

Microevolutionary responses in experimental populations of plants to CO₂-enriched environments: Parallel results from two model systems

(genetic diversity/global change/density-dependent competition/annuals/trees)

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ABSTRACT Despite the critical role that terrestrial vegetation plays in the Earth's carbon cycle, very little is known about the potential evolutionary responses of plants to anthropogenically induced increases in concentrations of atmospheric CO₂. We present experimental evidence that rising CO₂ concentration may have a direct impact on the genetic composition and diversity of plant populations but is unlikely to result in selection favoring genotypes that exhibit increased productivity in a CO₂-enriched atmosphere. Experimental populations of an annual plant (*Abutilon theophrasti*, velvetleaf) and a temperate forest tree (*Betula alleghaniensis*, yellow birch) displayed responses to increased CO₂ that were both strongly density-dependent and genotype-specific. In competitive stands, a higher concentration of CO₂ resulted in pronounced shifts in genetic composition, even though overall CO₂-induced productivity enhancements were small. For the annual species, quantitative estimates of response to selection under competition were 3 times higher at the elevated CO₂ level. However, genotypes that displayed the highest growth responses to CO₂ when grown in the absence of competition did not have the highest fitness in competitive stands. We suggest that increased CO₂ intensified interplant competition and that selection favored genotypes with a greater ability to compete for resources other than CO₂. Thus, while increased CO₂ may enhance rates of selection in populations of competing plants, it is unlikely to result in the evolution of increased CO₂ responsiveness or to operate as an important feedback in the global carbon cycle. However, the increased intensity of selection and drift driven by rising CO₂ levels may have an impact on the genetic diversity in plant populations.

Due to fossil fuel combustion, deforestation, and other human activities, atmospheric CO₂ is currently increasing, and levels of 500–700 μl/liter (ppm) are projected for the year 2050 (1). In addition to playing a potentially significant role in global climate change (2), as CO₂ is the primary substrate for photosynthesis, increasing CO₂ concentrations have profound implications for plant metabolism, growth, and development (3–8). Long-term CO₂-induced growth enhancements could result in increased productivity and carbon storage of terrestrial ecosystems. Consequently, enhanced carbon uptake of vegetation could lead to a deceleration in rates of atmospheric CO₂ increase (9). By influencing the genetic composition of plant populations (10) and the species composition of plant communities (11–16), rising CO₂ levels could also have significant long-term influences on the productivity and biogeochemistry of terrestrial ecosystems (17–19).

Much of the research investigating the responses of terrestrial vegetation to increased CO₂ has relied on comparative physiological and developmental studies of individually grown

plants. However, very few plants in nature develop in isolation. Through a variety of density-dependent interactions, including competition and facilitation, neighbors alter both the abundance and the distribution of local resources and environmental conditions. It is now well established that many of these factors (e.g., nutrients, light, moisture, and temperature) influence both the magnitude and duration of plants' responses to CO₂ (20–24). Competition studies with herbaceous species suggest that growth and developmental responses of individuals to increased CO₂ are substantially altered by both the numbers and the identities of neighboring plants and that competitive performance is often difficult to predict from that of individually grown plants (25–27). Equivalent studies with tree species are currently not available.

While much attention has been devoted to interspecific comparisons of species' CO₂ responsiveness, much less is known about intraspecific variation (28). Studies of cultivated crops (29) and a few noncultivated herbaceous species (10, 30, 31) have demonstrated the potential for intraspecific variation in CO₂ responsiveness. We know of no study which has examined the impact of competitive interactions on genetically variable responses to increased CO₂. It is thus unclear to what extent increased CO₂ can act as an important selective agent within natural plant populations (28, 32–34).

With respect to evolutionary responses to increased CO₂ in populations of competing plants, two alternative scenarios seem possible. If increased CO₂ differentially enhances growth responses of genotypes, then selection driven by increased CO₂ could favor increased growth responses to CO₂ in successive generations, and so ultimately act to enhance ecosystem-level carbon storage. However, by enhancing plant growth, increased CO₂ may also exacerbate density-dependent competitive interactions within plant populations and communities (35, 36). Density-dependent interactions have been shown to substantially alter genotype-specific performance in studies of "reaction norms" in plant populations (37–39) and often result in magnification of initial differences among genotypes (40). Thus, the primary selective effects of increasing CO₂ on the genetic composition of plant populations may be indirect, with increased CO₂ favoring genotypes that display high fitness under conditions of enhanced intra- or interspecific competition.

Several predictions follow from these considerations. First, the magnitude of growth responses to increased CO₂ is expected to be altered under competitive conditions, relative to the responses of plants grown individually. Second, genetic variability in growth responses to increased CO₂ may be greater under competitive conditions. Third, genotypes that are favored at elevated CO₂ levels may be different from those favored under present conditions, an effect detectable as a strong genotype–CO₂ interaction. If these conditions hold, we expect that overall selection intensities would be enhanced at

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elevated CO₂ concentrations, although this selection regime would not necessarily result in enhanced growth responses to CO₂ in subsequent generations.

MATERIALS AND METHODS

Model Systems. To address these questions, we conducted a set of reaction-norm experiments on genotypes of the annual plant *Abutilon theophrasti* (velvetleaf) and the deciduous tree species *Betula alleghaniensis* (yellow birch). The two species were grown both as individual plants in isolated pots and, as monospecific mixtures of genotypes, in dense stands in large growth containers. The experiments were carried out under atmospheres with ambient (350 ppm) and elevated (700 ppm) CO₂ levels in a controlled-environment facility. Eight genotypes of *Abutilon* and three maternal families of *Betula* were used in the experiments.

Seeds of *Betula* were collected from three mother trees within a 100-m² area in a mixed hardwood stand in the Harvard Forest, Petersham, Massachusetts. The *Abutilon* genotypes originated from an old field in central Illinois (Phillips Tract, University of Illinois Ecological Research Area, near Urbana). Seeds from which the original clones were derived were collected at 50-m intervals, and the resulting plants were clonally propagated by the axillary meristem enhancement method (Native Plants, Salt Lake City). Seeds used in the experiment were selfed progeny of the clonally propagated plants.

Experimental Design and Growing Conditions. The experiments were set up as factorial designs, with three blocks each split into two CO₂ levels. Stands were replicated twice and individually grown genotypes were replicated four times (*Abutilon*) and three times (*Betula*) within each block-CO₂ combination. Seedlings were transplanted into either 2.0-liter containers (individually grown plants) or into 22.5-liter tubs (high-density stands, with plants growing in a regular hexagonal grid in each tub). For *Abutilon*, each stand had 48 experimental plants, surrounded by 48 unmeasured edge plants of uniform genetic background, resulting in the density of 560 plants per m². A seedling of each *Abutilon* genotype was surrounded by six seedlings randomly selected from among the other seven genotypes. *Betula* stands had 24 experimental seedlings per container, with 24 additional edge plants (density of 280 plants per m²). *Betula* seedlings were planted such that a seedling from each maternal family was surrounded by equal numbers of all three families.

Plants from both CO₂ treatments were grown from seed in their respective CO₂ conditions. Soil and nutrient conditions approximated naturally occurring local systems in New England. All *Betula* pots and tubs were filled with reconstructed Harvard Forest soil profiles (7 cm of organic layer covering 8 cm of mineral soil), which resulted in roots with well-developed mycorrhizal infections. Roots were separated and retrieved for whole-plant biomass estimates. Seedlings were watered regularly and no nutrients were added to the soil. In the *Abutilon* experiment, naturally occurring sandy loam of eastern Massachusetts was used, with nutrients added as a slow-release balanced NPK fertilizer (Osmocote) at a rate corresponding to 150 kg of N per hectare per year. The experiment was continued through the first year's growth of *Betula* and through the entire life cycle of *Abutilon*, thus making possible quantitative genetic estimates of selection and drift on the basis of lifetime reproductive output for the latter species.

Statistical Analyses. Mixed-model analyses of variance were performed on untransformed data, with variation at the levels of stands (tubs) pooled with the error term. Genotypes were analyzed as a random factor in *Abutilon* and as fixed in *Betula* (due to a difference between the species in the sampling scheme employed in seed collection). The nature of the genotype-CO₂ interaction was further analyzed with a rank-

based approach, since the parametric analysis of variance does not detect the presence of qualitative (crossover) interactions (39, 41, 42). All data on total biomass or fruit biomass were converted into ranks, indicating relative performance of all plants in a given stand or, in the case of individually grown plants, in a given experimental module. Genotype-specific responsiveness to increased CO₂ was calculated as the difference in the geometric mean of biomass at elevated CO₂ and ambient CO₂ levels. Variation in responsiveness was in turn calculated as the variance in these genotype-specific responsiveness values.

Quantitative Genetic Analyses. Response to selection, R (i.e., the expected rate of increase in fitness under Fisher's fundamental theorem), is quantified as the product of fitness heritability and the variance in total relative fitness, or $R = h^2 V_w / W^2$ (where h^2 is narrow-sense heritability, and V_w and W are the variance and mean, respectively, of absolute fitness before selection) (43). h^2 was estimated as broad-sense heritability (H^2), calculated as the proportion of variance explained by genotype pooled across blocks. Although H^2 generally overestimates h^2 (due to incorporation of dominance and epistasis effects), the comparisons of relative magnitudes of estimated selection rates under different environmental conditions should be little affected by this bias. We tested for differences in the overall selective response, R , using a bootstrapping approach as previously applied in pairwise tests for differences in heritability estimates (44); 2000 iterations were used for each test. The "opportunity for selection," I , was calculated as the square of the coefficient of variation in fruit biomass.

The effects of altered reproductive distributions on genetic drift were quantified according to Heywood (45): $N_e/N = 1/[(1 + F)(s_b^2/z_b^2) + 1]$, where N_e/N is the ratio of effective to observed population size, F is the fixation index, and s_b and z_b are the standard deviation and mean of adult fecundity, respectively. For the purposes of these calculations we assumed a fixation index of 0, expected under outcrossing.

The rate of character change under directional selection was estimated according to a broadly accepted model of selection on correlated quantitative characters (46, 47). For the case of a single quantitative character correlated with fitness, the general multivariate model reduces to $\Delta z = \alpha R$, where Δz is the rate of character change per generation, α is the genetic correlation with fitness, and R is the response to selection as defined above. Here we examined the response to selection of genotype-specific CO₂ responsiveness, calculated as above.

RESULTS AND DISCUSSION

Density Effects. The results strongly support the hypothesis of a reduction in growth responses under high-density conditions. When plants were grown as individuals, both species exhibited pronounced responses to increased CO₂, with final biomass enhancement ratios (700 ppm/350 ppm) of 1.48 and 1.14 for *Betula* and *Abutilon*, respectively. In contrast, the overall stand-level responses for plants grown at high density were considerably lower, with corresponding ratios of 1.16 and 1.04. This decline in CO₂ growth response with density corresponds to a significant CO₂-density interaction effect in analyses of variance which was highly significant in *Betula* ($P = 0.0001$) and marginally significant in *Abutilon* ($P = 0.074$). However, the latter test had low power due to very few degrees of freedom available in the denominator (genotype-CO₂-density term, $df = 7$). Removing genotypes from the model yielded a highly significant CO₂-density interaction effect for *Abutilon* ($P = 0.0002$) in a two-way analysis of variance.

Genotype-CO₂ Interaction. In spite of the fact that the overall magnitude of response was reduced at high density, variance among genotypes in CO₂ responsiveness (measured as the logarithm of the ratio of mean performance at elevated and

ambient CO₂ concentrations) was higher under competitive conditions. In *Abutilon*, variance in genotype-specific CO₂ responsiveness was \approx 8-fold higher in dense stands than in individually grown plants (0.428 vs. 0.056; $P < 0.02$). In *Betula*, variance among maternal lines in CO₂ responsiveness was \approx 3-fold higher in dense stands (0.100) than in individually grown plants (0.027), though this difference was not statistically significant ($P > 0.25$).

For both species and at both densities, growth responses to increased CO₂ were genotype-specific (Fig. 1). Analyses of variance indicated a significant genotype-CO₂-density term in both *Abutilon* ($P = 0.017$) and *Betula* ($P = 0.035$). Analyses of variance were then repeated at each density separately and the sums of squares for genotype, CO₂, and genotype-CO₂ effects were expressed as percentages of their sum (i.e., excluding effects due to blocking). The main effect due to CO₂ (open bar in Fig. 1) was not significant at either density in *Abutilon* ($P > 0.1$), marginal in *Betula* stands ($P = 0.07$), and highly significant in *Betula* grown singly ($P = 0.0001$). The main effect due to genotype (solid bar) was significant in the high-density treatment ($P = 0.0001$) in both *Abutilon* and *Betula* and in singly reared *Abutilon* ($P = 0.017$), but not in singly reared *Betula* ($P = 0.384$). Genotype-environment (CO₂) interactions (hatched bar) were significant at both high ($P = 0.004$) and low ($P = 0.044$) density in *Betula*, but not in *Abutilon* ($P = 0.571$ and $P = 0.126$, respectively).

Shifts in genotypic ranks, as indicated by statistically significant genotype-CO₂ interaction terms, occurred in *Betula* stands ($P = 0.031$), but not in *Abutilon* stands ($P = 0.631$). Among individually grown plants, crossover interactions in genotypic ranks were marginally significant in both *Betula* ($P = 0.107$) and *Abutilon* ($P = 0.075$). Genotype-specific responses substantially altered the final distributions of biomass and reproductive output under increased CO₂ within experimental populations of both species (Fig. 2).

Quantitative Genetics of CO₂ Response. Two genetic processes may in theory contribute to a loss of genetic diversity under increased CO₂: (i) reductions in genetic variation due to directional selection (48, 49) and (ii) the effects of altered reproductive distributions on genetic drift (45). At high density the overall response to selection in *Abutilon* was nearly 3-fold higher at the elevated than at the ambient CO₂ level (responses to selection of 0.320 vs. 0.104, respectively; significant at $P = 0.02$). The response to selection among individually grown plants at both CO₂ levels was approximately an order of magnitude lower than in high-density stands, with values of 0.038 vs. 0.016, and not significantly different between the CO₂ levels ($P = 0.35$). The enhanced rates of selection at increased CO₂ correspond to an increase in relative variation of fitness at high density and elevated CO₂ concentration and to an increase in broad-sense heritability under increased CO₂ for both density treatments. At high density, the increase in relative variation in fitness also results in an increase in the

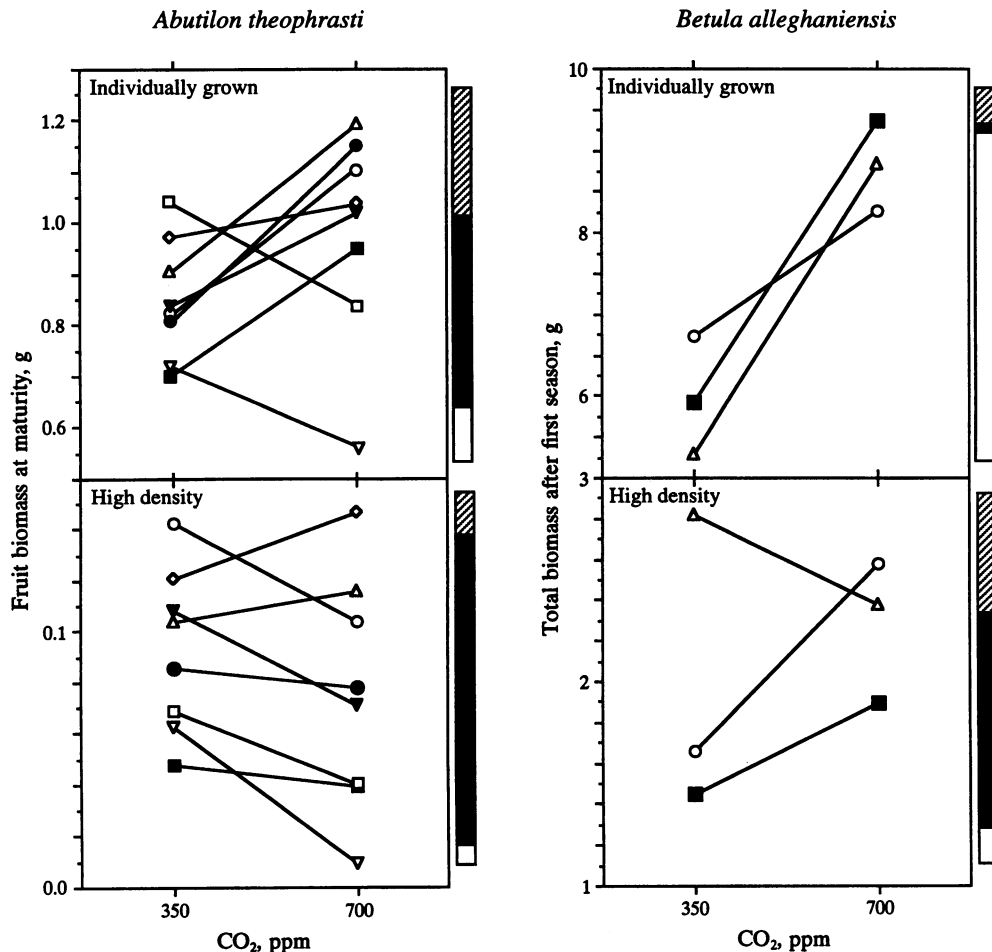


FIG. 1. Norms of reaction for performance of genotypes of *A. theophrasti* (Left) and *B. alleghaniensis* (Right) in response to atmospheric CO₂ concentration. Plants were grown either individually (Upper) or under high-density conditions (Lower). For *Abutilon*, each point represents an average of 12 (individually grown) and 36 (high density) plants; corresponding sample sizes for *Betula* are 9 and 48 plants, respectively. Bars adjacent to each panel indicate the proportion of the explained variance accounted by the CO₂ main-effect term (open bar), the genotype term (solid bar), and the CO₂-genotype interaction term (hatched bar).

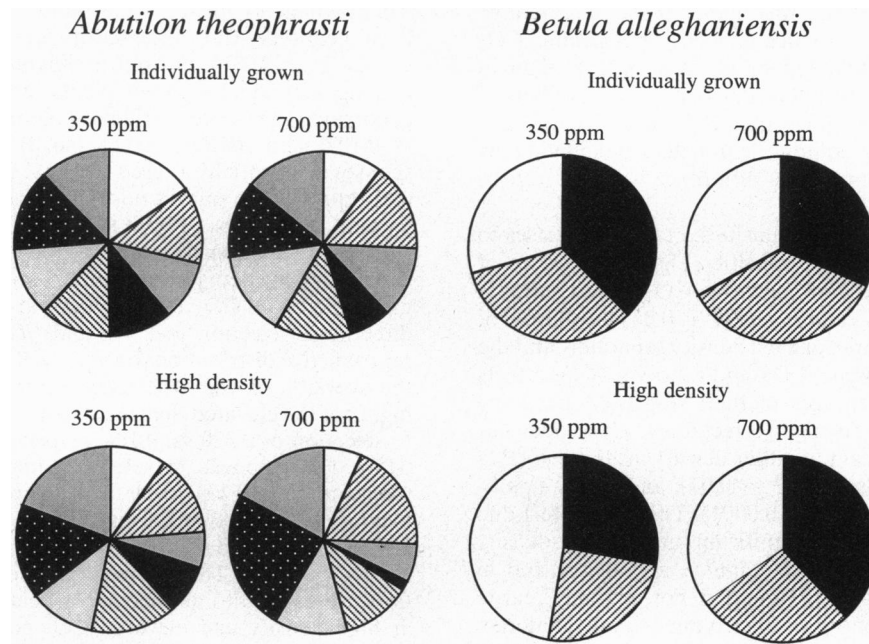


FIG. 2. Proportions of total fruit output (*Abutilon*) and end-of-season total biomass (*Betula*) in response to increased CO₂ for genotypes grown individually and at high density.

expected rate of genetic drift at the elevated CO₂ concentration ($N_e/N = 0.325$ vs. 0.246 at ambient vs. elevated CO₂, respectively). The opportunity for selection, I , for individually grown *Abutilon* plants was 0.31 and 0.16 at ambient and elevated CO₂, respectively; corresponding broad-sense heritabilities were 0.052 and 0.236 . For the high-density *Abutilon* plants values of I were 2.08 and 3.07 at ambient and elevated CO₂, respectively; corresponding broad-sense heritabilities were 0.050 and 0.104 .

The potential for selection to result in enhanced CO₂ responses in subsequent generations is a product of two factors: (i) the genetic correlation of genotype-specific growth responses with relative fitness under high CO₂ and (ii) the overall intensity of selection for CO₂-related enhancement of growth. At increased CO₂, genetic correlations of fitness with reproductive responsiveness were high (0.927 and 0.656 for individual and high-density treatments, respectively; $P < 0.05$ in both cases). However, the corresponding genetic correlations for biomass responsiveness were much lower (0.005 and 0.210 ; $P > 0.05$). Therefore, the estimated rate of character change was very low for CO₂ responsiveness, with projected increases of 0.02% and 0.94% per generation for individually grown and high-density plants, respectively.

Conclusion. In contrast to numerous studies investigating the evolutionary responses of plants to a wide range of anthropogenic stresses including heavy metals (50), atmospheric pollutants (e.g., SO₂, NO₂, and O₃) (51), and herbicides (52), very little is known about plant evolutionary responses to rising atmospheric CO₂ levels. It has been hypothesized that if rising CO₂ levels result in selection favoring genotypes that exhibit increased productivity in CO₂-enriched atmospheres, terrestrial ecosystem carbon storage may be significantly increased. As terrestrial ecosystems compose a significant component of the Earth's carbon cycle, the evolution of increased productivity could have a significant impact on current predictions regarding rates of atmospheric CO₂ increase in the future, and thus associated global climate change. Our results demonstrate that while the intensity of selection among competing plants is increased in elevated-CO₂ atmospheres, selection in these environments may not result in increases in plant growth responsiveness to CO₂. However, increased CO₂ may

greatly influence genetic composition of plant populations by selecting for other phenotypic traits; perhaps the most important class of traits favored will be those conferring greater relative fitness under enhanced competition for other limiting resources. Consequently, the overall effects of increasing CO₂ on the intensity of selection in plant populations may be surprisingly large, potentially resulting in substantial changes in the genetic diversity of natural plant populations.

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