Catching up on global change:
new ragweed genotypes emerge in elevated CO_2 conditions

Kristina A. Stinson,[1],† Caroline Brophy,[2,3] and John Connolly[2]

[1]*Harvard University, Harvard Forest, 324 North Main Street, Petersham, Massachusetts 01366 USA*
[2]*School of Mathematical Sciences, Environmental & Ecological Modelling Group, University College Dublin, Dublin 4, Ireland*

Abstract. Resource uptake by neighboring plants can be an important driver of natural selection in a changing environment. As climate and resource conditions are altered, genotypes that dominate within mixed populations today may differ markedly from those in future landscapes. We tested whether and how the dominance of different genotypes of the allergenic plant, common ragweed, may change in response to projected atmospheric CO_2 conditions. We grew twelve maternal lines in experimental stands at either ambient or twice-ambient levels of CO_2. We then constructed a model that combines classical quantitative genetics theory with a set of a priori predictions about the relative performance of genotypes in the two treatments. Our findings show a complete reversal in the genotypic size hierarchy of ragweed plants in response to projected atmospheric CO_2 conditions. Genotypes that are competitively suppressed in size at ambient levels become dominant under experimental doubling of CO_2. Subordinated plants, in turn, boost their reproductive allocation to that of dominants, shrinking the fitness gap among all genotypes in high CO_2. Extending our model to a contextual analysis framework, we further show that natural selection on size is reduced at elevated CO_2, because an individual's position within the size hierarchy becomes less important for reproduction than it is in ambient conditions. Our work points to potential future ecological and evolutionary changes in this widespread allergenic plant.

[3] Present address: Department of Mathematics & Statistics, National University of Ireland Maynooth, Maynooth, County Kildare, Ireland.

† E-mail: stinson@fas.harvard.edu

INTRODUCTION

Competition among neighboring plants determines resource allocation to growth and reproduction (Grime 1977, Tilman 1982), and is therefore likely to be an important driver of natural selection and determinant of genetic structure in populations (Bennington and Stratton 1998, Donohue et al. 2000). Several reviews of the literature show that elevated CO_2 alters competitive interactions in plant populations by favoring some species or individuals over others (Poorter and Navas 2003, Urban 2003). Genetic identity can also determine the outcome of inter- and intraspecific competition (Thomas and Bazzaz 1993, Weiner et al. 1997, Fridley et al. 2007). A handful of studies have detected significant $G \times CO_2$ interactions in plant growth and reproductive traits, but the large majority suggest there is no genotypic contribution to CO_2 response (Lau et al. 2007). However, only a few studies have investigated whether and how an

individual genotype's competitive position is likely to change in future environmental conditions (e.g., Thomas and Bazzaz 1993, Andalo et al. 2001, Fridley et al. 2007).

In stands of interacting plants, competitive size hierarchies become established as dominant individuals pre-empt the resource uptake of smaller, subordinate individuals, and can be determined by both genetic and environmental factors (Weiner 1990, Thomas and Bazzaz 1993). Plants will typically allocate growth to those structures that maximize efficient uptake use of the most limiting resource, increasing root:shoot ratios when nutrients are scarce and shifting allocation to light capture in shaded conditions (e.g., Tilman 1982). In light limiting conditions, CO_2-enrichment generally stimulates plant growth by enriching cellular levels of carbon dioxide for C-3 photosynthesis (Urban 2003). When dominant individuals receive the greatest physiological boost from supplemental CO_2, then competition increases and size differences among individuals become exacerbated (Thomas and Bazzaz 1993, Poorter and Navas 2003), i.e., "the rich get richer". In contrast, when subordinates experience a disproportionate growth boost from high CO_2, size and reproductive variation are reduced and smaller individuals "catch-up" to dominants (Wayne and Bazzaz 1997, Stinson and Bazzaz 2006).

Here, we tested whether subordinate genotypes "catch up" to dominants under elevated (720 vs 360 ppm) CO_2, in the widespread allergenic plant, common ragweed (*Ambrosia artemisiifolia* L., Asteraceae). Common ragweed is a weedy annual plant that forms dense, monospecific stands in disturbed habitats, old-fields, croplands, and roadsides of North America (Bassett and Crompton 1975). A major agricultural pest, this species is also a leading cause of fall hay fever allergies (Ziska et al. 2003, Epstein and Rogers 2004), and is becoming aggressively invasive across Europe (Dessaint et al. 2005, Taramarcaz et al. 2005). Elevated CO_2 enhances common ragweed's growth, reproduction, and pollen output, raising concern about its future status in the landscape and its long term impacts on human health (Wayne et al. 2002, Ziska et al. 2003, Epstein and Rogers 2004, Taramarcaz et al. 2005, Stinson and Bazzaz 2006). Recent work suggests that high CO_2 can alter the structure and magnitude of competitive size hierarchies in ragweed populations by differentially stimulating the photosynthesis and growth of small versus large individuals in a stand (Stinson and Bazzaz 2006), but the evolutionary implications of this phenomenon were previously unknown for *A. artemisiifolia* or any other species. To interpret the responses of competitively grown genotypes to climate change, we applied a mixed effects model to experimental data on maternal lineages of ragweed to estimate reaction norms, model genetic size hierarchies, and quantify the strength of selection on size in ambient and elevated CO_2 environments.

METHODS

Experimental common ragweed stands

We grew experimental monoculture stands of *Ambrosia artemisiifolia* in open top chambers at Harvard University's Concord Field Station, about 25 km east of the Boston urban area in Bedford (MA, USA). The chambers were constructed in a cleared field consisting of sandy soils that were augmented with 15.0 cm dry, commercially-produced loam and mechanically homogenized just prior to the experiments. Three chambers were maintained at ambient (360 µL L^{-1}) and three were maintained at elevated (720 µL L^{-1}) CO_2 via injection from an on-site liquid supply tank. An infra-red gas analyzer (LI-800, LiCor, Lincoln, NE) sampled air concentrations within each chamber at a frequency of <5 minutes in order to keep CO_2 levels to within ±50 µL L^{-1} of the set point. Air temperature was maintained within 1.5°C of ambient using electric fans to regulate air flow.

Seeds from 12 known maternal lines (genotypes) of second-generation seed stock of wild parental lineages were tagged and planted into two stands per chamber, in identical hexagonal grids consisting of 36 evenly spaced plants. Three replicates of each genotype were randomly assigned to positions within the grid, at a typical field density of 60 plants m^{-2}. In this design, the contribution of the maternal lineage to the trait variance is interpreted as the main genetic component in the analysis, assuming at least half sibling relatedness among genotypes (Fisher 1918); the contribution of maternal environment

to genotype performance during competition is usually small (Weiner et al. 1997) but has been experimentally removed here by the growth of second-generation stock under common conditions. We maintained all chambers at ambient CO_2 and misted germinants with water twice daily for the first two weeks. Thereafter, the CO_2 treatments were initiated and all chambers received natural rainfall. We provided equal amounts of supplemental water to all chambers during dry periods using an automated mist watering system suspended from the top of each chamber. To minimize edge effects, plants on the outermost edge of each stand were excluded from observation and only the central 24 plants were measured. To keep all chambers free of non-experimental plants, weeds were removed immediately after their germination (at least every 2–3 days).

Survival rates ranged from 99–100% per stand and averaged 97% and 98% in the ambient and elevated CO_2 treatments respectively. Strong photoperiodicity in this species led to a high degree of synchrony in flowering, fruiting, and senescence in all stands. Therefore, individuals were harvested during a single week, when all plants had demonstrated the onset of senescence and most live flowering heads had reached seed-set. Plants were dried to a constant mass and weighed for measurements of: total aboveground biomass (T), vegetative biomass (leaves and branches) (V), belowground/root structures (B), reproductive structures (R) and reproductive allocation (RA = reproductive biomass/aboveground biomass shoots, roots and reproductive parts). The sandy soils at our site, and our extensive experience with this species, allowed us to confidently separate root systems and estimate root biomass in most cases. Although a preliminary analysis indicated little variation in root mass among genotypes and treatments, B was omitted from further analysis due to insufficient replication across genotypes.

Model for genotypic size hierarchies

To test for genetic variation in size hierarchies between the two treatments, we fitted a nonlinear mixed effects model to the following plant biomass responses from our experiments: LT, LV, LR, and LRA, where a prefix of L indicates natural logarithm (log). In our model, μ_i is the mean response on the log scale for genotype i under ambient CO_2 and $a + b\mu_i$ is its mean response under elevated CO_2. The model on the log scale is

$$\text{Ambient: } \log(\text{Response}_{Aijkl})$$
$$= \mu_i + \omega_{Aj} + \eta_{Ak(j)} + \varepsilon_{Aijkl}$$

$$\text{Elevated: } \log(\text{Response}_{Eijkl})$$
$$= a + b\mu_i + \omega_{Ej} + \eta_{Ek(j)} + \varepsilon_{Eijkl}$$

Here, Response_{Aijkl} is for the lth individual (1 or 2) of the ith genotype (1 ... 12) from the kth stand (1 or 2) within the jth chamber (1 ... 3) under ambient CO_2 conditions and Response_{Eijkl} is similarly defined for elevated CO_2. We included multiple random components to allow for potential correlation between plants within stands nested within chambers (Verbeke and Molenberghs 2000). The notation $k(j)$ indicates the kth stand is nested within the jth chamber. ω, η, and ε represent chamber-to-chamber, stand-to-stand within chamber and within stand variability respectively. Random terms ω_{Aj}, ω_{Ej}, $\eta_{Ak(j)}$, $\eta_{Ek(j)}$, ε_{Aijkl} and ε_{Eijkl} are assumed normally distributed with mean zero and variance σ_{A3}^2, σ_{E3}^2, σ_{A2}^2, σ_{E2}^2, σ_{A1}^2 and σ_{E1}^2 respectively. The difference between ambient (A) and elevated (E) at each level of variability is tested.

The reaction norms generated by the model provide a visual and statistical assessment of genotypic performance within the context of competition within stands. The effect of CO_2 is determined by the coefficients a and b. The value of b distinguishes between five outcomes with respect to the $G \times CO_2$ interaction as detailed in Fig. 1. The last three categories (Fig. 1C–E) are various forms of a "catch-up" effect (i.e., each implies that subordinates gain proportionately more than dominants). Provided b is significantly less than 1 catch-up has occurred, but, if b is equal to or less than 0, then catch-up is even stronger. This is a model of interaction and the outcomes detailed above for the various values of b speak to the relative rather than the absolute performance of genotypes under ambient and elevated CO_2. The performance of a particular trait of subordinates could improve relative to dominants but all genotypes might decline with respect to that trait.

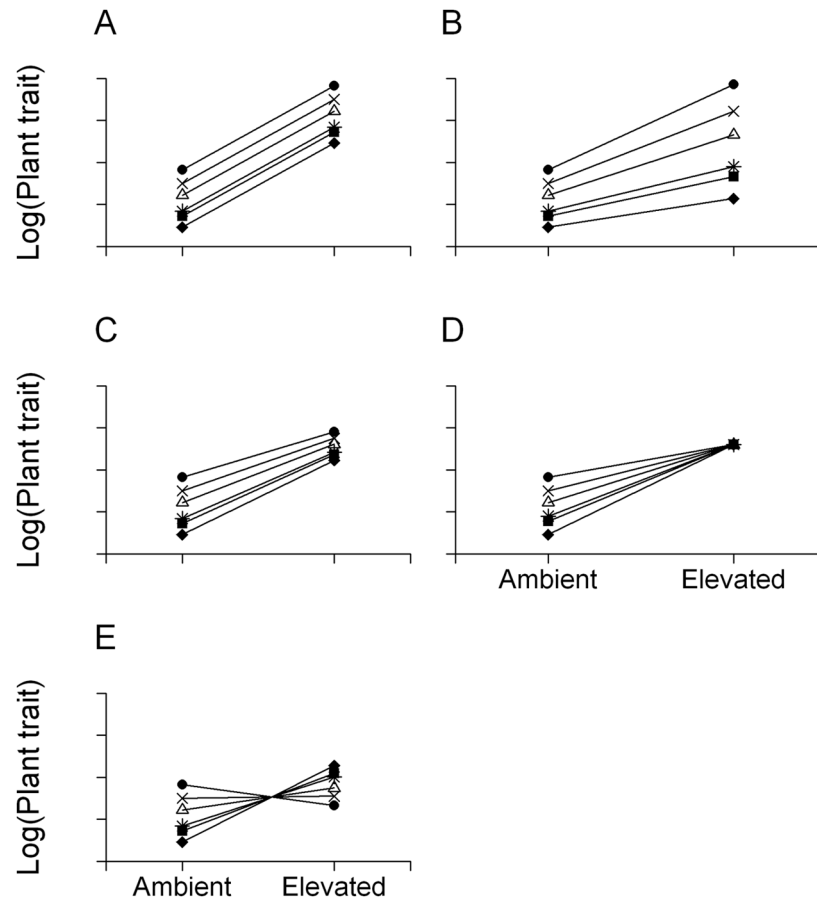Our model is an extension of the functional

Fig. 1. Hypothetical examples using six genotypes to illustrate the meaning of b in the mixed effects model. (A) b = 1, there is no interaction between CO_2 and genotype (indicated by parallel lines) and hence no change in genotypic dominance hierarchies. (B) b > 1, 'rich-get-richer', dominant genotypes at ambient CO_2 benefit proportionately more under elevated CO_2. Genotypic dominance hierarchy becomes more pronounced under elevated CO_2. (C) 0 < b < 1, 'simple catch-up'; subordinate genotypes under ambient CO_2 benefit proportionately more under elevated CO_2. Genotypic dominance hierarchy remains the same but is less pronounced under elevated CO_2. (D) b = 0, 'complete catch-up'; all genotypes tend to the same value under elevated CO_2. Subordinate genotypes under ambient CO_2 completely 'catch-up' to dominants and there is no genotypic dominance hierarchy under elevated CO_2. (E) b < 0, 'dominance reversal'; subordinate genotypes become dominant under elevated CO_2 causing a reversal in the genotypic dominance hierarchy under elevated CO_2.

relationship models by Kendall and Stuart (1973), in which b is the single interaction parameter which specifies a linear association between the mean genotype responses at ambient and elevated CO_2. (The model is nonlinear in that it involves the product of the coefficient b with μ_i terms and so is not amenable to the usual linear mixed models framework). The novelty of this approach is our interpretation of the interaction parameter b to distinguish between a range of possible hypotheses about the shape and varia-

tion in reaction norms, as shown in Fig. 1. Our approach is more flexible than the standard classical one (Fisher 1918) where the full G × E interaction is fit (i.e., $E[y] = \mu + \alpha_i + \beta_j + \alpha\beta_{ij}$ where $i = 1 \ldots 12$ for genotype, $j = 1, 2$ for CO_2 and $\alpha\beta_{ij}$ are parameters of interaction) in a standard linear mixed effects model. Instead, we partition the classical full 11 df G × E interaction into 1 df structure, identified by an a priori specification of a single coefficient b, and a 10 df random remainder. Partitioning the G × E interaction in

this manner has been employed elsewhere, motivated for example by variation in physiology or statistical dimension reduction (van Eeuwijk et al. 2005). Our approach captures the $G \times CO_2$ interaction in a single degree of freedom based on values of b, where b represents a specific predicted competitive outcome.

We also tested for the classical full $G \times E$ interaction and tested the remainder for any further structure. Models were fitted using maximum likelihood, implemented through the NLMIXED procedure in the SAS/STAT software, Version 9.1 of the SAS System for Windows. Model comparisons were made using likelihood ratio tests (Pawitan 2001).

Contextual analysis

To evaluate our results in an evolutionary context, we extended the functional relationship model for LRA to a contextual framework (Heisler and Damuth 1987, Weinig et al. 2007) by introducing two covariates measured at harvest time, log average stand biomass (LAv_T) and log relative size of an individual within the stand size hierarchy (LRatio = log(T/Av_T)).

The contextual equation 9 of Heisler and Damuth (1987) is

$$W_{ij} - \bar{W}_{..} = \beta_I (z_{ij} - \bar{z}_{..}) + \beta_C (\bar{z}_{i.} - \bar{z}_{..}) + \varepsilon_{ij}$$

where W_{ij} is a measure of individual fitness for the jth individual in the ith group (in our case RA_{ij} is the RA of the jth individual in the ith stand), z_{ij} is an individual character and $\bar{z}_{i.}$ a contextual character. $\bar{W}_{..}$ and $\bar{z}_{..}$ are averages over individuals and contexts. The regression model for a contextual analysis involving these two characters can be rearranged as

$$W_{ij} = W_{..} - (\beta_I + \beta_C)\bar{z}_{..} + \beta_I (z_{ij} - z_{i.}) + (\beta_I + \beta_C)z_{i.} + \varepsilon_{ij}$$

or

$$W_{ij} = \beta_0 + \beta_I (z_{ij} - z_{i.}) + (\beta_I + \beta_C)z_{i.} + \varepsilon_{ij}$$

In this form β_I is a within group coefficient as it measures the response to the difference between the value of the individual character and its group mean, whereas the response to variation at the group level is $\beta_I + \beta_C$. If there is no group effect in addition to the within group response then $\beta_C = 0$.

Using the notation of Heisler and Damuth's

contextual analysis approach, our extended functional relationship model is of the form

$$\text{Ambient: } \log(RA_{Aijkl}) = \mu_i + (\beta_{IA} + \beta_{CA})LAv\_T_{Ajk} \\ + \beta_{IA}LRatio_{Aijkl} + \omega_{Aj} \\ + \eta_{Ak(j)} + \varepsilon_{Aijkl}$$

$$\text{Elevated: } \log(RA_{Eijkl}) = a + b\mu_i \\ + (\beta_{IE} + \beta_{CE})LAv\_T_{Ejk} \\ + \beta_{IE}LRatio_{Eijkl} + \omega_{Ej} \\ + \eta_{Ek(j)} + \varepsilon_{Eijkl}$$

We take LT to be z_{ij} in the notation of Heisler and Damuth (1987) and our ratio variable on the log scale is LRatio = LT − LAv_T which is equivalent to their $z_{ij} - z_{i.}$. The coefficient of LRatio in our model is then β_I in their terms and the coefficient of LAv_T is $\beta_I + \beta_C$. The interpretation of the coefficient of LRatio is the same as their interpretation of β_I; it is a measure of response to within group variation. Because of the log scale this is equivalent to the effect of an individual's position on the within stand hierarchy relative to that of the mean of the stand. Since our model accounts for allometric variation among individuals (including that arising from ontogenetic effects or nonreproductive individuals), RA is an appropriate measure of fitness as a function of size for plants that are grown competitively in monoculture (Brophy et al. 2007).

We interpret β_{IA} and β_{IE} as the measures of direct natural selection on a given individual's size relative to its neighbors (Lande and Arnold 1983), and β_{CA} and β_{CE} as the contextual selection coefficients, at ambient (A) and elevated (E) CO_2. β_C is the difference between the coefficients of LAv_T and LRatio. The coefficients β_{IA} and β_{IE} measure the effect of an individual's size relative to the mean size of neighbors on its reproductive allocation (RA). The contextual selection coefficients measure any additional change in the fitness of an individual of any genotype arising from changes in the productivity of its stand.

RESULTS

CO_2 effects on genetic dominance hierarchies

Subordinate genotypes gained proportionately more total aboveground biomass than their dominant counterparts in elevated vs. ambient CO_2 conditions, as indicated by $b < 1$ for LT

Table 1. a) Estimates $\pm$ standard errors of a, b and μ_1 to μ_{12} and b) P-values for likelihood ratio tests on b for each response.

	Response			
Coefficient or test	log aboveground biomass (LT)	log vegetative biomass (LV)	log reproductive biomass (LR)	log reproductive allocation (LRA)
a) Coefficient				
a	1.56 ± 0.483	0.39 ± 0.248	0.46 ± 0.306	-0.57 ± 0.117
b	-0.87 ± 0.774	-1.06 ± 0.666	-0.05 ± 0.307	0.06 ± 0.086
μ_1	0.29 ± 0.368	-0.17 ± 0.275	-1.04 ± 0.824	-1.14 ± 0.353
μ_2	0.80 ± 0.365	0.24 ± 0.258	-0.20 ± 0.748	-1.23 ± 0.305
μ_3	0.39 ± 0.351	0.04 ± 0.235	-1.80 ± 0.803	-1.78 ± 0.346
μ_4	0.54 ± 0.311	0.04 ± 0.231	-0.82 ± 0.791	-1.32 ± 0.328
μ_5	0.12 ± 0.347	-0.29 ± 0.258	-1.34 ± 0.759	-1.33 ± 0.305
μ_6	0.77 ± 0.295	0.31 ± 0.229	-0.57 ± 0.798	-1.67 ± 0.301
μ_7	0.14 ± 0.347	-0.22 ± 0.245	-1.40 ± 0.759	-1.37 ± 0.308
μ_8	0.35 ± 0.325	-0.11 ± 0.247	-0.90 ± 0.777	-1.29 ± 0.317
μ_9	0.78 ± 0.302	0.27 ± 0.230	-0.61 ± 0.787	-1.32 ± 0.310
μ_{10}	0.47 ± 0.326	-0.03 ± 0.228	-0.25 ± 0.791	-0.94 ± 0.309
μ_{11}	0.33 ± 0.302	-0.13 ± 0.222	-0.58 ± 0.789	-1.03 ± 0.306
μ_{12}	0.46 ± 0.330	-0.07 ± 0.247	-0.75 ± 0.778	-1.29 ± 0.318
b) Likelihood ratio tests				
Catch-up ($b < 1$)	0.014	0.001	0.069	0.010
Dominance reversal ($b < 0$)	0.129	0.021	>0.999	0.439

(Table 1). Surprisingly, a result of $b < 0$ in LV further indicated complete dominance reversal in plant size: subordinate genotypes in ambient CO_2 became dominant in elevated CO_2, and the dominant genotypes became subordinate (Table 1; Fig. 2A). For LRA, the model suggested $b = 0$ ("complete catch-up"), i.e., all genotypes had a common ratio of reproductive to total aboveground biomass under elevated CO_2 (Table 1, Fig. 2B). There was also some evidence for $b < 1$ for LR, as subordinate genotypes achieved greater reproductive gains relative to dominants in elevated CO_2 (Table 1).

There was generally no evidence to suggest that chambers or repeated stands within chambers introduced correlations between responses (Table 2). No $G \times CO_2$ effects were detected with standard ANOVA, nor were remainder $G \times CO_2$ effects with the functional relationship model (Table 3).

Contextual effects of CO_2 and dominance hierarchies on natural selection

The position of a plant in the size hierarchy within a stand greatly affected its RA (β_{IA} and β_{IE} > 0, Table 4). For a plant of a given size, RA was greater the larger the plant was relative to its neighbors; but this effect was approximately three times greater at ambient than at elevated CO_2 ($\beta_{IA} > \beta_{IE}$, Table 4, Fig. 3). The contextual

effects (β_C) were positive at both ambient ($P = 0.034$) and elevated (NS) CO_2 and β_C was greater ($P = 0.054$) at ambient CO_2. Thus, there was positive but unequal direct and contextual selection on size at both ambient and elevated CO_2 (Table 4). Direct and contextual selection on size were both stronger at ambient than at elevated CO_2. In addition, there was strong evidence that subordinate genotypes catch-up to dominants in RA, with $b < 1$ ($P < 0.001$) and no evidence of $b \neq 0$ in the model (Table 4).

The hierarchical experimental design in our study (within stand, stand-to-stand and chamber-to-chamber) allowed us to further test for a difference in variability between ambient and elevated CO_2. The contextual analysis model fitted to the response variable LRA (log reproductive allocation) demonstrated the following results: Estimated within stand variability differed ($P < 0.001$) between ambient ($\hat{\sigma}^2_{A1} = 0.241$) and elevated ($\hat{\sigma}^2_{E1} = 0.017$) CO_2, where ˆ signifies an estimate. Estimated stand-to-stand variability also differed ($P < 0.001$) between ambient ($\hat{\sigma}^2_{A2} = 0.089$) and elevated ($\hat{\sigma}^2_{E2} \approx 0$) CO_2. Chamber-to-chamber variability did not differ between ambient and elevated CO_2 and was estimated at 0.002, indicating little difference in this component within or among our experimental treatments.
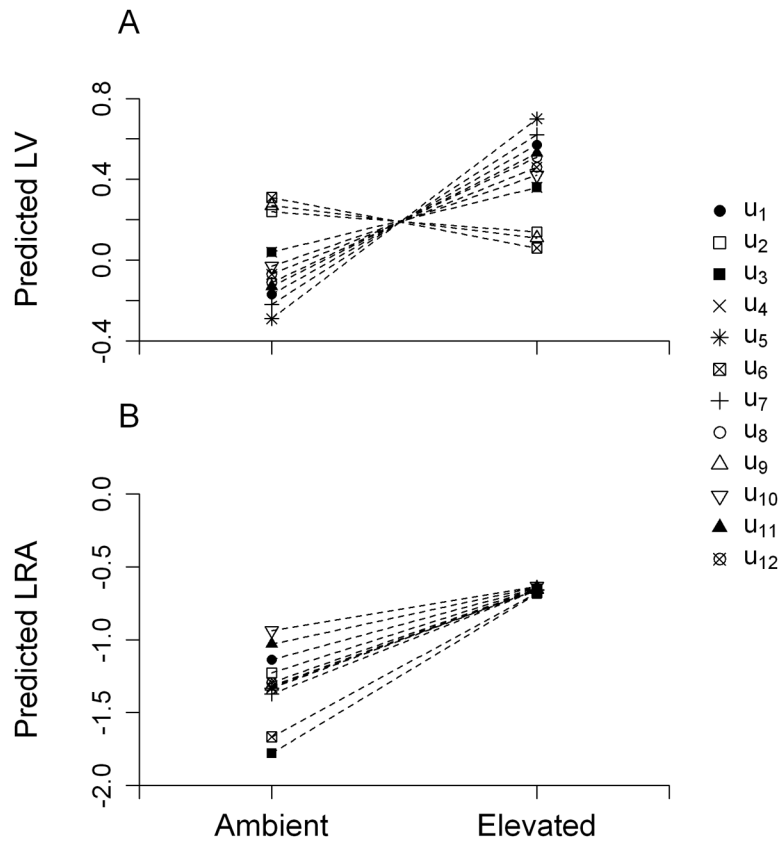
Fig. 2. Predicted (A) log vegetative biomass (LV) and (B) log reproductive allocation (LRA) versus level of CO_2 for each genotype (μ_1 to μ_{12}). Model estimates used to calculate these predictions are in Tables 1 and 4.

DISCUSSION

This work has implications for ecological research, and for the future status of *Ambrosia* *artemisiifolia* as a noxious, allergenic plant. First and most importantly, we show that future climate scenarios can favor genotypes that would otherwise be suppressed by their neighbors.

Table 2. *P*-values for likelihood ratio tests of the effect of CO_2 on variance components for each response.

Hypothesis	log aboveground biomass (LT)	log vegetative biomass (LV)	log reproductive biomass (LR)	log reproductive allocation (LRA)
$\sigma_{A3}^2 = \sigma_{E3}^2$	0.294	0.752	0.028	0.074
$\sigma_{A3}^2 = 0$	…	…	0.001	…
$\sigma_{E3}^2 = 0$	…	…	>0.999	>0.999
$\sigma_3^2 = 0$	0.065	0.138	…	…
$\sigma_{A2}^2 = \sigma_{E2}^2$	0.752	0.655	0.655	<0.001
$\sigma_{A2}^2 = 0$	…	…	…	<0.001
$\sigma_{E2}^2 = 0$	…	…	…	0.237
$\sigma_2^2 = 0$	0.221	0.294	…	…
$\sigma_{A1}^2 = \sigma_{E1}^2$	0.317	0.752	0.021	<0.001

Notes: The variance components are fitted initially allowing a separate variance component for ambient (A) and elevated (E) at each level of variability, giving the six components σ_{A3}^2 and σ_{E3}^2 (chamber-to-chamber), σ_{A2}^2 and σ_{E2}^2 (stand-to-stand) and σ_{A1}^2 and σ_{E1}^2 (within stand). If there was no evidence for a need to split the variance at a given level (hypotheses $\sigma_{A3}^2 = \sigma_{E3}^2$, $\sigma_{A1}^2 = \sigma_{E1}^2$), the model was re-fitted constraining the two components at that level to be equal (i.e., $\sigma_{A3}^2 = \sigma_{E3}^2 = \sigma_3^2$, $\sigma_{A2}^2 = \sigma_{E2}^2 = \sigma_2^2$ and $\sigma_{A1}^2 = \sigma_{E1}^2 = \sigma_1^2$).

Table 3. P-values for tests of the contribution of the functional relationship to the $G \times CO_2$ interaction by (1) the full $G \times CO_2$ interaction using classical ANOVA methods and (2) functional relationship model, for each response.

Test	df	log aboveground biomass (LT)	log vegetative biomass (LV)	log reproductive biomass (LR)	log reproductive allocation (LRA)
(1) Classical test for $G \times CO_2$ interaction	11	0.105	0.075	0.102	0.228
(2) Remainder of $G \times CO_2$ interaction having fitted the functional relationship model	10	0.358	0.629	0.178	0.687

Specifically, the disproportionate CO_2-induced growth gains to subordinate genotypes allow them to "catch-up" to dominants under elevated CO_2. The reaction norms in Fig. 2A show further that this can result in an extreme disruption of size hierarchies: genotypes that achieve size dominance in ambient conditions become suppressed at elevated CO_2, while the most subordinate genotypes become dominant. Thus, high atmospheric CO_2 promotes the growth of subordinate genotypes, reducing the competitive advantages to dominant genotypes and in some cases completely reversing the competitive hierarchy.

Second, we show that elevated CO_2 dramatically enhances reproduction by subordinate plants in this species. Subordinates preferentially allocate more of their CO_2-induced biomass gains to reproduction than dominant genotypes, and therefore catch up completely to dominants in terms of reproductive allocation. Such changes in reproductive allocation are sometimes ascribed to ontogenetic differences in enriched-CO_2 environments (Thomas et al. 1999), but we have shown in prior studies that strong photo-periodicity for reproduction and minimal CO_2-induced effects in early growth stages make this unlikely in *A. artemisiifolia* (Stinson and Bazzaz 2006). In addition, the present model accounts for possible variation in the allometric responses of individuals within a stand (Brophy et al. 2007). Thus, we conclude that elevated CO_2 disrupts the genetic dominance hierarchy by minimizing both size- and reproductive differences among genotypes within a stand. This work advances earlier findings (Wayne and Bazzaz 1997, Stinson and Bazzaz 2006) by showing that there is genetic variation in the degree to which CO_2 alters size, reproduction, and competitiveness in common ragweed.

A third contribution from this paper is evidence that two distinct processes—natural selection and competition—become simultaneously de-intensified by elevated CO_2 as a result of reduced variation in genotypic performance. This is best illustrated in Fig. 3, as a

Table 4. a) Estimates and tests for the model for log reproductive allocation (LRA) extended with the contextual analysis covariates: log average stand biomass (LAv_T) and log relative position within stand size hierarchy (LRatio = log(aboveground biomass/AV_T)) and b) tests of hypotheses among contextual analysis coefficients.

Coefficient or test	Estimate	P-value from likelihood ratio test
a) Coefficients		
a	−0.95	...
b	−0.05	<0.001†
(β_{IA} + β_{CA}) (coefficient of LAv_T at ambient)	0.88	<0.001
β_{IA} (coefficient of LRatio at ambient)	0.35	<0.001
β_{CA} (estimate = 0.88–0.35)	0.53	0.034
(β_{IE} + β_{CE}) (coefficient of LAv_T at elevated)	0.17	0.009
β_{IE} (coefficient of LRatio at elevated)	0.12	<0.001
β_{CE} (estimate = 0.17–0.12)	0.05	0.439
b) Hypothesis tests		
(β_{IA} + β_{CA}) = (β_{IE} + β_{CE})	...	0.011
β_{IA} = β_{IE}	...	<0.001
β_{CA} = β_{CE}	...	0.054

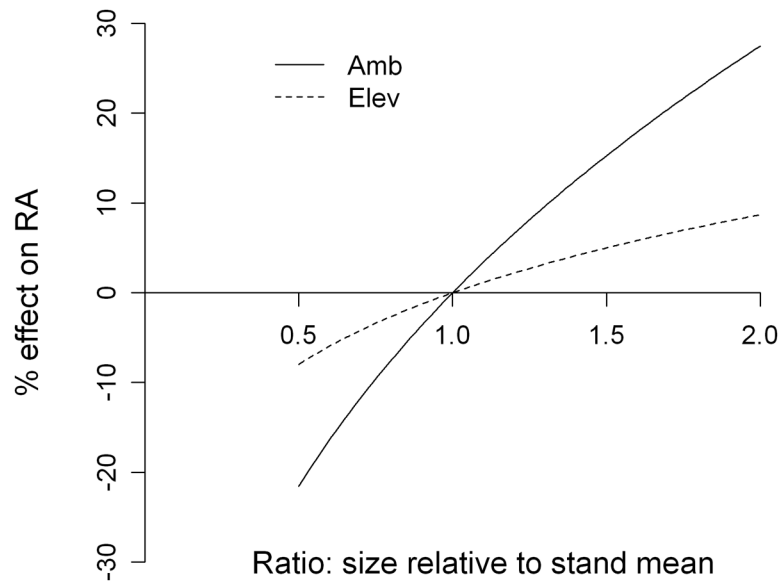†P-value is for the test b < 1, i.e., subordinates 'catch-up' to dominants.

Fig. 3. The effect on RA of plant size relative to stand mean size (ratio). The effect of ratio at ambient CO_2 is three times the size of the effect at elevated, indicated by the steeper line for ambient. The lines can be interpreted as the effect on direct natural selection of a given individual's size relative to its neighbors at ambient (solid line) and elevated (dashed) CO_2, having allowed for genotypic effects.

dampening effect of CO_2 on the reproductive advantages to larger plants within a stand. Here, the result of $b \approx 0$ in the contextual analysis can be interpreted as reduced variation among subordinate and dominant genotypes in their size-dependent reproductive success. In other words, natural selection on size is stronger, and size is more positively correlated with reproduction at ambient than at elevated CO_2. Thus, we demonstrate here a possible mechanism by which ragweed productivity and pollen production are predicted to increase at elevated CO_2 (Wayne et al. 2002, Ziska et al. 2003, Taramarcaz et al. 2005, Stinson and Bazzaz 2006).

The ecological and evolutionary implications of our results are complex. Changes in both direct and contextual selection, such as we show here for ragweed, suggest that high CO_2 could alter evolutionary trajectories and impact demographic properties of plant populations (Weinig et al. 2007). This finding is particularly concerning for plants that are considered noxious. For instance, elevated CO_2 has been shown to increase the biomass and toxicity of poison ivy (Mohan et al. 2006), while a number of global change factors are predicted to exacerbate forest pest and pathogen invasions (Dukes et al. 2009).

In the case of ragweed, relaxation of natural selection on size could create an opportunity for group selection, and may simultaneously retain genetic diversity in future populations by buffering selection against subordinates (Weinig et al. 2007). Relaxed size-related competition could also contribute to enhanced overall productivity and reproductive diversity within a stand, assuming that other resources are not limiting (Stinson and Bazzaz 2006). Moreover, changes in the genetic structure of ragweed populations could directly influence the performance of interspecific neighbors (Fridley et al. 2007), potentially altering community-level competitive interactions and other ecological processes (Fridley et al. 2007, Hughes et al. 2008). The health and resource management problems associated with increased growth and reproduction of this plant could therefore be larger than expected (Wayne et al. 2002, Ziska et al. 2003, Epstein and Rogers 2004, Taramarcaz et al. 2005).

Interpretation of our results requires the caveat that, as in many climate change experiments, the number of treatments is limited. While our experimental treatments represent only pre-elevated conditions and the predicted doubling of CO_2, climate change is likely to proceed in a

gradual pattern and will certainly occur in tandem with changes in temperature, precipitation and many other factors. Common ragweed naturally occurs in dense monoculture stands as simulated in this study, however, interspecific competitors, herbivores, and changes in resource use efficiency as determined by moisture, nutrient, and other abiotic conditions could also alter the responses we report here. Studies incorporating more complex environmental gradients and those that consider a multispecies community context are difficult to achieve due to the sample sizes needed, but are nevertheless important next steps.

Finally, it is worth mentioning that we found the previously-existing but not-widely-known modelling frameworks of the functional relationship model (Kendall and Stuart 1973) and contextual analysis (Heisler and Damuth 1987) to be useful in the interpretation of genotype by environment interactions and selection differentials in the context of competition. Using the interaction parameter b to distinguish among specific predicted competitive outcomes, our approach elucidates changes in the genetic hierarchy that were obscured by the error term in the classical ANOVA. We suggest that these methods may present new analytical opportunities where a priori predictions for genotypic performance and natural selection in a competitive context are considered.

In summary, this paper demonstrates that elevated CO_2 disrupts the genotypic size hierarchy and eliminates reproductive advantages to dominant genotypes, thereby altering genotypic dominance within populations of an allergenic, noxious weed. This work provides data on the potential broader importance of genotype-specific responses to global change for the structure and ecosystem function of natural populations (Bradley and Pregitzer 2007). Subsequent disruptions to ragweed's competitive and microevolutionary dynamics may have major long term and unpredictable effects on ecological, economic, and human health issues as atmospheric levels of CO_2 continue to rise.

Acknowledgments

Literature Cited

Andalo, C., I. Goldringer, and B. Godelle. 2001. Inter- and intragenotypic competition under elevated carbon dioxide in *Arabidopsis thaliana*. Ecology 82:157–164.

Bassett, I. J. and C. W. Crompton. 1975. Biology of Canadian Weeds 11. *Ambrosia artemisiifolia* L and *A. silostachya* Dc. Canadian Journal of Plant Science 55:463–476.

Bennington, C. and D. Stratton. 1998. Field tests of density and frequency dependent selection in *Erigeron annuus* (Compositae). American Journal of Botany 85:540–545.

Bradley, K. L. and K. S. Pregitzer. 2007. Ecosystem assembly and terrestrial carbon balance under elevated CO_2. Trends in Ecology & Evolution 22:538–547.

Brophy, C., D. J. Gibson, P. M. Wayne, and J. Connolly. 2007. A modelling framework for analysing the reproductive output of individual plants grown in monoculture. Ecological Modelling 207:99–10.

Dessaint, F., B. Chauvel, and F. Bretagnolle. 2005. Ragweed (*Ambrosia artemisiifolia* L): expansion history of a biological pollutant in France. M S-Medecine Sciences 21:207–209.

Donohue, K., D. Messiqua, E. Hammond-Pyle, S. M. Heschel, and J. Schmitt. 2000. Evidence of adaptive divergence in plasticity: Density and site-dependent selection on shade-avoidance responses in *Impatiens capensis*. Evolution 54:1956–1968.

Dukes, J., et al. 2009. Responses of pests, pathogens and invasive species to climate change in the forests of Northeastern North America: What can we predict? Canadian Journal of Forest Research 39:231–248.

Epstein, P. and C. Rogers. 2004. Inside the greenhouse: The impacts of CO_2 and climate change on public health in the inner city. Center for Health and the Global Environment, Harvard Medical School, Cambridge.

Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Transactions of the Royal Society of Edinburgh 52:399–433.

Fridley, J. D., J. P. Grime, and M. Bilton. 2007. Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. Journal of Ecology

95:908–915.

Grime, J. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

Heisler, I. L. and J. Damuth. 1987. A method for analyzing selection in hierarchically structured populations. American Naturalist 130:582–602.

Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Kendall, M. and A. Stuart. 1973. Functional and structural relationships. *In* The Advanced Theory of Statistics. Charles Griffin & Company, London.

Lande, R. and J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lau, J. A., R. G. Shaw, P. B. Reich, F. H. Shaw, and P. Tiffin. 2007. Strong ecological but weak evolutionary effects of elevated CO_2 on a recombinant inbred population of *Arabidopsis thaliana*. New Phytologist 175:351–362.

Mohan, J. E., L. H. Ziska, W. H. Schlesinger, R. B. Thomas, R. C. Sicher, K. George, and J. S. Clark. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO2. Proceedings of the National Academy of Sciences of the United States of America 103:9086–9089.

Pawitan, Y. 2001. In all likelihood: Statistical modelling and inference using likelihood. Oxford Science Publications, Oxford University Press, New York, USA.

Poorter, H. and M. L. Navas. 2003. Plant growth and competition at elevated CO_2: on winners, losers and functional groups. New Phytologist 157:175–198.

Stinson, K. A. and F. A. Bazzaz. 2006. CO_2 enrichment reduces reproductive dominance in competing stands of *Ambrosia artemisiifolia* (common ragweed). Oecologia 147:155–163.

Taramarcaz, P., C. Lambelet, B. Clot, C. Keimer, and C. Hauser. 2005. Ragweed (*Ambrosia*) progression and its health risks: will Switzerland resist this invasion? Swiss Medical Weekly 135:538–548.

Thomas, S. C. and F. A. Bazzaz. 1993. The genetic component in plant size hierarchies: norms of reaction to density in a *Polygonum* species. Ecological Monographs 63:231–249.

Thomas, S. C., M. Jasienski, and F. A. Bazzaz. 1999. Early vs. asymptotic growth responses of herbaceous plants to elevated CO_2. Ecology 80:1552–1567.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University press, Princeton, New Jersey, USA.

Urban, O. 2003. Physiological impacts of elevated CO_2 concentration ranging from molecular to whole plant responses. Photosynthetica 41:9–20.

van Eeuwijk, F., M. Malosetti, X. Yin, P. Struik, and P. Stam. 2005. Statistical models for genotype by environment data: from conventional ANOVA models to eco-physiological QTL models. Australian Journal of Agricultural Research 56:883–894.

Verbeke, G. and G. Molenberghs. 2000. Linear Mixed Models for Longitudinal Data. Springer, New York, USA.

Wayne, P., S. Foster, J. Connolly, F. Bazzaz, and P. Epstein. 2002. Production of allergenic pollen by ragweed (*Ambrosia artemisiifolia* L.) is increased in CO_2-enriched atmospheres. Annals of Allergy Asthma & Immunology 88:279–282.

Wayne, P. M. and F. A. Bazzaz. 1997. Light acquisition and growth by competing individuals in CO_2-enriched atmospheres: Consequences for size structure in regenerating birch stands. Journal of Ecology 85:29–42.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecology & Evolution 5:360–364.

Weiner, J., S. Martinez, H. MullerScharer, P. Stoll, and B. Schmid. 1997. How important are environmental maternal effects in plants? A study with *Centaurea maculosa*. Journal of Ecology 85:133–142.

Weinig, C., J. A. Johnston, C. G. Willis, and J. N. Maloof. 2007. Antagonistic multilevel selection on size and architecture in variable density settings. Evolution 61:58–67.

Ziska, L. H., D. E. Gebhard, D. A. Frenz, S. Faulkner, B. D. Singer, and J. G. Straka. 2003. Cities as harbingers of climate change: Common ragweed, urbanization, and public health. Journal of Allergy and Clinical Immunology 111:290–295.