processing dates. Formatting of tables was done with pander (Daróczi *et al.*, 2018). Packages rmarkdown (Allaire *et al.*, 2019) and knitr (Xie *et al.*, 2019) were used for creating a reproducible compendium. Package here (Müller, 2017) was used to ensure reproducibility on different platforms. Programming functions from R.utils (Bengtsson, 2019), string manipulation with mgsub (Ewing, 2019) and statistical tests and visualisations: rcompanion (Mangiafico, 2019).

The full analysis can be reproduced using code and data archived at https://mladencucak.github.io/AnalysisPLBIreland/.

3.5. Results

3.5.1. *Evaluation leaf wetness estimation*

A Wilcoxon signed rank test showed that there was a significant difference ($p<0.001$) between AUROC values for the models using the combined estimators as indicator for leaf wetness (RH ≥ 90% and rain ≥ 0.1mm) which were significantly higher than using only rain (≥ 0.1mm). The median AUROC for the method based on rain and RH thresholds was 0.735 compared to 0.695 for the method only using rain indicator (Figure 3.4).

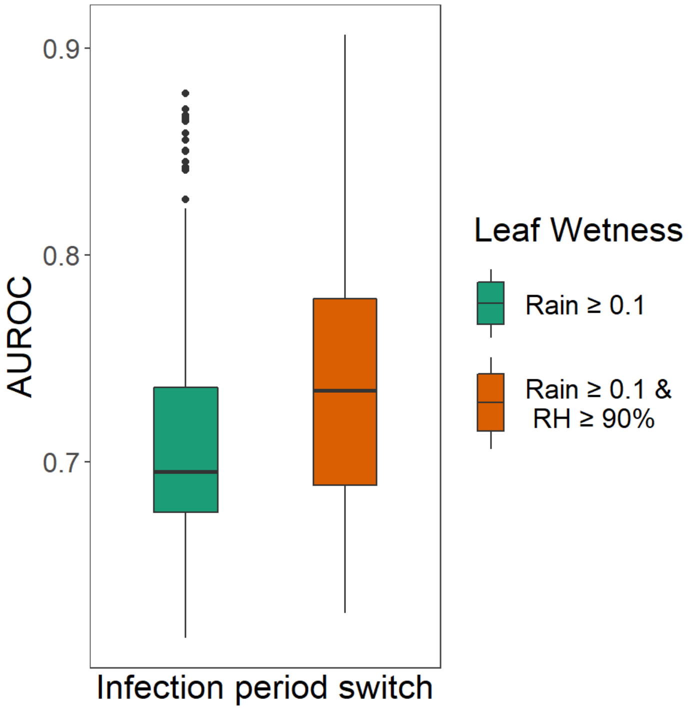


Figure 3.4. Group median difference between models with leaf wetness estimation using rain (rain ≥ 0.1mm) or the combined rain and relative humidity (rain ≥ 0.1mm and RH ≥ 90 %) as an estimator.

3.5.2. *Evaluation of main variable thresholds*

Scatterplots with LOESS smoothing and boxplots indicated a non-linear relationship with change in each factor level. The AUROC was found to increase when the thresholds for relative humidity and sporulation duration were reduced. Conversely, an increase in the temperature threshold resulted in an improvement in the predictive power of IR. For all variables, levels of predictor variables showing an increase in AUROC also show higher levels of dispersion, indicating the necessity to investigate the interactions.

A statistically significant cubic polynomial model ($F_{3,323} = 105.9$, $p < 0.0001$) was fitted to the AUROC data with the proportion of variance explained by the model of 0.8617 and 0.8535 for R^2 and adjusted R^2 values, respectively (Table 3.4). Diagnostic plots of residuals versus order of the data and histogram indicated no violation of the normality assumption. The 4th order polynomial model showed only a slight increase in the R^2 *and adjusted* R^2 value while the Shapiro-Wilks test indicated a lack of normality in the distribution of the residuals. Visual assessment of the response surface plotted with the

4th order model indicated a potential overfitting problem. Linear and quadratic fits had lower R^2 *and adjusted* R^2 values and were considered unsuitable. In addition, the predictions from the third-order polynomial model agreed the most with the local non parametric regression (concordance correlation coefficient (Lin, 1989) of 0.9896 (95% CI: 0.9876; 0.9913)), and hence this model was deemed to adequately reproduce the behaviour of the response surface.

Table 3.4. The table of fit statistics for polynomial models from first to fourth order fitted to AUROC data.

Order	**No. of Parameters**	**Degrees of Freedom**	**R2**	**Adj. R2**	**F statistic**	**p value**	**Shapiro -Wilk test**	**Shapiro – Wilk p-value**
1	4	339	0.637	0.634	198.68	<0.001	0.993	0.137
2	10	333	0.758	0.751	115.98	<0.001	0.997	0.813
3	20	323	0.861	0.853	105.89	<0.001	0.996	0.610
4	35	308	0.881	0.868	67.12	<0.001	0.990	0.030

The 3D response surface for the AUROC against any two independent variables while keeping the third independent variable at -3, 0, + 3 level, respectively, is presented in Figure 3.6. In total, nine 3D response surfaces were obtained by considering all possible variable combinations.

Figure 3.6 a-c depicts the interaction between RHt and Tt, keeping SDt at its -3, 0 and +3 level. Figure 3.6 a shows that AUROC increased with increasing Tt, up to 12 °C, and reducing RHt to 88% when SDt is set at 9h. If SDt is kept at the threshold of 12 hours, a decrease in the AUROC is evident (Figure 3.6 b), while an increase in SDt to 15h results in a significant reduction in model accuracy (Figure 3.6 c).

It can be observed from Figure 3.6 d-f, that the accuracy of the model increases with an increase in Tt and a reduction in SDt. The area of AUROC of above 0.85 is achieved with the reduction of sporulation period for 2 hours and an increase of the temperature threshold of 2 °C. This effect on the AUROC is reduced below 0.85 with SDt at the default threshold (12 hours); while increasing SDt results in a large reduction of the AUROC, to the level of an unacceptable prediction model.

Figure 3.6 g-i show the interaction between RHt and SDt, keeping Tt at its -3, 0 and +3 level. Increasing Tt positively influences the model accuracy. Over the range of the Tt factor levels, the area with the highest AUROC values is 0.79, 0.83, 0.87 associated with a temperature threshold reduced to 7 °C, the default and increased to 13 °C respectively.

Overall, results indicate that reducing RHt to 88 % and SDt to 10 hours and increasing Tt to 12 °C result in the largest improvements in the overall predictive performance of the model (Figure 3.5 a, b and i). Variations in Tt do not have the same magnitude effect on the model accuracy, as do the manipulations of RHt and SDt.

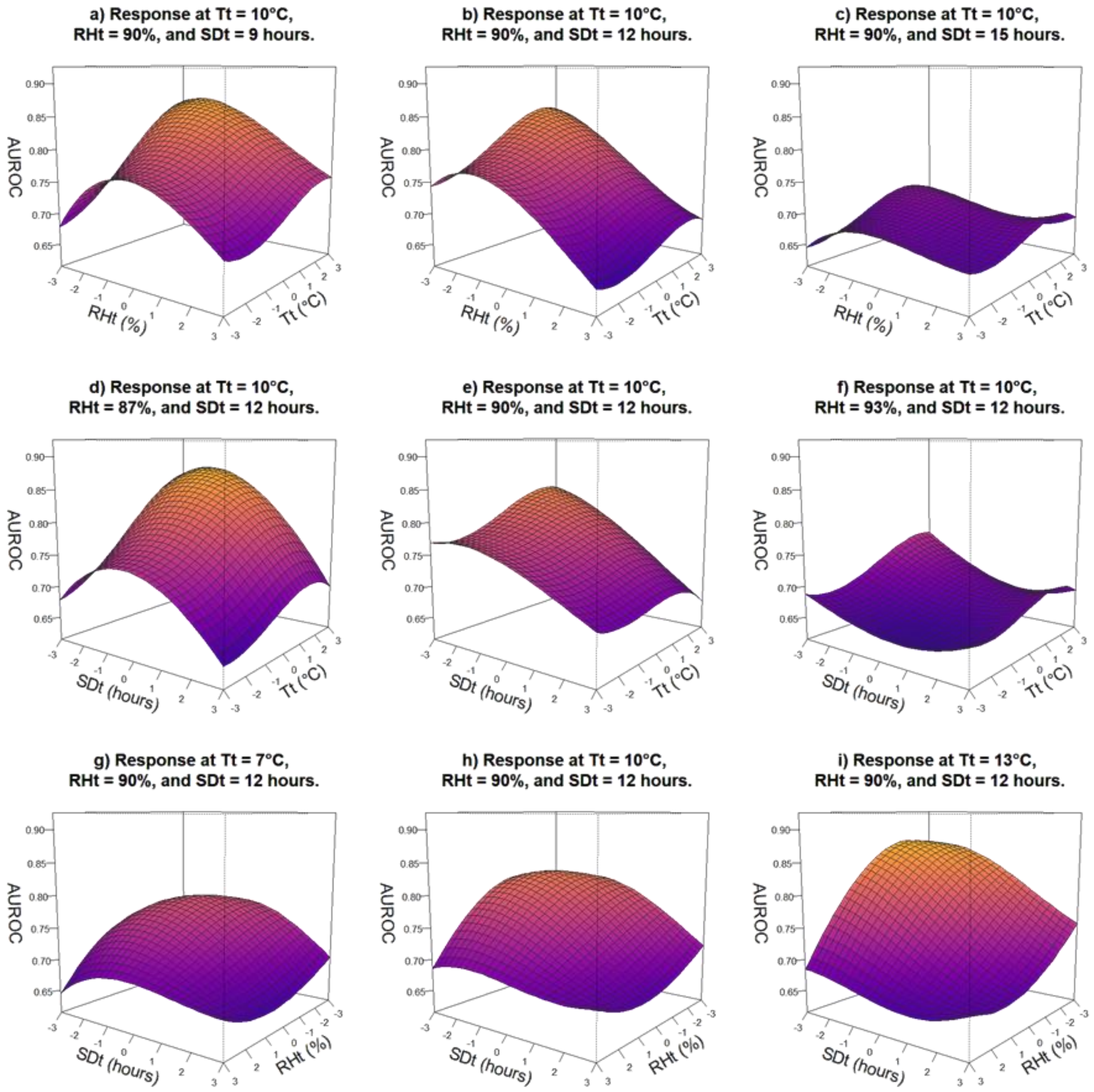
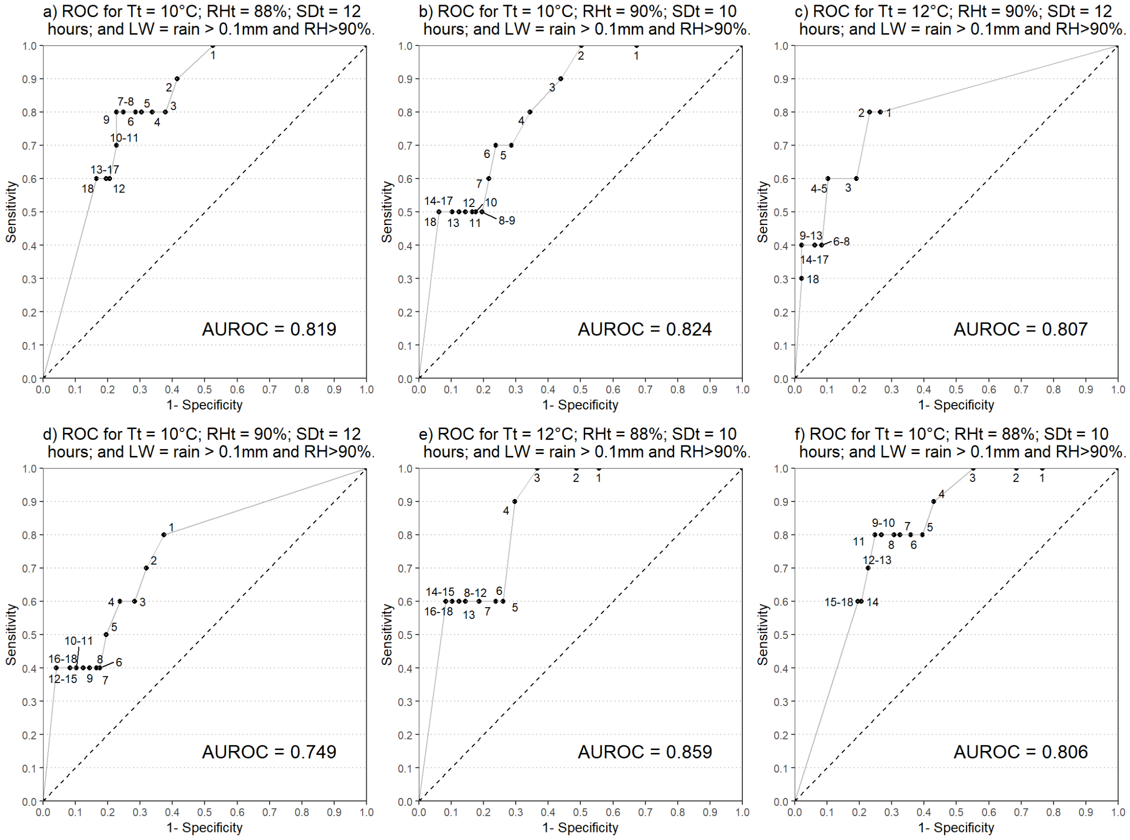

a) Response at Tt = 10°C, RHt = 90%, and SDt = 9 hours.
b) Response at Tt = 10°C, RHt = 90%, and SDt = 12 hours.
c) Response at Tt = 10°C, RHt = 90%, and SDt = 15 hours.
d) Response at Tt = 10°C, RHt = 87%, and SDt = 12 hours.
e) Response at Tt = 10°C, RHt = 90%, and SDt = 12 hours.
f) Response at Tt = 10°C, RHt = 93%, and SDt = 12 hours.
g) Response at Tt = 7°C, RHt = 90%, and SDt = 12 hours.
h) Response at Tt = 10°C, RHt = 90%, and SDt = 12 hours.
i) Response at Tt = 13°C, RHt = 90%, and SDt = 12 hours.

Figure 3.5 3D surface for interaction effect of two variables with third variable fixed on a specific level. 3D surface plots represent interaction between: Tt and RHt, with SDt of 9 (a)), 12 (b)) and 15 hours(c)); SDt and Tt, with RHt fixed at 87 % (d)), 90 % (e)), and 93 % (f)); and SDt with RHt, with Tt of 7 C° (g)), 10 C°(h)), and 13 °C(i)).

Figure 3.5 a-c depicts the ROC curves for the individual, selected model variable thresholds for RHt (88 %), SDt (10 hours) and Tt (12 °C), respectively. Adjusted RHt and SDt provides improvement in terms of model specificity with the grouping of cut-off points moving upwards in the ROC plane and having no associated FN; overall accuracy displays some improvement. Overall, adjusting RHt (Figure 3.5 b) resulted in the greatest improvement in the model accuracy, with sensitivity of 0.8 and high corresponding decision threshold scale of 3-9 EBH. Practically, this means that the risk accumulation of up to 9 EBH was necessary for the onset of the disease in 8 (out of 10) years. Adjusting

Tt only influenced the model performance with the sensitivity similar to the default model variable thresholds, having 2 FN predictions, indicating that the change in Tt had the least impact on the improvement in model performance (Figure 3.5 c).

The performance of the IR model with default variable thresholds is presented in Figure 3.6 d. ROC for the existing IR variable thresholds revealed a lack of specificity, with no risk accumulation in two years, while the current operational blight warning threshold was reached in only four out of ten years.



a) ROC for Tt = 10°C; RHt = 88%; SDt = 12 hours; and LW = rain > 0.1mm and RH>90%.

b) ROC for Tt = 10°C; RHt = 90%; SDt = 10 hours; and LW = rain > 0.1mm and RH>90%.

c) ROC for Tt = 12°C; RHt = 90%; SDt = 12 hours; and LW = rain > 0.1mm and RH>90%.

d) ROC for Tt = 10°C; RHt = 90%; SDt = 12 hours; and LW = rain > 0.1mm and RH>90%.

e) ROC for Tt = 12°C; RHt = 88%; SDt = 10 hours; and LW = rain > 0.1mm and RH>90%.

f) ROC for Tt = 10°C; RHt = 88%; SDt = 10 hours; and LW = rain > 0.1mm and RH>90%.

Figure 3.6 ROC curves for the model parameterizations according to the results of the sensitivity analysis. The IR model parameterizations with the change in a single model variable threshold: relative humidity (a), sporulation duration (b) and the sporulation duration (c), followed by the default (d), optimised (e) and low risk (f) model parametrization.

A model with variable thresholds recommended by the analysis of the response surface (SDt = 10 hours, RHt = 88 % and Tt = 12 °C), hereafter referred to as the **optimised model** (Figure 3.6 e), shows improved performance, with no FP. The disease outbreak was correctly indicated in all years of the study, although the sensitivity drops significantly in six years (corresponding to decision thresholds higher than 5 EBH), indicating that the maximum acceptable decision threshold for this model variation is 4 EBH, corresponding to sensitivity of 0.9.

An additional model variation was chosen for further analysis, hereafter referred to as the **low risk model**, with optimised SDt (10 hours) and RHt (88 %) and Tt kept at the original, default threshold of 10 °C (Figure 3.6 f). This was guided by the limited impact of changing the temperature threshold on the specificity of the model (Figure 3.6 c), limitations related to the size of the biological data set used in the evaluation, a lack of knowledge of the pathogen founder population and the risk associated with a possible disease outbreak. The ROC curve for this model showed improvement in the sensitivity of the model, with 8 years having up to 11 EBH accumulations. While a drop is evident in the AUROC value due to loss in specificity, the grouping of decision threshold points higher in the ROC plane allows consideration for another decision threshold as high as 11EBH with a sensitivity of 0.8.

3.5.3. *Treatment frequency and dose reduction*

Assuming the usual calendar spray practice was followed during the period investigated, the number of treatments calculated for the seven- and five- day calendar spray programmes were 15 and 22, respectively. The decrease in the number of recommended treatments with the increasing decision threshold approximated with the LOESS curve is presented in Figure 3.7. All model versions provide a reduction in the number of treatments compared to the standard five-day calendar treatment.

The number of treatments according to the default parametrization of IR is lower than the calendar practice across the range of decision thresholds (Figure 3.7a and d). In the case of the optimised model, the LOESS curve does not intersect any of the growers practice lines, indicating that the average number of treatments recommended by the model is lower than any grower practice schedule across the range of decision thresholds (Figure 3.7b and d). Given that the optimum decision threshold should not be lower than 4 EBH, the optimised model still provides an opportunity for a reduction in the number of treatments in all but one year and as low as five per season when compared to the seven-day programme.

The number of treatments advised by the low risk model when the decision threshold is set to 3 EBH (lowest observed risk accumulation prior to the disease outbreak) is lower than the 7-day treatment interval on average. However, this is not the case in years such as 2012 or 2007, when the number of treatments with a decision threshold of 7 EBH is close to the seven-day treatment frequency. However, the possibility to set higher decision threshold provides more opportunities for reducing the number of treatments, in the range from 5 to 11 EBH, with an average ranging from 12 to as low as 6 for the five-day strategy and 13 to 10 for the five to ten day strategy.

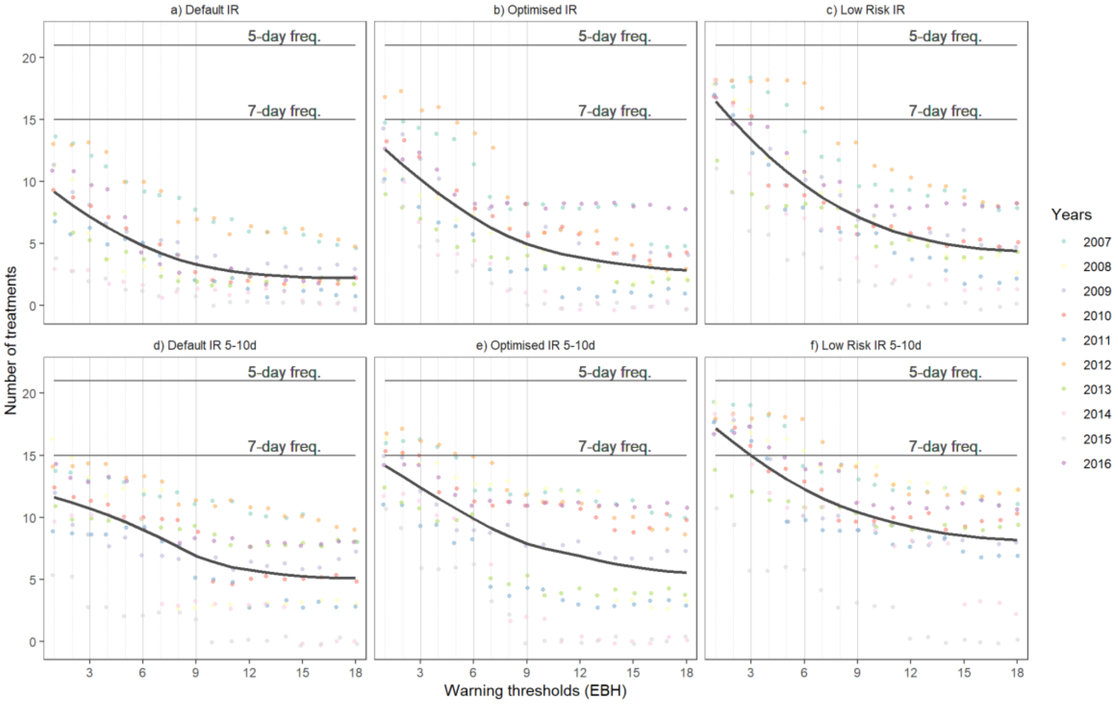


Figure 3.7. Difference between the model guided and the standard grower practice number of treatments over the range of decision thresholds. Figures a) to c) depict the sums of modelguided, d) to f) with model and calendar guided number of treatments per year. The dots represent the number of treatments per corresponding warning threshold in each year. LOESS curve represents the average potential benefit from the use of the model. The 5 and 7-day line represent number of treatments per estimated crop season. If the fitted smoothed line is above the estimated calendar frequency line, the model recommends more treatments than the usual standard calendar programme, on average.

The cumulative proportion of the total fungicide applied using model guided strategy and the number of treatments is compared to the 7-day calendar practice (Figure 3.8). All model versions provide reductions in both the total dose and the number of treatments applied. The reductions are lowest for the year 2012 which was one of the most severe ‘blight years’ on record (Fry *et al.*, 2015). Overall, the highest mean dose reduction is achieved by the default IR (0.248), followed by optimised IR (0.33); the lowest mean dose reduction is expectedly associated with the low risk IR (0.436).

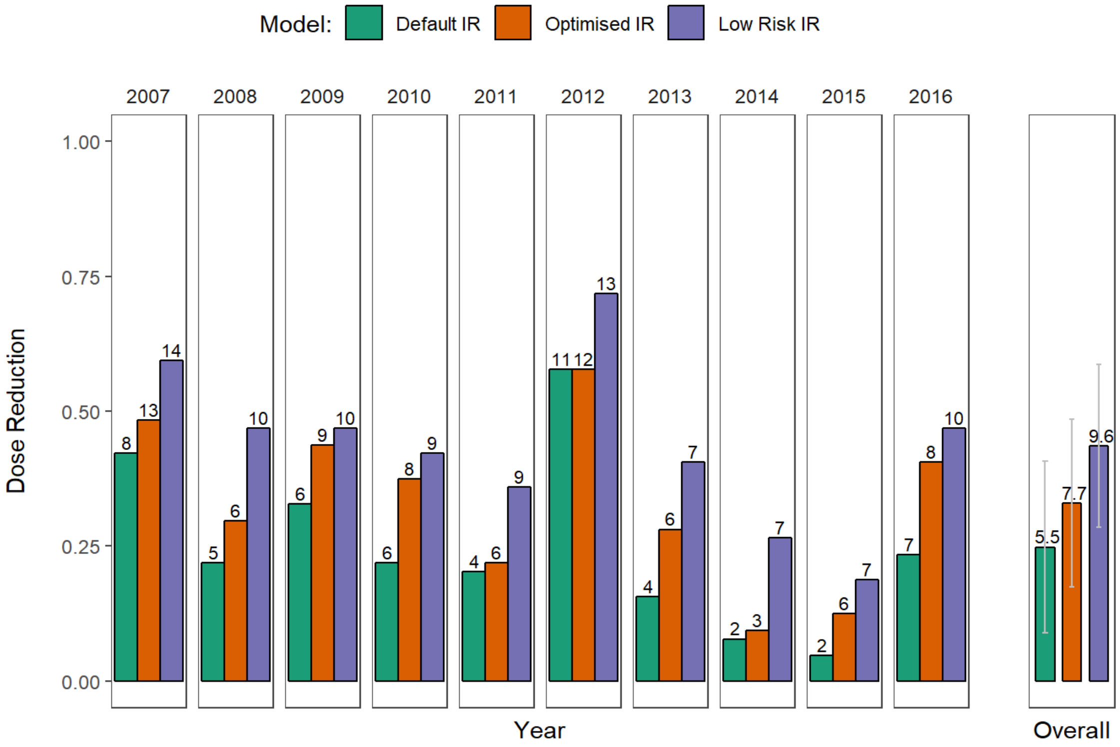


Figure 3.8 Dose reduction and a number of treatments recommended per year by the IR, optimized model and low risk model. Facets marked with the year on top represent summaries for individual years while the last facet represents the averages and variance across all years. In the facets for the individual years, the height of bars represents the proportion of the dose applied per model compared to the total dose, while numbers at the top of the bars represent the total number of treatments recommended by the model in each year. In the overall summary (facet on the far right), the height of the bar represents the mean dose reduction, the number above the bar is the mean number of treatments during the year, and the error bar represents the standard deviation.

3.6. Discussion

We presented an evaluation of the operational algorithm for potato late blight risk forecasting in Ireland. To evaluate the selected algorithm, a sensitivity analysis of the threshold values associated with the most important variables were assessed using empirical ROC curves derived from 10 years of historical weather and disease observation data. Guided by the results of the sensitivity analysis, current epidemiological knowledge and PLB risk awareness, two improved sets of model parameters and a range of operational thresholds are identified. Finally, three disease control strategies, based on these improved model thresholds and currently used model parametrisation, are compared to standard growers’ practice.

Crossovers between empirical and mechanistic models are a common approach in crop disease forecasting (Madden *et al.*, 2007); the IR model is one example. Mechanistic algorithms are a function-based estimation of conditions for the development and completion of several (or a single) segments of disease development; while, in the IR, these segments are limited to a threshold-based prediction of their completion. The threshold selection is often based on estimates by the model developer and may not be an accurate representation of the complex nature of biological processes (Yuen *et al.*, 2015). Such algorithms have their appeal in their simplicity, although biological processes, such as the development of disease epidemics, do not have a binary state but are a part of a complex system that encompasses soft transitions between minimum, optimum and maximum states (Hartill *et al.*, 1990). The semi mechanistic form of the IR adopted at the time for operational use in Ireland, required a number of simplifying assumptions. These favoured more “conservative” variable thresholds, to reduce the frequency of warnings. Our results indicate that the previously defined default thresholds of the Irish Rules are no longer fit for risk prediction in the new PLB pathosystem and based on the available data.

This study is in agreement with older reports stating that blight epidemics in Ireland are most often the second half of June (Dowley *et al.*, 2008) due to low night temperatures (Cooke, 1991). Average minimum daily temperature in Oak Park was low in April and May, 4.5 ˚C and 7.2 ˚C respectively, providing a potential explanation for the low pathogen activity during this period. Lower temperatures in the early stages of potato development can provide a certain level of protection until the plants reach a level of maturity where they are more resistant to attack (Grainger, 1979). This has been challenged in recent times due to the rise in aggressiveness of the newer pathogen strains active over a wider range of environmental controls (Cooke *et al.*, 2011; Fry *et al.*, 2015; Mizubuti *et al.*, 1998). The Irish Rules model uses a hypothetical lower temperature threshold of 10 ˚C without an upper boundary, consistent with a number of early prediction models employed in Northern Europe (Beaumont, 1947; Everdingen, 1926; Førsund, 1983; Schrödter *et al.*, 1967; Smith, 1956). Our results indicate that the development of *P. infestans* under typical Irish weather conditions is low if the temperature is less than 12 ℃. However, considering a relatively small gain in overall model accuracy, a more comprehensive evaluation would be necessary prior to recommending increasing the current temperature threshold. Previous research from areas with a diverse pathogen population cautions that blight epidemics will progress even if temperatures are lower than 10 ℃, under extended humid periods, although the rate of this progress is low (Grünwald *et al.*, 2002; Hermansen *et al.*, 2003). Additional years of data and knowledge of the founder population would be required to ensure that this is a robust conclusion, suitable for deployment on an operational basis.

Evidence exists for reducing the relative humidity threshold and duration of initial sporulation period. The diagnostic performance of the optimized model versions with these factors provides a ‘safer sleep’ for the farmer. Our results are in agreement with the report from Fennoscandia rejecting a relative humidity threshold of 90 % as a development threshold (Lehsten *et al.*, 2017). This threshold has been adjusted in a number of models used throughout Europe, i.e. the French model, Milsol, uses a threshold of 86 % (Gaucher, *personal communication*) and the Danish Blight management uses a threshold of 88 % (Hansen, *personal communication*). There are a number of reasons to opt for lower risk when deciding on which reported relative humidity threshold should be considered blight favourable, such as accuracy of measurements, distance between weather data source and the production area, topography of the area, physiological and phenological differences in crop haulm density and shaded areas of the production fields (Gent *et al.*, 2010; Magarey *et al.*, 2005a, 2017).

Leaf wetness estimation is one of the key parameters in agricultural meteorology controlling pathogen infection and determining disease development rates (Rowlandson *et al.*, 2014; Sentelhas *et al.*, 2008). In agricultural field conditions, leaf wetness may result from rain, fog, irrigation or distillation from the soil (Monteith *et al.*, 2007); our results indicate that a simple use of a precipitation threshold is not an appropriate estimator of leaf wetness in this context and should be supplemented with an additional estimator based on a simple empirical model for RH. Due to lack of in-field measurements, we have used a 'reverse' approach to test the validity of proposed estimation method by comparing the leaf wetness estimation to the disease occurrence (Beruski *et al.*, 2019). This estimation method has been successfully employed in a number of DSS worldwide (Gleason, 1994; Rowlandson *et al.*, 2014).

A low risk of three and four EBH was predicted by both the optimised and low risk models, prior to the disease onset during 2 of 10 years studied, 2011 and 2014. Possible reasons for this are the proximity and strength of the inoculum source or the aggressiveness of the pathogen lineage initiating the epidemics. The specific *P. infestans* lineages that initiated the epidemics in our data is not known, but it can be hypothesized that these infections were initiated by the more aggressive strains. Additionally, epidemics in both years were initiated later in the season, on 28 July and 1 August, possibly coinciding with a shift in the structure of pathogen population, increasing the probability that the infections were initiated by a more aggressive strain. Limited findings from our monitoring of the founder population at Oak Park, from 2016 to 2018, show that the epidemics are predominantly initiated by the older clonal EU_8_A1 genotype, while the population structure changes in favour of new genotypes EU_6_A1 and EU_13_A2 over the course of the season. This is in agreement with recent experimental evidence regarding the establishment of the new *P. infestans* genotypes under Irish conditions (Cooke, 2015; Kildea *et al.*, 2010; Stellingwerf *et al.*, 2018) exhibiting an increase in aggressiveness (Fry, 2008; Li *et al.*, 2012; Mizubuti *et al.*, 2000, 1998; Mariette *et al.*, 2016a). Hence, we can recommend 4 EBH as the minimum decision threshold to be considered under conditions of high disease pressure or if the outbreak of an aggressive strain of the pathogen is reported.

The optimised model offers significant potential to increase the model specificity and consequentially, reduction in the number of required treatments, compared to the low risk model in the high sensitivity range of the ROC curve, between 0.9 and 1. The difference between the optimised and low risk model, calling for caution, is the grouping of the cut-off points corresponding to the decision thresholds above 5 EBH. A number of decision thresholds for the low risk model is closer to the higher sensitivity area (5 - 11 EBH at 0.8 sensitivity) compared to the optimised model (all cut-off points higher than 5 EBH correspond to 0.6 sensitivity). Thus, determining a higher decision threshold, which requires fewer treatments, is possible for the low risk model at 0.8 sensitivity, although defining an exact threshold is difficult since values from 5 to 11 EBH correspond to the same sensitivity value. In the case of small sample sizes, the crude empirical estimate has the disadvantage of providing the same sensitivity values for different specificity values. The robust methodology and highly reproducible coding example allows for the regular updating and evaluation of the model leading to clearer definitions of the risk and/or benefit associated with each decision threshold as the new data becomes available.

It has been shown that on average, the use of risk prediction models offers a possibility for reducing fungicide inputs compared to standard Irish growers’ practice. Possible reductions in the dose and the number of treatments exhibit variation across the period studied. This reflects the nature of agricultural production and further empowers the need for IPM approach to defining the treatment intervals. While spray intervals should be longer than seven days, most of the time these intervals could be justifiably reduced during parts of the ‘blight year’. Currently, operational decision thresholds for issuing blight warnings are not clearly defined and based on experience. Hence, an estimation of risk associated with decision thresholds in the higher sensitivity range is provided. The accumulation of EBH needed to issue the warning at sensitivity levels of 0.9 and 1 is the same for both the optimised and low risk models, with the optimised model providing greater opportunities for reducing the number of fungicide treatments and/or the dose. However, an important advantage of the low risk model is related to the sensitivity, 0.8, providing more certainty in model outputs if the warning is considered at a higher decision threshold, from 5 to 11 EBH. Such situations may be considered when other factors necessary for the disease development are estimated lower, such as during the earlier part of potato growing season, if more resistant varieties are planted or low number of reported disease outbreaks in the region. The adoption of decision support systems and utilisation into everyday practice could have numerous benefits for growers, such as optimisation, as well as, justification of fungicide inputs (Taylor *et al.*, 2003). Our findings indicate that the original Irish Rules model parameters need to be altered for two model variables, which inevitably will result in an increase in the frequency of warnings. Optimisation of the control programme does not necessarily mean reduction in the number of treatments, and an effective forecasting scheme could advise at least as many fungicide treatments as the standard growers practice during seasons with blight favourable conditions (Doster *et al.*, 1991), which often occur with typical weather conditions experienced in Ireland. The decision on the level of risk acceptable by a grower is a complex one made according to the price of treatment, the value of production, legislative restrictions (Lehsten *et al.*, 2017) and the need for reduction to prevent the development of fungicide resistance (Cooke *et al.*, 2011). Hence, here we do not make a recommendation for the exact decision threshold but elaborate on possible reductions and varying levels of risk deemed acceptable by a producer. Met Éireann issues regional warnings and these warnings, and the quality of these warnings could be improved with information regarding the disease outbreaks and rapid identification of the pathogen lineage, due to reasons outlined above.

Decision support at the synoptic level is not a silver bullet to provide an ultimate solution for optimal environmentally friendly disease control, but merely another tool to get closer to it. Unfortunately, if it is not utilised as such and in an appropriate manner, it can lead to an opposite effect. Plant disease models are often parochial in nature, evaluated by researchers who developed them, and are often used without calibration when employed in agroecosystems different from those they were developed for (Harrison, 1995a; Shtienberg, 2013). The interdisciplinary nature of the work related to decision support in crop protection, requiring skills and knowledge in informatics, mathematics, meteorology, agronomy and biology are often a limiting factor for the sustainable development of this branch of plant disease epidemiology (Magarey *et al.*, 2017). One possible way to overcome some of the obstacles is the acceptance of open and reproducible methods. The importance and need for open-science in the field of phytopathology has been reported as a way include recruitment of experts from different fields, application of cutting-edge methods, and timely replication of data analyses as a way to increase the robustness of the findings (Kamoun *et al.*, 2019). Some of the relevant examples are coming from other fields of research related to potato late blight. The development of our understanding and knowledge of *P. infestans* population diversity has been empowered with POPPR, a widely used R package for enabling easier genetic analysis of clonal populations (Kamvar *et al.*, 2015). Also, Sparks *et. al.* (Sparks *et al.*, 2014) evaluated the possible implications of the climate change on potato late blight in the future. These do not have only a scientific value, but represent a significant contribution to the education of a new generation of phytopathologists, who will need to be equipped with such knowledge and skillsets to be able to keep up with the ‘fight’ against ever-evolving plant pathogens.

Easily accessible tools are necessary for validation and calibration of risk models using historical data prior to field evaluation in other climatic regions or re-evaluation in the original ecosystem, which could potentially save a considerable amount of time and money and lead to more sustainable use of decision support in plant protection. To the best of our knowledge, this is the first completely reproducible evaluation of a crop disease risk prediction model, implemented in a single computing environment, within a freely accessible software language. Such work, it is hoped, will empower the sustainable development of potato late blight and crop disease forecasting in general.

3.7. Conclusions

The results have shown that there is a need to revisit the parameters of the Irish Rules model, proposed for the different ecosystem and operational abilities at the time, as well as the operational use of the model. On the basis of the work presented here, we recommend the reduction of variable thresholds for relative humidity from 90 % to 88 % and sporulation duration from 12 to 10 hours; and adopting an additional leaf wetness indicator, incorporating both precipitation (≥ 0.1 mm) and relative humidity (≥ 90 %). Our analysis indicated that very little blight development was occurring at temperatures lower than 12 °C, however, this increase recommended operationally due to lack of certainty associated with the small data sample size and the high risk related to possible disease outbreaks and wider decision threshold range in the high sensitivity area of the ROC space for the low risk model. However, the thresholds identified here should be continuously evaluated after each growing season, facilitated here by the development of the methodology and associated model evaluation code. Our recommendation for the operational application of the model is to use the range of 4 to 11 EBH and set the threshold dynamically during the season based on the reports of the frequency of the disease outbreaks in the region of interest. Future development of the Irish PLB warning system should include rapid in-season identification of pathogen genotype distribution to be used as a guide for selection of the decision threshold.

Representation of the complex aetiology of *P. infestans* is omitted or generalized with synoptic empirical prediction algorithms, as well as other components of this pathosystem, such as pesticide protection status, crop resistance (Harrison, 1992b), quality of meteorological network coverage and distances between production field and weather stations (Taylor *et al.*, 2003), crop phenological stage (Hirst *et al.*, 1960) and pathogen genotype (Cooke *et al.*, 2011; Fry, 2016). Understanding the complexities of the agroecological system under investigation is crucial for interpreting the results of the analysis. Small data sets may carry high variability due to a limited number of observations (Yuen *et al.*, 2002). Hence, a note of caution is recommended when employing the model proposed here.

The exact methodology used in the development of early models, such as the IR, is not always clear, but the assumption is that they were a product of empirical, often trial and error based methodologies and weather data available at the time (Yuen *et al.*, 2015). Hence, the recommendation for future development is to explore the possibility of redesigning currently employed models to facilitate the transition from the threshold based binary estimation of stages of host parasite interaction, to a more realistic one, based on a functional relationship between host, parasite and the environment. Future work on development of risk prediction algorithms, should also take into consideration additional uncertainty introduced by forecasted weather data; avoiding the usual practice in crop disease modelling where models are developed with observed weather data and applied on forecasted weather with no evaluation of the impact of weather forecast uncertainty on model predictions (Magarey *et al.*, 2017). Approaches in IPM cannot be limited to a single discipline effort. The vast amount of data available nowadays that are currently under-utilized provides a number of opportunities for smarter farming (Kamilaris *et al.*, 2017)

The challenge still remains in front of the end-user to adequately employ information provided in the decision-making process with an awareness or knowledge of characteristics of the variety grown, growth stage, control measures used, risk from surrounding areas, accessibility of active ingredients and similar. The often hard-earned confidence by the final user could be maintained through constant evaluation of the system and adequate education regarding the appropriate use of decision support tools.

4. Optimising potato late blight management in the Republic of Ireland using risk prediction, varietal resistance and molecular tools

4.1. Preface

This chapter is submitted as:

Cucak, M., Moral, R., Fealy, R., Downes, P., Kildea, S. Optimising potato late blight management in the Republic of Ireland using risk prediction, varietal resistance and molecular tools. Submitted to *Phytopathology*.

Currently, due to the high risk involved with possible disease outbreaks, there is a high dependency on fungicides for the control of potato late blight. The environmental conditions on the island of Ireland provide opportunities for explosive epidemics and proposing sustainable IPM management solutions require a careful evaluation using an interdisciplinary approach. This study builds on the previous report on the re-evaluation of the IR, currently used potato late blight risk prediction model in the Republic of Ireland. The modified model is to be operationally deployed in the management of PLB, the disease, which, in case of outbreak due to wrong risk estimation, could rapidly lead to significant losses and endanger the livelihood of a farmer. Hence, the field validation was considered necessary, and for that purpose, we employed some of the major tools in the hands of a modern phytopathologist, encompassing an innovative field evaluation of an environmental disease risk prediction model, supplemented with the use of a molecular method to determine the full scope of possible benefits and/or repercussions. In an attempt to overcome inherited lack of trust in the use of DSSs, the approach we took here is to use a publicly available DSS to tailor the grower's usual management practice, rather than imposing a completely DSS dependent spray advice.

4.2. Abstract

Potato late blight remains the most significant threat to potato cultivation globally, often requiring expensive, time-consuming and environmentally unfriendly approaches to disease management. The goal of this research was to evaluate if the environmental risk estimation combined with increased varietal resistance can be reliably used to tailor the standard potato late blight management practice under growing conditions and contemporary *Phytopthora infestans* population in the Republic of Ireland. Using the modified Irish Rules model, it was possible to reduce fungicide usage compared to current standard practices used by Irish growers without adversely compromising disease control and yield. The delay in the initiation of the epidemics, the final foliar disease levels and the reduction of fungicide usage was correlated with increased host resistance levels. Although the epidemics on highly resistant varieties remained at low levels, a clear selection pattern towards the *P. infestans* genotypes EU_13_A2 and EU_6_A1 was observed. The rise in the frequency of strains of *Phytophthora infestans* with increased pathogenicity and virulence matching higher levels of host resistance was observed in the latter part of each of each growing season. Such variation in the population structure and possibility of the tuber blight infections calls for caution in the interpretation of the environmental risk estimation as the potato growing season progresses.

4.3. Introduction

Potato late blight (PLB) caused by the filamentous oomycete *Phytophthora infestans* is one of the world’s most devastating diseases of potato and tomato crops (Fry, 2008). Historically, failure of the potato crop due to PLB contributed to food shortages which resulted in dramatic changes in the demographics of Ireland mid-1800s (Bourke, 1964, p.64; Savary *et al.*, 2017). Globally, the cost of control and associated yield losses are estimated to exceed €1 billion annually (Haverkort *et al.*, 2008b). In Ireland, the annual loss from the disease has been estimated at 8% (Copeland *et al.*, 1993) with potential yield loss of 10.1 t/ha without fungicide protection (Dowley *et al.*, 2008). Potato late blight epidemics proliferate under conditions of cool and moist weather, typical in the northwestern part of Europe (Bourke, 1955b; Cooke *et al.*, 2011; Harrison, 1995b). Shifts in the pathogen population since the 1980s, the reliance on susceptible varieties and intensification of production make this disease a high-risk segment of production. Hence, disease control is supported by prophylactic fungicide applications with constantly increasing frequency. Fungicides are often applied at high rates and in short 5-7 day intervals, throughout the growing season (Cooke *et al.*, 2011; Kirk *et al.*, 2001). In addition to fungicide applications, management of the disease includes the use of the healthy seed, appropriate removal of inoculum (such as discarded tubers), frequent scouting of the crops and the use of support tools to aid decisions relating to the implementation of these measures. The reliability and subsequent adoption of these measures are continually challenged due to an increasingly unpredictable climate, the evolution of fungicide resistance and virulence, and the ability of these traits to move between populations due to increased global trade (Fry, 2016).

Phytophthora infestans is a heterothallic species generally requiring the presence of both A1 and A2 mating types for sexual reproduction and recombination (Fry, 2008; Goodwin *et al.*, 1994). Prior to the late 1970s, global *P. infestans* populations were dominated by strains belonging to the A1 mating type, hence limiting the diversity that existed in populations. Since then reports of the A2 mating type have increased (Goodwin *et al.*, 1997) facilitating the rise and spread of new lineages, some of which demonstrate increased fitness levels (Fry, 2016). Despite the low genetic diversity still often found in Western European *P. infestans* populations, they regularly undergo frequent and vital changes, with the rise of both EU_13_A2 (13A2) and EU_6_A1 (6A1) multilocus genotypes (MLG) as an example of such changes (Cooke *et al.*, 2011). The arrival and establishment of these two MLGs on the island of Ireland was likely delayed, probably due to its geographical location on the western fringe of Europe. Although the Irish population is dominated by EU_8_A1 (8A1), they have been reported in higher frequency recently, varying from year to year (Cooke *et al.*, 2014; Kildea *et al.*, 2010; Stellingwerf *et al.*, 2018). The relatively recent establishment of both 13A2 and 6A1 has greatly impacted control measures, with foliar resistance ratings of several cultivars being downgraded from resistant to moderately resistant or even susceptible (Lees *et al.*, 2012). These lineages also exhibit increased aggressiveness on susceptible varieties which dominate Western European production systems (Mariette *et al.*, 2016b). The Republic of Ireland is not an exception, with potato production dominated by susceptible varieties: Rooster (51.9%), Kerrs' Pink (15.1%), British Queen (8.6%) and Golden Wonder (4.0%) (Anonymous, 2011).

Reducing fungicide inputs for control of PLB on moderately resistant potato cultivars has been shown to be an effective control strategy (Bain *et al.*, 2014; Fry, 1975; Nærstad *et al.*, 2007; Spits *et al.*, 2007). Fry (1978) reported that combining cultivar resistance and regular applications of protective fungicides had an additive effect on controlling foliar PLB infections. More recently, Bain *et al.* (2014) demonstrated that, even in the presence of aggressive *P. infestans* populations, reduced rates of protectant fungicides slowed the progress of epidemics, and in doing so, varieties with moderate levels of resistance performed similarly to resistant varieties. However, *P. infestans* populations can adapt to locally dominant cultivars, irrespective of their resistance levels, and may render polygenic, partial resistance non-durable if not properly managed (Andrivon *et al.*, 2007). Even amongst the highly clonal *P. infestans* population currently present in Ireland, Stellingwerf *et al.* (2018) reported that 13A2 was found more often on varieties with some level of resistance, indicating the potential for the selection of increased virulence in local populations through varietal deployment. Numerous examples from early potato late blight breeding efforts show that the deployment of major resistance genes (R-genes), which offered a high level of resistance, became rapidly ineffective due to an increase in the frequency of the virulent isolates (Fry, 2008). The cultivar Pentland Dell in Scotland was known to contain genes R1, R2 and R3 and was resistant to the common race (Race 4), which led to its popularity, becoming the third most popular potato cultivar within three years and subsequent selection of a resistance-breaking biotype in a local pathogen population (Malcolmson, 1969). Currently, attention is shifting towards stacking R-genes by conventional resistance breeding or genetic engineering techniques (Leesutthiphonchai et al., 2019). A promising environmentally friendly strategy to prevent the resistance breakdown of potato cultivars under conditions of rapidly evolving pathogen population is to use disease risk prediction approaches to guide low input chemical protection (Kessel *et al.*, 2018).

The utilisation of decision support systems (DSS) to help guide and reduce the use of pesticides for the control of PLB has shown promise around the world (Bourke, 1959; Grünwald *et al.*, 2002; Hermansen *et al.*, 2003; Fry *et al.*, 1983; Small *et al.*, 2015b) and in Ireland (Bourke, 1953b; Dowley *et al.*, 2004). Due to technical and perceptual constraints, the update and utilisation of these systems in routine disease management has been perceived as slow (Gent *et al.*, 2010; Raatjes *et al.*, 2004; Shtienberg, 2013). In a case of high-risk disease, routine prophylactic applications of fungicide treatments appear to be economically justified unless a highly accurate disease risk model can be developed or during periods when the low disease pressure can be determined (Pethybridge *et al.*, 2009).

The Irish Rules (IR) (Bourke, 1953a) is a semi-empirical PLB risk prediction model developed to accommodate the PLB pathosystem, management practices and suitability of the meteorological network in Ireland during the 1950s. The IR is still utilized in their original form to support the blight warning service with issuing spray advice. The service is led operationally by the national meteorological service, Met Éireann (Dowley *et al.*, 2004). An evaluation of the IR by Dowley and Burke (2004) reported a significant reduction in fungicide usage, but with unsatisfactory disease control. More recently, these findings were confirmed through a theoretical comparison of the currently used PLB risk prediction models in Europe (Hansen *et al.*, 2017). This study has shown that the Irish Rules model produces the lowest risk accumulations, due to its conservative set of parameters. Considerable changes in the PLB pathosystem since the establishment of the rules, limited evaluation of the model and questions regarding its performance (Dowley *et al.*, 2004; Hansen *et al.*, 2017) prompted us to evaluate and re-calibrate the model and the decision strategy (Cucak *et al.*, 2019). The following changes of the model thresholds were recommended: 1) reduction of the thresholds for relative humidity and an initial period duration from 90% and 12 h to 88% and 10 h, respectively; 2) keeping the temperature threshold at 10°C, and 3) adopting an additional leaf wetness indicator which incorporates both precipitation (0.1 mm) and relative humidity (90%). Based on the re-parameterised model, our results have shown that a minimum of 3 and a maximum of 11 effective blight hours (EBH) are necessary for the disease outbreak. While the reduction of the model variable thresholds inevitably results in an increase in risk estimation, the results of the simulation analysis showed that the re-parametarised model still provides reductions in fungicide usage when compared to the current grower practice.

Given the potential risks to the production associated with failing to control PLB under Irish growing conditions, a field evaluation of the revised model and decision strategy was implemented in order to validate the previously conducted theoretical analysis. Our aim is to show how subtle adjustments of the standard grower’s practice using a reliable, publicly available decision support tool is possible under Irish conditions. Our specific goals are to compare the performance of fixed and environmental adjustment of standard grower’s potato late blight chemical control on foliar disease control and the effect on yield of varieties varying in disease resistance levels under field conditions. Additionally, the pathogen population was monitored to evaluate the implications of developed disease management strategies. An open and reproducible presentation of the methods and the analysis employed is provided, to facilitate further evaluation and development of IPM strategies, following the principles set in our previous study.

4.4. Methods

Frequently used abbreviations in are presented in Table 8.1.

4.4.1. *Trial design and cultural practices*

Field trials were conducted at the Teagasc Crops Research Centre at Oak Park, Carlow, Ireland (latitude: 52.85, longitude: -6.91) during the period 2016-2019. Fertilization and non-experimental pesticide applications, pre-emergence herbicide and insecticides, were applied according to local potato growing practices. In each season the preceding crop was spring barley, with the potato crop representing the non-cereal break crop in a five-year rotation. For each trial, the soil was a free draining medium sandy loam. The planting dates were approximately one month later than the standard grower’s practice to avoid plant senescence towards the end of the season. The disease was allowed to develop naturally. Due to an extended dry period in early July 2018, the trial was irrigated on two occasions to prevent abiotic impacts of drought. The irrigation had no impact on disease development since the first disease occurrence was not noted until 20 August. The entire trial was desiccated in late September and harvesting took place in October of each season. Drills in each plot were mechanically lifted and tubers were then hand-picked from the soil surface. Potatoes were stored in open storage for at least two weeks to allow tuber blight symptoms to develop. Dates of the agronomic operations are presented in Table 8.2.

The trial was designed as a split plot, with two factors; fungicide programme randomised to the whole plots and variety to sub-plots, with 4 replications. The sub-plot consisted of 20 tubers of each variety per replicate. Factors are described below. The trials were planted into pre-formed 81 cm wide ridges, with a planting distance and the distance between tuber centres was 31 cm. Each main plot was made up of six drills 11.3 m long, with sub-plots consisting of two drills with ten plants each. To facilitate harvesting 1 m was left unplanted at the end of each sub-plot. In addition, the middle two drills of each plot were planted with the variety King Edward to allow a uniform development of the disease. A 3 m divider strip was left between the replicates to facilitate fungicide application and avoid interplot interference. Spraying was carried out with a conventional sprayer mounted on a utility vehicle with an independent power source. The spray volume was 200 1 ha^{-1} and the spray pressure was 3 bars to give a medium/fine spray quality using anti-drift spray nozzle number 4110-20.

4.4.2. *Cultivars*

Six potato varieties (Table 4.1) were included in the trials and were selected as they either represent those most widely cultivated in Ireland, or the extremes of resistance and susceptibility currently available. The breeding clone T5821/11, bred within the Teagasc breeding programme, was also included to represent an elite variety with a high level of partial resistance. The seed was acquired from commercial sources, with the exception of T5821/11, which was propagated as part of the Teagasc potato breeding programme.

Table 4.1 Potato cultivars and breeding clones used in the field trials, their foliar and tuber resistance to *Phytophthora infestans* (scale from 1 to 9, with 9 being the most resistant), and growing season lengths.

Variety/ breeding clone	**Foliage resistance: Field**	**Tuber resistance: Laboratory**	**Maturity**
King Edward	3	5	Maincrop
British Queen*1	3	4	Second Early
Rooster*1	3	5	Late
Setanta	6	7	Maincrop
T5821/11	8	8	Late
Sarpo Mira	8	9	Very late

*1Included after 2016

4.4.3. *Disease control*

We followed the approach outlined by Madden and Ellis (1988a), that an appropriate validation of a warning system should include a comparison of a DSS generated programme with a standard spray programme and a no-fungicide control. All infections were natural. The application of fungicides commenced when the plants were beginning to meet within the drills. Six late blight control strategies based on weekly intervals were employed in the trials; 1: untreated control, 2-3: full and half label dose of fungicide programme considered as standard growers practice (further referred to as the full and half dose), respectively, and 4-6: dose adjustment of the standard growers fungicide programme based on the disease risk prediction for the following seven days determined as follows:

4. Irish Rules (IRp): full-dose applied if the IR model output reached the threshold of 12 EBH as per Bourke (1953a);

5. Blight Management (BMp, included during period 2017-2019): adjusted dose applied based on a limited version of Blight Management including only model A (for susceptible varieties) as per Nielsen et al. (2015) (Table 8.3) without altering our fungicide programme (curative treatments recommended by the Blight Management were not implemented);

6. Modified Irish Rules (MIRp): adjusted dose applied based on risk predicted by the MIR model as per Cucak *et al.* (2019), with doses applied (five categories: no treatment, quarter, half, three quarters and the full dose) reflective of respective risk accumulations of effective blight hours (EBH): 0, 1-3, 4-6, 7-9 and 10-12.

The fungicide programmes were typical of locally applied programmes including the following fungicides applied in rotation (the active substance and the label dose are indicated in brackets): Ranman (cyazofamid 400 g/l, 0.5 l/ha); Shirlan (fluazinam 500 g/l, 0.4 L/ha); Infinito (fluopicolide 625 g/l + propamocarb 62.5g/l, 1.6 L/ha); and Revus (mandipropamid 250 g/l, 0.6 L/ha). In all cases, the recommended label dose was considered as the full dose. See Table 8.4 for further details on dates of application and doses applied for each treatment.

An automated service to run the above-described risk prediction models was implemented in the R programming language. For each blight control strategy, the risk was calculated based on the observed and forecasted hourly weather relevant for the trial location. The historical weather files contain the hourly values for the following variables: mean air temperature (°C) and relative humidity (%) at 2 m and the total hourly precipitation (mm) measured at the Oak Park synoptic weather station operated by Met Éireann. All trials were within a radius of up to 500m from the meteorological station. The weather forecast was extracted from the nearest grid point of the high-resolution forecast (HRES) atmospheric model, operationally run by the European Centre for Medium-Range Weather Forecasts (ECMWF). The HRES grid resolution is approximately 9 km. The provided weather forecast data consisted of three files with intervals from 0 to 90, 120 and 240 hours lead time with the corresponding 1, 3 and 6-hour temporal resolutions, respectively. Files were merged for the entire 240 hour period prioritising forecasts with lower temporal resolutions (0-90 hours: 1-hourly forecast, 91-120 hours: 3-hour forecast and 121-240 hours: 6-hour forecast). Temperature and relative humidity were downscaled to hourly resolution by spline interpolation using the Forsythe, Malcolm and Moler method (Forsythe *et al.*, 1977); while the rain totals were divided by 3 for 3-hourly and 6 for 6-hourly files. Data files were obtained from Met Éireann daily at 09:30 UTC; the observed files are then concatenated with the 240 hours weather forecast, starting from the midnight of the current day. The automated service ingests the weather data and generates the dose calculation for the respective fungicide application on the current day and graphical outputs of the model calculations for the following 7 days (Figure 4.1).

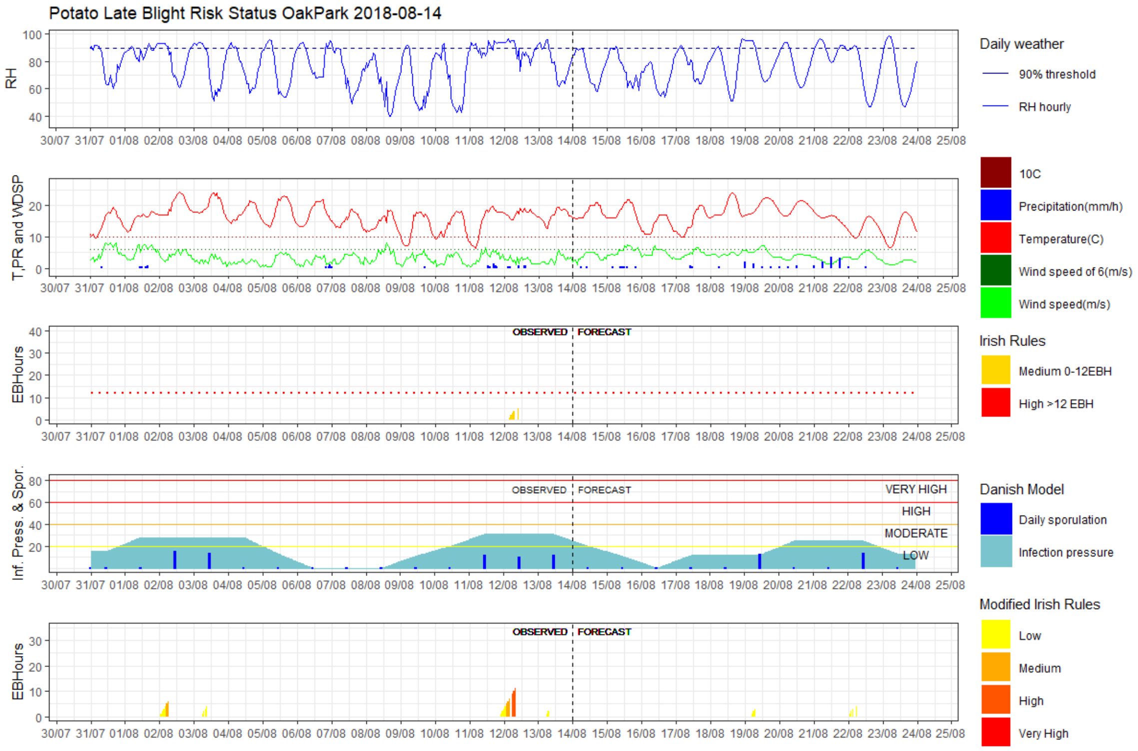


Figure 4.1 An example output of the system providing the outputs of the risk prediction models.

4.4.4. *Disease and yield assessments*

Disease severity, identified as the proportion of diseased crop tissue in each sub-plot plot, was estimated visually in accordance with ADAS potato late blight foliage assessment key (Anonymous, 1976) every 3 to 7 days. The assessments were initiated after the disease was first observed in the trial site and continued until the untreated control plots were completely necrotic or plants were naturally senescing.

Following harvesting and storage, tubers between 45 and 85 mm were considered as marketable yield (further on referred to as yield). Yields were estimated by harvesting tubers and re-scaling actual yields to tonnes per hectare, without adjusting for the effect that small plot sizes have on yields. Each subplot was mechanically harvested with tubers subsequently picked by hand. Following harvesting, the tubers were stored at ambient temperature for 3-6 weeks prior to grading.

4.4.5. *Pathogen sampling and molecular characterization*

Collection and isolation

Pathogen collection was completed by sampling infected potato leaflets from each plot with visible disease symptoms at the end of the epidemic in 2016 and at different stages of the epidemic development during years 2017 - 2019 (See Table 8.5 for sampling dates and Table 8.6 for the number of isolates per variety and factor per year). The number of samplings was dictated by the duration of epidemics and weather conditions allowing their implementation. The number of samples varied per plot and sampling date. To avoid disturbing the progress of epidemics, the first samples from a plot were taken when at least two lesions were found in plot and only half the lesion (and leaflet) was collected, the exception being late infections on the resistant cultivars, T5821/11 and Sarpo Mira. The number of lesions collected per plot was reciprocal to the disease progress with the maximum number of 4 lesions per plot. Single *P. infestans* lesions were identified and pressed onto Whatmann FTA cards (GE Healthcare), with the exception of 2017, when live cultures were also isolated as follows; cuttings of the sporulating lesions were placed underneath pea agar medium (160 g peas per L and 1.5% w/v agar) amended with antibiotics: rifampicin (37.5 mg/L), ampicillin (10 mg/L) and nystatin (37.5 mg/L). Petri dishes were closed with parafilm and incubated at 18°C in darkness. When clear aerial mycelial growth was visible, approximately 5-7 days after isolation, a piece of mycelium was transferred to the fresh pea-agar medium using a sterile scalpel blade and incubated at 18 °C. Axenic isolates of *P. infestans* were transferred to pea-agar for subsequent DNA extraction and transferred onto the rye agar slopes (Caten *et al.*, 1968) for long term maintenance at 4 °C.

DNA extraction

A single 2 mm disc was punched from the FTA cards and transferred into 1.5 ml 96 well PCR plates. The disc was washed three times with 400 µl of the FTA purification reagent (Whatman Inc., USA) followed by two rinses with 400 µl Tris-EDTA buffer (10mM Tris and 0.1 mM EDTA). The disks were dried for 2 hours in a laminar flow after which they were kept at 4 °C. PCR amplification was implemented within the following four days.

For the *P. infestans* isolates, pieces of lyophilized mycelium were placed in a 2-mL polypropylene vial with glass beads and homogenized. The tissue was disrupted using a mixer mill (MM400 Retsch). DNA extracted using the MagMAX™ Plant DNA Kit (A32580, ThermoFisher) on King-Fisher 96DW instrument (Thermo Scientific) and stored at -20 °C. DNA concentration was measured using NanoDrop 2000 Spectrophotometer (Thermo Scientific, United States) and adjusted to 10 ng/µl.

Microsatellite genotyping

Polymorphic simple sequence repeat (SSR) regions of *P. infestans* isolates were amplified using previously designed standardized set of twelve microsatellite markers (Pi02, Pi4B, G11, Pi04, Pi63, Pi70, D13, SSR2, SSR4, SSR6, SSR8 and SSR11) (Knapova *et al.*, 2002; Lees *et al.*, 2006; Li *et al.*, 2010). Amplification of the SSR markers was carried out as previously described (Li *et al.*, 2013). PCR reactions were performed with Qiagen Type-it Microsatellite PCR kit (Qiagen Corporation) in accordance with the manufacturer's instructions (Qiagen, Hilden, Germany). Primers labelled with a fluorescent dye (G5 dye set: 6-FAM, NED, VIC; Applied Biosystems) were used. Samples from 2016 were analysed using ABI 3130xl, and 2017 - 2019 using ABI 3500XL capillary DNA sequencer according to the manufacturer's instructions (Applied Biosystems). SSR allele size was determined relative to GeneScan 500 LIZ standard and scoring was done using GeneMapper version 3.7 (Applied Biosystems). MLGs were assigned as per allele sizes per Stellingwerf *et al.* (2018).

4.4.6. *Data analysis*

Software Used for the Analysis and the Reproducibility

The entire analysis was implemented using a freely available tool for statistical programming, R language (R Core Team, 2018). The research compendium, containing the entire data analysis is archived at: https://mladencucak.github.io/PLBFieldTrial/index.html

The list of packages that were not used directly for the analysis is provided here. A portion of the data was imported using readxl (Wickham *et al.*, 2019). Packages used for data munging: tidyverse (Wickham, 2017). Packages used for visualisations: ggplot2 (Wickham, 2016), cowplot (Wilke, 2018), and ggthemes (Arnold *et al.*, 2019). Univariate series imputation was implemented using functions from package imputeTS (Moritz *et al.*, 2017). Package zoo (Zeileis *et al.*, 2005) was used for processing dates. Formatting of tables was done with pander (Daróczi *et al.*, 2018). Packages rmarkdown (Allaire *et al.*, 2019) and knitr (Xie *et al.*, 2019) were used for creating a reproducible compendium. Package here (Müller, 2017) was used to ensure reproducibility on different platforms. Programming functions from R.utils (Bengtsson, 2019), string manipulation with mgsub (Ewing, 2019).

Disease control and yield analysis

The disease observations were used to calculate the relative area under the disease progress curve (rAUDPC) (Campbell *et al.*, 1990) to enable comparison between treatments with different assessment periods. The rAUDPC was calculated using the R “agricolae” package (De Mendiburu, 2014). The values of the response variable, rAUDPC are proportions, beta GLMMs with a logit link were fitted using package “glmmTMB” (Brooks *et al.*, 2017). Generalized linear mixed models (GLMM) can be used for the analysis of the data with greater heterogeneity of the disease incidence than would be expected from the random pattern (Madden *et al.*, 2002). Models were fitted to the first year, and remaining years separately, due to lack of two levels of both treatments in 2016. The effects of block and plot were included as random in the linear predictor of the model. The deterministic (fixed-effect) components were fungicide programme, variety and the interaction between fungicide programme and variety for 2016 data, and for the remaining years of the study, the three-way interaction between programme*variety*year was also included. The two-way interaction between the programme, variety (model fit 2016) and the three-way interaction between factors year, programme and variety were significant, hence all of the terms were kept in the model. A linear mixed effect model was fitted to the yield data using the package “lsmeans” (Lenth *et al.*, 2018) following the same procedure. The same interactions were observed to be significant and all terms were kept in the model.

Goodness-of-fit of the models was evaluated using plots of residuals. ANOVA-like tables were calculated using Wald Chi-Squared Test statistics for comparisons, using the Anova function from the “car” package (Fox *et al.*, 2018). For multiple comparisons and *post hoc* tests, the estimated marginal means, standard errors and confidence intervals were calculated using the “emmeans” package (Lenth *et al.*, 2019) and compact letter displays of all pairwise comparisons using the “multcomp” package (Hothorn *et al.*, 2019). The estimates were combined for both models and presented with the point chart with error bars. A linear mixed effects model was fitted to the yield data using the same modelling procedure and *post hoc* testing. In addition to plots of residuals, half normal plots with simulation envelopes were used to assess the goodness-of-fit of the fitted models, using package “hnp” (Moral *et al.*, 2017).

Analysis of the microsatellite data

The genotyping data and metadata was collated into a single file and subsequently formatted as GenAlEx comma separated files to be imported as a genclone object. Frequency charts of genotype proportions per variety and fungicide programme were created for the two-way contingency tables to explore possible selection patterns.

Selection patterns between fungicide programme, variety and year.

The Bruvo distance among MLGs was calculated and minimum spanning networks (MSN) were constructed to visualise the structure of the population across the studied years using the “Poppr” package (Kamvar *et al.*, 2014). Clustering of genetically similar individuals was sought using the Discriminant Analysis of Principal Components (DAPC), a multivariate method that uses genetic data to describe the differences between pre-defined biological populations (Jombart *et al.*, 2010), using the “Adegenet” package (Jombart *et al.*, 2018). In DAPC, data is first transformed using Principal Component Analysis and, subsequently, clusters are identified using the k-means clustering algorithm. The number of clusters (K) was allowed to vary from 5 to 25 and the optimal K was determined based on the Bayesian information criterion (BIC).

In-season temporal variation of population structure.

To provide an overview of how the epidemics progressed in relation to the dynamics of the different *P. infestans* MLGs the number and the proportion of samples assigned to specific MLGs for each sampling date were calculated for the complete collection, from 2017 to 2019 (Table 8.7). As MLGs relating to 2016 were collected from a single sampling time point they were excluded from the analysis. To reduce the potential impacts that the more resistant varieties/fungicide treatments may have had on the *P. infestans* population a subset of data consisted of samples from susceptible the varieties (King Edward, British Queen and Rooster) plots where the epidemics were allowed to develop unimpeded (untreated controls and IRp) were also analysed. The data is presented using frequency plots.

4.5. Results

4.5.1. *Climatic conditions and disease progress*

Conduciveness of weather conditions (Figure 8.1), and subsequently, potato late blight disease progress (Figure 8.2), varied considerably throughout the years studied. The disease pressure developed to extreme levels due to high foliar disease levels in eight untreated and Irish Rules plots with susceptible varieties (King Edward and British Queen), in all years except in 2018 when the highest mean foliar disease level was 25 %. 2016 and 2017 were similar to average blight years in Ireland, while 2018 late blight season was impeded in June and the first half of July, due to uncharacteristically high temperatures and lack of rainfall (Figure 8.1). A severe blight epidemic prevailed in 2019, due to extremely blight conducive weather conditions throughout, and especially in the latter half of August. The first detections of PLB in the trial site were on 25 July 2016, 3 July 2017, 26 July 2019, which was in accordance with the 25-year average (Dowley *et al.*, 2008), with the exception of the extraordinarily dry 2018, when the disease was not observed until 20 August 2018. Epidemics in untreated control plots of the highly resistant potato varieties, T5821/11 and Sarpo Mira, started later and developed very slowly reaching from 0 to 0.5 and 5% disease foliage on T5821/11 and Sarpo Mira, respectively.

4.5.2. *Fungicide applications*

The number of fungicide applications and the proportion of the total label dose for all years of the trial and the overall averages for 2017-2019, due to the missing levels in 2016, are presented in Figure 4.2. Over the four-year period of the experiment, the average number of fungicide applications was 9.3 for the fixed 7-day programmes, with 8 applications in all years except in 2017 with 12 applications; while the DSS programmes varied from 1 to 9.3. The IRp received an average of 1 application and 9.7% of the total dose applied in the full dose programme. The BMp did not provide any reductions in the number of applications, while the average total dose ranged from 87.5% to 43.6%, with a three-year average of 79.2%. The MIRp received an average of 8.7 fungicide applications and an average total dose of 41.3% of the full programme applied.

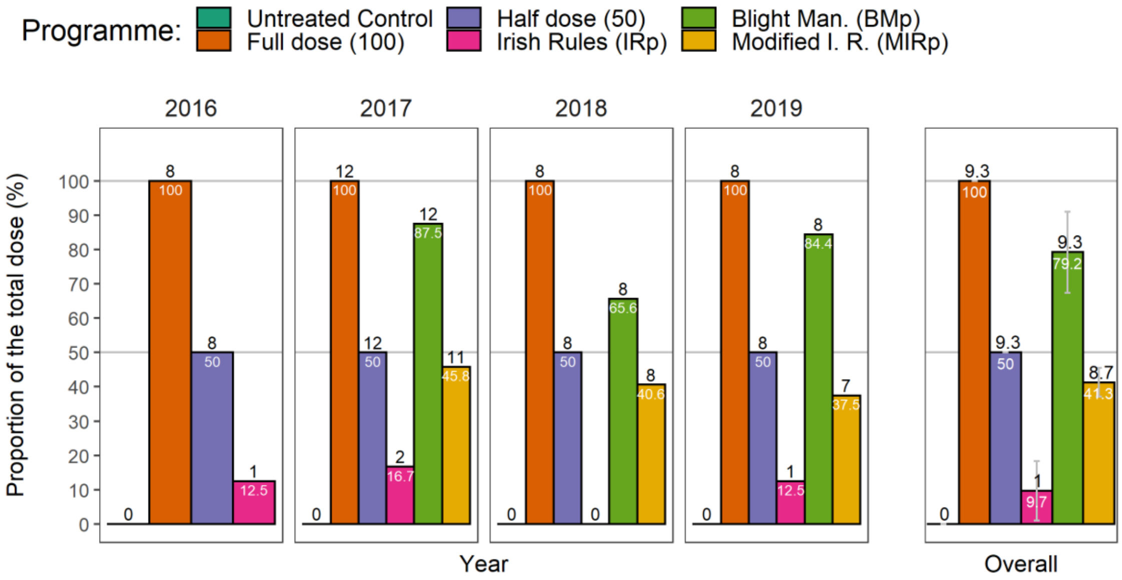


Figure 4.2 The proportion of the total label dose and the number of pesticide applications recommended per year by the fixed and varying dose programmes. Facets marked with the year on top represent summaries for individual years while the last facet represents the overall averages and variance per programme. In the facets for the individual years, the height of the bars represents the proportion of the dose applied per model compared to the total dose (number of applications x 100%), while the numbers at the top of the bars represent the total number of applications recommended by the model in each year. The overall summary (facet on the far right) includes years 2017 - 2019 because of the missing levels in 2016, where the height of the bar represents the mean dose reduction, the error bars represent the standard deviation and the number above the bar is the mean number of applications during the year.

4.5.3. *Disease control and the impact on the yield*

The higher order interactions were significant, between fungicide programme and variety in 2016 ($p < 0.001$ and $p = 0.004$, for the foliage disease and yield, respectively); and year, fungicide programme and variety in the remaining years ($p = 0.0014$ and $p < 0.001$, for the foliage disease and yield, respectively). Observed values, the estimated means and confidence intervals of each treatment combination ($\alpha = 0.05$) showing the variation of the foliage disease and the yield in relation to fungicide programme and variety in different years are presented in Figure 4.3.

The performance of fungicide programmes followed a similar trend across the studied period (Figure 4.2 a). Foliar disease levels were highest in the IRp, while half dose, MIRp and BMp were similar to the standard growers' practice for the susceptible and moderately resistant varieties. The yield levels followed a similar pattern, except in the low-disease, warm and dry 2018, when there was no difference between the programmes. In the other seasons, the differences were significant only for the susceptible varieties. No differences between fungicide programmes were identified between the resistant varieties T5821/11 and Sarpo Mira in terms of either foliar disease control or yield between irrespective of fungicide programme or year.

A single fungicide application recommended by the IR at the beginning of the season in 2016 provided a significant reduction in foliar disease levels compared to the untreated control but was not comparable to the levels of protection provided by the other programmes. However, this was not reflected in yield, and the IRp was not significantly different from the untreated control. In the case of the prolonged epidemic experienced in 2017, the two fungicide applications recommended by the IRp were not sufficient to provide significantly different levels of disease control compared to the untreated controls of susceptible and moderately susceptible varieties. The same effect was observed in terms of yield, except for the medium resistant Setanta. Due to late disease onset and slow epidemics in 2018, the overall rAUDPC was low and the season finished with low disease levels. There was no significant difference between IRp and untreated control for susceptible varieties, B. Queen, K. Edward and Rooster and between the remaining levels of factors. Warm and dry weather conditions caused the final yield to be lower than the historical average. Lower foliar disease control achieved by IRp and untreated control did not significantly reflect on the yield, which was not significantly different between the fungicide programmes.

The environmental conditions were favourable for blight development in 2019 (Figure 8.1). The rAUDPC values were the highest, compared to the other years the trials were conducted. Disease control by IRp was not significantly different from the untreated control for B. Queen and K. Edward. ‘Related’ models MIRp and IRp recommended a full dose fungicide programme on 15 August, prior to the onset of severe blight weather (Table 8.4). This led to a significant reduction of the disease levels on Rooster and Setanta compared to the untreated control but still higher than all other programmes. Similar to 2016, the disease control by the IRp on Roster and Setanta was significantly reduced compared to the untreated control, although it was still higher than the rest of the fungicide programmes.

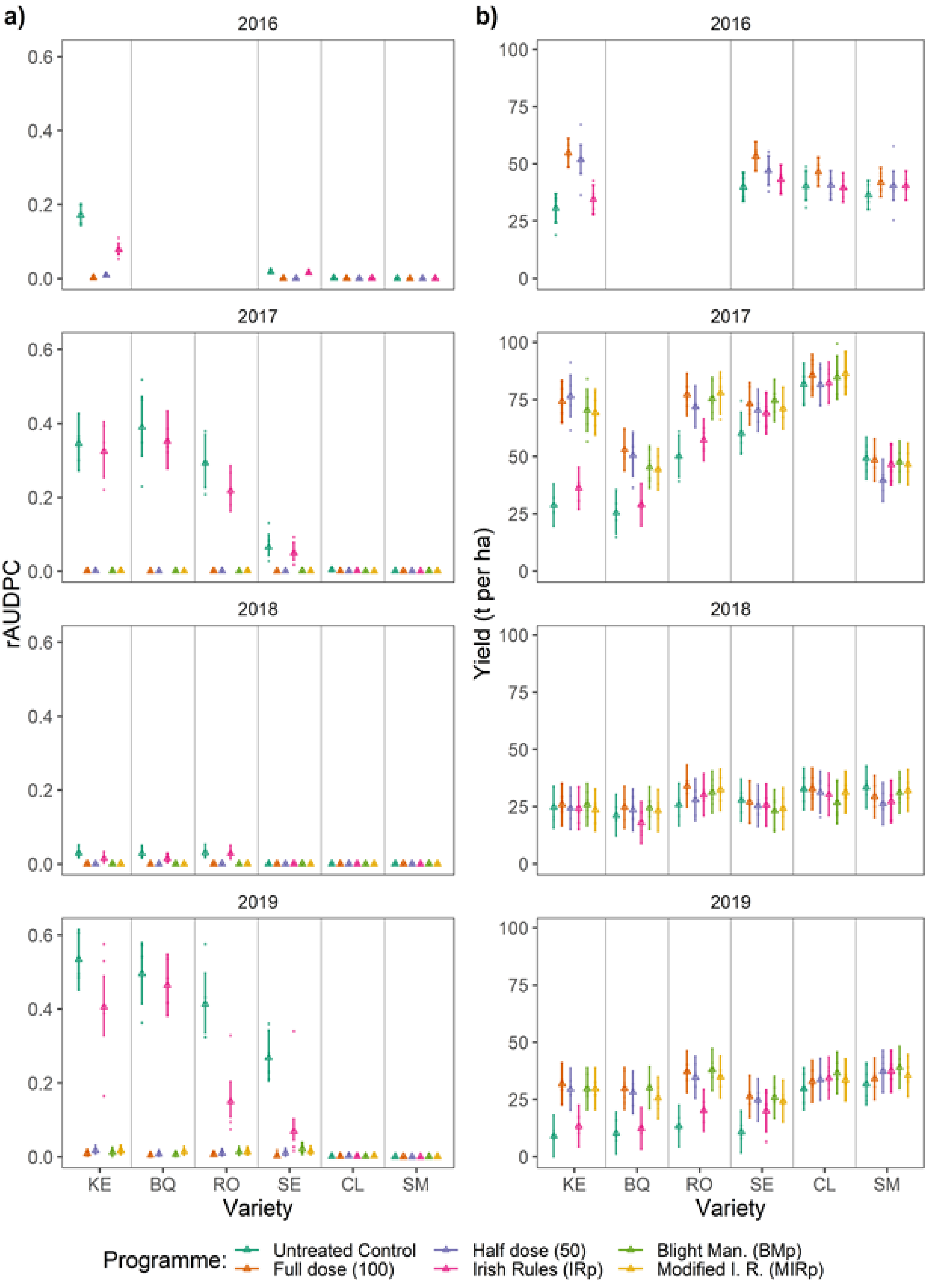


Figure 4.3 The estimated marginal means and 95% confidence intervals of the three-way interactions between year, variety and fungicide programme for models fitted to: a) the disease and b) the yield data. Observed values are presented as dots. The colour-coding is according to the fungicide programme. For both, the disease and yield data, separate models were fitted, one to the 2016 data set, due to the lack of two fungicide programmes and varieties, and the second one to 2017-2019 data set. Varieties are presented as discrete values on the x-axis with increasing level of resistance from (left to right): King Edward (KE), British Queen (BQ), Rooster (RO), Setanta (SE), the clone from Teagasc breeding programme T5821/11 (CL) and Sarpo Mira (SM).

4.5.4. *Population structure and selection patterns between fungicide programme, variety and year*

A total of 1287 single lesions were successfully genotyped and used to characterise the response of the local population, fungicide programme and potato variety during period 2016-2019. The population remains simple and all samples were associated with previously identified MLGs 8A1, 6A1 and 13A2, with the exception of a single isolate from 2019, associated to EU_36_A2 (36A2) MLG (Figure 4.4) This is the first report of the 36A2 MLG in the Republic of Ireland. Due to low frequency of 36A2, this isolate was was not considered in further analysis.

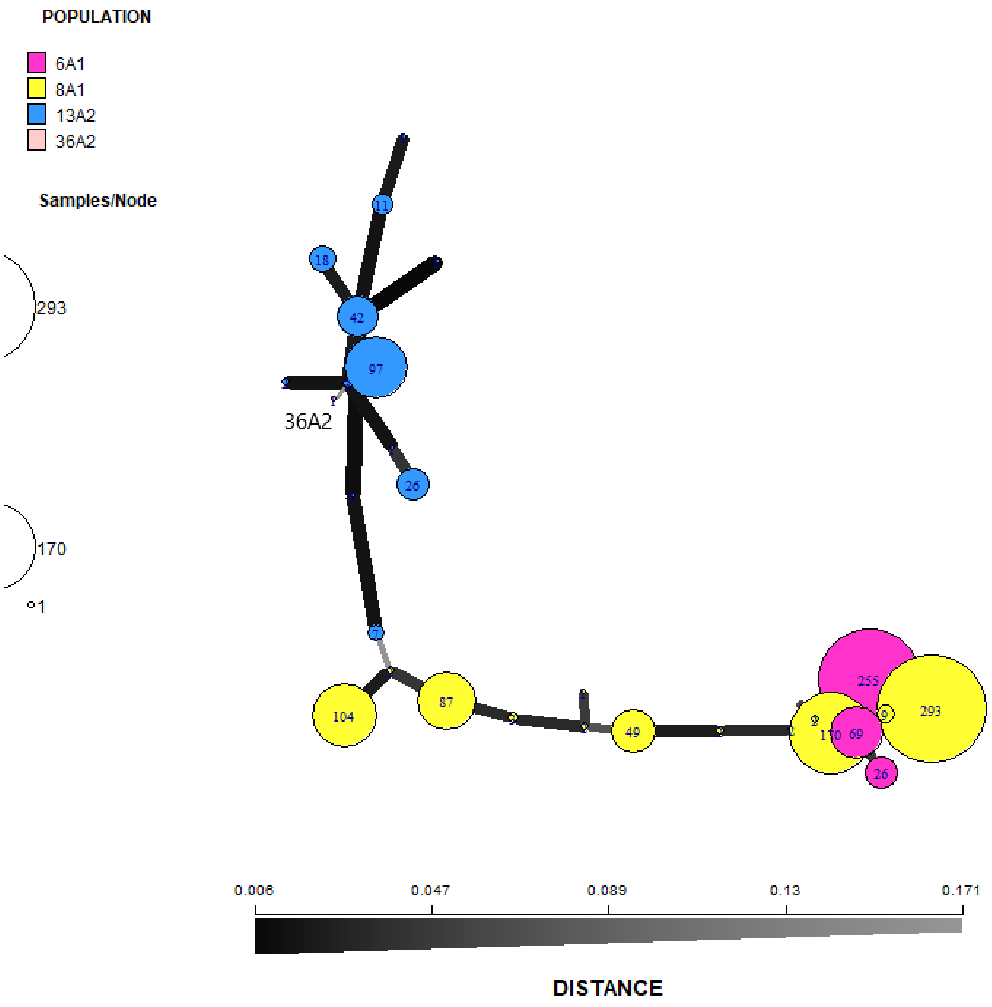


Figure 4.4 Minimum spanning networks (MSN) for *Phytophthora infestans* isolates collected at the field trial at Oak Park, 2016-2019. The allelic variation between *Phytophthora infestans* field samples was estimated using standardized multiplex short sequence repeat (SSR) marker assay. Each node represents grouping and the node sizes are proportional to the number of the isolates. Genetic similarity between MLGs is indicated with shared nodes, while Bruvo genetic distance determines the thickness of the node connectors

With the exception of the resistant variety Sarpo Mira, large collections of *P. infestans* were established from the different varieties (Figure 4.5). 13A2 was found at greater frequencies on varieties with increased foliar resistance levels. Conversely, 8A1 was found more frequently on the susceptible cultivars and in similar frequencies (67.3, 64.9, 66.2, on K. Edward, B, Queen and Roster, respectively).

The corresponding DAPC analysis of the data confirmed the differentiation indicated by the frequency distributions of the clonal MLGs per variety. While clusters of varieties were overlapping, varieties with increasing levels of resistance were further from the complete overlap of the three susceptible varieties, indicative of the population shift obvious in the frequency charts. Both the frequency charts and the corresponding DAPC analysis for fungicide treatments suggest limited if any impacts of the different fungicide programmes on the population structure. Frequencies of the clonal MLGs varied over the years of the study, with the most obvious difference observed in dry and warm 2018, when 90.3% of samples belonged to 8A1 genotype. DAPC indicated differences between the annual populations, showing the shift of the population in 2018, after which the population from 2019 remained in the same cluster.

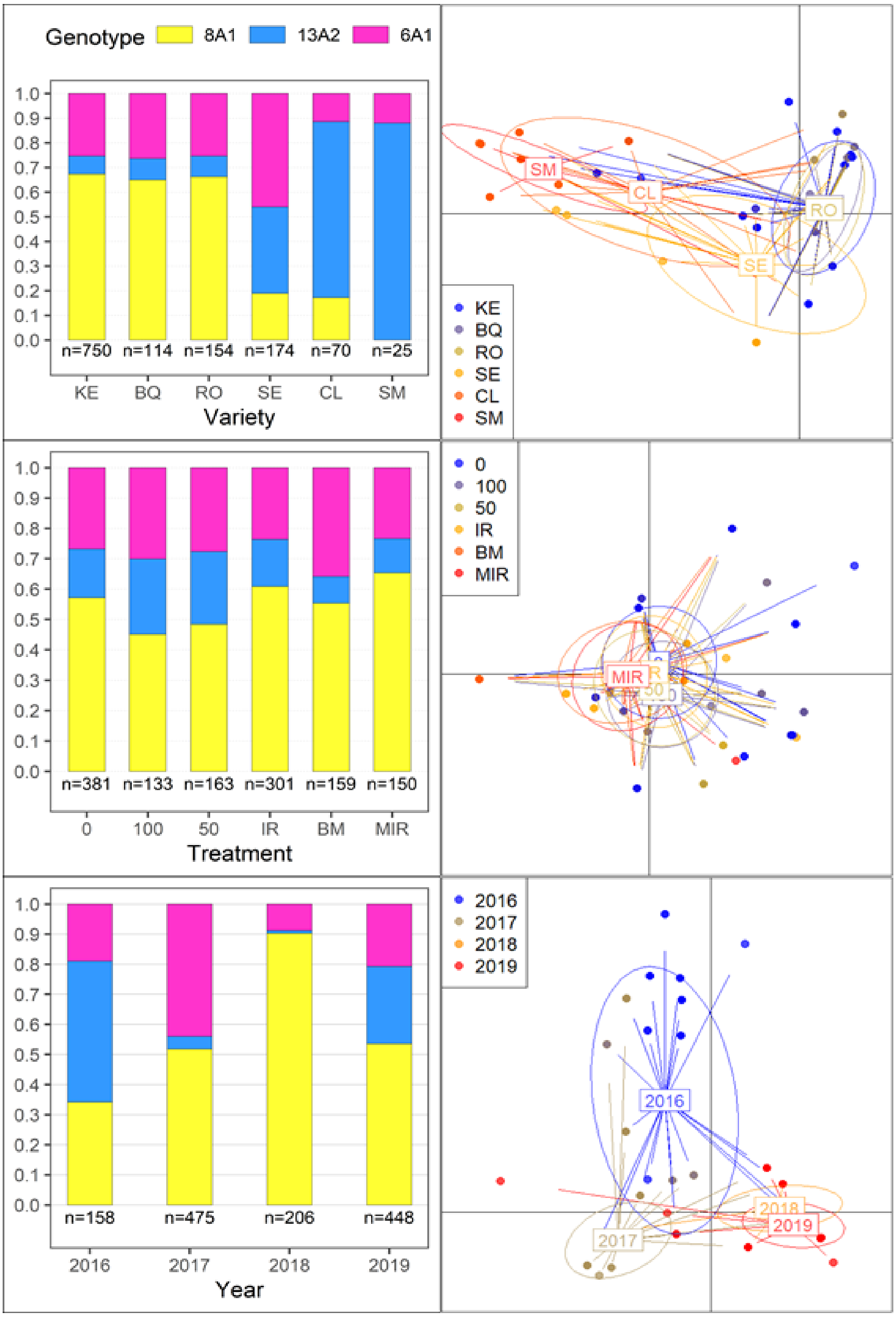


Figure 4.5 Relative frequencies (the bar charts on the left) and discriminant analysis of principal components (DAPC) (right) of *P. infestans* populations sampled at the field trial at Oak Park, 2016-2019. Samples were pooled per variety (top row), fungicide programme (middle row) and year (bottom row), disregarding the sampling date. Varieties are presented as discrete values on the x-axis with increasing level of resistance from (left to right) (upper left chart) and labels (upper right DAPC scatterplot): King Edward (KE), British Queen (BQ), Rooster (RO), Setanta (SE), the clone from Teagasc breeding programme T5821/11 (CL) and Sarpo Mira (SM). Programmes are presented as discrete values on the x axis: Untreated control (0), half dose (50), full dose (100), Irish Rules (IR), Blight management (BM) and Modified Irish Rules (MIR).

4.5.5. *In-season temporal variation of population structure*

A total of seven, four and two individual samplings were implemented in 2017, 2018 and 2019, respectively. An apparent temporal population shift is observed in all years of the study, with the founder population consisted of the old clonal lineage 8A1, being replaced with newer strains (6A1 and 13A2) as the epidemics progressed (Figure 4.6). In the final sampling in 2017 and 2019, 87.2% and 80% of all samples and 92.3 and 64% of the subset samples belonged to 6A1 and 13A2. This shift was not as expressed in 2018 when frequencies of 6A1 and 13A2 remained at a low level (11.5 and 17.2 for full and the subset of data, respectively. However, the population structure at that stage of the epidemics (approx. 25% in control plots with susceptible varieties) in 2018 is directly comparable to the similar level of epidemics in 2017 and 2019 when the same level of the foliar disease occurred at an earlier date.

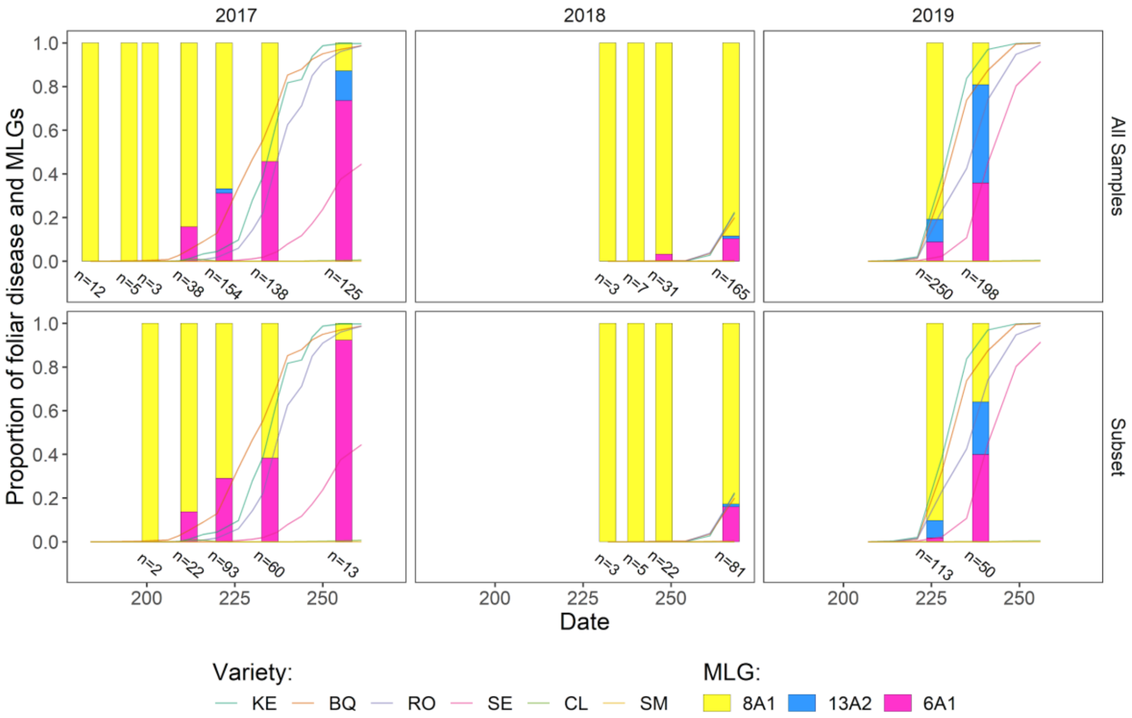


Figure 4.6 In-season temporal variation of *P. infestans* population structure and the potato late blight disease progress 2017-2019 in the field trial at Oak Park. Bars represent the proportion of samples belonging to specific clonal maximum locus genotype (MLG) per sampling. Horizontal rows of facets represent MLG frequencies in the entire collection (upper row) and the subset samples collected from plots with unimpeded disease development (lower row). The number of samples per sampling date is presented below bars. Lines represent the mean disease progress in control plots.

4.6. Discussion

The results of an interdisciplinary study assessing possibilities for the integration of economically and environmentally friendly strategies in standard potato late blight management practices to control potato late blight, a notorious plant disease, under Irish conditions are presented. Currently, potato production is completely reliant on the prophylactic use of pesticides, and potato producers are facing the challenge to reduce pesticide inputs for controlling the disease. This is largely through legislative demands, namely, the European Community Directive 128/2009 on the Sustainable Use of Pesticides (European Commission, 2009, 2009), as well as increased demands by the supermarket chains to reduce the use of pesticides for crop disease control (Rossi *et al.*, 2012). It has been shown here that the subtle modification of the standard grower's potato late blight management practice can lead to reduced usage of chemicals to control the disease. In addition, the response of the pathogen population to treatments was monitored, to understand possible implications on the decision making in disease management. Our findings indicate that although the Irish population of *P. infestans* remains simple, frequency of virulent strains matching the host resistance is increased in latter parts of the potato growing season. Publicly available DSS can be used to preserve the durability of varietal resistance and prevent selection patterns under conditions of high disease pressure, since the MIR successfully indicated periods of severe disease pressure.

All three forecasting schemes provided significant reductions in fungicide usage compared to the full label fungicide dose programme considered as the standard grower's practice. Both the IRp and the MIRp also required lower inputs than the half dose programmes, while BMp required a mean total dose of 79.2%. The higher mean fungicide usage required by the BMp may in part be due to a limited implementation of the Blight Management DSS. The limitations were as follows: only model A (for susceptible varieties) was used due to our experimental design constraints; later planting dates causing dose correction to be based mostly on the high infection pressure tiers of the model dose correction and pre-defined fungicide programme was not altered to accommodate the curative treatments recemented by the system. The dose correction was employed due to the split-plot design constraints, as each main plot received the same fungicide treatment. Most importantly for Irish potato cultivation, the IRp failed to provide acceptable levels of foliar disease control on varieties with lower and medium levels of blight resistance, which constitute the majority of the Irish potato production. However, levels of control achieved by both the BMp and the MIRp were not different from either the half dose or full dose fungicide programme. Interestingly, there was also no significant difference between the half dose and full dose programmes in terms of disease control, even on the most susceptible varieties in the trial.

Disease control and the yield achieved across fungicide programmes were not different for the resistant varieties included in trials. For the two most resistant varieties, disease levels remained low across the years, with epidemic onset only late in the season. These epidemics were likely initiated due to the high disease pressure, an inflow of the aggressive strains and the maturity induced reduction of the polygenetic resistance (Fry *et al.*, 1986). This scenario is especially dangerous when the environmental conditions are very conducive, as occurred in 2019, if the resistant varieties are not protected. PLB is a classic example of a polycyclic disease with a pronounced exponential phase (Van der Plank, 1963) and rapid disease cycles which could lead to resistance breakdown and act as a primary inoculum pool for surrounding potato fields, under conducive conditions. Both the IRp and the MIRp have indicated such periods in August 2019 and recommended full label dose fungicide application, indicating that the algorithm is suitable for the PLB prediction in the Irish ecosystem.

Crop disease risk prediction models are routinely developed and calibrated using the historical weather data, without evaluating the uncertainty introduced by employing the forecasted weather data (Magarey *et al.*, 2017). Crop disease DSSs that utilize real short-term weather forecasts created by operational numerical weather prediction models are not very common (Caffi *et al.*, 2011; Fernandes *et al.*, 2011). Surprisingly, results shown here indicate that the use of a 7-day weather forecast with high temporal resolution resulted in a reliable risk prediction. This could perhaps be explained by the simplicity of the models employed in the study, which do not require very precise predictions beyond the developmental thresholds. An empirical approach is often applied for the development of territorial models operated on the mesoscale, while the field models operating on the microscale are frequently based on more fundamental (mechanistic) approach (Gommes *et al.*, 2010). It appears that the simpler models representing a combination of the two, such as the IR (and MIR), are currently a good compromise when employed ‘between scales' using the extended short-range weather forecast, up to seven days. This indicates that the reliability of using weather forecast data in disease risk prediction is significantly improved. Due to technical and experimental constraints, we did not include possible adaptable treatment windows, i.e. 5-10 days, as proposed in Cucak *et al.* (2019), which seems to be a realistic possibility based on the current findings. These results are encouraging considering constant improvements and the increasing spatial resolution of weather forecasts. High-risk diseases on valuable crop require frequent interventions throughout the season (Pethybridge *et al.*, 2009) and the risk estimation is based on short-range forecasted weather, which could potentially alleviate the need for expensive on-site stations.

One of the key inputs for effective management of potato late blight disease is information regarding the population dynamics and structure of the causal agent *P. infestans* (Fry *et al.*, 2013). Similar to previous reports by Kildea *et al.* (2010) and Stellingwerf *et al.* (2018), SSR analysis indicated that the genetic composition of the *P. infestans* population remained relatively simple with only three major clonal lineages found in all years (13A2, 6A1 and 8A1). None of the strains belonging to 5A1 genotype was found, which have been previously detected by Stellingwerf *et al.* (2018). The older clonal lineage 8A1 is being displaced by newer strains with increased levels of aggressiveness (e.g. 13A2, 6A1) in Northwest Europe (Cooke *et al.*, 2012; Mariette *et al.*, 2016). The 'always more aggressive' hypothesis is often advocated to explain such clonal lineage replacements in *P. infestans* populations (Day *et al.*, 1997; Cooke *et al.*, 2012). Conversely, findings of this study are in agreement with previous reports and the 8A1 still remains a dominant lineage in Ireland (e.g. Cooke *et al.*, 2014; Kildea *et al.*, 2010), which appears to be well accommodated to the Irish climatic conditions.

Observed selection patterns related to varieties with increased blight resistance levels are in agreement with those from Stellingwerf *et al.* (2018), indicating that more resistant varieties are selecting more aggressive strains. This is especially pronounced in the case of Sarpo Mira and 13A2. Highly resistant, Sarpo Mira contains multiple R genes (Rietman *et al.*, 2012). Hobby and organic growers mostly rely on resistant varieties, with Sarpo Mira being one of the popular choices in Ireland. Due to low input crop protection by these groups and a high potential for selecting fittest strains is leading to a risk increase as the season progresses (Fry, 2008). However, Stellingwerf *et al.* (2018) have also reported selection patterns between the susceptible varieties Desire and King Edward. Contrary to their findings, such pattern was not observed between the three susceptible varieties included in our trials, King Edward, British Queens and Rooster, of which the last two constitute over two-thirds of the conventional Irish potato production (Anonymous, 2011). It was also confirmed that there was no selection pressure caused by the use of reduced dosages across fungicide programmes.

Whilst the findings regarding the monitoring of the temporal structure of the pathogen population originate from the field trials, which may not be representative of typical potato production systems in which will often be a single variety and high levels of disease are avoided, clear patterns of selection were observed. Firstly, the epidemics were exclusively initiated by the 8A1, and secondly, its frequency reduced in favour of the 13A2 and 6A1 genotypes as the epidemic progresses, with the rate of change depending on the rate of disease progression. Such findings may be explained by trade-offs between pathogenicity (within-season fitness) or survival (between-season fitness) shaping the invasive potential of lineages (Andrivon *et al.*, 2013). Higher aggressiveness (e.g. short latency period, high spore production, high lesion growth rate) provide a comparative advantage at the beginning and, consequently, during epidemics (Montarry *et al.*, 2007) but may reduce asexual transmission between seasons (Andrivon *et al.*, 2007). Highly aggressive isolates on the foliage could decrease the number and size of daughter tubers, which will be severely infected and rot in soil, limiting the overwintering inoculum pool thus reducing the number of volunteer plants (Andrivon *et al.*, 2007; Flier *et al.*, 1998).

Pathogenicity trade-off in combination with the overall weather conditions between and at the beginning of the potato growing seasons dictate the composition and amount of the initial inoculum pool. For example, the cold winter 2017/18 and a period of dry and uncharacteristically warm weather in the spring of 2018 led to a significant reduction of the pathogen survival, delay in disease onset and ultimately, 'mild' epidemics for Irish conditions. Even after the dry period ended and the typical wet Irish weather conditions began in the second half of July - the first infections were not observed until 20 August due to severe reductions of the pathogen inoculum availability. The disease levels and the final proportion of fitter strains remained at a low level of 9.7% at the end of the season. Conversely, the weather conditions prior to and especially during August of 2019 allowed uninterrupted and continuous disease cycles which led to an exponential increase in the size of the pathogen population, and most importantly those aggressive strains, resulting in a severe blight epidemic. This, in turn, affected all of the disease control programmes, even the full dose standard growers practice programme.

Integrated and multifaceted strategies have the best chance for successful and environmentally friendly management of late blight (Fry *et al.*, 2013). Incorporation of information regarding the pathogen population and recognising and understanding pathosystem patterns in the ecosystem of interest is crucial in order to incorporate environmental risk prediction into disease management advice. It is expected that the availability of big data technologies, easier data collection and the transfer will result in improved DSSs (Andrivon, 2018). The direct integration of this information into risk prediction models is still under development. Hence, each model output should go through a human filter before being turned into a practical advice (Rossi *et al.*, 2012) and the inherently complex provision of pest risk forecasts clearly requires a collaborative, multidisciplinary approach involving researchers with expertise in pest biology, crop management, meteorology, and information technology (Magarey *et al.*, 2017). Building an infrastructure to support the environmental disease risk prediction would lead towards sustainable IPM, such as a functional spore sampling network (Fall *et al.*, 2015) and rapid pathogen molecular characterisation (Fry *et al.*, 2013) and interactive reporting of disease outbreaks (Anonymous, 2019).

A key challenge for research is to evaluate and propose economically and environmentally friendly and yet still effective strategies to control the PLB. This study combines major tools in the hands of a modern phytopathologist enabling one to start moving towards the IPM; from a classical field evaluation built on the basis of extensive epidemiological evaluation of an environmental disease risk prediction model, supplemented with the use of molecular methods to determine the full scope of possible benefits or repercussions of their use. Additionally, the analysis is highly reproducible, providing a prime example of an integrated approach in plant pathology experimentation, enabling the extensive and accessible review and possible improvement of the implemented work using a single open-access computing platform, the R language. Such resources are lacking in the field of plant pathology and are as important for a new plant pathologist entering the field, as well as for the experienced ones.

5. Rethinking crop disease risk modelling: BlightR, a new potato late blight forecasting model

This chapter is due for submision:

Cucak, M., Esker, P., Kildea, S., Downes, P., Fealy, R. (2020) Rethinking crop disease risk modelling: BlightR, a new potato late blight forecasting model.

The initial refinement and field evaluation of IR brought significant improvement of the model performance but also pointed out its core deficiencies which limit further improvements of the model's operational capabilities. Over the duration of this research, new disease outbreak data became available and information regarding the temporal shift in the pathogen population structure (outlined in Chapter 4). For these reasons, it was necessary to develop a more comprehensive model which could facilitate more detailed risk estimation, calibrated to the level of *P. infestans* genotype.

Additionally, the motivation behind this research was to establish a precedent in the way crop disease risk prediction models are developed, evaluated and validated. The approach applied here allows easier and more accessible peer review; improve credibility and reproducibility of research; enable validation and re-calibration over time in the ecosystem it is intended for as well as its easy transfer to any intended ecosystem.

5.1. Abstract

Crop production systems are threatened by numerous pathogens endangering sustainable food production. Decision support systems have often been developed to tailor crop disease management programmes. However, their use remains limited due to several issues regarding their development, application, evaluation and re-calibration. Here, a new potato late blight risk prediction model is proposed, aimed to tackle these issues. This research is aimed to help steer the future of crop disease risk prediction models

towards more reproducible and transferable resources, providing opportunities for global transferability. The model pathosystem is potato late blight, the devastating disease of potato and tomato. The model retains the simplicity required to reach a compromise between uncertainties introduced with modelling assumptions regarding *Phytophthora infestans* lifecycle and those entailed with the numerical weather prediction. The proposed model was developed, evaluated and calibrated for the use under a highly conducive environment in the Republic of Ireland using recent disease observations and weather data. Additionally, the proposed model was compared with the currently used model, the Irish Rules, in terms of diagnostic performance and accuracy using forecasted weather data as model inputs. Accessibility and reproducibility of the model and approach enables prompt re-calibration of the model to respond to frequent shifts of the *P. infestans* population, resulting in occurrence and establishment of clonal lineages active over different environmental conditions. The results indicate that the proposed model can safely extend current 7-day standard grower practice fungicide application intervals up to 11-days. Resources such as this should help reduce ever-increasing trend of reliance on the prophylactic use of fungicides to control the potato late blight, as well as empower the development and application of IPM approaches in cropping systems globally.

5.2. Introduction

Crop production systems are threatened by numerous pathogens (Fisher *et al.*, 2012) which have the potential to cause severe epidemics and lead to interruptions of food supply chains (Chakraborty *et al.*, 2011). Population factors (such as the emergence of new strains), environmental influences (such as weather and climate impacts on inter- and intra- season pathogen population), and disease management intervention-driven pathosystem interactions (such as crop breeding and pesticide-driven population selection) are important factors in disease risk mitigation (Newlands, 2016). These are likely to be further complicated by changes in climate which could have profound effects on future plant disease dynamics (Garrett *et al.*, 2011; Pautasso *et al.*, 2012; Savary *et al.*, 2011) and the evolution of pesticide resistance, as well as virulence matching host resistance, all of which require an increasing need to manage, and mitigate the impacts of pests. As a consequence, integrated pest management (IPM) is facing numerous challenges (Lamichhane *et al.*, 2016). Trans-national networking can help overcome some of the increasing internal IPM challenges, including decreasing trends in budget allocation, scarcity of expertise, inter- and intra- country communication gaps and the lack of inter- and trans- disciplinary IPM research (Lamichhane *et al.*, 2016). In relation to plant pathology, and more specifically crop disease forecasting, problems such as a lack of generalised encyclopaedia-like generic models, and their implementation and accessibility, are limiting cooperation pathways and the development of the discipline (Magarey *et al.*, 2007; Bregaglio *et al.*, 2012).

Potato late blight (PLB), caused by *Phytophthora infestans,* is the cause of major crop losses in potato and tomato production globally (Savary *et al.*, 2017). An integrated approach to PLB control encompasses the reduction of primary inoculum sources (e.g. dumps and volunteers and seed hygiene) and cultivation of PLB resistant varieties (Schepers *et al.*, 2009). Efforts to breed varieties resistant to PLB have been hampered, due to market-driven demand for more well known, traditional varieties which tend to have low blight resistance levels. In parallel, the *P. infestans* population has undergone significant changes since the 1980s leading to the rise of strains with higher levels of aggressiveness worldwide (Fry *et al.*, 2015) and in Ireland (Cooke, 2015; Kildea *et al.*, 2010). Hence, chemical protection, which represents a substantial cost burden for growers, is often applied preventively, based on perceived, rather than actual, risk (Carisse *et al.*, 2009); in the case of PLB, chemical protection is applied at a constant 5 to 7-day calendar-based interval due to a zero-tolerance management approach to this disease (Cooke *et al.*, 2011; Kirk *et al.*, 2001). Such a high pesticide input approach, besides being costly, leads to selection pressure and the emergence of more pesticide tolerant strains (Chen, 2007; Nielsen, 2014; Schepers *et al.*, 2018) and is associated with detrimental environmental and human health impacts (Newlands, 2016).

The use of mathematical models to understand plant disease epidemics in order to inform their management has a relatively long history (e.g. van der Plank, 1968). In general, crop disease prediction models can be divided into empirical, often applied for creating territorial models, and mechanistic (fundamental), often employed for field-based approaches (Gommes *et al.*, 2010). While this is a general division, many of the models lie between these two ends of the continuum (Madden *et al.*, 1988a). Numerous risk prediction models have been developed to aid practical day-to-day PLB management decisions. While mechanistic models simulating the entire life cycle of the pathogen have been developed since the 1960s (i.e. Andrade-Piedra *et al.*, 2005; Michaelides, 1991; Skelsey *et al.*, 2009; Van Oijen, 1991; Waggoner, 1968), their use in practical PLB disease management remains low due to uncertainty caused by the numerous assumptions regarding the pathogen biology and complexities involved in their integration into Decision Support Systems (DSS) (Harrison, 1992a). Early models employed in the PLB DSSs were mostly of a qualitative empirical nature, based on simple threshold rules (e.g. Försund *et al.*, 1958; Hyre *et al.*, 1955; Smith, 1956; Van Everdingen, 1926; Wallin, 1962). Over time, models have integrated mechanistic features, describing the suitability of environmental conditions in a more realistic, quantitative manner (Bourke, 1970). Such models were developed using statistical relationships which described the relationship between the weather and disease development from field trials (e.g. the Negative Prognosis (Schrödter and Ullrich, 1967) or reported disease outbreaks and theoretical knowledge (e.g. Irish Rules (Bourke, 1953a); Simphyt I (Kluge and Gutsche, 1990) and MILSOL (Ladeveze, 1988)). Contemporary PLB risk prediction models are mainly based on a matrix-type accumulation of risk values within crudely defined threshold criteria for disease outbreaks. The descriptions of a number of models are available at the UC Davis website (http://ipm.ucanr.edu/DISEASE/DATABASE/potatolateblight.html) and those currently used in Europe can be found on the EuroBlight website (Hansen *et al.*, 2017).

Phytophthora infestans populations have been continuously evolving since the 1980s, with unique clonal lineages arising with differences in pathogen fitness and pathogenicity, potentially impacting epidemiology of the disease (Cooke *et al.*, 2011; Fry *et al.*, 2015). Isolates with clonal lineage, or asexual descendants of a single genotype, share the same genotypic (e.g. mating type and SSR profile) and similar phenotypic characteristics (e.g. fungicide sensitivity) which are routinely evaluated and reported (Fry, 2008). Other epidemiologically important phenotypic characteristics, such as sporulation or infection, have been less frequently quantitatively explored in the past. While genotypic differences have been studied using simulation models (Andrade-Piedra *et al.*, 2005; Andrade-Piedra *et al.*, 2005; Seidl Johnson *et al.*, 2015), they have not been employed for the purpose of practical disease forecasting. Recent efforts to monitor *P. infestans* population, and quantify the pathogenicity traits of current genotypes (e.g. Andrivon *et al.*, 2017) will inevitably lead to some extension of their practical application into PLB disease forecasting systems. However, empirical and crude threshold-based models currently employed cannot readily accommodate the integration of such information in practical risk prediction models.

In the past, a lack of technical ability has led, by necessity, to numerous compromises and over-simplifications being required in PLB risk estimation modelling. An increasing knowledge about the pathogen population and phenotypic traits of the dominant pathogen lineages, as well as the accessibility and quality of observed and forecasted weather data and accessibility of high-speed computing, requires a re-evaluation of some of these simplifications. In doing so it may increase the accuracy, flexibility and usability of risk prediction in PLB management decision making. Hence, the objective of this study was to develop a simple PLB model, representing an optimum compromise between pathogen biology interpretation and the constraints associated with the practical application of models to improve the reliability of the DSS for PLB. The proposed model, intended for use in a high risk ecosystem, is evaluated under Irish conditions and outputs are compared with the simpler, threshold-based, IR model, currently used operationally in Ireland. Additionally, a structured, comprehensive, reproducible and open access of the model implementation and evaluation methodology, using observed and forecasted weather data and disease outbreak information, is provided as means to accommodate further community-based model development, refinement and applications across different ecosystems.

5.3. Methods

A schematic overview of the study is presented in Figure 5.1. The model development framework employed here is based on what Magarey and Sutton (2007) defined as the most important factors (and common obstacles) in the development of reliable pest risk prediction models: environmental inputs, model construction and parameterization, validation, and implementation. Initially, a background to the modelling approach is provided, followed by a description of the sub-components and the subsequent calculation of the risk. Model subcomponents can be switched on, depending on data availability, resulting in a number of model variants. The proposed model variants were compared with the current IR model and assessed using the ratio of model sensitivity and its economic value for a number of decision thresholds. The uncertainty of the risk predictions with a ten-day lead time were also evaluated using forecasted weather data.

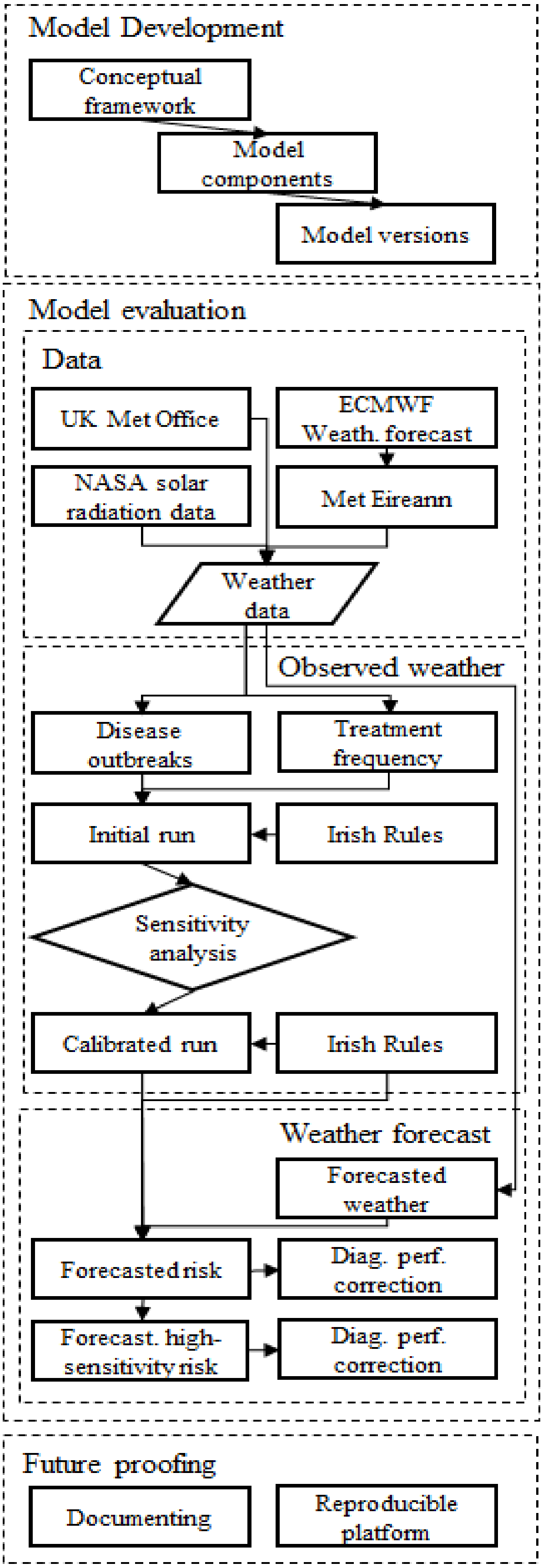


Figure 5.1 Simplified presentation of major steps undertaken in this research (Diag. perf. =diagnostic performance).

5.3.1. *Model development*

Conceptual framework

The model outlined here, which was developed to be applied at the synoptic scale, was built on well-known and accepted scientific knowledge regarding the environmental conditions influencing the life cycle of *P. infestans*. Explosive PLB epidemics are driven by environmental conditions and a high reproduction rate of the pathogen. Extended periods of humid weather with mild temperatures are known as blight favourable weather conditions and have been widely employed in blight forecasting since the initial development of models (Fry, 1982); here, a refinement of this approach is proposed. However, compromises are still inevitable when deploying synoptic models, as certain aspects of the life cycle are omitted due to the existing gap between the scale of development of pests and diseases (e.g. micrometeorological scale, canopy layer) and the representative reference scales of available weather information. For example, sporangia are released due to a rapid drop in relative humidity resulting in the break-up of the sporangiophores; this usually occurs in the morning (Fry *et al.*, 2012). It is considered that, due to the high spatial variability associated with relative humidity, such precision could not be expected for the intended synoptic scale application of the model.

The Irish Rules (IR) (Bourke, 1953) is a PLB forecasting model developed in the 1950s and has remained largely unchanged since then. The IR was revolutionary at the time, as it was the first PLB quantitative model that mimics the life cycle of the pathogen using a set of empirical threshold-based processes. Cucak *et al.* (2019) previously described and evaluated the model in detail and suggested simple modifications to parameter and decision thresholds. This modified version of the IR (hereafter MIR) exhibited a certain loss of specificity but resulted in a significant improvement in model accuracy. However, this work clearly highlighted the need to transition from a threshold-based binary estimation of stages of host-parasite interaction to a more biologically realistic one, based on a functional relationship between pathogen and its environment. For example, Cucak *et al.* (2019) highlighted the disadvantages of employing a crude threshold-based approach for risk estimation; indicative with regards to the temperature threshold, employed as a single lower limit estimator for all life stages of the pathogen. While it was clear that pathogen activity was low at the existing model threshold value of 10 °C, Cucak *et al.* (2019) did not advise increasing the temperature threshold due to zero risk PLB tolerance, even though it was clear that pathogen activity was low at the existing model threshold value of 10 °C.

In our approach to infection modelling, an attempt was made to upgrade the current IR model towards a more fundamental approach (Madden *et al.*, 1988a; Magarey *et al.*, 2007) or one which mimics the nature of the biological system under investigation. For example, temperature-moisture response functions for estimating sporulation and infection conditions as an adaptation of a widely used method proposed by Duthie (1997) and Magarey *et al.* (2005b) were implemented, as they are based on biologically meaningful parameters.

Although numerous crop disease risk prediction models are based solely on the estimation of the infection conditions, it is of value to include additional stages of the life cycle, such as the pathogen inoculum availability (Magarey *et al.*, 2007) or pathogen survival (e.g. Skelsey *et al.*, 2007). Sporangia are structures enabling the spread of the disease aerially on longer distances (Aylor *et al.*, 2011) or locally by rain splash (Fry, 2013). Their long-distance dispersal is rare due to the reduction of germinative power after exposure to sunlight (Bashi *et al.*, 1983; De Weille, 1964; Mizubuti *et al.*, 2000; Wallin, 1962). Hence, levels of sporulation estimated are based on the local conditions, assuming that inoculum originates from nearby sources. Solar radiation has a major impact on the viability of detached oomycete sporangia (Bashi *et al.*, 1983; De Weille, 1964; Mizubuti *et al.*, 2000;

Wallin, 1962). In the current work, a model recently proposed by Skelsey *et al.* (2007) is employed for estimating the probability of *P. infestans* spore survival; once the sporangium is deposited on the plant surface it requires moisture to germinate and establish the infection, either directly, by forming a germ tube, or indirectly by releasing biflagellate zoospores (typically 8 to 12) (Fry *et al.*, 2013). Infection efficiency is directly related to the temperature during periods when leaf wetness is present (Rotem *et al.*, 1978) and the proposed model estimates conditions for both infection pathways during the period when the leaf is wet.

While numerous approaches have been suggested for estimating leaf wetness, ranging from very simple empirical to complex physical to models, there is a general consensus that a simple relative humidity threshold is satisfactory for estimating leaf wetness when there is a high probability that the plant surface is wet (Rowlandson *et al.*, 2014). However, this threshold varies spatially and temporally, and numerous researchers have proposed a range of values, from 85 to 92% relative humidity (Rowlandson *et al.*, 2014). While there is a greater likelihood that the plant surface is wet if the RH is > 95%, lower thresholds are often utilised to prevent false negative estimates associated with minor instrument errors or precision (Bourke, 1970). However, leaf wetness is not a binary process, the upper layer of potato haulm is most often wetted before the inside layers, while the drying process is a reversal of this (Jacobs *et al.*, 2009). As far as the authors are aware, no research has been conducted with regards to leaf wetness under Irish conditions. However, our previous analysis has shown that PLB infections can occur below 90% RH, which raises the question on the usefulness of this approach in humid ecosystems, such as on the island of Ireland. Hence, an adapted method was employed, in the form of a scaled leaf wetness risk estimate, to derive a probability that the leaf is wet for values below a threshold of 95% relative humidity.

The model consists of three subcomponents which estimate risk based on: 1) **sporulation** on the first night; 2) **survival** during the first day; and 3) **infection** during the first day and the second night. The model inputs are based on readily available meteorological measurements obtained at standard synoptic heights for variables: the average hourly air temperature (°C) and relative humidity (%) at 2m and total daily solar radiation (MJ/m^2/day). The model output is a daily risk estimation. The model requires three days of weather data for the risk estimation on the second day, hence the first and last day of the weather data do not have an associated estimation of risk.

General functions

Temperature response function. The impact of temperature on sporulation and infection risk was modelled using an adapted five parameter beta distribution density function, commonly applied in modelling crop growth, after Yan and Hunt (Yan *et al.*, 1999). While (Magarey *et al.*, 2005b) proposed a simplified version of this function with only three parameters, defining cardinal (minimum, maximum and optimum) temperatures, it was considered that the two parameters left out in Magarey *et al.* (2005b) are relevant for estimating the development of *P. infestans*, especially if the model is going to be applied using pathogen genotype corrected parameterization. Consequently, the model was defined as follows:

$$\boldsymbol{r(t)} = \begin{cases} \boldsymbol{Rmax}\left[\left(\dfrac{\boldsymbol{T(t)-Tmin}}{\boldsymbol{Topt-Tmin}}\right) * \left(\dfrac{\boldsymbol{Tmax-T(t)}}{\boldsymbol{Tmax-Topt}}\right)^{\frac{\boldsymbol{Tmax-Topt}}{\boldsymbol{Topt-Tmin}}}\right]^{\boldsymbol{c}} & \boldsymbol{if\ Tmin \le T(t) \le Tmax} \\ \boldsymbol{0} & \boldsymbol{else} \end{cases} \qquad \boldsymbol{5.1}$$

Equation 5.1 Temperature response function

Where *r* represents the hourly risk contribution of the modelled process and the five parameters in the equation are the three cardinal temperatures (*Tmin*, *Topt* and *Tmax*), the maximum rate *Rmax* at *Topt*, and parameter *c* which determines the shape of the curve

(Figure 5.2a). The purpose of the parameter *c* is to adjust the estimation of sporulation and infection rates on sub-optimal temperatures. In practical terms, this means that increasing the shape parameters narrows the curve around the optimum temperature. The parameter *Rmax* determines the rate of the process. Initial parameters of the model, cardinal temperatures, *c* and *Rmax* were obtained from the literature.

Sunrise and sunset calculations. Sunrise and sunset were estimated using a modified function ‘suncalc’ from the package RAtmosphere (Biavati *et al.*, 2013) based on the methods proposed by Teets (2003).

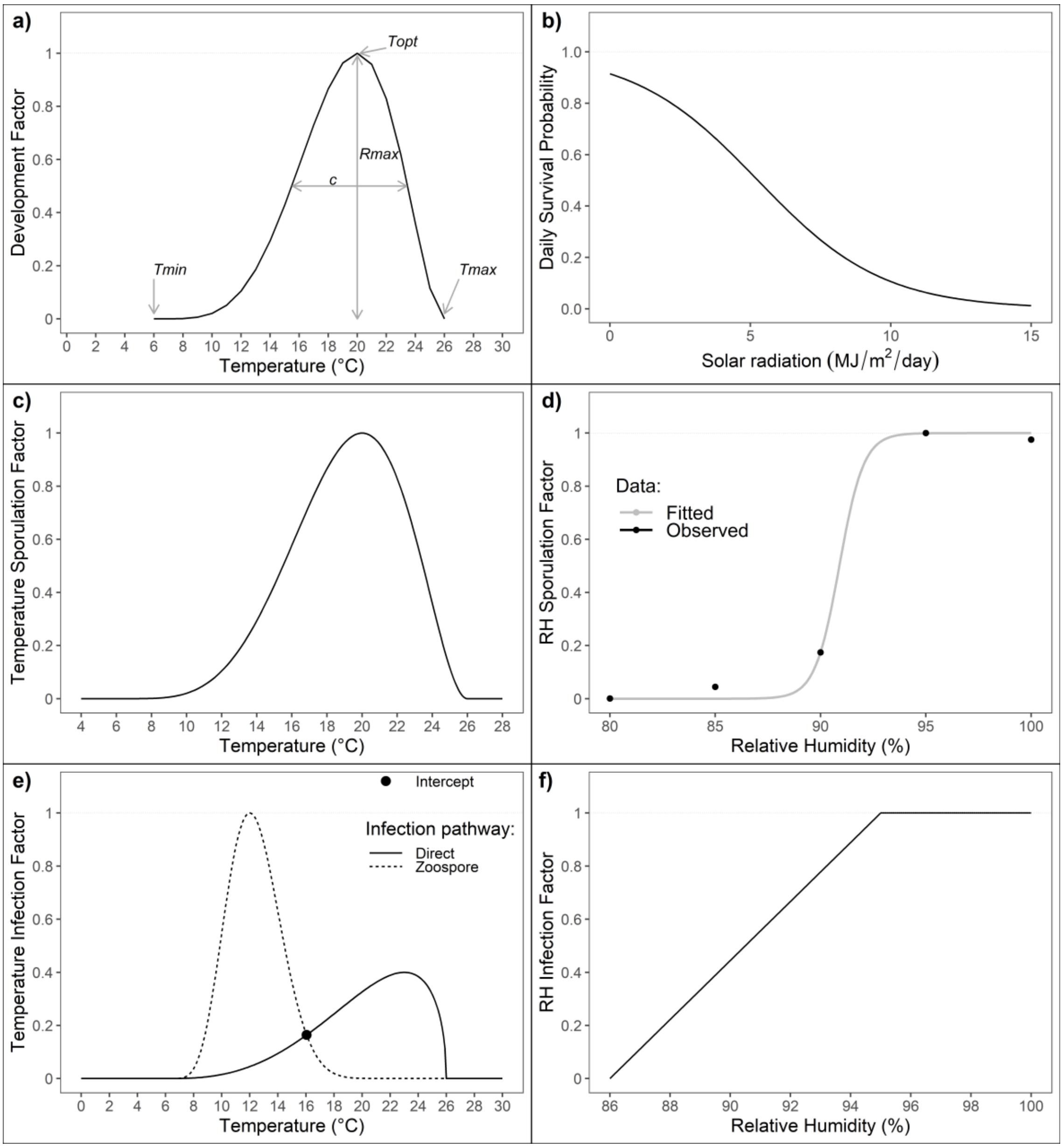


Figure 5.2 Functions used in the proposed model: a) general presentation of beta function; b) probability of spore survival; c) impact of temperature on sporulation; d) impact of relative humidity on sporulation; e) impact of temperature on infection; and f) relative humidity infection factor.

5.3.2. *Model Subcomponents*

Parameter descriptions and their values for modelled life stages are presented in Table 5.1. If not stated in the description of the subcomponents, default parameter values were obtained from Crosier (1934). Parameter names correspond to the model code provided in the supplementary material.

Table 5.1 The code, description and values of model parameters.

Parameter	Description (unit)	Default	Parameter corrections
Sporulation			
TminSpor	Minimum sporulation temperature (°C)	6	7
ToptSpor	Optimum sporulation temperature (°C)	20	21
TmaxSpor	Maximum sporulation temperature (°C)	26	25
RfactSpor	The maximum sporulation rate (unitless)	1	unchanged
ShapeSpor	The shape of the sporulation curve(unitless)	2	4
KSpor	Maximum carrying capacity	97049.81	unchanged
n0Spor	Initial population size	6.05E-04	unchanged
rSpor	The growth rate	1.734924	unchanged
spor_dur	The minimum duration of sporulation conditions (h)	10	unchanged
hr_before_spor	Initiate sporulation counter before the first night (h)	5	unchanged
hr_after_spor	Terminate sporulation counter after the first night (h)	5	unchanged
Spore mortality			
B0	Derived coefficient of the logistic function (unitless)	2.37	unchanged
B1	Constant term of the logistic function (unitless)	0.45	unchanged
Infection			
TminInf (Tmin)	Minimum indirect infection temperature (°C)	6	unchanged
ToptInf (Topt)	Optimum indirect infection temperature (°C)	12	14
TmaxInf	Maximum indirect infection temperature (°C)	26	unchanged
RfactInf	The maximum indirect infection rate (unitless)	1	unchanged
ShapeInf	The shape of the indirect infection curve(unitless)	15	unchanged
TminInfDir	Minimum direct infection temperature (°C)	6	unchanged
ToptInfDir	Optimum direct infection temperature (°C)	23	unchanged
TmaxInfDir	Maximum direct infection temperature (°C)	26	unchanged
RfactInfDir	The maximum direct infection rate (unitless)	0.4	unchanged
ShapeInfDir	The shape of the direct infection curve (unitless)	0.5	unchanged
RhminInf	Lower leaf wetness relative humidity threshold (%)	86	unchanged
RhoptInf	Optimum leaf wetness relative humidity threshold (%)	95	unchanged
hr_after_inf	Termination of infection counter after the second night (h)	5	unchanged

Sporulation

Sporulation period. Sporulation is inhibited during hours of high light intensity (Cohen *et al.*, 1975; Xiang *et al.*, 2014). Hence, it was considered that the sporulation conditions start 5 hours before sunset (*hr_before_spor*) and ends 5 hours after the sunrise (*hr_after_spor*). Under typical summer daylength conditions experienced at the latitude of Ireland, this approximately equates to the period from 15:00 to 11:00 hrs on the following day.

Temperature effect on sporulation. Crosier (1934) reported that while no sporangia were formed outside the range from 3 to 26 °C, very few were formed below 9 °C (Mizubuti and Fry, 1998). Hence, it was considered that the lower developmental temperature (*TminSpor*) to be the midpoint at 6 °C. A left-skewed beta function was fitted for the estimation of the effect of temperature on sporulation (SPORt) (Figure 5.2c).

$$\boldsymbol{SPORtemp(t)} = \begin{cases} \boldsymbol{RfactSpor}\left[\left(\frac{\boldsymbol{T(t) - Tmin}}{\boldsymbol{Topt - Tmin}}\right) * \left(\frac{\boldsymbol{Tmax - T(t)}}{\boldsymbol{Tmax - Topt}}\right)^{\frac{\boldsymbol{Tmax-Topt}}{\boldsymbol{Topt-Tmin}}}\right]^{\boldsymbol{ShapeSpor}} & \boldsymbol{if\ Tmin \le T(t) \le Tmax} \\ \boldsymbol{0} & \boldsymbol{otherwise} \end{cases} \qquad \mathbf{5.2}$$

Relative humidity effect on sporulation. Harrison and Lowe (1989) reported that the formation of sporangia occurs under conditions of high saturation vapour pressure surrounding infected tissue. Hence, the functional relationship between relative humidity and sporulation is modelled using the data they reported on, employing a logistic equation (parameter descriptions in Table 5.1) that is solved analytically, as follows:

$$\boldsymbol{SPORrh(t)} = \frac{\boldsymbol{KSpor} * \boldsymbol{n0Spor} * \boldsymbol{e^{rSpor\,RH}}}{\boldsymbol{KSpo} + \boldsymbol{n0Spor} * (\boldsymbol{e^{rSpor\,RH}} - \mathbf{1})} \qquad \mathbf{5.3}$$

Eqn 5.3. was fitted to the reported sporulation at a wind speed of 1.4 m/s, using the ‘nlsLM’ function from the ‘minpack.lm’ package (Elzhov *et al.*, 2016) (Figure 5.2d).

The estimated hourly sporulation was calculated as a product of temperature and relative humidity effects on sporulation:

$$\boldsymbol{SPOR(t) = SPORtemp(t) * SPORrh(t)} \qquad \mathbf{5.4}$$

Daily sporulation risk estimation. PLB lesions require extended humid periods for the production of sporangia (Crosier, 1934; Schrödter and Ullrich, 1967; Harrison, 1995; Hartill *et al.*, 1990). While Bourke (1953) considered that the minimum duration of this period is 12 hours, Cucak *et al.* (2019) indicated that this period should be reduced to 10 hours. Hence, it was considered that the minimum conditions for sporulation have been met if there was a continuous period of 10 hours (spor_dur) where the hourly sporulation conditions have been met (SPOR(t) >0). If the sporulation duration conditions are met, the daily sporulation risk is calculated as a sum of hourly sporulation; otherwise, the risk of sporulation is set to zero.

$$\boldsymbol{daySPOR} = \begin{cases} \sum_{t=1}^{n} \mathbf{SPOR(t)} = \sum_{t=1}^{n} \mathbf{SPORtemp(t)} * \mathbf{SPORrh(t)} & \boldsymbol{if\ spor\_dur = TRUE} \\ \mathbf{0} & \boldsymbol{otherwise} \end{cases} \qquad \mathbf{5.5}$$

Survival

An estimate of the daily survival rate of the detached *P. infestans* sporangia was calculated as a function of the daily solar radiation (Figure 5.2b) (after Skelsey *et al.*, 2017), as follows:

$$\boldsymbol{daySURV} = \frac{\mathbf{1}}{\mathbf{1} + \boldsymbol{exp}^{-(\boldsymbol{B}-\boldsymbol{B_0X})}} \qquad \mathbf{5.6}$$

where daySURV is the probability of spore survival and B and B_0 are logistic function parameters.

Infection

Temperature effect on infection. There is no general consensus regarding the exact cardinal temperatures of the two infection pathways (Harrison, 1992a), as outlined previously, due to differences in experimental conditions between laboratories, or reference plant and pathogen strains used for the experimentation (Madden *et al.*, 1988a). However, it is widely accepted that the indirect germination pathway favours cooler temperatures (10 – 15 °C) and the direct pathway tends towards somewhat higher temperatures (18 – 24 °C) although with a lower rate of success which was accounted for with a lower rate for the direct infection (*RfactInfDir*) (Crosier, 1934; Fry *et al.*, 2013). Consequently, the temperature effect on infection is estimated by using two beta functions, for zoospore infection (zooINFtemp):

$$zooINFtemp(t) = \begin{cases} RfactInfZoo\left[\left(\frac{T(t)-TminInfZoo}{ToptInfZoo-TminInfZoo}\right)*\left(\frac{TmaxInfZoo-T(t)}{TmaxInfZoo-ToptInfZoo}\right)^{\frac{TmaxInfZoo-ToptInfZoo}{ToptInfZoo-TminInfZoo}}\right]^{ShapeInfZoo} & if\ Tmin \le T(t) \le Tint \\ 0 & otherwise \end{cases} \quad 5.7$$

and direct infection (dirINFtemp):

$$dirINFtemp(t) = \begin{cases} RfactInfDir\left[\left(\frac{T(t)-TminInfDir}{ToptInfDir-TminInfDir}\right)*\left(\frac{TmaxInfDir-T(t)}{TmaxInfDir-ToptInfDir}\right)^{\frac{TmaxInfDir-ToptInfDir}{ToptInfDir-TminInfDir}}\right]^{ShapeInfDir} & if\ Tmin \le T(t) \le Tint \\ 0 & otherwise \end{cases} \quad 5.8$$

Parameters were obtained from the literature (e.g. Crosier, 1934; Fry *et al.*, 2012; Mizubuti and Fry, 1998) (Table 5.1). The intersection point between both approaches was calculated using the function 'curve_intersect' from the package reconPlots (not on CRAN). For temperature values below and above the intersection point, the infection risk was calculated using functions parameterized for the indirect (zooINFt) and direct infection (dirINFt), respectively (Figure 5.2e).

$$INFtemp(t) = \begin{cases} zooINFtemp(t) & if\ Tmin \leq T(t) \leq\ Tint \\ dirINFtemp(t) & if\ Tint <\ T(t) \leq Tmax \\ 0 & otherwise \end{cases} \tag{5.9}$$

Effect of leaf wetness duration on infection. The risk of the plant surface being wet is scaled linearly from 0 to 1 for the values in the range from 86% to 95% RH, respectively, and the leaf is considered wet for RH values higher than 95% (Figure 5.2f), as follows:

$$INFlw(t) = \begin{cases} 1 & if\ RH(t) \geq RhoptInf \\ -9.556 + RH(t) * 0.110 & if\ RhminInf \leq\ RH(t) < RhoptInf \\ 0 & if\ RH(t) < RhminInf \end{cases} \tag{5.10}$$

Daily infection risk estimation. The risk of infection is calculated as a function of temperature and leaf wetness risk factors. The hourly risk of infection (INF(t)) estimation starts after the minimum sporulation duration conditions have been met. The risk of infection is then calculated as a product of the temperature (INFtemp(t)) and leaf wetness (INFlw(t)) infection risk functions. The accumulation breaks if the infection conditions were not met for more than 3 hours (infstop), which leads to spore die-off. The risk of infection is calculated as follows

$$dayINF = \begin{cases} \sum_{t=1}^{n} \mathrm{INF(t)} = \sum_{t=1}^{n} \mathrm{INFtemp(t)} * \mathrm{INFlw(t)}, until\ \sum_{t}^{t+2} \mathrm{INF(t)} = 0 & if\ spor\_dur =\ TRUE \\ 0 & otherwise \end{cases} \tag{5.11}$$

5.3.3. *Calculation of the daily risk*

Different stages of the pathogen life cycle have been employed to estimate the risk of disease outbreak (Madden *et al.*, 1988a; Magarey *et al.*, 2005b). The model, as currently described, outputs a daily estimate of risk. To evaluate if the inclusion of all three modelled life stages represents an improvement over the simpler, two-stage, threshold-based IR model, evaluated three model versions or variants were evaluated (Figure 5.3) where the daily risk is estimated as the product of the following model subcomponents:

1. Sporulation, survival and infection risk (hereafter referred to as the R model variant),

2. Sporulation and infection risk (the Rsi model variant); and

3. Survival and infection risk (the Rmi variant).

For all model variants, the infection estimated risk is calculated from the morning of day 1 until the morning of day 2 and survival during day 1.

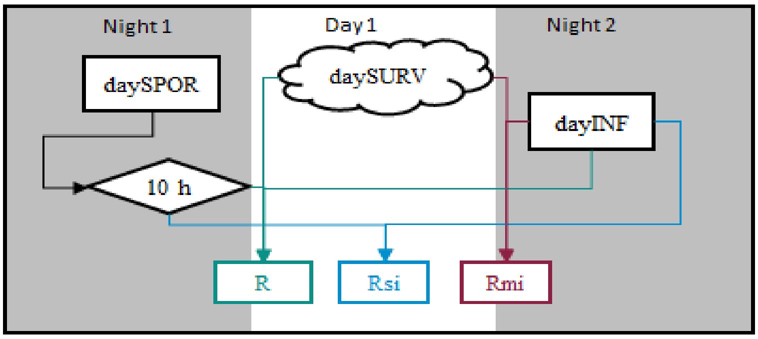


Figure 5.3 Simplified scheme of the daily risk calculation for different versions of the model.

5.3.4. *Model Evaluation*

The model was evaluated using disease outbreak and weather data obtained from Northern Ireland and the Republic of Ireland (ROI).

Data

Weather data.

Hourly weather data for the historical period 2002 -2018, was acquired from Met Éireann for the Republic of Ireland and the UK Met Office (UKMO) for Northern Ireland (Met Office, 2012). The weather variables obtained include hourly air temperature (°C) and relative humidity (%) at 2m and total hourly precipitation (mm). Quality control and data imputation for temperature, relative humidity and rain were implemented according to methods previously described (Cucak *et al.*, 2019). Solar radiation measurements were not available for Northern Ireland; estimated daily solar radiation (MJ/m^2/day) was obtained from the NASA POWER global meteorology and surface solar energy climatology data (Stackhouse Jr *et al.*, 2018) using the function ‘get_power’ from the ‘nasapower’ package (Sparks, 2018). The accuracy of the estimated solar radiation data was evaluated using measured data from 11 synoptic stations in the Republic of Ireland, using the concordance correlation coefficient (CCC) (Lin, 1989). CCC of 0.947 (95% CI: 0.946 - 0.948) was considered satisfactory to use the data in the analysis (Figure 5.4).

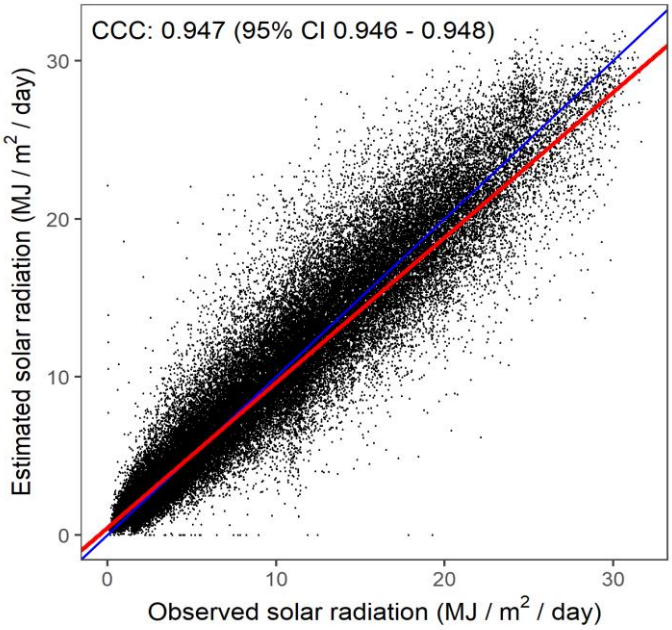


Figure 5.4 Concordance correlation coefficient of measured and estimated daily solar radiation for 11 synoptic stations in the Republic of Ireland. The blue line represents the perfect agreement between the observed and estimated data and the red line is the concordance line.

Observed Weather data subset for testing model specificity.

The initial data set consisted of 54 weather stations distributed across the island of Ireland. In an effort to obtain a geographically representative sample of stations, a subset of 34 stations was selected for further analysis. All agronomic stations were kept in the data set; the final selection also included a number of coastal stations, including airport stations. From the subset of 34 stations (Figure 5.5), only station years with less than 1% of missing values for the period from 1 May until 30 September were kept, resulting in 371 station/year environments (Figure 8.3).

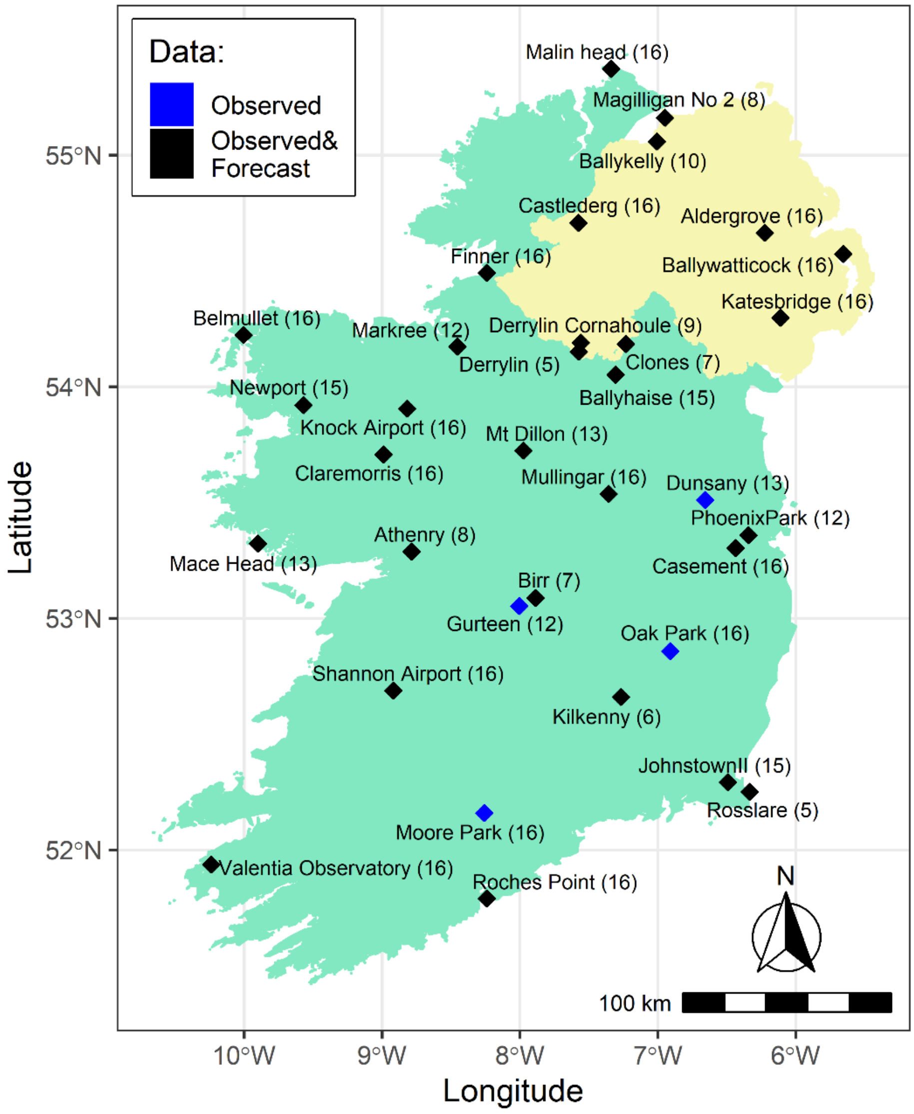


Figure 5.5 Map of the weather stations included in the model evaluation. The number of years of historical weather observations per weather station is indicated in brackets. The stations marked with the blue triangle are locations of both observed and forecasted weather data.

Numerical Weather forecast data.

Numerical, gridded weather forecast data was obtained for 5 weather stations, representative of the most important potato growing regions in the Republic of Ireland (Table 5.2), for the period 2017 to 2019. For each year, the forecast data was subsetted for the part of the potato growing season when the PLB risk is estimated, starting from 1 May and ending on 30 September. The forecast data was extracted from representative model grid from the high-resolution (HRES) atmospheric model (grid resolution approx. 9 km), operationally run by the European Centre for Medium-Range Weather Forecasts

(ECMWF). Weather forecast datasets were delivered as three files with intervals from 0 to 90, 120 and 240 hours lead time with the corresponding 1, 3 and 6-hour temporal resolutions, respectively. Files were merged for the entire 240-hour period prioritising forecasts with lower temporal resolutions. Temperature and relative humidity were temporally scaled to an hourly resolution, consistent with the observed weather data, by spline interpolation using the Forsythe, Malcolm and Moler method (Forsythe *et al.*, 1977). Solar radiation totals were not interpolated since the model only requires daily totals. NWP derived solar radiation values were converted from W/m^2 to (MJ/m^2) prior to ingesting into the model. Files containing 240 hours of interpolated and simulated weather forecast data were then concatenated with the observed weather data, starting from midnight of day one.

The final data set consisted of 2010 ten-day daily sets after removing 95 (4.51%) data sets which contained missing values after the interpolation procedure was applied. To enable model runs and the calculation of risk estimates for each of the ten days, a day of observed data was attached before day one and after day ten for each of the station files. Risk estimation for all models was calculated based on the observed and forecasted hourly weather data.

Table 5.2 Locations of stations included in the analysis and coordinates of the high-resolution forecast (HRES) atmospheric model grid points.

Station name	Latitude	Longitude	Grid point lat.	Grid point long.
Dunsany	53.51	-6.656	53.533	-6.68
Gurteen	53.052	-8.005	53.04	-8.016
Johnstown	52.292	-6.491	52.337	-6.469
Moorepark	52.158	-8.258	52.127	-8.227
Oakpark	52.857	-6.909	52.83	-6.89

Disease outbreak data.

The disease outbreak data consisted of the date and coordinates of 352 late blight outbreaks from across NI over an 11- year period (2005-2014) and 10 outbreaks from Oak Park, ROI, for a similar period (2007-2016). The NI data were collected every year as part of the Agriculture and Horticulture Development Board (AHDB) Potatoes 'Fight Against Blight' campaign (https://potatoes.ahdb.org.uk/). The disease outbreak data from Oak Park was acquired from the Teagasc breeding program field trial records.

The coordinates of blight outbreak locations were obtained using the 'geocoding' function from the 'ggmap' package (Kahle and Wickham, 2013) and confirmed manually. The 'haversine' formula was used to calculate the great-circle distance between outbreaks and surrounding weather stations. The closest weather station, with less than 1% of missing data, was then found iteratively and the weather data was assigned to each outbreak. The average distance between outbreaks and the weather stations of 14.73 km (IQR = 7.3 - 20.7 km) was considered acceptable for the intended purpose and no outliers and possible false values were detected regarding the date of the reported disease outbreaks (Figure 5.6).

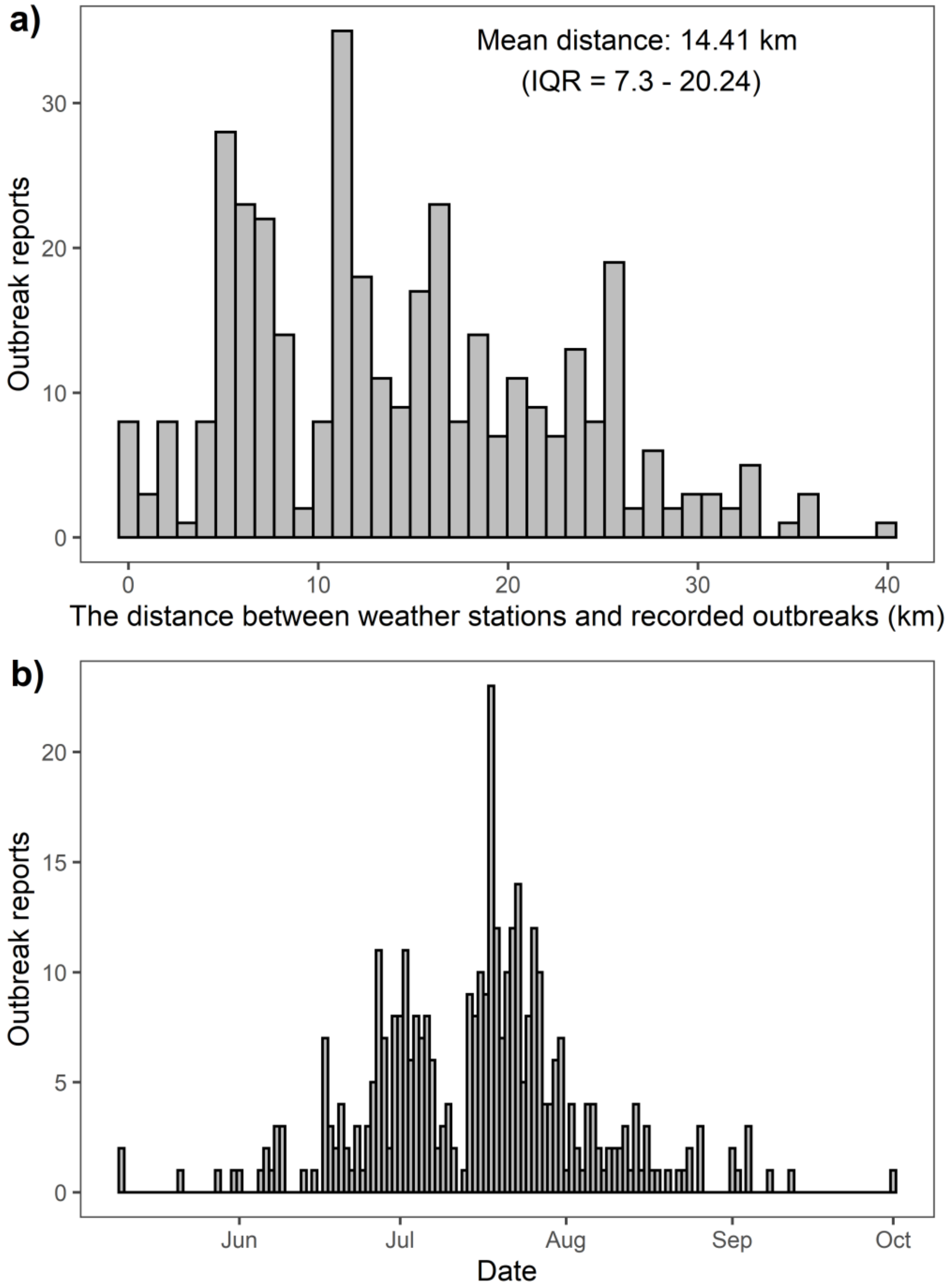


Figure 5.6 Bar charts showing the number of outbreak reports per: a) the distances up to 40 km from weather stations; and b) per each date from 1st July to 1st October..

Evaluation of diagnostic performance

The concept of applying information theory to diagnostic decision making based on the assessment of probabilities in plant disease management was introduced in the 1990s (Hughes *et al.*, 1999) and remains a commonly used method for the evaluation of the diagnostic performance of crop risk prediction models (e.g. Gent *et al.*, 2010; McRoberts *et al.*, 2011; Skelsey *et al.*, 2017; Yuen *et al.*, 1996). It is based on the premise that a known value of a prior probability of a disease can be utilised with a prediction that allows the prior probability to be updated to a posterior probability of disease. Most applications of information theory to epidemiology are concerned with the designation of comparison and reference probabilities, followed by calculation of information contents and their expectations in order to characterise predictions and the diagnostic tests used to make them (Hughes, 2017). The application of these principles requires the presence of controls (no disease) and cases (disease present). The application of the methodology is limited in the case of potato late blight due to a lack of ability to assess the 'negative events', the controls, and no defined way to measure the false positive rate. Here, an alternative measure of the diagnostic performance based on the estimation of sensitivity, the true positive rate, and adapted estimation of the model specificity was proposed. This methodology is based on the approach presented in Cucak *et al.* (2019) but adapted for the current data set.

To evaluate the diagnostic performance of the models, risk estimates were categorised. Contingency tables were then created for a range of risk cut-off points, representing a fungicide application decision threshold, as follows: the range of values from minimum to maximum observed daily risk estimation for each model in all years of the study were cut into 4% quantiles, resulting in 26 cut-off points. This comparison was not possible for the IR and MIR models due to its semi mechanistic nature, where the risk is calculated on an hourly basis and expressed as an effective blight hour (EBH). Hence, the diagnostic performance for MIR and IR was calculated for the values from 1-26 EBH.

Diagnostic performance curves were generated using the model performance indicators for each cut-off point, calculated as a ratio of:

- True positive rate (TPR): Proportion of the outbreaks successfully predicted prior to the disease outbreak. The prediction was considered successful if the threshold was reached during the time window starting 14 days and ending 4 days prior to the disease being observed in the field. A risk warning of disease outbreak 10 days ahead has been reported as an optimum warning time, and a period of four days was considered to be a minimum incubation period.

- Treatment reduction rate (TRR): Calculated as a proportion of the maximum number of treatments during potato vegetation. While potatoes are grown from March to October, the typical plant protection season lasts from May until September, inclusively. The length of each year/season environment data set was 138 days and 19.7 (138/7) fungicide treatments would normally be applied under the standard seven-day grower's practice. The number of fungicide applications recommended by each model was calculated as follows: Fungicide was applied when the risk threshold was reached; it was considered that each application would keep the plants protected for a minimum period of seven days when no application was recommended. For example, if a fungicide treatment was applied on day one, no treatments would be applied in the following seven days, but if the decision threshold was reached then a new fungicide application would follow on the seventh day.

Considering the high risk associated with a possible disease outbreak, the high TPR decision thresholds for the PLB management was considered, maximising the model TPR with an associated 'cost' in the treatment reduction rate. Partial area under the curve (pAUC) in the high sensitivity region (TPR > 0.8) was used to estimate the diagnostic performance of each model variation. Additionally, the maximum achieved TRP (%) was calculated.

The pAUC was calculated as follows: the maximum TPR value was extrapolated to the highest TRR value (TRR= 1) as a horizontal line and the cut-off value for TPR = 0.8 was linearly interpolated between the two closest TPR values. The pAUC was then calculated using the trapezoidal rule (Rosner, 2015).

Sensitivity analysis and parameter correction

A local sensitivity analysis to changes in parameter values was implemented by varying each model parameter value from -3 to +3 units from their default values, within a sensible parameter space (Table 8.8). The exception was the *r* factor for sporulation and direct infection, where six units below the default maximum value of 1 were evaluated. The sensitivity of the model to parameter changes was compared using diagnostic performance in the high sensitivity region the pAUC and maxTPR.

Based on the evaluation of model sensitivity, model parameters indicating significant overall improvement of pAUC were altered, guided by the knowledge of biology and assumptions made in the model development, and the updated-parameterized models were re-evaluated.

5.3.5. *Uncertainty of the risk estimation based on the forecasted weather data*

Initially, verification statistics were used to assess the accuracy and identify biases for each weather variable used to run the models. The statistics included root mean square error (RMSE) and the concordance correlation coefficient (CCC) (Lin, 1989). The statistics were calculated for 10-day and 240-hour lead time for relative humidity and temperature and 10-day lead time for solar radiation.

The agreement between the observed and predicted outputs of the risk prediction models over the ten-day lead time was assessed with CCC. To remove bias and diminish the effects of high-risk estimations, the value-to-rank transformation was implemented. Risk outputs are converted into risk groups based on the evaluation of the model performance, as follows: 1: low (TPR = 1-0.95), 2: medium (TPR = 0.95-0.9), 3: high (TPR = 0.9 - 0.85), 4: very high (TPR = 0.85-0.8) and 5: extreme (TPR < 0.8). The corresponding risk ranks were then grouped per day and compared using the Spearman correlation coefficient.

5.4. Results

5.4.1. *Diagnostic performance*

The diagnostic performance of models evaluated in this study is presented in Figure 5.7. The proposed models covered the entire TRR space, allowing flexibility in the selection of the decision threshold. Overall, the proposed models Rsi, R, and Rmi performed similarly in terms of pAUC (0.049, 0.046 and 0.044, respectively) as the MIR (0.048). The default IR model failed to estimate any risk for 12.15% of disease outbreaks (no risk accumulation prior to 12.15 % of outbreaks), which led to low performance in the high sensitivity AUC region (pAUC = 0.027), although it did provide the highest TRR in that region. With the exception of the IR model, all models provided the possibility for a reduction in treatments compared to standard 7-day growers' practice, ranging from an average of an 8-9-day schedule for TRR for 0.95 - 1 to 10-12-day schedule in the TRR 0.8 - 0.85 range.

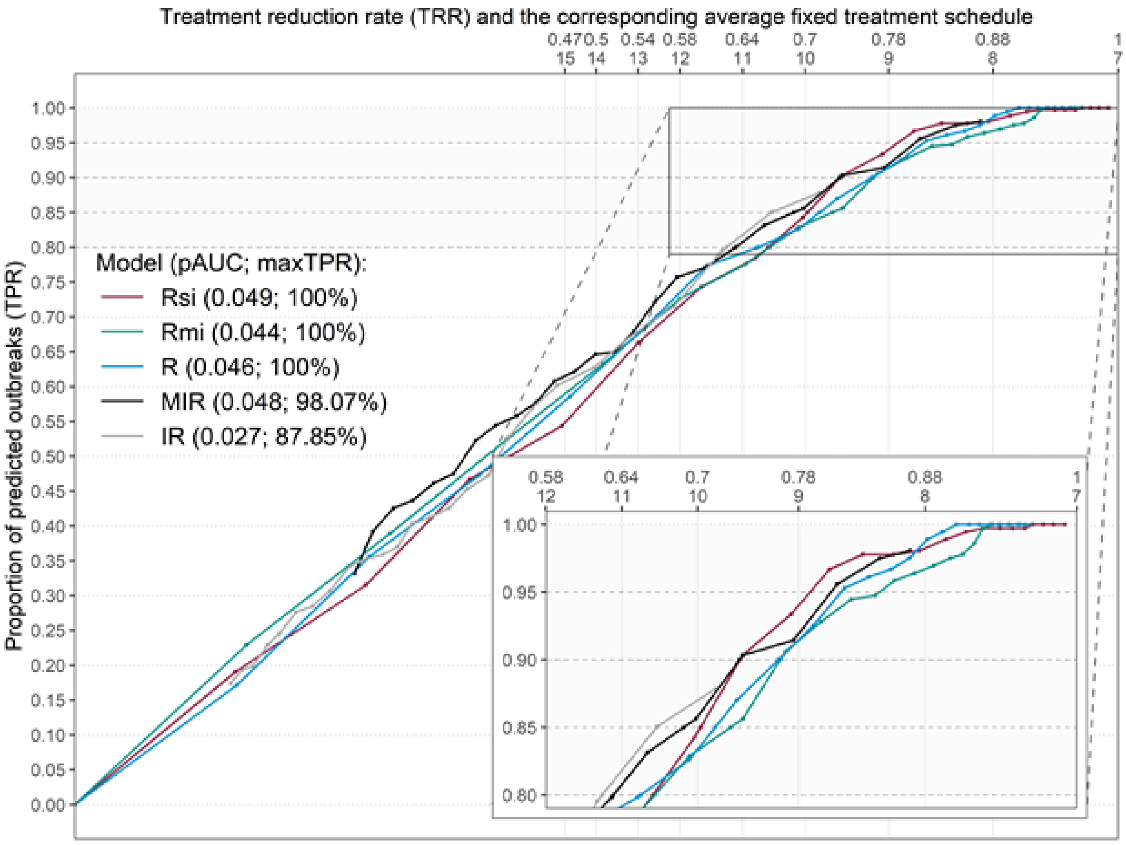


Figure 5.7 The diagnostic performance of models included in the analysis.

5.4.2. *Sensitivity analysis of proposed models*

The results of the sensitivity analysis expressed as an effect of parameter changes on pAUC are presented in Figure 5.7. The most consistent improvement of the model performance was observed with an increase in the optimum temperature for the direct infection (ToptInf). Increasing the lower leaf wetness indicator threshold (RhminInf) led to a decrease in pAUC, which had the highest effect on R, the model which is based only on infection and mortality. Reducing the impact of suboptimal temperatures (ShapeInf) on the indirect infection has a positive impact on R and Rsi pAUC and negative on Rmi pAUC.

A major impact on the model performance was observed with changes in parameter values for the sporulation subcomponent, indicating a need to narrow the area under the temperature response function. The observed improvements were: a decrease of the impact of sub-optimal temperatures by increasing ShapeSpor (model R does not have the sporulation subcomponent); increasing the optimum (ToptSpor) and minimum (TminSpor) values, and decreasing the maximum sporulation temperature (TmaxSpor) parameters.

While no consistent response with parameter changes in the mortality subcomponent was observed, one of the parameters determining the model temporal boundaries had an impact; increasing the minimum sporulation duration (spor_dur) led to a decrease in the maxTPR (Figure 8.4) and pAUC. Changes to some of the models' parameters resulted in an inconsistent response in terms of performance, which could be explained as the model is based only on a limited set of the life stages.

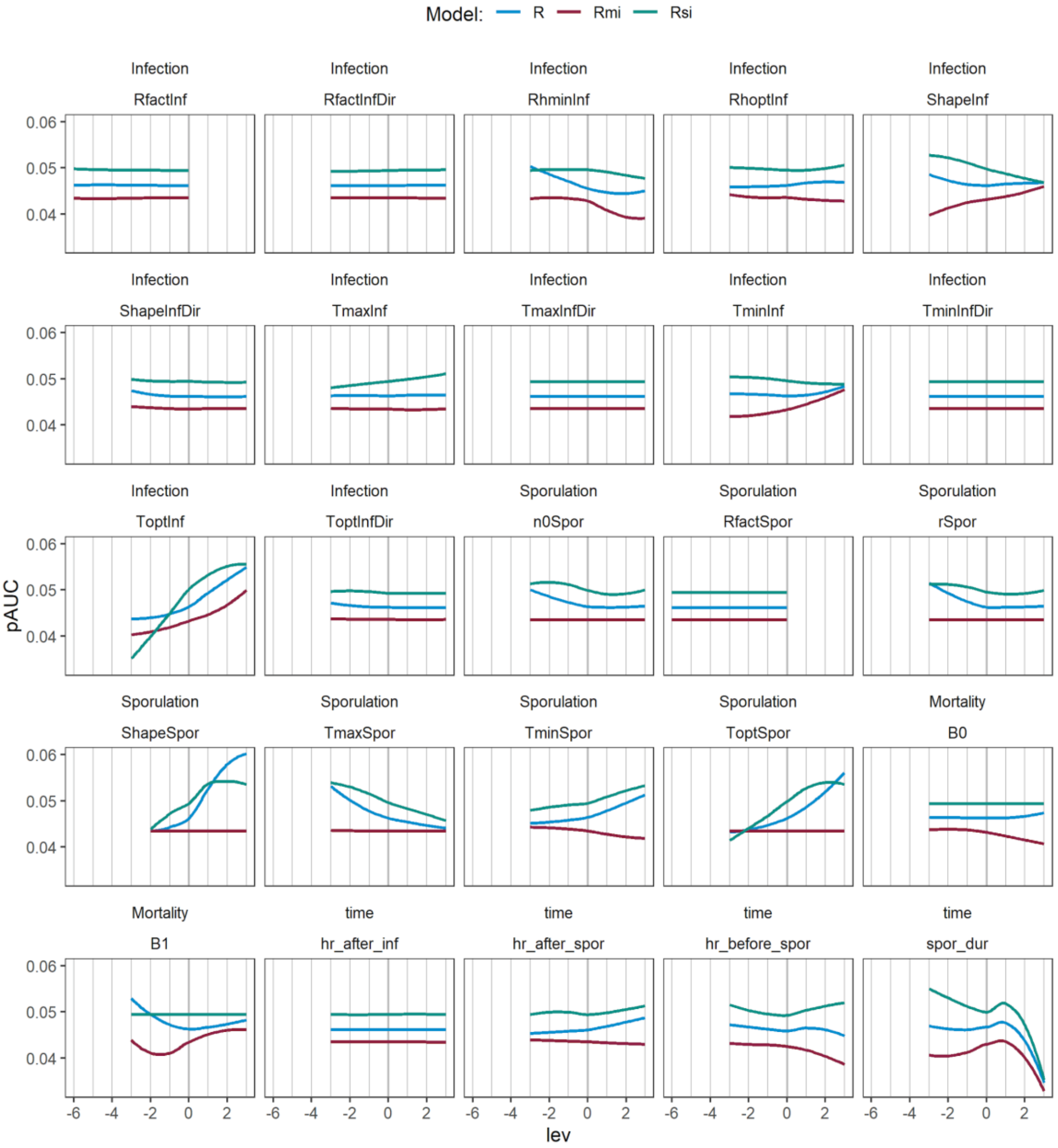


Figure 5.8 Local sensitivity analysis of the proposed model parameter variations +/-3 units from the default values (from 0 to -6 levels for RfactInf and RfactSpor). Smoothed lines were fitted to the pAUC response using the LOESS method for the three proposed models.

5.4.3. *The diagnostic performance of models after the parameter correction*

After reviewing the results of the sensitivity analysis, a model with corrected parameters was evaluated and the diagnostic is shown in Figure 5.8. The parameter correction led to an increase in the overall performance of all three proposed models. The two best performing models were R and Rsi, achieving pAUC values of 0.06 and 0.055, respectively. While R and Rsi achieved similar performance in the 0.9 to 1 TPR region, R offers higher TRR equalling to 11 to 12 day- programme in 0.8 to 0.9 TPR region.

However, Rmi achieved pAUC of 0.046, representing a low overall increase of 0.002 compared to the default model run.

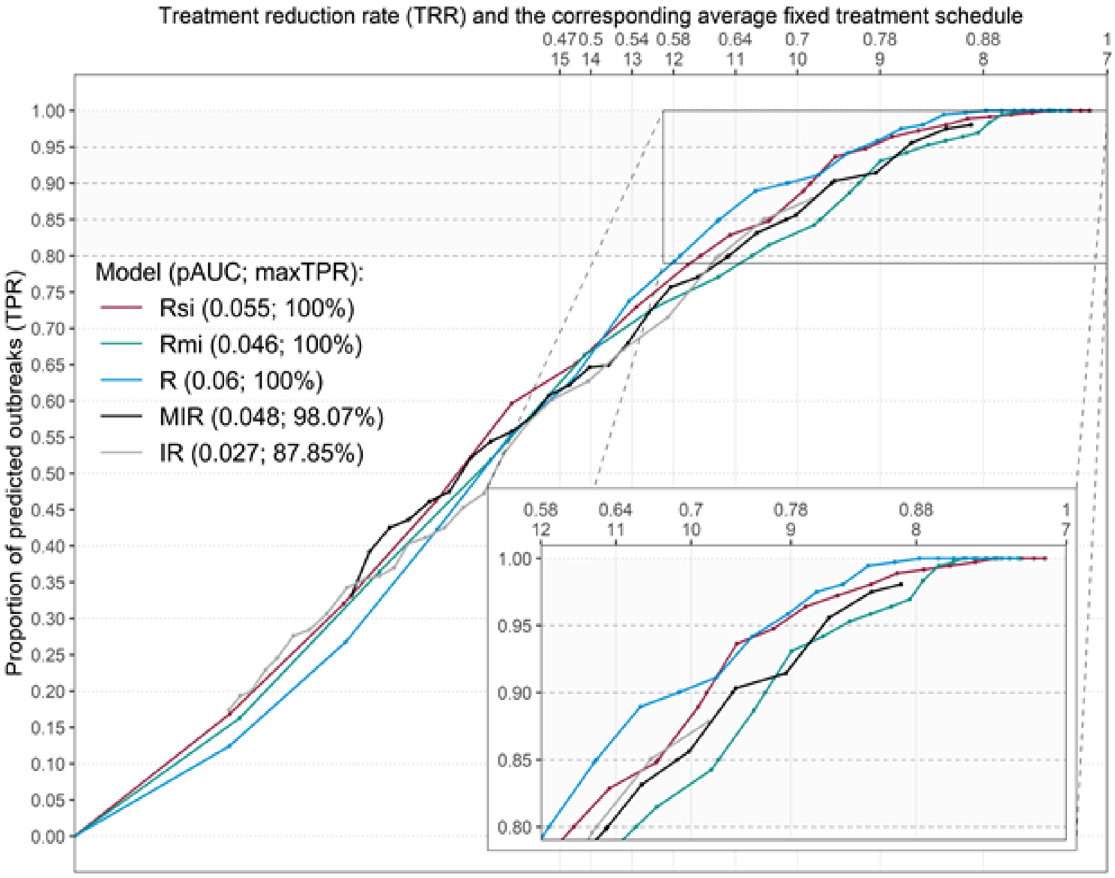


Figure 5.9 The diagnostic performance of models included in the analysis after the parameter corrections.

5.4.4. *Uncertainty of the risk estimation based on the forecasted weather data*

The mean daily concordance correlation coefficients of the three weather forecast variables used to run the models (Figure 5.10 a) indicated that the drop in agreement starts after the lead day 3 and is most prominent on day 5 of the 10-day forecast. The agreement between the forecasted and the observed temperature was the best of the three variables, overall. A low RMSE peak for the predicted hourly temperature is observed in the late evening hours in the first 3 lead-time days, which becomes more exponentiated after day 4 accompanied by a similar anomaly during the morning hours (Figure 8.5 a). The daily RMS linearly progressed over the lead time from 1.38 on the lead day 1, to 3.78 on day 10. Although the forecasted solar radiation shows somewhat better agreement with the observed values, the predictions are of similar quality between the 2 and 5-day lead time (Figure 8.6). The RMSE of the hourly relative humidity predictions rises approximately twice in size during the morning hours, goes through a certain level of correction during the day and then returns to a similar level as in the morning hours in the evening, after which it drops notably before midnight, where it stays until the morning. This pattern of the anomaly repeats and increases over time, with the morning anomaly being even more exponentiated after the 5-day lead.

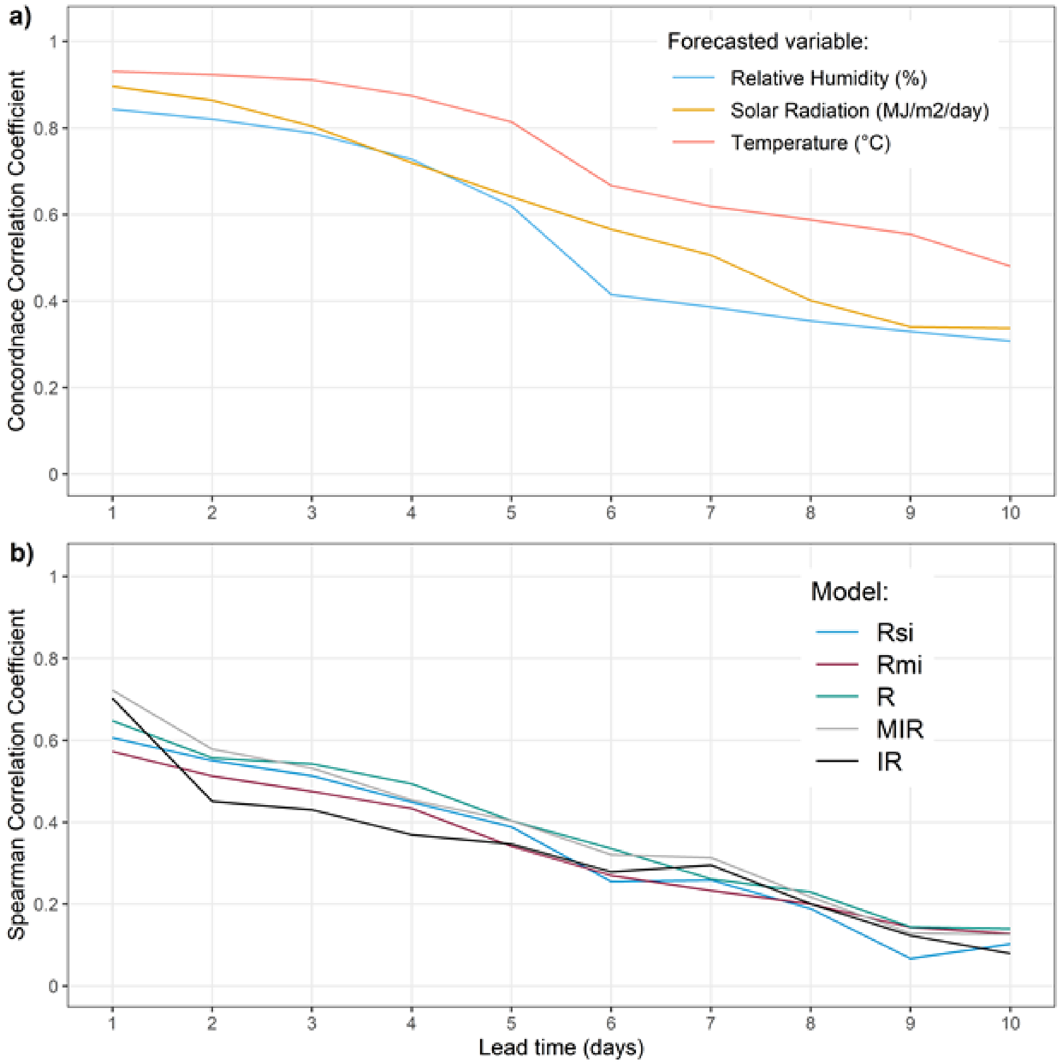


Figure 5.10 Daily mean concordance correlation coefficients between observed and predicted weather variables used for running the potato late blight risk prediction models employed in this evaluation; b) Spearman correlation coefficient between the ranked values of the observed and predicted outputs of the risk prediction models for 10-day lead time.

The CCC of predicted versus the observed values for each lead time day is presented in the Figure 8.6. The MIR and IR consistently achieved a better agreement across the entire lead time period than the proposed models. All of the model outputs based on the forecasted weather underpredicted the risk. This trend was more evident for the proposed models and increased with forecast lead time. The best performance between the proposed models was achieved by Rsi, the model based on sporulation and infection subcomponents which require only forecasted values of relative humidity and temperature.

The gap in the predictive ability of models was reduced after the value-to-rank correction, with the proposed models showing an increase and “the IR based models” (IR and MIR) a decrease of predictive ability (Figure 5.10 b). The most notable difference is the drop in the accuracy of ranked predictions is based on the IR model risk estimation, due to the presence of a low number of risk cutoff points (3 EBH) in the high sensitivity range (see Figure 5.7). Unsurprisingly, the accuracy pattern follows a similar trend as the CCC of the forecasted weather variables (Figure 5.10 a), although predictions are less accurate, most notably in the first 3-lead days. Additionally, the lack of agreement is most notable during July across models (Figure 5.11), with the skill of predictions by the lead day 6 not different from a random predictor ($0 < r^2 < 0.15$). This coincides with the period when most of the recorded blight outbreaks in the data (see Figure 5.6).

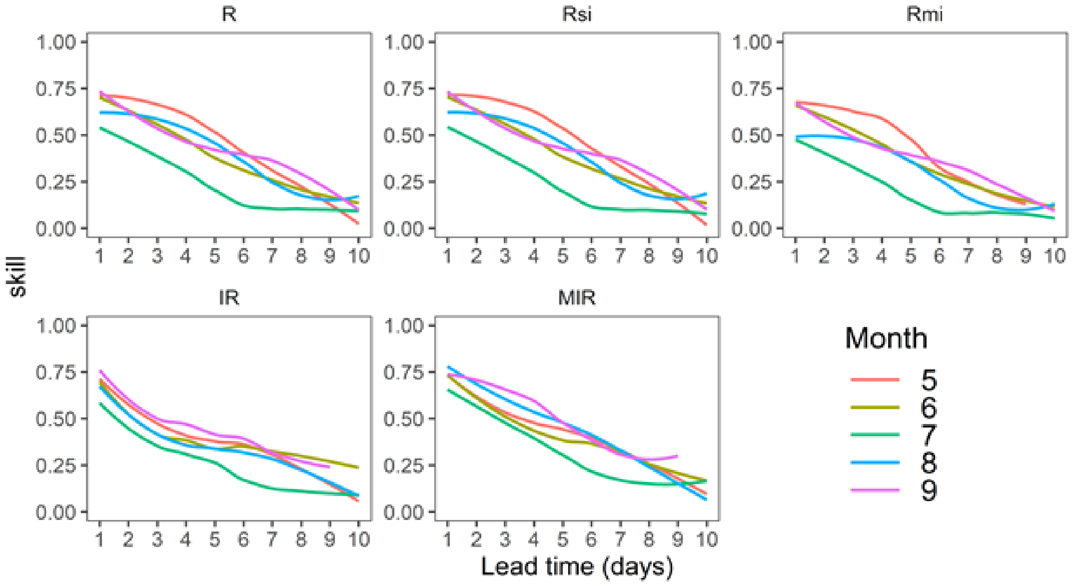


Figure 5.11 Spearman correlation coefficient between the ranked values of the observed and predicted outputs of the risk prediction models for 10-day lead time for each month of the potato growing season.

5.5. Discussion

The PLB risk prediction models proposed here are developed using an adapted version of an established simple generic model and a semi-empirical model used in Ireland (See Bourke, 1953). We presented a complete development cycle of the new model, evaluation of the diagnostic performance in comparison with the simpler model; estimation of decision thresholds within the high sensitivity region of the diagnostic performance curve; and estimated the uncertainty introduced by the risk estimation using the forecasted weather data. Additionally, this is the first reproducible open-source example of development and evaluation of a crop disease risk prediction model. Such resources can be used for further development and ongoing re-evaluation of the proposed model of the PLB decision support system in the Republic of Ireland and elsewhere.

The climatic conditions and reliance on traditional varieties with depleted PLB resistance on the island of Ireland do not allow for a large reduction of fungicide usage, based exclusively on the estimated environmental conditions for disease development. Our results indicate that the standard 7-day schedule can be reliably extended to an average

10- or 11- day schedule, based on the MIR and R models, respectively. The models containing an estimation of sporulation as one of the submodels (R and Rsi), achieved a better diagnostic performance than the model limited on the estimation of spore survival and infection risk (Rmi) (as seen in Figure 5.9). Essentially, the R and Rsi rely on two-day risk estimation, compared to the Rmi, in which the sporulation conditions on the first night are not considered. A two-day approach has been employed explicitly in northwest Europe since the inception of the PLB forecasting, with Smith rules (not Hutton Criteria) in the UK (Dancey *et al.*, 2017; Smith, 1956) and implicitly in the IR model (Bourke, 1953). Another reason for that could be that the estimated solar radiation was used as model input, although the estimated data displayed a good agreement with the measured data in the Republic of Ireland. This is further substantiated by the lack of consistency after varying the parameters as indicated in the sensitivity analysis. However, the Rmi model was kept for the purpose of further evaluation and application in different ecosystems, where a more appropriate data set may be available.

Our results show that the currently employed version of the IR model had the lowest diagnostic performance with a very high number of false-negative predictions, confirming findings from previous reports (e.g. Cucak *et al.*, 2019; Dowley and Burke, 2004; Hansen *et al.*, 2017). The modified version of the Irish rules (Cucak *et al.*, 2019) achieved performance comparable to that of the proposed models. Nonetheless, models proposed here offer a number of benefits over the simpler, empirical, threshold-based models with regards to flexibility, operational deployment and ability to integrate new knowledge of the pathosystem through the biologically meaningful parameters. The proposed models could be calibrated to accommodate frequent phenotypic fitness changes due to an increasing diversity of the pathogen population. In order to provide an adequate crop disease risk estimation, prediction models need to be based on an optimum compromise between the knowledge of pathogen biology and the ability of the weather recording and forecasting network. Hence, the coding example including the model development and evaluation proposed models could be employed to follow the advancements in meteorology as well as accumulation of knowledge of the increasing pathogen phenotypic differentiation within the pathogen population.

Applying crop disease risk prediction models on a synoptic scale requires compromises and simplifications of the life cycle representation. However, technological development and accumulating biological knowledge are not allowing us to settle down with the outdated (over)simplistic approaches. For example, our research indicates that while the initial epidemics are initiated by less aggressive older clonal population, the frequency of fitter strains able to overcome higher levels of the host resistance is increasing as the potato season progresses (Section 4.5.5). The rate of this shift in the *P. infestans* population is dependent on the environmental conditions. Although the exact mechanism is not modelled, integrating parameterisations for less- and more aggressive lineages would lead to improved risk estimation, and further fungicide usage reductions. Although the importance of preserving the PLB varietal resistance durability has received increasing emphasis in theoretical (e.g. Skelsey *et al.*, 2007) as well as applied research (e. g. Kessel *et al.*, 2018), the models proposed in this study represent the first decision support tool that could be used for differentiating risk of more virulent pathogen lineages.

Our modelling framework is based on well-known facts regarding the pathosystem, including the idea that spores are mostly produced overnight, their viability is reduced by the solar radiation, and infections could start from the morning and the longer the conditions last during the day and the following night, the higher the risk. However, this is only a simplification of a complex pathosystem, “adjusted” to minimize the probability of the false-negative predictions of the high-risk disease in the high-risk ecosystem and on a synoptic level. Such simplifications inevitably lead to a loss of the model specificity due to an increase in the number of true positive predictions. For example, spore germination and infection are impossible without the leaf wetness, which, at the same time, prevents the spore release from the sporulating lesions (Rotem *et al.*, 1978). This was not included in the model. Hence, major biological improvements of the model algorithm resulted in only limited improvements of the model diagnostic performance in the operationally employed high sensitivity region. However, the parameter correction guided by a simple sensitivity analysis led to the improvement of the diagnostic performance.

The increasing complexity of the risk prediction algorithms has been reported as a prerequisite for a successful disease risk prediction (e.g. Rossi *et al.*, 2010b). In case of a crop disease requiring high fungicide treatment frequency, such as PLB, the treatment decision depends largely on the forecasted weather data. Our results indicate that this advantage could be questioned in case of zero tolerance crop disease, such as PLB. The risk estimation is based on the latter end of the disease cycle, 24 - 48 hours prior to possible infection event, leading to the necessity for a management decision, implying a level of reliance on the forecasted weather. Increasing the number and complexity of driving variables in defining the transition of life stages and quantifying the risk, needs to be balanced with the uncertainty of the input variables. Hence, the underlying uncertainty introduced with the application of the model on the synoptic level is further amended with the uncertainty of the weather forecast. The results presented here indicate that even simple modifications of the model, such as the one proposed here, results with a ‘complexity penalty’ within the entire range of risk estimates. However, the agreement between the predicted and observed risk estimation between models is not notably different within the operationally employed highly sensitive range, except for the IR model. The underperformance of the IR model is due to poor performance within the high sensitivity region which caused a rank deficiency when the agreement in the high sensitivity region was compared.

However, environmental risk estimation should be employed only as a decision support tool, rather than an executive one. A number of additional tools should be in place to further improve the tactical decision making in PLB management, such as reporting the disease outbreaks; implementation of MLG distribution map and spore sampling.

Several underlying problems have led to the poor performance of the DSSs when compared to ‘safe sleep’ solutions offered by the prophylactic use of pesticides in disease management, especially in the case of a zero-tolerance disease, such as PLB. Issues of complexity, user accessibility, accuracy and robustness have been common problems leading to poor utilisation of promising ideas and concepts standing behind robust epidemiological research. The interdisciplinary nature of the path needed for delivery of such complex mechanism has often proven to be a stepping stone for the delivery of robust decision support in crop protection; often needing constant inputs and communication in development, delivery and evaluation of such systems between agronomist, agrometeorologist, software engineer, modeller and ultimately the final user (Magarey and Isard, 2017). The speed of development of these systems would have been substantially faster had there been real cooperation between countries or groups of researchers. In order to withstand funding reductions, it is necessary for the development of new DSSs that collaboration between researchers and research groups internationally increases significantly in the near future (Bouma, 2007). The approach presented here offers one pragmatic way to improve communication and collaboration channels leading to the further development of the discipline. In the era of re-emerging and new crop diseases, threatening global crop security, ever-decreasing number of new plant pathologists need to use all the tools available to achieve sustainable disease management (Saunders *et al.*, 2019).

Some of the most important issues in the development of useful crop disease forecasting models have been tackled here: Most of the models go through a biological evaluation, lacking the economic evaluation and interpretation of the decision thresholds (Magarey and Sutton, 2007); fail to account for and quantify the uncertainty of the risk estimation introduced by the weather forecast (Gleason *et al.*, 2008) and lack of reproducibility and ease of access for further development of the model and the sub-discipline, in general (Lamichhane *et al.*, 2016). Reproducibility of the model development and evaluation platform allows it to be employed worldwide. However, we call for caution regarding the assumptions employed in the model development and operational application characteristic to the Irish potato late blight pathosystem and meteorological network ability.

6. General discussion and conclusions

The aim of the current thesis was to evaluate the possibilities for the integration of alternative, environmentally friendly and economically viable options to control potato late blight based on the environmental risk estimation under Irish conditions. In seeking to achieve this aim, several steps were pursued, following principles of reproducible science and employing an interdisciplinary approach, that combined knowledge of plant pathology, plant disease epidemiology, agrometeorology and potato production systems. A general review of modelling principles, the diverse history and current state of potato late blight forecasting in Ireland and worldwide is provided in Chapter 2. The main focus of Chapters 3 and 4 was on the evaluation and re-calibration of the Irish Rules model, based on historical disease observations and extensive field evaluation, respectively. In Chapter 5, building on the previous evaluation of the IR model, a new model was proposed in order to facilitate ongoing and future development of PLB risk prediction, aiming to overcome a number of limitations associated with models currently employed, both operationally and in a research context. Additionally,, both models were assessed regarding the uncertainty introduced with forecasted weather used as in input for the disease risk prediction. Finally, the general discussion and conclusions regarding the work done in this thesis is presented in this chapter, including recommendations for modification of the current PLB forecasting system in the Republic of Ireland and possible future implications. Suggestions for future research directions are also outlined. Finally, an outlook to the disease management practice implications of this thesis is presented.

6.1. Discussion

While aspects presented in the introductory chapters and manuscripts I-III are examined separately, the findings of each chapter are drawn together and discussed here, including linkages between them. Each of the manuscripts offers an innovative, transferable and reproducible methodology and presentation of results, such as: the assessment of diagnostic performance of the high risk crop disease model; the field evaluation incorporating advanced plant pathology research tools, and finally the first complete report covering all stages of a responsible and holistic crop disease risk forecaster development, respectively. Hence, it is argued that the research undertaken and reported in this thesis represents a significant and new contribution to knowledge beyond the targeted ecosystem, presented as a coherent body of work.

There is no single simple solution to the global late blight management problem (outlined in Chapter 1). Recent migrations of *P. infestans* population have led to the situation where both mating types (A1 and A2) are present worldwide and opportunities exist for sexual reproduction and recombination. This has led to an increase in diversity, resulting in occurrence of new strains and the establishment of new populations exhibiting higher levels of aggressiveness and virulence and fungicide resistance. Although physically isolated, these changes in *P. infestans* population have not bypassed the Republic of Ireland. Hence, potato production today is heavily reliant on managing PLB based on the prophylactic and protective use of fungicides. Although fungicides are an effective disease control tool, their efficacy is compromised by adverse environmental effects and by the emergence of insensitive or resistant strains. Such an approach is not only expensive, but inconsistent with current efforts to reduce the negative impacts of the global food production system. Integrated management of potato late blight is a suite of tools designed to improve the disease management in an environmentally friendly manner. While host resistance is seen as the most cost-effective and eco-friendly form of management, new varieties with increased levels of PLB resistance coming out of breeding programs have not yet found their way to the market. Potato production in the Republic of Ireland, and globally, is reliant on well-known traditional varieties with low levels of PLB resistance. There is hope that the application of genetic engineering technologies will lead to the improvement of current varieties. However, these efforts are still within the research domain due to perceived human health concerns.

Hence, sensible, short- and long- term approaches to effectively managing the potato late blight problem requires the global research community to develop and improve integrated potato late blight management strategies. One of the most important IPM tools for the reduction of the environmental impact of potato production, besides sanitation measures, host resistance and fungicide protection is PLB risk forecasting (Schepers, 2009; Cooke, 2011). A wider adoption of PLB risk forecasting could have several benefits both for growers and consumers, such as optimised disease control, as well as providing a justification for fungicide use and lead to improvements of the overall economics of production. Additionally, combined with other IPM measures, such as the use of resistant varieties and improved sanitation measures, risk forecasting would greatly improve the sustainability of potato production as recommended in the European Community Directive 128/2009 on the Sustainable Use of Pesticides (European Commission, 2009). However, crop disease DSSs are often poorly constructed, misunderstood and misused; due to a lack of a comprehensive technical or knowledge base during their development, combined with overenthusiastic expectations and poor sustainability plans (Gent *et al.*, 2013; Rossi *et al.*, 2012; Shtienberg, 2013). Due to the increased awareness of these issues and risks associated with highly conducive blight environment, such as in the Republic of Ireland, the approach taken in this research was to tackle these issues through the use of sensible biological and statistical evaluation techniques leading to the re-calibration of the currently used model; thereby, reducing the risk of false negative predictions; informing a potential end-user regarding the benefits of the use of resistant varieties under current Irish *P. infestans* population rather than determining the exact thresholds due to awareness of the downfalls of territorial models (Chapter 2); providing the new modelling platform to facilitate enhancements of the risk estimation; and finally, providing the entire workflow in a robust, accessible and reproducible manner through a single programming language ensuring the sustainability, and subsequent development, of the approach.

An overview of PLB risk prediction modelling approaches and the history of PLB DSSs presented in Chapter 2 reveals insights into the manner and approaches taken in the development of potato late blight crop disease models and DSSs, as well as highlighting potential pathways for future developments and improvements. Numerous risk prediction models that inform DSSs worldwide remain diverse in terms of their complexity and structure, as well as the DSSs themselves. The models applied on the territorial scale are typically less complex and considered inherently less accurate compared to the more complex models applied on the microscale, which feature inherently more accurate estimates. However, territorial models are still appealing for several reasons, such as: simplicity of implementation and accessibility to a regular user and ready availability of the required input weather data. Importantly, their simplicity is of benefit due to the lower demands for precision from the weather data produced by numerical weather prediction models (see Chapter 5). Additionally, increasing the complexity of a model additionally increases the uncertainty of the risk estimation and demands more frequent updates.

Hence, the approach taken in this thesis was to evaluate the Irish Rules model, a well-known and long-established PLB risk prediction model in the Republic of Ireland. The IR model has been used for the purpose of potato late blight forecasting for 70 years in the Republic of Ireland; it is well known to Irish producers and it is based on fundamental knowledge of PLB epidemiology. However, evolving *P. infestans* population active over wider environmental conditions and changing demands of potato production have imposed a need to re-evaluation the model, as well as its decision thresholds.

6.1.1. *The modified IR (MIR) model*

The Irish Rules model was revolutionary in its approach to quantify the risk of disease development (as outlined in Chapters 2 and 3). However, the model was based on the needs of potato production and the epidemiological patterns of the 1950s. At the time, the expectations from crop disease management programme were lower; Large (1959) stated that a good commercial fungicide programme could be expected to prolong the haulm growth for two weeks until the end of August, during blight years, leading to an average 15% yield increase. Such expectations are marginal in contemporary potato production. The validity of the Irish Rules was first questioned under field conditions in the 1990s (e.g. Dowley *et al.*, 2004; Leonard *et al.*, 1999), around the time when the Smith Period (Smith, 1956) from the UK was reported to be increasingly inaccurate due to the complicated interactions between the pathogen, environment and the unknown growth parameters of the newer genotypes (Taylor *et al.*, 2003). These reports are dated before the genotype 13A2 or 6A1 were detected within the population. Prior to the establishment of these new genotypes, missing a few critical periods may not have carried such high risk and potential for negative consequences as it does nowadays, when failure to predict critical periods may lead to severe blight pressure for the grower (Flier *et al.*, 2002). Changes in production patterns and the epidemiology of the disease highlighted the need to initially evaluate the Irish Rules model and subsequently re-calibrate the model, to ensure that the model continues to reflect the changes.

Following the evaluation of the IR model, presented in Chapter 4, modifications to the existing thresholds were proposed which led to a significant improvement in the overall diagnostic performance of the modified model, most notably in the high sensitivity region of the ROC curve, which corresponds to the operational range of the model. The analysis of the data from Oak Park indicated that the operational range of 0-11 EBH corresponds to a 0.8-1.0 sensitivity range. The same method used in this analysis could not be undertaken for the data set from Northern Ireland, due to a lack of information regarding the presence of host foliage. Consequently, an adapted version of the evaluation methodology, presented in Chapter 3, was developed in order to analyse the wider data set and the results of this analysis, which are presented in Chapter 5. While the specificity of the model was calculated using the available data for the host presence in Chapter 3, the specificity of the model for the wider data set presented in Chapter 5 was calculated as a proportion, indicating a reduction in the number of treatments following the standard 7-day interval practice. Importantly, both analyses are in agreement regarding the overall conclusion that the original thresholds employed in the IR model were not fit for purpose due to large proportion of false negative predictions; these were significantly decreased with the new model thresholds (see Figure 3.6 and Figure 5.9). Although the results using these different methods could not be directly compared due to these methodological differences, both indicate a similar operational range of the model within the high sensitivity region (specificity 0.8-1), 0-11 EBH for the initial evaluation presented in Chapter 4 and 0-8 EBH for the analysis presented in Chapter 6. The difference is also potentially caused by the lack of smoothness of the diagnostic curve in the Chapter 4 analysis, due to a low number of data points associated with only ten years of the disease data.

Subsequent to the evaluation of the model using the historical data, a field trial was established to evaluate the relative performance of the model under field conditions, and the results are presented in Chapter 5. This study was implemented in a manner different to a classical DSS evaluation, particularly with regards to the treatment schedule. Due to the high perceived risk posed by possible disease outbreaks, PLB management is heavily reliant on the frequent use of pesticides, typically on 7-day intervals in western Europe (Cooke *et al.*, 2011), including the Republic of Ireland. Hence, the research outcomes were oriented towards informing the adjustment of the standard grower’s practice, rather than imposing a completely new, or untested, management strategy. Additionally, the evaluation of the environmental risk estimation was complemented with the evaluation of the role of varietal resistance and the effect on the local *P. infestans* population. Results presented indicate that the MIR model provides both satisfactory disease control as well as achieving higher environmental standards, resulting in more economical disease management. Such encouraging results require further investigation, largely on the possibilities for the reduction of, not only the dose, but also treatment frequency. For example, if a treatment costs 100 Euro per ha (including PPP, human hour and amortisation) and if we consider that 10000 ha are currently planted with potato, a saving of 1 million Euro could be obtained, on average. These reductions have even bigger savings, keeping in mind the environmental benefit. Additionally, the model was successful in identifying periods of extreme risk, when the use of fungicides is necessary and justified, and could potentially save the production.

As outlined in Chapter 2, there are numerous components of the PLB pathosystem that need to be considered when making a decision regarding an appropriate PLB management strategy, such as: potato variety and pathogen population and presence; as well as the impact of human interventions, such as selection and implementation of the agrotechnical operations. Integration of these segments into non-commercial, wide-use, and usually government owned PLB DSSs is challenging (e.g. Chapter 2). Although such systems exist, such as BlightPro (e.g. Small *et al.*, 2015a), their long term reliability is questionable due to issues of maintenance and lack of updating varietal resistance and fungicide efficacy information. For example, the evolving pathogen population has been known to be able to quickly degrade the resistance rating of a potato cultivar (Lees *et al.*, 2012), potentially leading to very costly disease management errors. Although the results presented in Chapter 5 are in agreement with previous findings, indicating that the Irish population remains simple (Kildea *et al.*, 2010; Stellingwerf *et al.*, 2018), the newer populations, which consist of genotypes 6A1 and 13A2, are exhibiting increased levels of aggressiveness compared to the older 8A1 genotype populations. However, these genotypes have been relatively recently established under Irish conditions and any DSS proposed prior to their establishment requires re-evaluation. A lack of any long term sustainability plan, when DSSs are proposed is a serious and reoccurring limitation of these systems in crop protection and the more complex the system is, the greater the need for constant validation and updating (Shtienberg, 2013). This problem is better managed by personalised commercial DSS such as “Agrovision” (previously known as Prophy, see Nugteren, 2004) which are built on constantly generated and updated databases and have the possibility for manual data entry by a producer.

Hence, considering the territorial application of the IR model, no risk adjustment was recommended as an outcome of this thesis, but the system is calibrated to minimise the risk of the disease outbreak. Successful application of DSSs in crop protection depends on intensive communication between meteorologists, field crop advisors, researchers and end-users (Magarey *et al.*, 2017) which should be an immediate priority in the operational application of the Irish potato late blight warning service.

6.1.2. *The new model*

The MIR model has shown its potential as an accurate tool for predicting the disease outbreaks (e.g. Chapters 4 and 5). Due to its simplicity, it places lower demands on the accuracy of the weather forecast (as seen in Chapter 6) and is easy to understand and implement. However, during the implementation of this research, potential issues limiting future improvements in the MIR became apparent, suggesting room for further improvements. For example, the crude threshold base of the model was a key limiting factor, most notably highlighted in Chapter 4, where an increase in the temperature threshold could not be recommended although the analysis indicated low pathogen activity below 12 °C. Growth of *P. infestans* will still occur even below 10 °C (Crosier, 1934) with the majority of the 11 UK genotypes tested by Chapman (2012) being able to infect at 8 °C, although at a very low percentage. Another problem is a lack of an upper temperature threshold in the MIR model. Although current temperatures during the potato growing season are predominantly within the temperature range of *P. infestans* under current Irish conditions, this may no longer hold in future due to climate change (Garrett *et al.*, 2011). Besides these potential issues, possibilities also exist for the improvement of prediction in terms of accuracy of risk estimation, presented in Chapter 5. For example, continued improvements in the weather network and numerical weather prediction, evolving pathogen population as well as the knowledge of the new rising strains and constantly increasing the risk of potato production demand improvements in the tools for management of the disease. Additionally, the quantitative nature of the model enables easier selection and adjustment of operational thresholds and determination of risk categories.

6.2. Recommendations on the operational application of the MIR model

Based on the results of the work presented in this thesis, the recommendations for the operational application of the MIR model output are as follows:

- **Risk classification** into five categories: very low, low, medium, high and very high, reflective of respective risk accumulations of effective blight hours (EBH): 0-3, 4-6, 7-9, 10-12 and > 12.
- **Information delivery:** Blight warnings in Ireland are currently issued several days in advance (as seen in Chapter 2), while it was shown (Chapter 5) that the agreement of the model estimates using observed and forecasted data drops drastically after lead time of four days. Hence, the error probability of model output based on forecasted data should be incorporated into the visualisation of model outputs (e.g. shading or

“alpha” of graphs applied to corresponding lead times) and considered in the practical application of the model outputs, most importantly when issuing blight warnings.

- **Information accessibility**: Blight maps and meteograms used internally by Met Éireann for specific locations should be available publicly following examples from other DSS (e.g. Dancey *et al.*, 2017; Hansen *et al.*, 2017; Small *et al.*, 2015). While these outputs are currently not publicly available due to justified concerns regarding the interpretation of model outputs, their availability to the public would improve the timelines required for disease management activity, whether deciding on a dose, interval or active ingredient for a fungicide treatment, implementing scouting activity, and similar.

However, it should be clearly indicated how the risk should be interpreted. Here, the general guidelines are provided but varietal resistance, phenological stage of plant and inoculum pressure (e.g. Chapter 1, 2 and 5) represent an important factor in the translation of risk into advice or an operational decision.

Further advice on the interpretation of the MIR risk outputs

The previously determined minimum of three disease cycles (Muller *et al.*, 1953) and maximum of five generations for the initiation of epidemics (Bourke, 1953b) is still valid based on the analysis of the available data. This period was proposed as an initial, exponential stage (Muller *et al.*, 1953) of sigmoid-shaped disease progress curve, describing compound-interest polycyclic disease progression (van der Plank, 1968). Hence, the probability of disease outbreak in the field depends on the conditions for the multiplication of pathogen population, proximity of the inoculum source and phenological stage of the crop, with the risk of the disease outbreak being low until crops start closing their canopy.

The current calibration of the model and recommended operational thresholds is suitable for typical potato late blight risk under Irish weather conditions. However, there are differences between, as well as within, seasons. Results indicate that the interval between treatments can be extended during dry summers, such as the one in 2018 (see Chapter 5). Following the same population dynamics principle elaborated in the previous section, the pathogen population undergoes a severe reduction during periods of dry weather and needs a few reproduction cycles to reach the stage of high inoculum pressure. Conversely, under typical Irish conditions, uninterrupted disease cycles occur during spring and summer, and the inoculum pressure culminates typically during July when most of the disease outbreaks are reported (Figure 5.6 and (Dowley *et al.*, 2008)). If these conditions continue during August, allowing uninterrupted disease cycles, that year can have pandemic proportions; such conditions were observed in 2019 (e.g. Chapter 5). Similar observations are reported by Keane (1982) who states that an epidemic year is characterized with 2 or 3 risk periods within 14 days, as indicated by the default, and more conservative, IR model.

6.3. Future (and current) priorities for research and practical application of PLB DSS in the Republic of Ireland

There are numerous ways for improving the management of PLB based on the environmental risk estimation. While some of methods described below are still expensive and/or limited to research purposes, there are accessible ways to improve the content of information regarding the possibility of disease outbreak and guide appropriate management decisions.

6.3.1. *Improving the disease risk estimation*

Extending the knowledge of PLB epidemiology

The *P. infestans* inoculum causing primary infections originate from potato tubers infected in the previous season (Zaag, 1956), oospores (Andersson *et al.*, 1998) or alternative hosts (Flier *et al.*, 2003). While the conditions for oospore infections have not been confirmed in western Europe (Cooke *et al.*, 2011), the role of alternative hosts remains unclear (Flier *et al.*, 2003); it is assumed that the primary infections predominantly originate from the infected tubers (Schepers *et al.*, 2009). Furthermore, due to strict seed quality control and five-year crop rotation, it could be assumed that the primary *P. infestans* inoculum originates from outside of the crop, from the tubers infected in previous seasons, surviving either as volunteers left in the field after harvest or in waste piles. Mild Irish winters provide an increased possibility for the inter-season survival of tubers infected by *P. infestans.* Quantifying the survival of both infected and non-infected tubers, which can play an important role in primary disease cycles, would be beneficial for the purpose of forecasting the initial outbreak in the field. Additionally, such research could provide insights into the dynamics of the population structure between seasons and help elucidate the persistence of the 8A1 genotype under Irish conditions, despite incursions by other genotypes.

Another research necessity, related to the new *P. infestans* population in Ireland, is to understand the phenotypic characteristics of established genotypes in relation to the environment, specifically temperature, moisture and solar radiation. There is a lack of knowledge regarding the suboptimal temperature effect on new pathogen lineages, either in terms of latent growth or re-infection of the new tissue. Such information could provide pointers regarding these characteristics and gaps in knowledge regarding new strains, will be available from currently implemented evaluations in Europe (Andrivon *et al.*, 2017).

Such information would help better parametrisation and further development of the new model proposed in this thesis (Chapter 5).

Application of molecular tools

Information regarding the pathogen population, crucial for selecting an appropriate management tactic (Carlisle *et al.*, 2001; Cooke *et al.*, 2012; Stellingwerf *et al.*, 2018), was discussed in more detail in Chapter 5. The importance of such information was clearly identified after 2009, which was a severe 'blight' year worldwide (Cooke *et al.*, 2011; Fry *et al.*, 2013), and served as a reminder of the devastating power of PLB. This led to extensive research efforts to find alternative strategies for disease management. Fungicide resistance and aggressiveness differences between *P. infestans* clonal lineages have led to increased efforts for establishing tools for rapid determination of the structure of the pathogen population over time (during a season) and space (different locations) (Fry *et al.*, 2013). Polymerase chain reaction (PCR) based microsatellite markers are a relatively fast and widely used molecular characterisation method to separate multilocus genotypes of the pathogen (Lees *et al.*, 2006). Microsatellite markers could be used on small samples, with the results obtained within 24 h, making them an irreplaceable tool for predicting the traits of the pathogen in any given sample (Fry *et al.*, 2013). Besides its crucial importance for informing the management tactics due to fungicide insensitivity of some pathogen lineages, the clear pattern of change in the structure of *P. infestans* population (as seen in Figure 4.6) can be further used for dynamic in-season calibration of the new model proposed in Chapter 5 of this thesis.

6.3.2. *Practical model application*

Field evaluation

The initial evaluation of the MIR model under field conditions was implemented with a degree of caution. The results of the trials (as presented in Chapter 4) and the fungicide trials implemented in the 2019 season (results not shown here) offers the potential to safely increase the intervals between fungicide applications. Hence, further field trials evaluating the incorporation of environmental risk-adjusted selection of active ingredients, dose and interval for fungicide application would likely yield further improvements in the proposed strategies.

Monitoring inoculum

Risk prediction models used in practice are often based only on the estimation of environmental conditions for infection (Magarey *et al.*, 2007), and the ones employed in PLB DSSs are no exception (Schepers *et al.*, 1995). Complementing the environmental risk estimation with other tools from the IPM toolbox leads to improved risk estimation and more informed advice to the end-user (Rossi *et al.*, 2012). For example, the fungicide treatments to control PLB are often recommended when the pathogen inoculum is not present (Taylor *et al.*, 2003). Tools, such as Burkhard spore traps, have been used to record the initial occurrence and monitor the seasonal intensity of pathogen inoculum (Agrios, 2006). Although they have a slow turnaround-time of 7-days, they have been reported as a reliable tool for the detection of incoming pathogen inoculum and a counterweight to model risk estimation for timing fungicide treatments (Fall *et al.*, 2015). A solution for the high-maintenance and low speed of manual spore samplers is on the horizon with the development of rapid low-cost biosensors which could be deployed in the field. Such biosensors could aid early detection and biological recognition of air-borne *P. infestans* sporangia but cannot differentiate between viable and non-viable inoculum, which is where the models estimating the survival could compensate for this shortcoming (Skelsey *et al.*, 2017).

Disease outbreaks

At present, the accessibility of smartphone technology is almost universal and costs of transmission are low; this presents numerous opportunities to improve the quantity of information available to end-user when deciding on crop management tactics (Fabregas *et al.*, 2019). Reporting of disease outbreaks complemented with environmental risk calculation could be readily converted into maps on the distribution of risk. These maps could provide simplistic spatial and temporal representations of risk distribution; make DSS outputs easier to understand for system users and perhaps initiate the need for the system in non-users. Improvements of the timeliness, cost-effectiveness and accessibility could help wider use and reliance on the DSS.

Remote sensing

Recent technological and scientific developments led to the introduction of non-destructive, sensor-based methods for crop disease detection as part of an international movement towards precision agriculture practices (Mahlein *et al.*, 2018). Blight in potatoes is a zero-tolerance disease and the early detection of the disease outbreak is crucial for integrated pest management measures (Schepers *et al.*, 2009). Visual assessments by humans in production fields, as well as assessments of disease progress in research fields, are time-consuming. Hyperspectral sensors and imaging techniques have shown an enormous potential to tackle this issue (Mahlein *et al.*, 2018). Problems with such techniques are lack of differentiation between biotic and abiotic caused stress and unified spectral image of the diseased plant across different phenological stages (Madden *et al.*, 2007). However, recent *in-vitro* research on the spectral response of different potato cultivars (Gold *et al.*, 2019) as well as the clonal lineage discrimination in latent phases of the infection (Gold *et al.*, 2019) shows promise.

6.4. Final conclusions

The goal of this thesis was to revise the potato late blight decision support system based on environmental risk estimation, in the Republic of Ireland. This goal was achieved through the combination of epidemiological modelling and field and laboratory experimentation. The Irish Rules model, which has been used operationally since the 1950s was evaluated, modified and tested in the field, yielding positive results. The modified IR model and the new risk prediction model, as well as providing a clear methodology for their ongoing evaluation was proposed and was provided as a completely reproducible open source tool to facilitate the future improvement of models and decision thresholds. Accessibility to such methods and tools is becoming increasingly important, due to a need to monitor frequently evolving *P. infestans* populations which lead to emergence of new lineages characterised with new traits and different environmental requirements. Such information could be used to inform environmental risk prediction and management tactics. It has been shown that varietal resistance has shown great potential, but it needs to be protected because even simple *P. infestans* populations, such as in Ireland, can deplete the genetic resistance potential.

It seems likely that with an increased ability to measure and forecast the weather, increased knowledge of pathogen population and ability to monitor its structure, will inevitably lead to increased use of DSSs in potato late blight management. Collectively, the results of this thesis contribute towards the development of more effective and eco-friendly integrated management of potato late blight disease in the Republic of Ireland, and elsewhere.

The new modelling platform was proposed that could help improve the accuracy of risk estimation. However, each new crop disease model needs an extensive evaluation before it is employed in practice (Magarey *et al.,* 2007; Rossi *et al.,* 2010a). Hence, we do not recommend the instant application or operational use of the new models but instead propose a gradual transition. Initially, the model should be tested under field conditions and used side by side with the MIR model operationally.

7. References

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8. Appendix 1: Supplementary Information

8.1. Supplementary material for Chapter 4

Table 8.1 List of frequently used abbreviations along with their full forms.

Abbreviation	Full Form
GLMM	Generalized linear mixed model
IPM	Integrated pest management
PLB	Potato late blight
rAUDPC	Relative area under the disease progress curve
BQ	British Queen
KE	King Edward
RO	Roster
SE	Setanta
CL	Clone form Teagasc breeding programme
SM	Sarpo Mira
IRp	Irish Rules programme
MIRp	Modified Irish Rules programme
BMp	Blight Management programme
EBH	Effective blight hours

Table 8.2 Dates of the agronomic operations.

Year	Planting	Disease Outbreak	Desiccation	Harvest	Grading
2016	02/06	25/07	30/09	13/10	06/12
2017	17/05	03/07	28/09	15/10	07/12
2018	07/06	20/08	28/09	13/10	10/01/19
2019	22/05	26/07	20/09	16/10	15/12

Table 8.3 Dose model A used in Blight Management. The recommended dose depends on the local infection pressure for late blight and the proximity of the location where the late blight is recorded.

Model A **Infection Pressure**		**Stage 1 No outbreak in the country**	**Stage 2 An outbreak in the country**	**Stage 3 Outbreak in region (25-50 km)**	**Stage 4 Outbreak in the field plot**	**Stage 5 Late blight not active**
> 60	Very High	50	50	75	100	100
40-60	High	50	50	50	100	100
20-39	Moderate	0	0	50	75	50
1-19	Low	0	0	50	50	50
0	No Risk	0	0	50	50	50

Table 8.4 Dates, fungicides and the dose applied over the course of the study.

Year	Active Substance	Date	Control	Full Dose	Half Dose	Irish Rules	Blight Management	Modified Irish Rules
2016	Ranman	7/11/2016	0	100	50	100	-	-
	Revus	7/19/2016	0	100	50	0	-	-
	Revus	7/27/2016	0	100	50	0	-	-
	Ranman	8/4/2016	0	100	50	0	-	-
	Ranman	8/12/2016	0	100	50	0	-	-
	Shirlan	8/20/2016	0	100	50	0	-	-
	Shirlan	8/28/2016	0	100	50	0	-	-
	Shirlan	9/5/2016	0	100	50	0	-	-
2017	Revus	6/23/2017	0	100	50	100	100	100
	Revus	7/3/2017	0	100	50	0	100	25
	Ranman	7/10/2017	0	100	50	0	100	25
	Ranman	7/18/2017	0	100	50	0	75	50
	Revus	7/25/2017	0	100	50	0	50	25
	Revus	8/1/2017	0	100	50	0	75	50
	Ranman	8/8/2017	0	100	50	0	75	25
	Infinito	8/16/2017	0	100	50	0	100	75
	Infinito	8/24/2017	0	100	50	0	100	25
	Shirlan	8/31/2017	0	100	50	100	100	100
	Shirlan	9/7/2017	0	100	50	0	75	0
	Infinito	9/14/2017	0	100	50	0	100	50
2018	Infinito	8/2/2018	0	100	50	0	50	25
	Revus	8/9/2018	0	100	50	0	50	25
	Revus	8/16/2018	0	100	50	0	50	25
	Ranman	8/23/2018	0	100	50	0	75	50
	Ranman	8/30/2018	0	100	50	0	100	50
	Infinito	9/6/2018	0	100	50	0	100	100
	Infinito	9/13/2018	0	100	50	0	50	25
	Ranman	9/20/2018	0	100	50	0	50	25
2019	Revus	7/18/2019	0	100	50	0	50	25
	Revus	7/26/2019	0	100	50	0	50	0
	Ranman	8/1/2019	0	100	50	0	75	25
	Ranman	8/8/2019	0	100	50	0	100	25
	Revus	8/15/2019	0	100	50	100	75	100
	Revus	8/22/2019	0	100	50	0	100	50
	Ranman	8/29/2019	0	100	50	0	100	50
	Ranman	9/5/2019	0	100	50	0	100	25

Table 8.5 Sampling dates and number of samples per sampling.

2016		2017		2018		2019	
10/6/2016	158	7/14/2017	5	8/20/2018	3	8/14/2019	250
		7/20/2017	3	8/28/2018	7	8/27/2019	198
		7/3/2017	12	9/24/2018	165		
		7/31/2017	38	9/5/2018	31		
		8/10/2017	154				
		8/23/2017	138				
		9/13/2017	125				

Table 8.6 Counts of genotyped isolates per year, programme and variety, over the course of study.

Year	Prog.	KE	BQ	RO	SE	CL	SM
2016	0	16	0	0	16	8	6
	100	9	0	0	10	7	5
	50	16	0	0	8	6	1
	IR	16	0	0	16	9	9
2017	0	66	17	23	33	14	0
	100	36	1	0	5	1	0
	50	53	0	5	1	0	2
	IR	54	11	19	15	3	0
	BM	56	0	1	0	0	0
	MIR	50	3	6	0	0	0
2018	0	31	8	19	10	2	0
	100	10	0	1	2	3	0
	50	13	0	4	0	0	0
	IR	36	10	7	7	0	0
	BM	24	1	4	0	0	0
	MIR	9	3	2	0	0	0
2019	0	54	12	17	19	9	1
	100	26	4	6	6	1	0
	50	33	10	5	6	0	0
	IR	52	15	13	7	2	0
	BM	46	7	9	8	2	1
	MIR	44	12	13	5	3	0

Table 8.7 The number and the proportion of samples assigned to specific MLGs for each sampling date were calculated for complete collection 2017 – 2019

Year	**Date**	**All samples**					**Subset**				
		No. of Samples	**8A1 (%)**	**13A2 (%)**	**6A1 (%)**	**13A2 +6A1 (%)**	**No. of Samples**	**8A1 (%)**	**13A2 (%)**	**6A1 (%)**	**13A2 +6A1 (%)**
2017	7/3	12	100	0	0	0	0	0	0	0	0
	7/14	5	100	0	0	0	0	0	0	0	0
	7/20	3	100	0	0	0	2	100	0	0	0
	7/31	38	84.2	0	15.8	15.8	22	86.4	0	13.6	13.6
	8/10	154	66.9	1.9	31.2	33.1	93	71	0	29	29
	8/23	138	54.3	0	45.7	45.7	60	61.7	0	38.3	38.3
	9/13	125	12.8	13.6	73.6	87.2	13	7.7	0	92.3	92.3
2018	8/20	3	100	0	0	0	3	100	0	0	0
	8/28	7	100	0	0	0	5	100	0	0	0
	9/5	31	96.8	0	3.2	3.2	22	100	0	0	0
	9/24	165	88.5	1.2	10.3	11.5	81	82.7	1.2	16	17.2
2019	8/14	250	80.8	10.4	8.8	19.2	113	90.3	8	1.8	9.8
	8/27	198	19.2	44.9	35.9	80.8	50	36	24	40	64

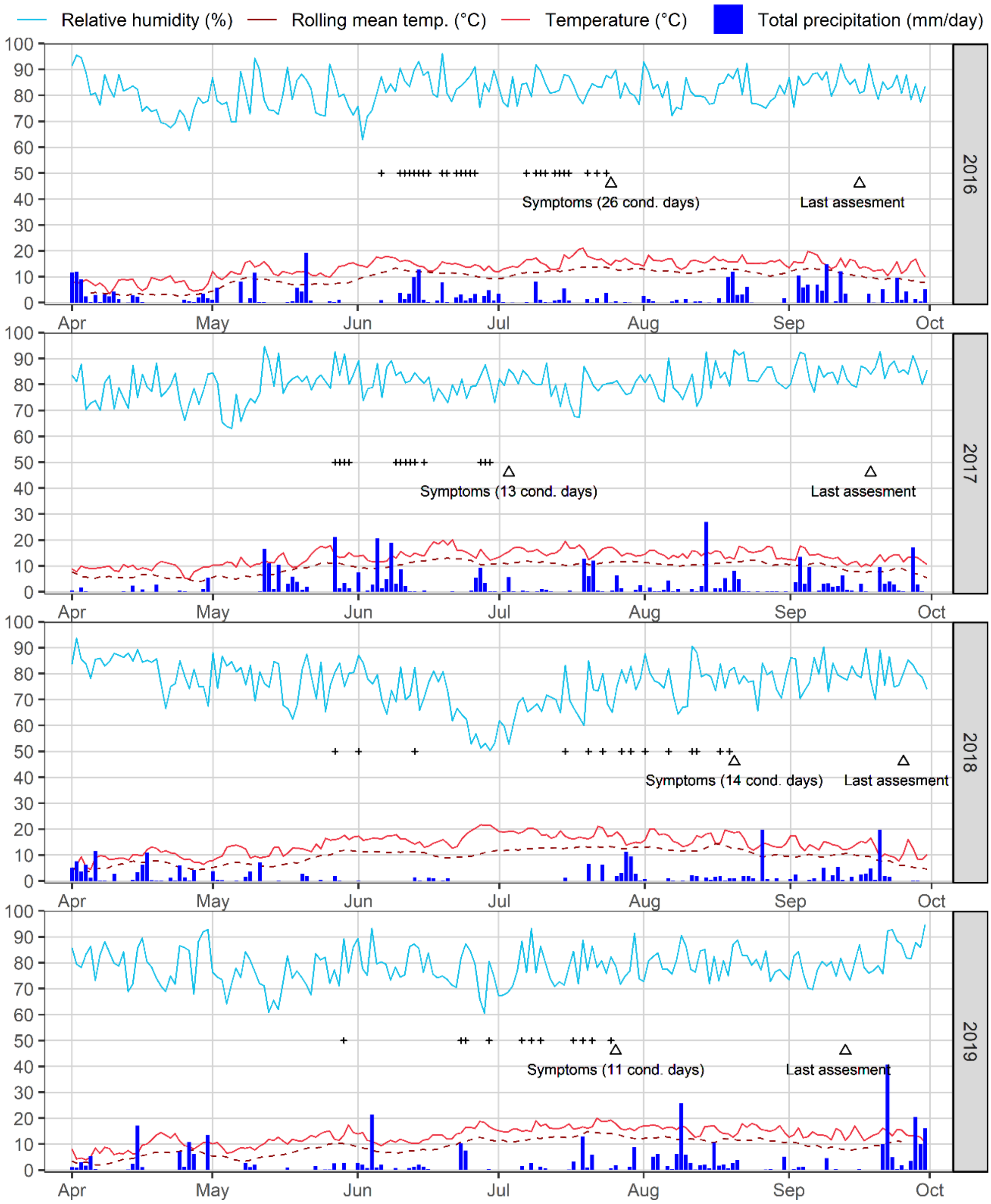

Figure 8.1 Daily weather conditions (average temperature and relative humidity, total rain, 10 day-rolling mean temperature), disease outbreak and the last assessment periods, and conducive days for the disease outbreak, over the course of the study, from 2016 to 2019, inclusively. Days were considered conducive if a minimum of conditions for blight development were recorded (minimum daily temperature ≥ 10 °C, average daily relative humidity ≥ 80% and total daily precipitation ≥ 0.2).

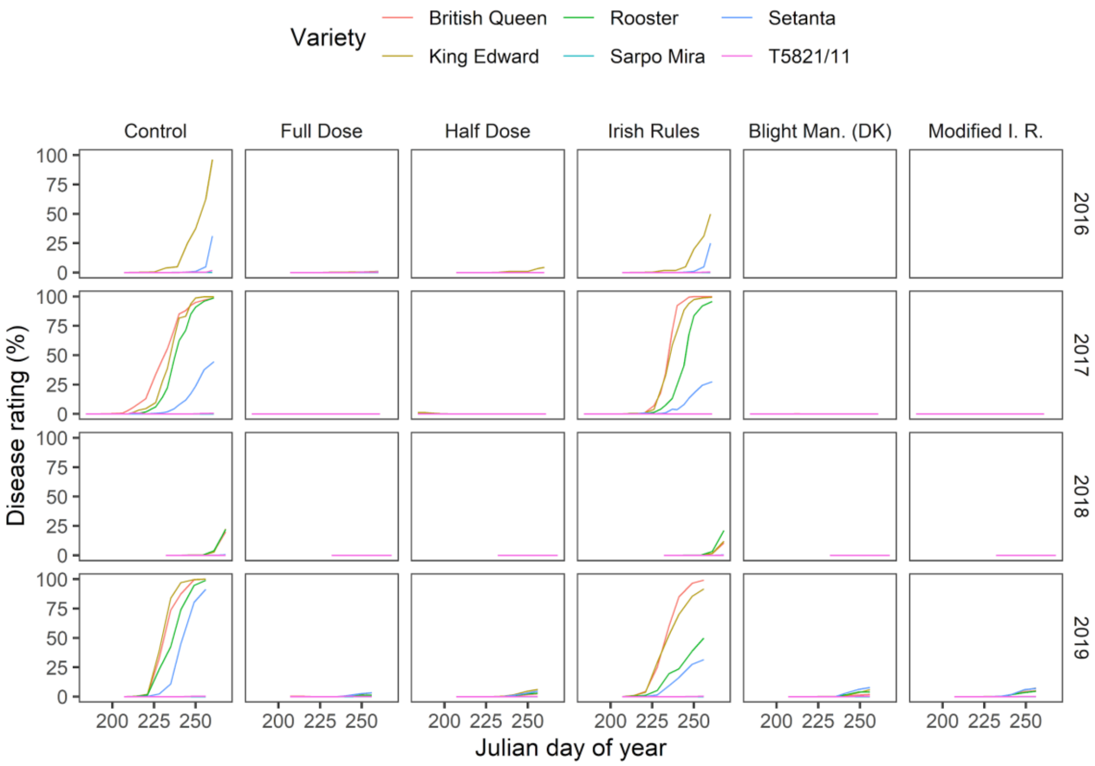

Figure 8.2 Disease progress curves representing means over replicates for all cultivar (different curves), programme (vertical facets) and year (horizontal facets) combinations from the field trial at Oak Park.

8.2. Supplementary material for Chapter 5

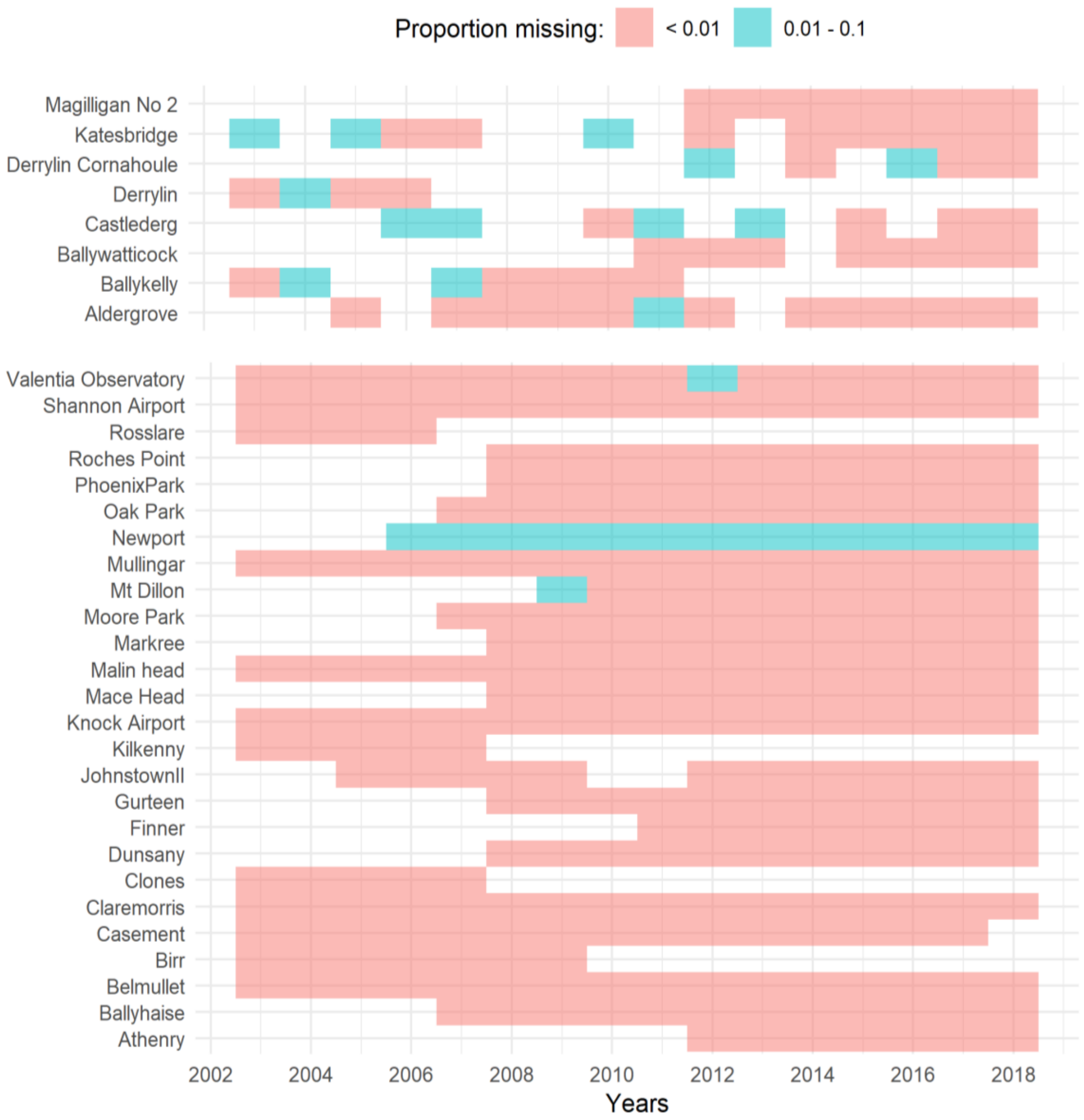

Figure 8.3 Weather stations selected for the model diagnostic performance evaluation.

Table 8.8 Sensitivity analysis parameter values.

	Levels						
Parameter	-3	-2	-1	0	1	2	3
TminInf	3	4	5	6	7	8	9
ToptInf	9	10	11	12	13	14	15
TmaxInf	23	24	25	26	27	28	29
ShapeInf	1	5	10	15	20	25	30
TminInfDir	3	4	5	6	7	8	9
ToptInfDir	20	21	22	23	24	25	26
TmaxInfDir	23	24	25	26	27	28	29
RfactInfDir	0.1	0.2	0.3	0.4	0.5	0.6	0.7
ShapeInfDir	0.01	0.1	0.25	0.5	0.75	1	2
RhminInf	83	84	85	86	87	88	89
RhoptInf	92	93	94	95	96	97	98
B0	0.01	0.37	1.37	2.37	3.37	4.37	5.37
B1	0.15	0.25	0.35	0.45	0.55	0.65	0.75
TminSpor	3	4	5	6	7	8	9
ToptSpor	17	18	19	20	21	22	23
TmaxSpor	23	24	25	26	27	28	29
ShapeSpor	0.5	1	1.5	2	4	8	12
n0Spor	$6.05*10^{-7}$	$6.05*10^{-6}$	$6.05*10^{-5}$	0.000605	0.00605	0.0605	0.605
rSpor	1.1	1.3	1.5	1.73	2	2.3	2.7
spor_dur	4	6	8	10	12	14	16
hr_before_spor	2	3	4	5	6	7	8
hr_after_spor	2	3	4	5	6	7	8
hr_after_inf	2	3	4	5	6	7	8
	Levels						
	-6	-5	-4	-3	-2	-1	0
RfactInf	0.4	0.5	0.6	0.7	0.8	0.9	1
RfactSpor	0.4	0.5	0.6	0.7	0.8	0.9	1

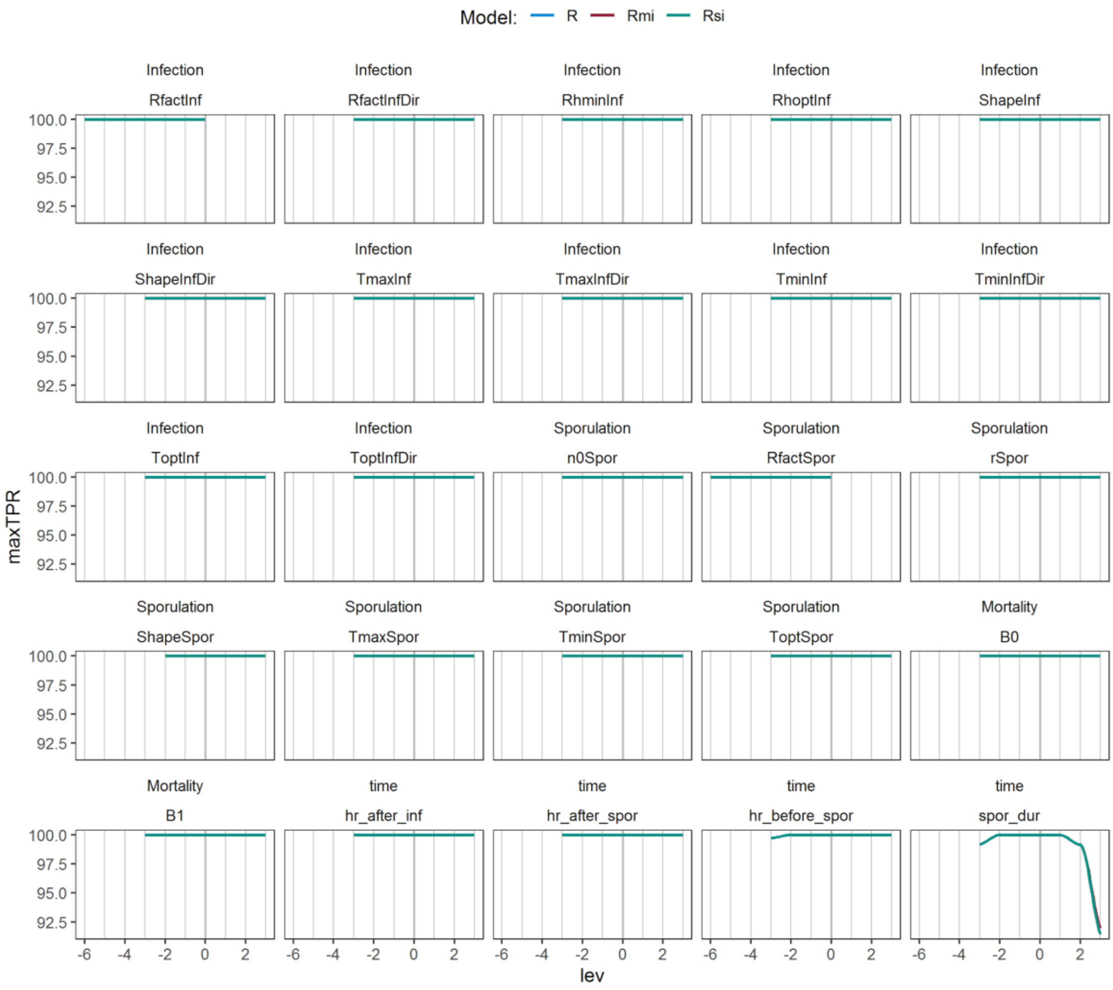

Figure 8.4 Local sensitivity analysis of the proposed model parameter variations +/-3 levels from the default values (from 0 to -6 levels for RfactInf and RfactSpor). Smoothed lines were fitted to the maximum achieved true positive rate (TPR) response using the LO

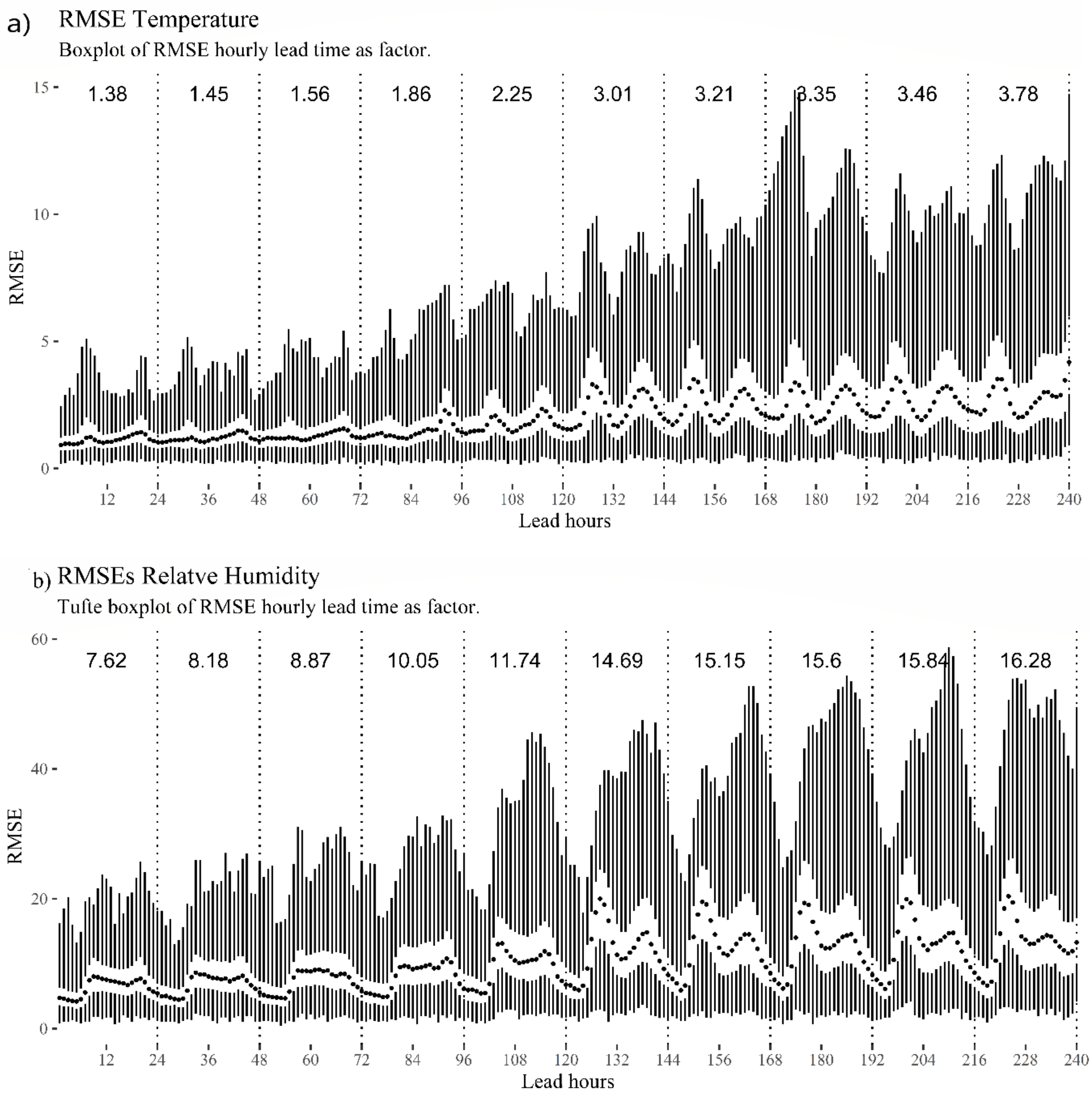

Figure 8.5 Root mean square errors of the 2 m HRES of: a) air temperature and b) relative humidity depending on the lead time.

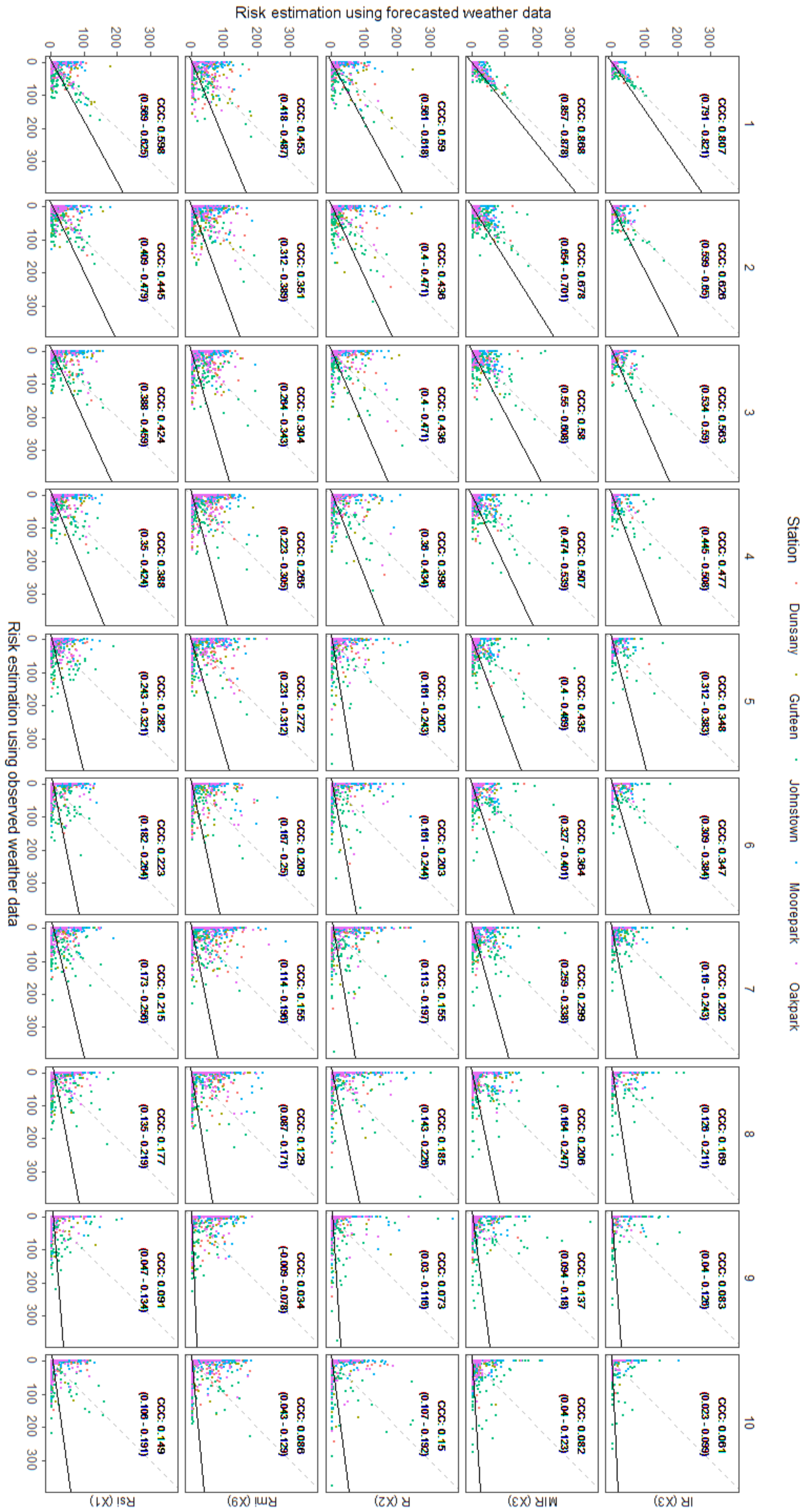

Figure 8.6 Concordance correlation coefficients and 95% confidence intervals between observed and predicted outputs of the risk prediction models over the 10-day lead time. Grey dashed line represents the line of perfect agreement and the black line the calculated

9. Appendix 2: Declarations of Co-authorship

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Authorship Declaration Form

Publication Details:

Thesis Chapter/Pages	3
Publication title	Evaluation of the 'Irish Rules': The Potato Late Blight Forecasting Model and Its Operational Use in the Republic of Ireland
Publication status	Published
Type of publication	Research article
Publication citation	Cucak, M., Sparks, A. H., Moral, R., Kildea, S., Lambkin, K., Fealy, R. (2018) Evaluation of Irish Rules, the Potato Late Blight Forecasting Model and its Operational use in Republic of Ireland. *Agronomy* 2019. 9: 515

Nature/extent of my contribution to the work detailed above is as follows:

Nature/Extent of Contribution	**Lead author**
For this paper, I conceived and developed the research design, acquired the data, implemented the code, analysed the results and wrote the manuscript	☒ Yes ☐ No

The following co-authors contributed to the work (all contributing co-authors):

Name	**Nature of contribution**
Adam Sparks	Software, visualisation and proof-reading
Rafael de Andrade Moral	Discussed the statistical analysis
Stephen Kildea	Contributed to discussions on research design
Keith Lambkin	Contributed to data curation and proof-reading
Rowan Fealy	Contributed to discussions on research design, proof-reading, minor comments to the text

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-author's contribution to this work

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Publication Details:

Thesis Chapter/Pages	4
Publication title	Optimising potato late blight management in the Republic of Ireland using risk prediction, varietal resistance and molecular tools.
Publication status	Under review in *Phytoathology*
Type of publication	Research article
Publication citation	Cucak, M., Moral, R., Fealy, R., Lambkin, K., Kildea, S. Optimising potato late blight management in the Republic of Ireland using risk prediction, varietal resistance and molecular tools.

Nature/extent of my contribution to the work detailed above is as follows:

Nature/Extent of Contribution	**Lead author**
For this paper, I conceived and developed the research design, implemented the field trials, isolate sampling and molecular characterisation, implemented the code, analysed the results and wrote the manuscript	☒ Yes ☐ No

The following co-authors contributed to the work (all contributing co-authors):

Name	**Nature of contribution**
Rafael de Andrade Moral	Consultation on the statistical analysis
Rowan Fealy	Contributed to discussions on research design and proof-reading
Keith Lambkin	Contributed to data curation and proof-reading
Stephen Kildea	Contributed to the research design and provided comments and edits on text

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-author's contribution to this work

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Authorship Declaration Form

Publication Details:

Thesis Chapter/Pages	5
Publication title	Rethinking the crop disease risk modelling: development of BlightR, the new potato late blight forecasting model.
Publication status	Manuscript ready for submission
Type of publication	Research article
Publication citation	Cucak, M., Esker P., Moral, R., Downes, P., Kildea, S., Fealy, R. Rethinking the crop disease risk modelling: development of BlightR, the new potato late blight forecasting model.

Nature/extent of my contribution to the work detailed above is as follows:

Nature/Extent of Contribution	**Lead author**
For this paper, I conceived and developed the research design, acquired the data, implemented the code, analysed the results and wrote the manuscript	☒ Yes ☐ No

The following co-authors contributed to the work (all contributing co-authors):

Name	**Nature of contribution**
Paul Esker	Discussed the research design and provided comments and edits on the manuscript
Rafael de Andrade Moral	Discussed the presentation of the model and results
Stephen Kildea	Contributed to discussions on research design
Paul Downes	Contributed to data curation and proof-reading
Rowan Fealy	Contributed to discussions on research design, proof reading, minor comments/edits to text

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-author's contribution to this work

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10. Appendix 3: Published Manuscripts

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Article

Evaluation of the ‘Irish Rules’: The Potato Late Blight Forecasting Model and Its Operational Use in the Republic of Ireland

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Received: 9 July 2019; Accepted: 2 September 2019; Published: 6 September 2019

Abstract: Potato late blight caused by *Phytophthora infestans* is one of the most important plant diseases known, requiring high pesticide inputs to prevent disease occurrence. The disease development is highly dependent on weather conditions, and as such, several forecasting schemes have been developed worldwide which seek to reduce the inputs required to control the disease. The Irish Rules, developed in the 1950s and calibrated to accommodate the meteorological network, the characteristics of potato production and the *P. infestans* population at the time, is still operationally utilized by the national meteorological agency, Met Éireann. However, numerous changes in the composition and dynamics of the pathosystem and the risks of production/economic consequences associated with potato late blight outbreaks have occurred since the inception of the Irish Rules model. Additionally, model and decision thresholds appear to have been selected ad hoc and without a clear criteria. We developed a systematic methodology to evaluate the model using the empirical receiver operating curve (ROC) analysis and the response surface methodology for the interpretation of the results. The methodology, written in the R language, is provided as an open, accessible and reproducible platform to facilitate the ongoing seasonal re-evaluation of the Irish Rules and corresponding decision thresholds. Following this initial analysis, based on the available data, we recommend the reduction of the thresholds for relative humidity and an initial period duration from 90% and 12 h to 88% and 10 h, respectively. Contrary to recent reports, we found that the risk of blight epidemics remains low at temperatures below 12 °C. With the availability of more comprehensive outbreak data and with greater insight into the founder population to confirm our findings as robust, the temperature threshold in the model could potentially be increased from 10 °C to 12 °C, providing more opportunities for reductions of pesticide usage. We propose a dynamic operational decision threshold between four and 11 effective blight hours (EBH) set according to frequency of the disease outbreaks in the region of interest. Although the risk estimation according to the new model calibrations is higher, estimated chemical inputs, on average, are lower than the usual grower’s practice. Importantly, the research outlined here provides a robust and reproducible methodological approach to evaluate a semi-empirical plant disease forecasting model.

Keywords: *Phytophthora infestans*; potato late blight; plant disease forecasting; decision support system; reproducibility

1. Introduction

Potato late blight (PLB) caused by *Phytophthora infestans* (Mont.) de Bary [1] is amongst the most destructive diseases of potato crops [2]; due to its fast reproductive cycle and aggressiveness, if left untreated, it can rapidly lead to the total destruction of the crop, either in the field or in storage, following harvest [3]. In Ireland, historical outbreaks of potato blight have had a significant cultural and economic impacts, and are partly attributed to mass starvation and the subsequent migration of large portions of the population fleeing from famine during the 1840s [4]. In Ireland alone, an estimated €5 million is spent annually on fungicides to control PLB, whilst globally the cost of control and losses are estimated to exceed €1 billion annually [5]. Although *P. infestans* can form overwinter oospores, under Irish conditions that is not believed to occur (Louise Cooke, personal communication), and typically the pathogen overwinters in infected tubers (in dumps, volunteers or infected seeds) [6]. The rate of late blight epidemic progression is highly dependent on the weather, with temperature, relative humidity and precipitation being the most important variables, the latter two closely being related [7]. Prolonged periods of humid and cool weather provide conditions favorable for pathogen sporulation [8]; short-lived sporangia subsequently spread through a mixture of rain splash and wind dispersal [9]. The disease impacts yield both indirectly and directly; indirectly, by reducing photosynthetic surface, and directly, when zoospores washed from foliage infect tubers in the ground [6].

Since the late 1970s, increasing globalization has resulted in the worldwide migrations of pathogen genotypes of both mating types, leading to the displacement of dominant, older clonal lineages or genotypes commonly referred to as US-1 [10]; this has facilitated the development and spread of new lineages, some of which demonstrate an increased aggressiveness [11]. This rise of new genotypes has introduced changes in the ecology of *P. infestans* [12–15]. The increasing genetic variability of *P. infestans* is likely reducing the durability of late blight resistance based on R gene stacks [16,17]. Although the structure of the Irish *P. infestans* population shows little genetic variation, it is dominated by a few clonal genotypes comprised of the more aggressive EU_13_A2 and EU_6_A1 strains [18,19]. New genotypes have established in Ireland and have been reported in higher frequencies in recent years [20–22]. In addition, the majority of potato production in Ireland is based on more susceptible potato cultivars, guided by market demand [23]. Population diversification, coupled with the influence of climate change [24], has led to increased difficulties controlling PLB [25,26]. Presently, due to the high risk of PLB epidemics in high-input agriculture, associated with increased aggressiveness of the pathogen, intensive fungicide regimes are routinely used; in Western Europe this equates to more than 10 applications per season [5,27], while in some countries crops can receive as many as 20 fungicide applications [28]. The need to develop late blight forecasting models for use as decision support tools has been long acknowledged as one of few integrated pest management (IPM) approaches available for PLB management, motivated by both environmental and economic factors [29–31]. In response to the environmental challenges posed from increased pesticide usage, the European Community Directive 128/2009 on the Sustainable Use of Pesticides provides strict guidelines for the sustainable use of plant protection products in order to reduce risks to human health and the environment [32]. Reliable disease forecasting offers the potential to reduce yield losses and crop inputs during unfavorable blight weather conditions, while also supporting an ex post facto justification for the use of plant protection products [3,31] in compliance with national and international regulations. Kessel et al. [33] have shown the necessity for environmental risk prediction to guide low input chemical protection to prevent the resistance breakdown of currently resistant potato cultivars. Forecasting systems that involve numerous alerts have been shown to be useful in that regard, when applied on a pathosystem involving a valuable crop and rapid disease [34].

At their core, crop disease forecasting systems employ algorithms, either mechanistic (fundamental) or empirically based, to predict disease cycles. Mechanistic based models are developed from laboratory experiments in controlled environment chambers, greenhouses or fields, and describe one or more segments of the host-parasite relationship as influenced by the environment [34]. Initially, the development of such models centered around the use of weather events to predict the development and onset of epidemics, and were mainly empirical in nature [35], based on the duration of weather events beyond a crude weather threshold (e.g., [36,37]) and phenological stage [38]. More recently, the use of mechanistic approaches have increasingly been employed in an effort to encompass more complex components of PLB epidemics, along with crop growth, chemical protection and cultural practices [11,33]. Due to its historical and relative economic importance, Ireland has a long history in the development of forecasting systems for use in PLB management.

Austin Bourke, one of potato late blight forecasting pioneers, developed the PLB model referred to as the 'Irish Rules' (IR). This model sought to include knowledge of the disease life cycle as opposed to being an entirely empirical approach [39]. For example, the selection of suitable weather criteria was determined from previously published laboratory experiments [8], rather than a retrospective analysis of historical weather during blight outbreaks, such as in the development of the 'Dutch rules' [36] and 'English rules' [40]. Bourke [41] found that the frequency of warnings produced by these latter models was too high under Irish conditions, and consequently, the IR were devised as an intermediate solution between empirical and process-based approaches [7,42], the aim of which was to increase the accuracy of disease life cycle interpretation.

The first attempt to undertake an evaluation of the IR dates back to the 1970s, when Frost [43] found no significant relationship between disease outbreaks at a site located in the south east of the country, Oak Park, Co. Carlow (now a Teagasc research center), and risk accumulation derived from weather data from two nearest synoptic weather stations, Mullingar and Kilkenny. Following re-analysis of this work, Keane [44], who included two additional surrounding weather stations, reported that IR were able to predict those outbreaks, although the exact evaluation methodology is not well documented. Reported field evaluations of the IRperformance have shown that the control according to the model outputs results in a significant reduction in fungicide usage, but with unsatisfactory disease control compared to the Negfry Decision Support System (DSS) [45] or routine fungicide protection [46]. More recently, as part of a pan-European initiative, a theoretical comparison of the risk accumulation between several European PLB risk prediction models has shown that the IR model simulates the lowest estimate of risk, due to its strict criteria [47].

The uptake and use of DSS in blight forecasting worldwide is limited largely due to the level of risk associated with a costly disease outbreak [31,48,49]. Risk adverse farmers use DSS to support an increased number of chemical treatments [34], which is often the case in Ireland. The main incentive for producers to use plant disease risk prediction in recent times is to increase economic benefit through cost reduction, and to comply with pesticide use policies required by supermarket chains [3,48]. Irish producers use, but do not necessarily rely on, operational blight warnings, hence it is now timely to review the IR and undertake an evaluation with a view toward refining the rules in light of recent changes in disease and plant ecology.

The aim of this study was, therefore, to provide a comprehensive, systematic and transparent method to facilitate an ongoing evaluation of the IR model, and its operational application, in the context of changes in the disease epidemiology and increasing regulation (market/policy). The impact of the proposed modifications on the potential number of treatments and fungicide usage is also determined and presented. Additionally, this research provides the first completely reproducible report in the area of plant disease forecasting, with a view to inspire and enable researchers elsewhere to modify, adapt and use the proposed methods and the code outlined here.

2. Data and Methods

The paper is structured as follows; initially we provide an overview of the site and available biological and weather data. The Irish Rules model is described, after which we present the evaluation of the model's parameter thresholds, currently employed operationally. Proposed model modifications and identified decision thresholds are further assessed by a comparison of treatment frequency and dose reduction. A schematic of the workflow is outlined in Figure 1. The list of frequently used abbreviations is presented in Table 1.

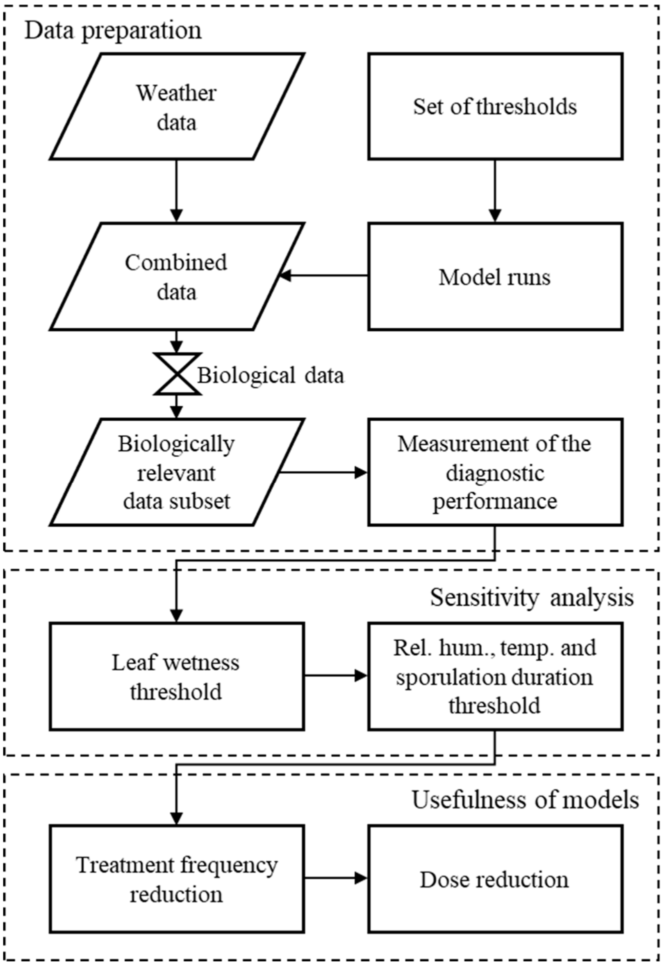

Figure 1. Simplified flowchart of the steps taken in Irish Rules (IR) model evaluation.

Table 1. List of frequently used abbreviations in the manuscript along with their full forms.

Abbreviations	Full Form
IPM	Integrated Pest Management
DSS	Decision Support System
PLB	Potato late blight
IR	Irish Rules
RHt	Relative humidity threshold
Tt	Temperature threshold
SDt	Sporulation duration threshold
LWt	Leaf wetness threshold
EBH	Effective blight hours
ROC	Receiver operating characteristic
AUROC	Area under the ROC curve
FP	False positive
TP	True positive
FN	False negative
TN	True negative

2.1. Site Description

Oak Park, Co. Carlow, Ireland (latitude: 52.8560 and longitude: −6.9121), a Teagasc (Irish agricultural advisory body) research center, is located in the south east of Ireland. Soils are composed of light limestone gravelly soils and heavy textured soils derived from limestone till.

Typical weather conditions calculated over the growing period (April to October) for the period 2007 to 2016 indicate that average daily relative humidity values were typically high throughout the potato growing season, which is a characteristic of Irish conditions more generally. The mean temperature over the period was 13 °C, relative humidity was 80.2% and average sum of precipitation was 398.31 mm. The night time temperatures during the early part of the potato growing season were low, with averages of 6.6 °C in April and 9.2 °C May.

2.2. Data

2.2.1. Biological Data

Planting dates and primary disease outbreak data were acquired from the Teagasc breeding program field trial records for the period 2007 to 2016. The breeding program trials consisted of 25–60 potato varieties in all years, representing all levels of susceptibility to potato late blight. Trials were laid out in randomized complete block design, with six blocks and plots of 20 plants. The seeds were propagated in accordance with the seed certification scheme of the Irish Department of Agriculture, Food and the Marine (DAFM) to ensure no latently infected tubers; the *P. infestans* inoculum originated from natural sources. Crop rotation was undertaken on a five-year cycle. Plots did not receive any fungicide treatments. All plots were visually inspected for disease occurrence on a weekly basis, from crop emergence, and generally more frequently during periods of humid weather. That data provided the information about the disease outbreaks used in the model analysis and evaluation outlined herein.

Planting dates in the biological data are somewhat later compared to the usual agricultural practice in Ireland, which is suitable for the analysis because the healthy green tissue is present throughout summer. Outbreak dates vary from 26th of June to 23rd of August.

2.2.2. Weather Data

Hourly weather data for the historical period under investigation, was acquired from the Met Éireann synoptic weather station at Oak Park. The weather variables obtained include the hourly air temperature (°C) and relative humidity (%) at 2m and the total hourly precipitation (mm). The trial sites were within a radius of 500 m of the weather station in all years and were located on flat ground with no physical barriers in between them.

Availability of good quality weather and biological data is crucial for successful calibration and evaluation of plant disease forecasting models [50]. Quality control of the available weather data and appropriate imputation of missing values is often disregarded in agriculture, which could lead to imprecise or incorrect results [47,51]. Post-processing of the weather data undertaken as part of this study included checking for duplicate entries and recording values outside of 'expected' ranges, determined using histograms. The data had only 6 missing values for both precipitation and temperature, and 7 missing values for relative humidity, over the period of interest. These short intervals of consecutive hours of missing data for temperature and relative humidity were imputed by spline interpolation using the Forsythe, Malcolm and Moler method [52], as suggested by Shah et al. [53].

2.2.3. The IR Model and Its Operational Use

According to original Irish Rules [41], illustrated in Figure 2, periods with temperatures ≥ 10 °C and relative humidity ≥ 90% provide the necessary environmental conditions considered conducive for potato late blight. These periods are further split into:

- Sporulation period—the initial stage considered necessary for the formation of sporangia is set to a minimum of 12 consecutive hours;
- Infection period—starts after the 12 hour sporulation period is completed. If the surface of the plant is not wet at the beginning of the infection period, effective blight hours (EBH) begin accumulating from the 16th hour (12 h sporulation period + 4 h = 16 h); when the surface of the plant is wet at the beginning of the infection period, the effective blight hours' (EBH) accumulation is reduced by a period of 4 h (16 h − 4 h = 12 h). The leaf (surface) wetness (LWt) is considered present if there was a considerable amount of precipitation (≥ 0.1 mm) during the time window of 3 h before and 3 h after the 12th consecutive hour of sporulation. The infection period lasts until conditions (temperatures ≥ 10 °C and relative humidity ≥ 90%) are not broken for more than 5 consecutive hours, required for spore survival.

Hours fulfilling these criteria are termed effective blight hours (EBH). The risk of potato late blight outbreak estimation is based on the longevity of the infection period, expressed as a sum of the EBH.

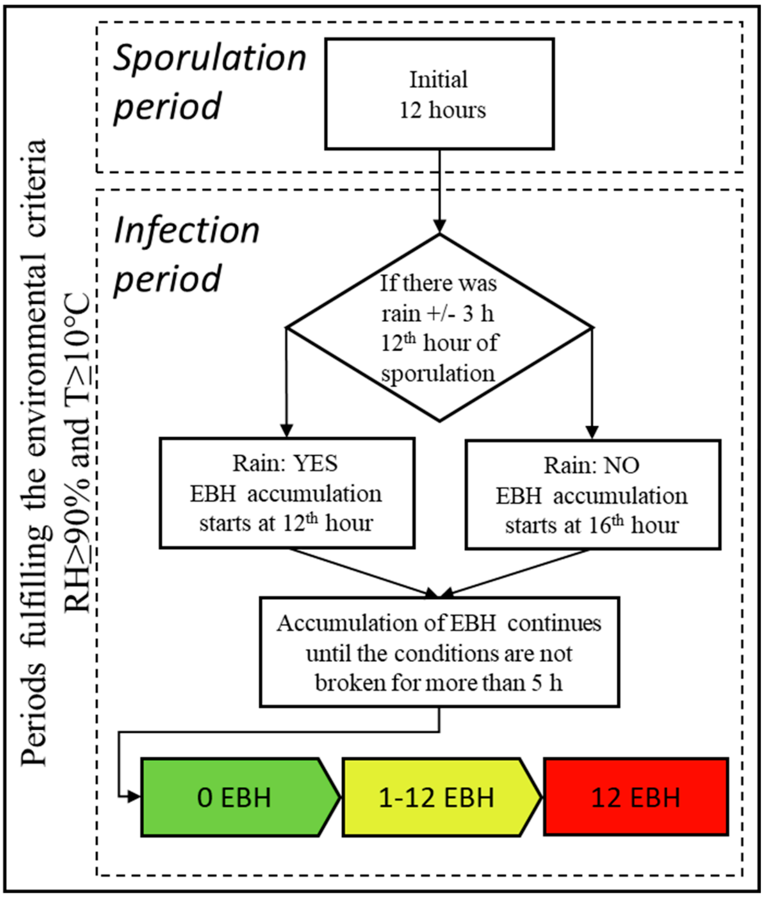

Figure 2. Simplified presentation of the Irish Rules algorithm. The operational warning threshold scale is presented as the "traffic light" scheme, ranging from green (no warning), to yellow when the warning considered and red when the warnings are issued without delay.

Currently, the warning system is used operationally by the national meteorological service, Met Éireann. The IR are utilized in their original form to support the blight warning service with issuing spray advice [44,46]. The decision on issuing a blight warning and its termination is determined by the meteorological officer on duty after visual inspection of the IR model outputs based on a 10-day numerical weather prediction (NWP) model forecast from the European Centre for Medium-range Weather Forecasts (ECMWF). Warnings are disseminated through the Met Éireann web portal, radio and television weather broadcasts and mobile application. Operationally, a decision threshold to issue a blight warning is considered for an accumulation of 12 EBH. Additionally, if a continuous spell of mild, humid and damp weather lasting 24 h or more is expected, a blight warning may be considered, even if it does not explicitly meet the warning criteria. Blight warnings are typically issued 2 to 6 days in advance and include information about areas likely affected, duration of the spell and opportunities for spraying, where possible. The decision threshold of 12 EBH was established from operational experience since the 1950s (for example, between 1950 and 2000, a network of blight scouts reported on regional blight outbreaks and the progress of epidemics) although it was not systemically documented. Currently, the May 1st is the 'Zero date'. a date threshold after which warnings are considered valid.

2.3. Evaluation Procedure

2.3.1. Model Thresholds under Evaluation

The IR is a set of processes mimicking the 'behavior' of a mechanistic model. The transition between these processes is determined by an empirically derived set of thresholds, which ultimately influence the risk estimation expressed as the duration of an infection period. Four of these primary thresholds were subjected to a sensitivity analysis. The environmental thresholds for relative humidity (RHt), temperature (Tt) and the duration of period considered as necessary for the inoculum production—the sporulation duration threshold (SDt), were varied from −3 to +3 units of their respective default values (Table 2). To assess the leaf surface wetness indicator, the default estimation using rain (>0.1 mm) was compared to using the combined rain and relative humidity thresholds as indicators (Rain > 0.1 mm and RH ≥ 90). The model was run using all combinations of model variable thresholds. Outputs were then combined with the hourly weather data for further analysis.

Table 2. Model variable threshold variations evaluated in the analysis.

Range	Relative Humidity (%) (RHt)	Temperature (°C) (Tt)	Sporulation Duration (hours) (SDt)
+3	93	13	15
+2	92	12	14
+1	91	11	13
Existing	**90**	**10**	**12**
−1	89	9	11
−2	88	8	10
−3	87	7	9

2.3.2. Analysis of Diagnostic Performance

The period considered in the sensitivity analysis was from planting date to the recorded disease outbreak in each season, which was further split in two segments (Figure 3):

- **No infection period:** Considered the period when the healthy (susceptible) host was present, but no infections were observed. This period lasted from emergence, which was estimated to start three weeks after planting, to 14 days prior to the first observation of the disease in the field. Specificity or true negative rate was measured during this period. It was considered that each warning during this period activated a chemical treatment which provided protection for the subsequent period of 7 days, and was considered as a false positive (FP). True negatives (TN) were calculated as a proportion of the remaining period, when fungicide protection was not recommended.
- **Warning period:** Considered a period when infections occurred and was assigned a 10-day time window, starting 14 days and ending 4 days prior to the disease being observed in the field. A risk warning of disease outbreak 10 days ahead has been reported as an optimum warning time [54], and a period of four days was considered to be a minimum incubation period. Sensitivity or

true positive rate was assessed during ‘warning period’. Warning periods where the value of the warning threshold was reached and would trigger a fungicide treatment, is considered as a true positive (TP) and if the warning was not issued false negatives (FN).

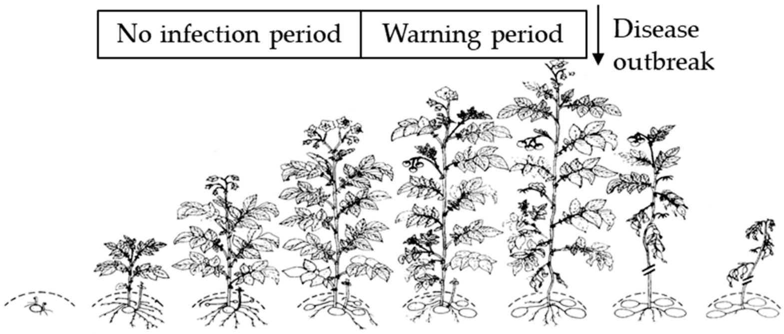

Figure 3. Simplified schematics illustrating the temporal split of the data for the diagnostic performance calculation (source [55]).

Contingency tables were created with sensitivity and specificity values from a confusion matrix (as shown in Table 3) for each evaluated disease warning decision threshold for all model outputs. The range of decision thresholds used as cut-off points, or the level of risk leading to treatment, was from 1 to 18 EBH.

Table 3. Confusion matrix used for calculating the cutoff points for contingency tables.

Disease Forecast	**Disease Observed**	
	Yes	**No**
Yes	TP Warning period	FP No infection period
No	FN Warning period	TN No infection period
Measures of the performance	Sensitivity TP/(TP + FN)	Specificity TN/(TN + FP)

2.3.3. Receiver Operating Characteristic (ROC) Curves

The performance of each model was assessed using receiver operating characteristic curves (ROC). An ROC curve is a graphical technique for assessing model predictive ability through the relationship of specificity and sensitivity [56,57]. Empirical ROC curves were constructed with cut-off points for different thresholds on a discrete scale. Specificity (i.e., 1-specificity) on the x-axis and the sensitivity on the y-axis was plotted for each cut-off point. The accuracy of the model was evaluated based on the area under the ROC curve (AUROC), serving as a single measure of the discriminatory ability of the model [58,59]. The area under the curve (AUROC) was calculated for model outputs using the trapezoidal rule [59]. In general, an AUROC of 0.5 suggests no discrimination (i.e., the model is no better than a random predictor); as the value of AUROC approaches 1, the better the predictive value of the model are [60].

2.4. Statistical Analysis

2.4.1. Evaluation of Leaf Wetness Estimation

In order to evaluate the LWt estimation, two indicators are evaluated; values of hourly rain (rain > 0.1 mm) and rain and humidity (rain ≥ 0.1 mm and RH ≥ 90%). The model runs were split in two groups, with each run having a measure of the LWt indicator in each group. The difference between paired samples was calculated; and normality of the sample distribution was visualized using a histogram and density plot, and assessed with the Shapiro–Wilk test. Where samples did not conform to a normal distribution, a non-parametric paired two-sample Wilcoxon rank sum test was carried out to assess the difference between groups. Model outputs with higher performing LWt indicators were kept for further analysis.

2.4.2. Evaluation of Main Variable Thresholds

Boxplots were used for the initial visualization of change in model accuracy, with a change in each factor level of a single variable. A polynomial surface, using locally estimated scatterplot smoothing (LOESS), was fitted to the AUROC data using each variable as a predictor and all possible interactions, to model the trend of AUROC response with change for each variable threshold individually.

An orthogonal polynomial regression model was used to study the sensitivity of the AUROC with the change in the model variable thresholds and their interactions. Polynomial response models have shown to be useful for summarizing relationships [61]. The response surface methodology [62] consists of a group of mathematical and statistical procedures used for approximating the functional relationship between a selection of control variables which have an influence on the response variable [63]. The polynomial models were fitted sequentially, starting from first order and adding higher degree terms up to the fourth order. Model fits were assessed with their respective R^2-value and an R^2 adjusted-value, a Shapiro–Wilk test of residuals and examination of the fitted surface, until overfitting was indicated on the response surface plane. Additionally, the non-parametric local regression (LOESS) was used to obtain predicted values for the four-dimensional response surface, using RHt, Tt and SDt, and all three and two-way interactions as the predictors. The extent of agreement was then compared between polynomial regressions and the LOESS regression to aid in choosing the degree of the polynomial regression, measured using the concordance correlation coefficient [64]. The lowest-degree polynomial that accomplished the required degree of approximation was subsequently adopted. The higher degree polynomial models offer increased flexibility in the response surface, but they need to be fitted with caution due to the potential to 'overfit' these models [61].

The fitted polynomial equation was then expressed in the form of three-dimensional (3D) surface plots, in order to visualize the interaction between the changes in thresholds (Table 2) and the response variable. The graphical representation provides a method to visualize the relationship between the response and experimental levels of each variable, and the types of interactions between the test variables.

Due to awareness of constraints of the limited data set, we relied on current knowledge of PLB disease epidemiology as a guide for interpretation of the results. Hence, a suite of model versions was selected based on the results of the sensitivity analysis, which were subjected to further examination based on the position and grouping of the cut-off points in the ROC space. Defining an optimal decision threshold is not a trivial task [56]. The high cost of false negatives (FN) associated with potential onset of PLB epidemics [14,65] predetermines that the decision threshold should lie closer to the upper right-hand corner of the ROC curve, in order to minimize the associated risk of the disease development [66].

2.5. Treatment Frequency and Dose Reduction

The crop risk prediction model is useful only if it provides the same level of protection as the standard practice, while reducing necessary costs and labor [32,34]. In this theoretical study, we do not account for the differences in the active ingredient or the type of the fungicide, but merely try to associate a reasonable estimation of possible reductions in the number of treatments or/and dose reduction with predictive power at predefined decision thresholds. After defining the 'optimum' sets of model thresholds, it was necessary to compare the number of treatments and the pesticide usage recommended by the model versions compared to standard growers' practice. This was done in order to determine if the recommended model parametrizations are economically and environmentally viable. Currently, spray intervals range from 5 to 7 days under Irish conditions, which are the intervals we accounted for in this study. We evaluated three model parametrizations—the IR with the default parameters (Section 2.2.3, The IR Model and Its Operational Use), and two improved parametrizations as identified in the subsequent analysis.

We assume that planting starts the day after the daily average soil temperature is greater than 8 °C for three consecutive days after the 1 April. This is a common practice in Ireland, in line with recommendations from the national advisory body, Teagasc. Farmers typically start fungicide treatments as soon as the emergence progresses over 50% and continues until the potatoes' above-ground potato haulm completely die off, typically three weeks after desiccation. Here, we assume that the growing season lasts 120 days. However, the pesticide protection continues during these three weeks, until the potato above-ground potato haulm is desiccated.

The difference between standard growers' practice and model versions is evaluated in two ways:

1. Reduction in the number of treatments, split into:
    - Model guided: A fungicide treatment is applied every time the warning threshold is reached with a minimum period of 5 days prior to following treatment, and;
    - Model and calendar guided: A minimum of 5 and maximum of 10 days between treatments.

The sum of recommended treatments is calculated for all decision thresholds and seasons. The resulting summaries are presented visually as point graphs. A LOESS curve was fitted to estimate the minimum decision threshold where the protection according to the model is for fewer treatments then the usual 5 or 7-day practice.

2. Dose reduction based on 7-day calendar treatment. Currently, Irish growers do not rely on the operational warnings issued by the Met Éireann, but do increase the dose or use stronger, often less environmentally friendly, formulations during those periods identified as at risk. Possible dose reductions are calculated for the usual 7-day calendar treatment. The dose reductions are based on the maximum risk calculated by the model during the 7-day period between treatments. The maximum dose is applied if the risk is over 12 EBH, which is the current warning decision threshold in Ireland.

2.6. Software Used for the Analysis and the Reproducibility

This analysis has been implemented in R, a freely available statistical programming language [67]. A portion of the data was imported using readxl [68]. Packages used for data munging: tidyverse [69], zoo [70], data.table [71] and pracma [72]. Packages used for visualisations: ggplot2 [73], cowplot [74], ggrepel [75], rsm [76] and ggthemes [77]. Univariate series imputation was implemented using functions from package imputeTS [78]. Package zoo [70] was used for processing dates. Formatting of tables was done with pander [79]. Packages rmarkdown [80] and knitr [81] were used for creating a reproducible compendium. Package here [82] was used to ensure reproducibility on different platforms. Programming functions from R.utils [83], string manipulation with mgsub [84] and statistical tests and visualizations: rcompanion [85].

The full analysis can be reproduced using code and data archived at https://mladencucak.github.io/AnalysisPLBIreland/.

3. Results

3.1. Evaluation Leaf Wetness Estimation

A Wilcoxon signed rank test showed that there was a significant difference ($p < 0.001$) between AUROC values for the models. Using the combined estimators RH ≥ 90% and rain > 0.1 mm as indicators for leaf wetness, were significantly higher than using only rain > 0.1 mm. The median

AUROC for the method based on rain and RH thresholds was 0.735 compared to 0.695 for the method only using rain indicator (Figure 4).

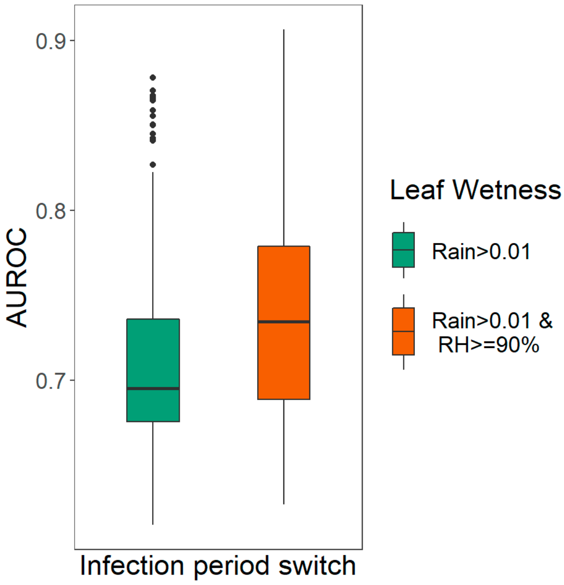

Figure 4. Group median difference between models with leaf wetness estimation using rain (>0.1 mm) or the combined rain and relative humidity (rain > 0.1 mm and RH ≥ 90%) as an estimator.

3.2. Evaluation of Main Variable Thresholds

Scatterplots with LOESS smoothing and boxplots indicated a non-linear relationship with change in each factor level. The AUROC was found to increase when the thresholds for relative humidity and sporulation duration were reduced. Conversely, an increase in the temperature threshold resulted in an improvement in the predictive power of IR. For all variables, levels of predictor variables showing an increase in AUROC also show higher levels of dispersion, indicating the necessity to investigate the interactions.

A statistically significant cubic polynomial model ($F_{3,323} = 105.9$, $p < 0.0001$) was fitted to the AUROC data with the proportion of variance explained by the model of 0.8617 and 0.8535 for R^2 and adjusted R^2 values, respectively (Table 4). Diagnostic plots of residuals versus order of the data and histogram indicated no violation of the normality assumption. The forth order polynomial model showed only a slight increase in the R^2 and adjusted R^2 values, while the Shapiro–Wilks test indicated a lack of normality in the distribution of the residuals. Visual assessment of the response surface plotted with the 4th order model indicated a potential overfitting problem. Linear and quadratic fits had lower R^2 and adjusted R^2 values and were considered unsuitable. In addition, the predictions from the third-order polynomial model agreed the most with the local non parametric regression (concordance correlation coefficient [64] of 0.9896 (95% CI: 0.9876; 0.9913)), hence this model was deemed to adequately reproduce the behavior of the response surface.

Table 4. The table of fit statistics for polynomial models from first to fourth order fitted to area under the receiver operating curve (AUROC) data.

Order	No. of Parameters	Degrees of Freedom	R^2	Adj. R^2	F Statistic	p Value	Shapiro -Wilk Test	Shapiro – Wilk p-Value
1	4	339	0.637	0.634	198.68	<0.001	0.993	0.137
2	10	333	0.758	0.751	115.98	<0.001	0.997	0.813
3	20	323	0.861	0.853	105.89	<0.001	0.996	0.610
4	35	308	0.881	0.868	67.12	<0.001	0.990	0.030

The 3D response surface for the AUROC against any two independent variables while keeping the third independent variable at −3, 0 and +3 levels, respectively, is presented in Figure 5. In total, nine 3D response surfaces were obtained by considering all possible variable combinations.

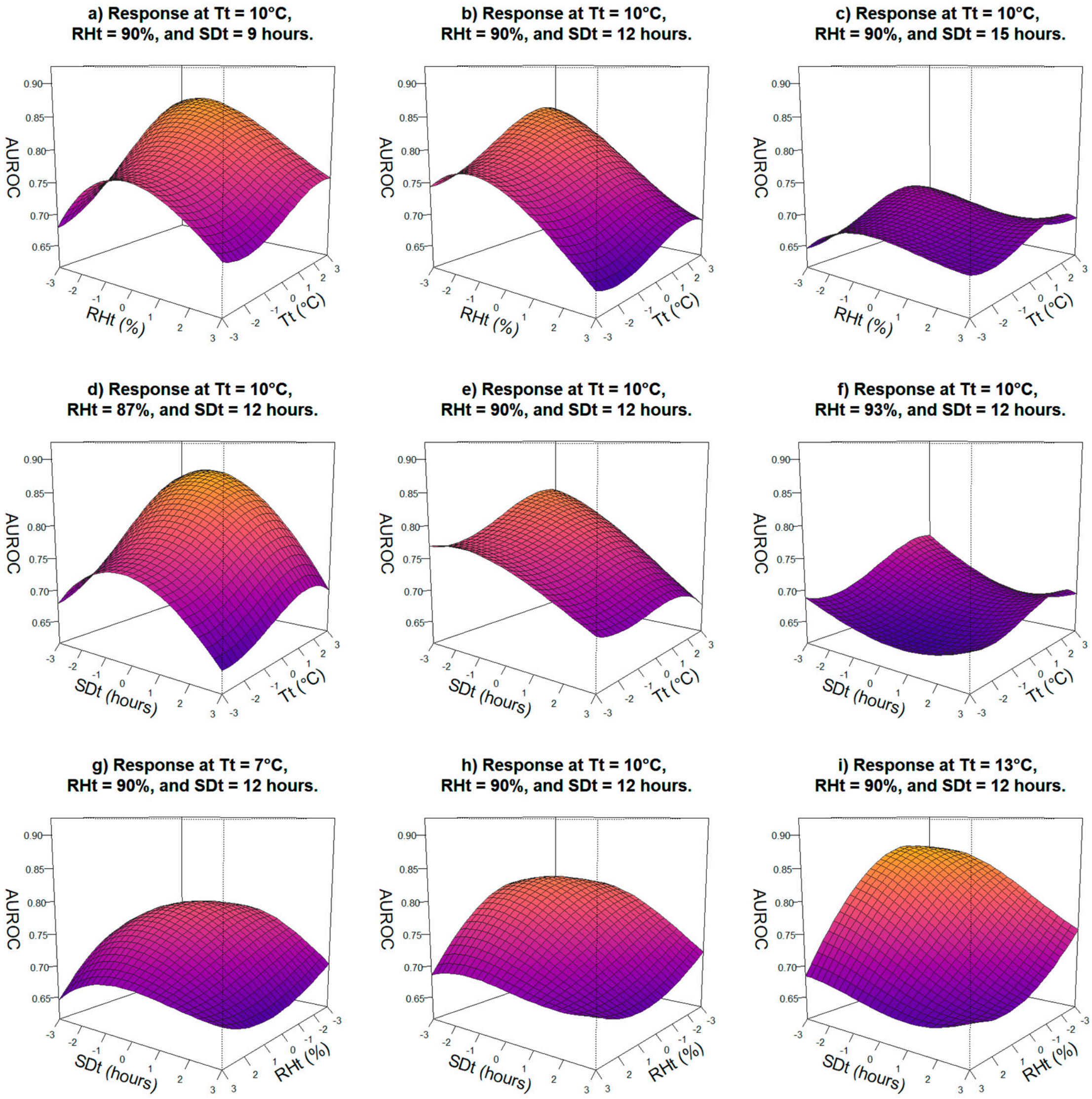
a) Response at Tt = 10°C, RHt = 90%, and SDt = 9 hours.
b) Response at Tt = 10°C, RHt = 90%, and SDt = 12 hours.
c) Response at Tt = 10°C, RHt = 90%, and SDt = 15 hours.
d) Response at Tt = 10°C, RHt = 87%, and SDt = 12 hours.
e) Response at Tt = 10°C, RHt = 90%, and SDt = 12 hours.
f) Response at Tt = 10°C, RHt = 93%, and SDt = 12 hours.
g) Response at Tt = 7°C, RHt = 90%, and SDt = 12 hours.
h) Response at Tt = 10°C, RHt = 90%, and SDt = 12 hours.
i) Response at Tt = 13°C, RHt = 90%, and SDt = 12 hours.

Figure 5. 3D surface for interaction effect of two variables with third variable fixed on a specific level. 3D surface plots represent interaction between: Tt and RHt, with SDt of 7 (**a**), 10 (**b**) and 13 h (**c**); SDt and Tt, with RHt fixed at 87% (**d**), 90% (**e**), and 93% (**f**); and SDt with RHt, with Tt of 7 °C (**g**), 10 °C (**h**), and 13 °C (**i**).

Figure 5a–c depicts the interaction between RHt and Tt, keeping SDt at its −3, 0 and +3 levels. Figure 5a shows that AUROC increased with increasing Tt, up to 12 °C, and reduced RHt to 88% when SDt was set at 9 h. If SDt is kept at the threshold of 12 h, a decrease in the AUROC is evident (Figure 5b), while an increase in SDt to 15 h results in a significant reduction in model accuracy (Figure 5c).

It can be observed from Figure 5d–f, that the accuracy of the model increases with an increase in Tt and a reduction in SDt. The area of AUROC of above 0.85 is achieved with the reduction of sporulation period for 2 h and an increase of the temperature threshold of 2 °C. This effect on the AUROC is reduced below 0.85 with SDt at the default threshold (12 h); while increasing SDt results in a large reduction of the AUROC, to the level of an unacceptable prediction model.

Figure 5g–i shows the interaction between RHt and SDt, keeping Tt at its −3, 0 and +3 levels. Increasing Tt positively influences the model accuracy. Over the range of the Tt factor levels, the area with the highest AUROC values is 0.79 by 0.83 by 0.87, associated with a temperature threshold reduced to 7 °C, the default threshold and the one increased to 13 °C.

Overall, results indicate that reducing RHt to 88% and SDt to 10 h and increasing Tt to 12 °C results in the largest improvements in the overall predictive performance of the model (Figure 5a,b,i). Variations in Tt do not have the same magnitude effect on the model accuracy, as the manipulations of RHt and SDt do.

Figure 6a–c depicts the ROC curves for the individual, selected model variable thresholds for RHt (88%), SDt (10 h) and Tt (12 °C), respectively. Adjusted RHt and SDt provides improvement in terms of model specificity, with the grouping of cut-off points moving upwards in the ROC plane and having no associated FN; overall accuracy displays some improvement. Overall, adjusting RHt (Figure 5b) resulted in the greatest improvement in the model accuracy, with sensitivity of 0.8 and high corresponding decision threshold scale of 3–9 EBH. Practically, this means that the risk accumulation of up to 9 EBH was necessary for the onset of the disease in eight (out of 10) years. Adjusting Tt only influenced the model performance with the sensitivity similar to the default model variable thresholds, having two FN predictions, indicating that the change in Tt had the least impact on the improvement in model performance (Figure 5c).

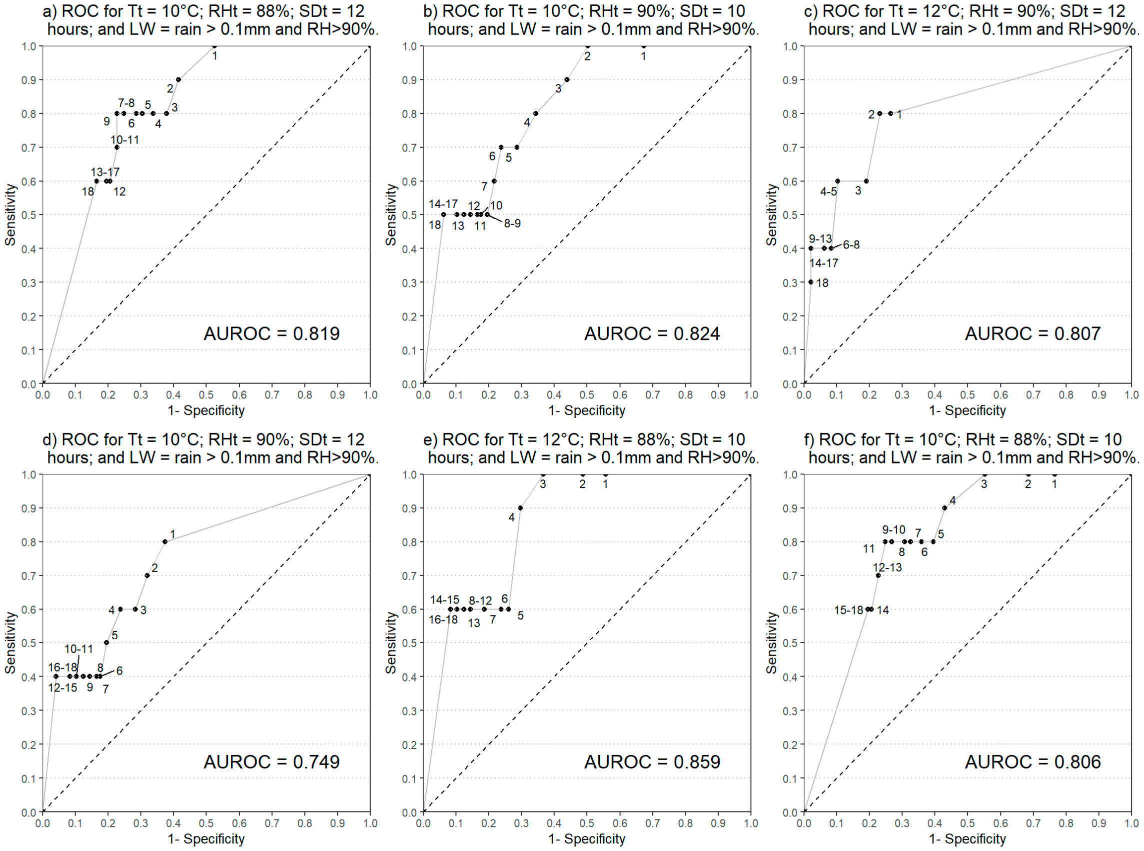

Figure 6. ROC curves for the model parameterizations according to the results of the sensitivity analysis. The IR model parameterizations with the change in a single model variable threshold: relative humidity (**a**), sporulation duration (**b**) and the sporulation duration (**c**), followed by the default (**d**), optimized (**e**) and low risk (**f**) model parametrization.

The performance of the IR model with default variable thresholds is presented in Figure 6d. ROCs for the existing IR variable thresholds revealed a lack of specificity, with no risk accumulation in two years, while the current operational blight warning threshold was reached in only four out of ten years.

A model with variable thresholds recommended by the analysis of the response surface (SDt = 10 h, RHt = 88% and Tt = 12 °C), hereafter referred to as the optimized model (Figure 6e), shows improved performance, with no FP. The disease outbreak was correctly indicated in all years of the study, although the sensitivity dropped significantly in six years (corresponding to decision thresholds higher than 5 EBH), indicating that the maximum acceptable decision threshold for this model variation is 4 EBH, corresponding to sensitivity of 0.9.

An additional model variation was chosen for further analysis, hereafter referred to as the low risk model, with optimized SDt (10 h) and RHt (88%); Tt kept at the original, default threshold of 10 °C (Figure 6f). This was guided by the limited impact of changing the temperature threshold on the specificity of the model (Figure 6c), limitations related to the size of the biological data set used in the evaluation, a lack of knowledge of the pathogen founder population and the risk associated with possible disease outbreak. The ROC curve for this model showed improvement in the sensitivity of the model, with eight years having up to 11 EBH accumulations. While a drop is evident in the AUROC value due to loss in specificity, the grouping of decision threshold points higher in the ROC plane allows consideration for another decision threshold as high as 11 EBH with a Sensitivity of 0.8.

3.3. Treatment Frequency and Dose Reduction

Assuming the usual calendar spray practice was followed during the period investigated, the number of treatments calculated for the seven and five-day calendar spray programs were 15 and 22, respectively. The decrease in the number of recommended treatments with the increasing decision threshold approximated with the LOESS curve is presented in Figure 7. All model versions provide a reduction in the number of treatments compared to the standard five-day calendar treatment.

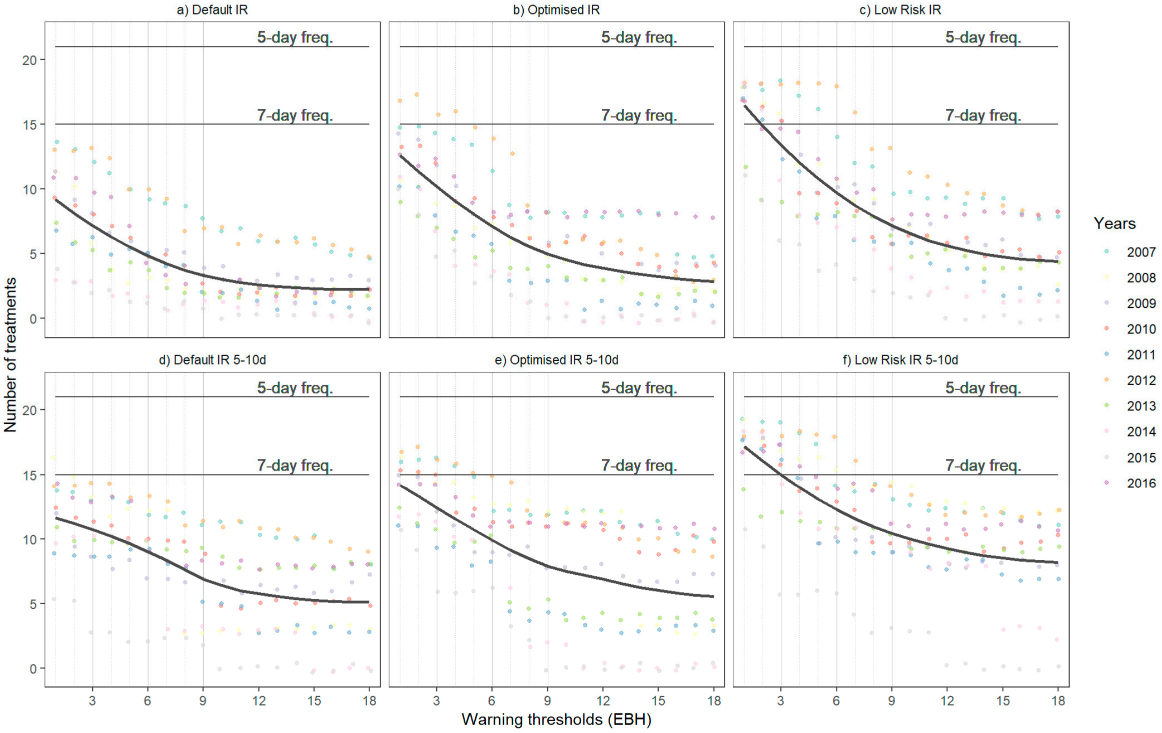

Figure 7. Difference between the model guided and the standard grower practice number of treatments over the range of decision thresholds. Figures (**a**–**c**) depict the sums of guided model; (**d**–**f**) the model and calendar guided number of treatments per year. The dots represent the number of treatments per corresponding warning threshold in each year. LOESS curve represents the average potential benefit from the use of the model. The 5 and 7-day lines represent number of treatments per estimated crop season. If the fitted smoothed line is above the estimated calendar frequency line, the model recommends more treatments than the usual standard calendar program, on average.

The number of treatments according to the default parametrization of IR is lower than the calendar practice across the range of decision thresholds (Figure 7a,d). In the case of the optimized model, the LOESS curve does not intersect any of the growers practice lines, indicating that the average number of treatments recommended by the model is lower than any grower practice schedule across the range of decision thresholds (Figure 7b,d). Given that the optimum decision threshold should not be lower than 4 EBH, the optimized model still provides an opportunity for a reduction in the number of treatments in all but one year and as low as five per season when compared to the seven-day program.

The number of treatments advised by the low risk model when the decision threshold set to 3 EBH (lowest observed risk accumulation prior to the disease outbreak) is lower than the 7-day treatment interval on average. However, this is not the case in years such as 2012 or 2007, when the number of treatments with a decision threshold of 7 EBH is close to the seven-day treatment frequency. However, the possibility to set higher decision threshold provides more opportunities for reducing the number of treatments, in the range from 5 to 11 EBH, with an average ranging from 12 to as low as six for the five-day strategy, and 13 to 10 for the five to ten day strategy.

The cumulative proportion of the total fungicide applied using model guided strategy and the number of treatments is compared to the 7-day calendar practice in Figure 8. All model versions provide reductions in both the total dose and the number of treatments applied. The reductions are lowest for the year 2012 which was one of the most severe 'blight years' on record [86]. Overall, the highest mean dose reduction is achieved by the default IR (0.248), followed by optimized IR (0.33); the lowest mean dose reduction is expectedly associated with the low risk IR (0.436).

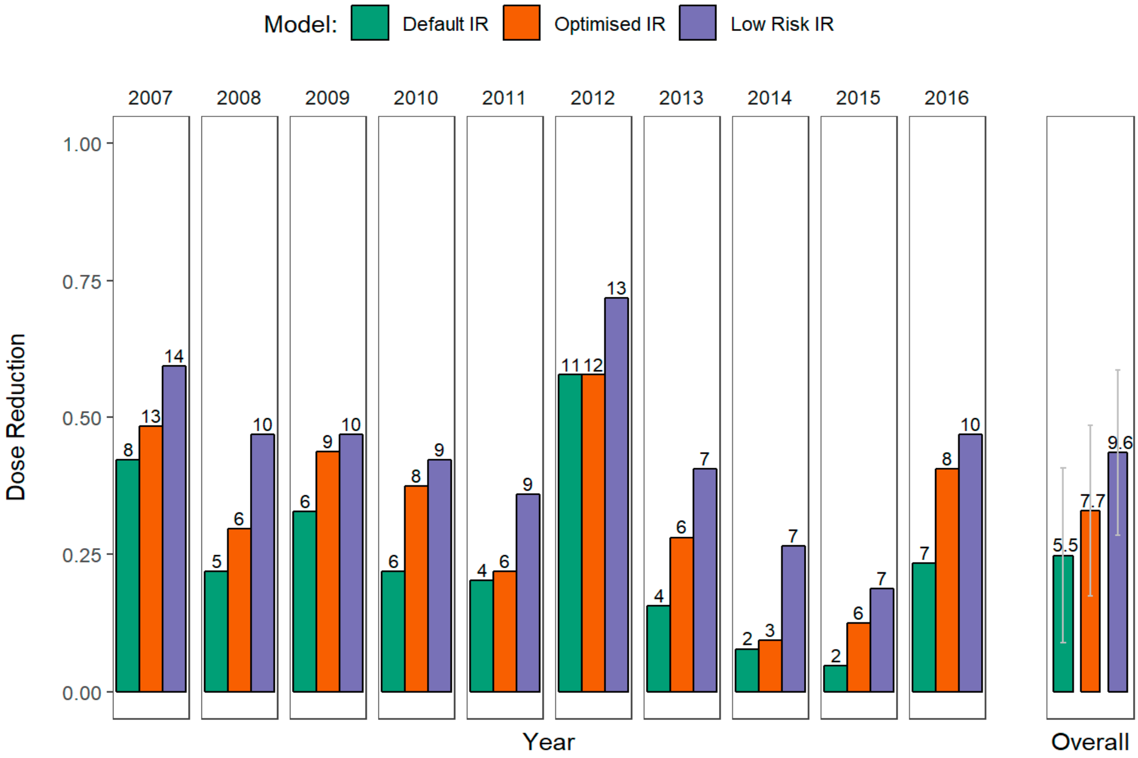

Figure 8. Dose reduction and number of treatments recommended per year by the IR: optimized model and low risk model. Facets marked with the year on top represent summaries for individual years while the last facet represents the averages and variance across all years. In the facets for the individual years, the height of bars represents the proportion of the dose applied per model compared to the total dose, while numbers at the top of the bars represent the total number of treatments recommended by the model in each year. In the overall summary (facet on the far right), height of the bar represents the mean dose reduction, the number above the bar is the mean number of treatments during the year and the error bar represents standard deviation.

4. Discussion

We presented an evaluation of the operational algorithm for potato late blight risk forecasting in Ireland. To evaluate the selected algorithm, a sensitivity analysis of the threshold values associated with the most important variables were assessed using empirical ROC curves derived from 10 years of historical weather and disease observation data. Guided by the results of the sensitivity analysis, current epidemiological knowledge and PLB risk awareness, we identified two improved sets of model parameters and a range of operational thresholds. Finally, three disease control strategies, two based on these improved model thresholds and currently using model parametrization, are compared to standard growers' practice.

Crossovers between empirical and mechanistic models are a common approach in crop disease forecasting [42]; the IR model is one example. Mechanistic algorithms are a function-based estimation of conditions for the development and completion of several (or a single) segments of disease development, while in the IR, these segments are limited to a threshold-based prediction of their completion. The threshold selection is often based on estimates by the model developer and may not be an accurate representation of the complex nature of biological processes [87]. Such algorithms have their appeal in their simplicity, although biological processes, such as the developments of disease epidemics, do not have a binary state but are a part of a complex system that encompasses soft transitions between minimum, optimum and maximum states [88]. The semi mechanistic form of the IR adopted at the time for operational use in Ireland, required a number of simplifying assumptions. These favored more "conservative" variable thresholds, to reduce the frequency of warnings. Our results indicate that the previously defined default thresholds of the Irish Rules are no longer fit for risk prediction in the new PLB pathosystem, and are based on the available data.

This study is in agreement with older reports stating that blight epidemics in Ireland are not initiated before the second half of June [27] due to low night temperatures [89]. Average minimum daily temperature in Oak Park was low in April and May, 4.5 °C and 7.2 °C respectively, providing a potential explanation for the low pathogen activity during this period. Lower temperatures in the early stages of potato development can provide a certain level of protection until the plants reach a level of maturity where they are more resistant to attack [90]. This has been challenged in recent times due to the rise in aggressiveness of newer pathogen strains active over a wider range of environmental controls [12,28,86]. The Irish Rules model uses a hypothetical lower temperature threshold of 10 °C without an upper boundary, consistent with a number of early prediction models employed in Northern Europe [37,40,91–93]. Our results indicate that the development of *P. infestans* under typical Irish weather conditions is low if the temperature is less than 12 °C. However, considering a relatively small gain in overall model accuracy, a more comprehensive evaluation would be necessary prior to recommending increasing the current temperature threshold. Previous research from areas with a diverse pathogen population cautions that blight epidemics will progress even if temperatures are lower than 10 °C, under extended humid periods, although the rate of this progress is low [94,95]. Additional years of data and knowledge of the founder population would be required to ensure that this is a robust conclusion, suitable for deployment on an operational basis.

Evidence exists for reducing the relative humidity threshold and duration of initial sporulation period. The diagnostic performance of the optimized model versions with these factors provides a 'safer sleep' for the farmer. Our results are in agreement with the report from Fennoscandia rejecting a relative humidity threshold of 90% as a development threshold [96]. This threshold has been adjusted in a number of models used throughout Europe; i.e, the French model, Milsol, uses a threshold of 86% (Gaucher, personal communication) and the Danish Blight management uses a threshold of 88% (Hansen, personal communication). There are a number of reasons to opt for lower risk when deciding on which reported relative humidity threshold should be considered blight favorable, such as accuracy of measurements, distance between weather data source and the production area, topography of the area, physiological and phenological differences in crop haulm density and shaded areas of the production fields [49,97,98].

Leaf wetness estimation is one of the key parameters in agricultural meteorology controlling pathogen infection and determining disease development rates [99,100]. In agricultural field conditions, leaf wetness may result from rain, fog, irrigation or distillation from the soil [101]; our results indicate that a simple use of a precipitation threshold is not an appropriate estimator of leaf wetness in this context and should be supplemented with an additional estimator based on a simple empirical model for RH. Due to lack of in field measurements, we used a 'reverse' approach to test the validity of proposed estimation method by comparing the leaf wetness estimation to the disease occurrence [102]. This estimation method has been successfully employed in a number of DSS worldwide [99,103].

A low risk of three and four EBH was predicted by both the optimized and low risk models, prior to the disease onset during two of 10 years studied, 2011 and 2014. Possible reasons for this are the proximity and strength of the inoculum source or the aggressiveness of the pathogen lineage initiating the epidemics. The specific *P. infestans* lineages that initiated the epidemics in our data is not known, but we can hypothesize that these infections were initiated by the more aggressive strains. Additionally, epidemics in both years were initiated later in the season, on July 28th and August 1st, possibly coinciding with a shift in the structure of pathogen population, increasing the probability that the infections were initiated by a more aggressive strain. Limited findings from our monitoring of the founder population at Oak Park, from 2016 to 2018, show that the epidemics are predominantly initiated by the older clonal EU_8_A1 genotype, while the population structure changes in favor of new genotypes EU_6_A1 and EU_13_A2 over the course of the season. This is in agreement with recent experimental evidence regarding the establishment of the new *P. infestans* genotypes under Irish conditions [20–22] exhibiting an increase in aggressiveness [12–15,17]. Hence, we can recommend 4 EBH as the minimum decision threshold to be considered under conditions of high disease pressure or if the outbreak of aggressive strain of the pathogen is reported.

The optimized model offers significant potential to increase the model specificity and consequentially, reduction in the number of required treatments, compared to the low risk model in the high sensitivity range of the ROC curve, between 0.9 and one. The difference between the optimized and low risk model, calling for caution, is the grouping of the cut-off points corresponding to the decision thresholds above 5 EBH. A number of decision thresholds for the low risk model are closer to the higher sensitivity area (5–11 EBH at 0.8 sensitivity) compared to the optimized model (all cut-off points higher than 5 EBH correspond to 0.6 sensitivity). Thus, determining a higher decision threshold, which requires less treatments, is possible for the low risk model at 0.8 sensitivity, although defining an exact threshold is difficult since values from 5 to 11 EBH correspond to the same sensitivity value. In the case of small sample sizes, the crude empirical estimate has the disadvantage of providing the same sensitivity values for different specificity values. The robust methodology and highly reproducible coding example allow for the regular updating and evaluation of the model, leading to clearer definitions of the risk and/or benefit associated with each decision threshold as the new data becomes available.

We have shown that on average, the use of risk prediction models offers a possibility for reducing fungicide inputs compared to standard Irish growers' practice. Possible reductions in the dose and the number of treatments exhibit variation across the period studied. This reflects the nature of agricultural production and further empowers the need for IPM approach to defining the treatment intervals. While spray intervals should be longer than seven days, most of the time these intervals could be justifiably reduced during parts of the 'blight year.' Currently, operational decision thresholds for issuing blight warnings are not clearly defined and based on experience. Here we provide an estimation of risk associated with decision thresholds in the higher sensitivity range. The accumulation of EBH needed to issue the warning at sensitivity levels of 0.9 and one is the same for both the optimized and low risk models, with the optimized model providing greater opportunities for reducing the number of fungicide treatments and/or the dose. However, an important advantage of the low risk model is related to the sensitivity, 0.8, providing more certainty in model outputs if the warning is considered at a higher decision threshold, from 5 to 11 EBH. Such situations may be considered when other factors necessary for the disease development are estimated lower, such as earlier part of season, more resistant varieties or low number of reported disease outbreaks in region. The adoption of decision support systems and utilization into everyday practice could have numerous benefits for growers, such as optimization, as well as, justification of fungicide inputs [54]. Our findings indicate that the original Irish Rules model parameters need to be altered for two model variables, which inevitably will result in an increase in the frequency of warnings. Optimization of the control program does not necessarily mean reduction in the number of treatments, and an effective forecasting scheme could advise at least as many fungicide treatments as the standard growers practice during seasons with blight favorable conditions [104], which often occur with typical weather conditions experienced in Ireland. The decision on the level of risk acceptable by a grower is a complex one, made according to price of treatment, value of production, legislative restrictions [96] and the need for reduction to prevent the development of fungicide resistance [33]. Hence, here we do not make a recommendation for the exact decision threshold but elaborate on possible reductions and varying levels of risk deemed acceptable by a producer. Met Éireann issues regional warnings and these warnings, and the quality of these warnings, could be improved with information regarding the disease outbreaks and rapid identification of the pathogen lineage, due to reasons outlined above.

Decision support at the synoptic level is not a silver bullet to provide an ultimate solution for optimal environmentally friendly disease control, but merely another tool to get closer to it. Unfortunately, if it is not utilized as such, and in an inappropriate manner it can lead to an opposite effect. Plant disease models are often parochial in nature, evaluated by researchers who developed them, and are often used without calibration when employed in agroecosystems different from those they were developed for [31,105]. The interdisciplinary nature of the work related to decision support in crop protection, requiring skills and knowledge in informatics, mathematics, meteorology, agronomy and biology are often a limiting factor for the sustainable development of this branch of plant disease epidemiology [49]. One possible way to overcome some of the obstacles is acceptance of open and reproducible methods. The importance and need for open-science in the field of phytopathology has been reported as a way include recruitment of experts from different fields, the application of cutting-edge methods and timely replication of data analyses to increase the robustness of the findings [106]. Some of the relevant examples are coming from other fields of research, related to potato late blight. The development of our understanding and knowledge of *P. infestans* population diversity has been empowered with POPPR, a widely used R package for enabling easier genetic analysis of clonal populations [107]. Moreover, Sparks et. al. [108] evaluated the possible implications of the climate change on potato late blight in the future. These do not have only a scientific value, but represent a significant contribution to the education of a new generation of phytopathologists, who will need to be equipped with such knowledge and skillsets to be able to keep up with the 'fight' against ever-evolving plant pathogens.

Easily accessible tools are necessary for validation and calibration of risk models using historical data prior to field evaluation in other climatic regions or re-evaluation in the in the original ecosystem, which could potentially save a considerable amount of time and money and lead to more sustainable use of decision support in plant protection. To the best of our knowledge, this is the first completely reproducible evaluation of a crop disease risk prediction model, implemented in a single computing environment, within a freely accessible software language. Such work, it is hoped, will empower the sustainable development of potato late blight and crop disease forecasting in general.

5. Conclusions

The results have shown the there is a need to revisit the parameters of the Irish Rules model, proposed for the different ecosystem and operational abilities at the time, and the operational use of the model. On the basis of the work presented here, we recommend the reduction of variable thresholds for relative humidity from 90% to 88% and sporulation duration from 12 to 10 h; and adopting an additional leaf wetness indicator, incorporating both precipitation ($\geq$0.1 mm) and relative humidity

(≥90%). Our analysis indicated that very little blight development was occurring at temperatures lower than 12 °C; however, we do not recommend this increase operationally due to the lack of certainty associated with the small data sample size and the high risk related to possible disease outbreaks and wider decision threshold range in the high sensitivity area of the ROC space for the low risk model. However, the thresholds identified here should be continuously evaluated after each growing season, facilitated here by the development of the methodology and associated model evaluation code. Our recommendation for the operational application of the model is to use the range of 4 to 11 EBH and set the threshold dynamically during the season based on the reports of the frequency of the disease outbreaks in the region of interest. Future development of the Irish PLB warning system should include rapid in-season identification of pathogen genotype distribution to be used as a guide for selection of the decision threshold.

Representation of the complex aetiology of *P. infestans* is omitted or generalized with synoptic empirical prediction algorithms, and other components of this pathosystem, such as pesticide protection status, crop resistance [7], quality of meteorological network coverage and distances between production field and weather stations [54], crop phenological stage [6] and pathogen genotype [11,28]. Understanding complexities of the agroecological system under investigation is crucial for interpreting results of the analysis we have implemented. Small data sets may carry high variability due to a limited number of observations [57]. Hence, we add a note of caution when employing the model proposed here.

The exact methodology used in the development of early models, such as the IR, is not always clear, but the assumption is that they were a product of empirical, often trial and error based methodologies and weather data available at the time (Yuen and Mila, 2015). Hence, the recommendation for future development is to explore the possibility of redesigning currently employed models to facilitate the transition from the threshold based binary estimation of stages of host parasite interaction, to a more realistic one, based on a functional relationship between host, parasite and the environment. Future work on development of risk prediction algorithms, should also take into consideration additional uncertainty introduced by forecasted weather data, avoiding the usual practice in crop disease modelling where models are developed with observed weather data and applied on forecasted weather with no evaluation of the impact of weather-forecast uncertainty on model predictions [49]. Approaches in IPM cannot be limited to a single discipline's efforts. The vast amount of data available nowadays that are currently under-utilized provides a number of opportunities for smarter farming [109]

The challenge still remains in front of the end user to adequately employ information provided in the decision-making process with an awareness or knowledge of characteristics of variety grown, growth stage, control measures used, risk from surrounding areas, accessibility of active ingredients, etc. The often hard-earned confidence by the final user could be maintained through constant evaluation of the system and adequate education regarding the appropriate use of decision support tools.

Author Contributions: Conceptualization, M.C. and S.K.; methodology, M.C.; software, M.C. and A.S.; validation, M.C., and R.d.A.M.; formal analysis, M.C.; investigation, M.C.; data curation, M.C. and K.L.; writing—original draft preparation, M.C.; writing—reviewing and editing, M.C., R.F., R.d.A.M., S.K. and K.L.; visualization, M.C. and A.S.; supervision, R.F. and S.K.; project administration, R.F. and S.K.; funding acquisition, S.K. and R.F.

Funding: This research was funded under the Department of Agriculture, Food and the Marine STIMULUS project 'EPIC' (14/S/879).

Acknowledgments: I would like to thank to Jim Grant and Jonatan Yuen for interesting discussions which helped to implement this work.

Conflicts of Interest: The authors declare no conflict of interest.

Repository: https://github.com/mladencucak/AnalysisPLBIreland.

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