INTER- AND INTRAGENOTYPIC COMPETITION UNDER ELEVATED CARBON DIOXIDE IN *ARABIDOPSIS THALIANA*

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Abstract. The consequences of elevated CO_2 on plant growth have been well studied on individual plants. The response of a more complex system with several plants interacting is less understood—a situation that limits our capacity to predict the response of natural plant communities. In this study we analyzed the effect of CO_2 enrichment on intergenotypic competition in *Arabidopsis thaliana.* Seeds of five genotypes collected from different natural populations were used. Each genotype was cultivated in a pure stand and in a mixture with each of the other four genotypes in two CO_2 conditions (ambient and elevated). At harvest time, genotype fitness was estimated by the number of fruits and seeds produced per plant. At current levels of CO_2, genotypes performed better in a pure stand than in a mixture. Kin selection, associated with the low seed dispersal and autogamous reproductive regime of *A. thaliana,* is invoked to explain these positive responses among plants of similar genotype. Surprisingly, in a high-CO_2 atmosphere (700 μL/L) the reverse situation was observed: plants performed better in mixtures than in pure stands. Positive frequency-dependent selection under ambient CO_2 concentration became negative under elevated CO_2, which could lead more easily to the maintenance of genetic variation. This hypothesis was tested with a simple model of competition. At equilibrium, the simulation did not show coexistence among more genotypes under elevated CO_2 than under ambient CO_2 concentration. However, this study allows predictions about evolutionary trajectories under high-CO_2 conditions. In *A. thaliana,* genotypes that will maintain the most their ability to grow well in pure stand should be selected under increasing CO_2.

Key words: Arabidopsis thaliana; *elevated CO_2 and competition among genotypes; fitness; genotype; global change, implications of elevated CO_2; intraspecific competition; kin selection; selection, frequency dependent.*

INTRODUCTION

Atmospheric CO_2, the primary substrate for photosynthesis, is currently increasing in concentration. A doubling of the present (ambient) concentration is expected to be reached by the end of the next century (Keeling et al. 1989). The implications of this for individual plant metabolism, growth, and development are profound and are now well known. However, these physiological changes are not easy to relate to fitness or demographic changes, notably since competitive interactions are modified in ways that are not easily predicted. Likewise, the effects of elevated CO_2 concentrations on temperature are difficult to predict. For simplicity, our study focused on increasing CO_2 and did not attempt to simulate global warming.

A major effect of increasing CO_2 is to increase competition for other resources by speeding up plant growth (Bazzaz and McConnaughay 1992), perhaps influencing population demographic parameters. For example,

simulated population dynamics of *Abutilon theophrasti* at high CO_2 exhibited greater oscillations as a result of higher fecundity combined with overcompensating dependence of fecundity on density (Bazzaz et al. 1992). A second effect of elevated CO_2 concentrations is to modify the outcome of competition. At the interspecific level, for example, Wray and Strain (1987) showed that CO_2 enrichment increases the competitive ability of *Aster pilosus* so that it suppresses the growth of *Andropogon virginicus.* Thus, many studies predict that CO_2 enrichment will affect plant communities in terms of productivity and species composition (Bazzaz and Carlson 1984, Bazzaz and Garbutt 1988, Leadley and Stöcklin 1996, Potvin and Vasseur 1997).

At the intraspecific scale, one might also expect major changes in population composition through modification of the competitive process. A few studies provide direct empirical evidence of modifications of competition in high CO_2. For example, Bazzaz et al. (1995) showed that variance in genotype-specific CO_2 responsiveness was far greater in dense stands of *Abutilon theophrasti* and *Betula alleghaniensis* than in individually grown plants. Genotypes with the largest growth

PLATE 1.   Left: Wild population of *Arabidopsis thaliana* in Orsay, France. Intraspecific competition between individuals is strong (photograph by Bernard Godelle). Right: In each plot of the competition experiment, 20 plants were cultivated in pure stands or in pairwise mixtures. The experiment was conducted under ambient and elevated CO_2 (photograph by Christophe Andalo).

responses to CO_2 in the absence of competition did not have the greatest fitness in a competitive stand. These results at the population scale show that competition should not be neglected if we are interested in understanding evolutionary processes associated with increasing CO_2. In addition, it is now well established that traits that are important for determining the outcome of competition between plants (phenology, resource allocation, growth, fecundity, or germination) are often modified in genotypically specific ways under elevated CO_2 (see Norton et al. 1995, Zhang and Lechowicz 1995, Andalo et al. 1996, Ward and Strain 1997, Andalo et al. 1998, for research on *Arabidopsis thaliana*). Genotypes will then modify their own competitive ability in very different ways, and high CO_2 will probably change the competitive interrelationships of numerous species.

Details of intergenotypic competition have been well studied in some crop species in order to understand how the outcome of competition is determined (Goldringer et al. 1994). In *A. thaliana* Griffing (1989) provided a genetic analysis of complex competitive interactions among three genotypes (two genotypes and their F_2 hybrid) across several environments. However, as far as we know, there have been no studies of intergenotypic competition in wild species in relation to the global-climate-change scenario. The intraspecific competition of *A. thaliana* is usually quite large because of poor seed dispersal (Harper 1977), rapid colonization of freshly perturbed sites, and a relatively synchronous seed germination (Ratcliffe 1961, Baskin and Baskin 1971). Moreover, there are numerous different

life-history strategies (e.g., for flowering time, growth rate, rosette size, see Kuittinen et al. [1997]) that may be related to genotypic competitive ability. For these reasons, we have chosen this annual species with a short generation time to study the intergenotypic competition in different CO_2 concentrations.

Our study investigates the CO_2 effect on the interactions among five genotypes collected from different natural populations of *A. thaliana.* Each genotype was cultivated in a pure stand and in a mixture with each of the other four genotypes. We used a simple model to study the potential frequency-dependent processes resulting from intergenotypic competition. Frequency-dependent patterns of interaction have often been described (Bell 1997) and could be an indication of powerful forces causing the retention of variability in populations. Do such interactions exist among natural genotypes of *A. thaliana*? Can we predict their evolution in the CO_2 concentration forecast for the next century and their consequences for the selective process?

MATERIALS AND METHODS

Study species

Arabidopsis thaliana is a small, predominantly selfing (Abbott and Gomes 1989) species that is widely distributed in many parts of the north-temperate zones of the world (see Plate 1). This annual weed grows in open habitats (Ratcliffe 1961) like cliffs, sandy bluffs, roadsides, borders of paths, and gardens. This species is characterized by high fecundity. Natural populations are generally referred to as ''ecotypes,'' which are usu-
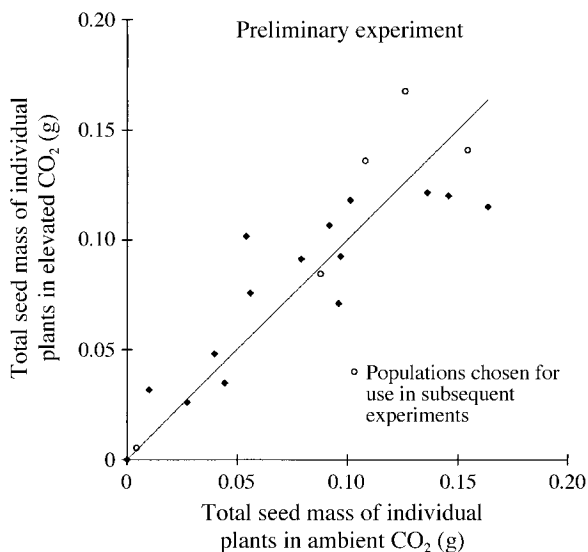
Fig. 1. Seed production by *Arabidopsis thaliana* in a preliminary experiment with two CO$_2$ treatments for 20 genotypes (from different populations near Paris, France). Ambient = 350 μL CO$_2$/L of air; elevated = 700 μL/L. From this experiment we selected five genotypes with contrasting seed production and response to elevated CO$_2$.

ally classified as early or late flowering. Early flowering ecotypes (winter annual) germinate in the autumn and flower early in the spring while late-flowering ecotypes (summer annual) complete their life cycle in the same season. In Central Europe these two ecotypes are common and can be found together in the same populations.

Preliminary experiment

In late May–early June 1996 seeds from 20 maternal plants, each sampled from a different population near Paris (France), were harvested and stored in a seed cabinet at 5°C and 35% humidity. Progenies from a single parent plant are considered to be genetically homogenous because of the high selfing rate of the species, and will be referred to as belonging to the same "genotype" hereafter.

On 5 December 1996 the seeds were sown in pots (28 × 20 × 10 cm) filled with a mixture of peat and compost and covered with a glass plate (see Plate 1). Each pot contained 10 rows of 10 seeds, each row corresponding to a particular genotype. To break seed dormancy the pots were pre-incubated in a cold chamber in the dark at 4°C for 7 d. The 16 pots were then put in eight greenhouses, four with ambient CO$_2$ and four CO$_2$-enriched (see Andalo et al. [1998] for greenhouse characteristics and environmental conditions). In each greenhouse, each one of the 20 genotypes was represented by two rows of seeds located in two different pots.

On 10 February 1997, with none of the fruits having yet ripened, all the plants were watered for the last time and a transparent plastic film was put among rows.

Three months later, the total seed pool produced in each row was collected and weighed. Within each row the number of plants that reached maturity from the original 10 seeds was counted, and the average seed mass produced by individual plants was calculated as a simple arithmetic average.

Our method of harvest constrained this experiment to a length that was probably shorter than the life cycle of some of the genotypes used. Consequently a few genotypes produced no or only few seeds (Fig. 1). Because of this problem, we did not pursue analysis of these data, but used the results to select five genotypes with contrasting seed production (probably related to contrasting length of life cycle) and response to elevated CO$_2$ (Fig. 1).

Preparation of plant material

On 12 August 1997 the seeds from these five genotypes were sown in pots filled with a mixture of peat and compost and covered with a petri dish. To break seed dormancy the pots were pre-incubated in a cold chamber in the dark at 4°C for 7 d and then kept 2 wk in the greenhouse as described in Andalo et al. (1998). Seeds of each genotype were sown in different pots, one for each CO$_2$ treatment (700 and 350 μL CO$_2$/L of air, 10 pots overall). Seedlings in these pots were then used in the experiment below.

Experimental design

On 4 and 5 September 1997 seedlings were transplanted to plastic pots (17 × 13 × 6 cm) with 20 plants per pot (905 plants/m^2) and placed outside in four unheated growth tunnels (2 × 0.5 × 1 m), two with ambient CO$_2$ and two with CO$_2$-enriched air with a constant flow of industrial CO$_2$ pumped in from one side. All tunnels had slightly higher pressure than ambient air because of the constant air inflow, and air escaped through large holes at the opposite end of the tunnels. To minimize a potential tunnel effect we moved individual pots among tunnels and changed CO$_2$ treatments among tunnels four times during the experiment. During the study period, average daily air temperature ranged from −4.4°C to 21.9°C, and average daily radiation from 0.83 MJ/m^2 to 28.8 MJ/m^2.

To separate intra- and intergenotypic effects of competition we grew plants in pure stands and in pairwise mixtures of five genotypes (A, B, C, D, and E). For the pairwise mixtures, we generated all 10 combinations between genotypes: A + B, B + C, C + D, D + E, A + C, B + D, C + E, A + D, B + E, and A + E. For each combination, we varied the frequency of the two genotypes (20:80 and 80:20). There were two pots in each CO$_2$ treatment (100 pots overall). For each pot, we counted the number of fruits on four plants at two dates: two months after sowing, when the plants of genotype D (which had the shortest life cycle of the five genotypes) had completed fruit production, and at the end of the experiment, when all plants had died

TABLE 1. ANOVA results for *Arabidopsis thaliana* competition sensitivity calculated with data from the second harvest.

Source of variation	Effect	df	MS	F	P
CO_2	fixed	1	73 022	9.07	0.0046*
Geno	fixed	4	1 674	0.21	0.9324
GenoN	fixed	4	27 336	3.4	0.018*
Pot(CO_2 × Geno × GenoN)	random	38	8 049	1.72	0.0091*
CO_2 × Geno	fixed	4	40 104	4.98	0.0025*
CO_2 × GenoN	fixed	4	24 115	3	0.0304*
Geno × GenoN	fixed	11	15 804	1.96	0.0611
CO_2 × Geno × GenoN	fixed	10	22 015	2.74	0.0122*
Error		212	4 683		

Note: The effects of genotype (Geno), genotype of the neighbor (GenoN), CO_2 treatment (CO_2), pot, and all the interactions were tested (mixed model).

* *P* values are significant at the 0.05 level.

and aboveground biomass was dry. For the pairwise mixture the four plants were those sown at the low relative frequency. The two dates of measurements (referred to as ''first harvest'' and ''second harvest'' hereafter) may mimic two types of disturbance: the first may represent an environment in which not all plants can complete their life cycle, the second may represent environmental conditions persisting long enough to allow all plants to reproduce completely.

For each genotype in each pot 10 unripened fruits were harvested on a randomly chosen plant of the four plants on which the fruit number was measured. The seed number (from the 10 fruits) was counted and we calculated the mean seed number per fruit.

Statistical analysis

We investigated the relationship between fruit number and seed number per fruit using correlation analysis. Independent of their environment or genotype, individual plants were considered as statistically independent observations. As the fruit number and the seed number per fruit (i.e., the total seed number) were positively and significantly correlated (see *Results*), all subsequent analyses were based on the total fruit number (measured on four plants per pot) as a measure of individual fitness (noted ''W'' hereafter).

For the pure stands we averaged data over the two pots (eight plants in total) per CO_2 treatment to generate a measure of fitness in competition only with individuals of the same genotype, $\bar{W}_{ii}$. For the mixed stands in each CO_2 treatment and for the different pairwise combinations, we calculated, for each plant of genotype *i* cultivated with plants of genotype *j* (mixture with 20% of *i* and 80% of *j*; eight plants for a particular combination), its competition sensitivity as $\bar{W}_{ii} - W_{ij}$. The data from the two harvests were analyzed separately. Using SAS software (SAS Institute 1990) and analysis of variance, we tested the effects of genotype, genotype of the neighbor, CO_2 treatment, pot (nested within the three previous factors), and all the interactions.

Model

Because our statistical analysis revealed complex interactions between pairs of genotypes and the CO_2 treatment (see *Results,* below) we performed numerical simulations using the model of Schutz et al. (1968) to tease apart these complex effects. This is a simple model for pairwise competition, initially used by Schutz et al. (1968) to investigate competitive feedback mechanisms that may allow coexistence among different homozygous lines in a population of soybeans and other autogamous plant species.

We considered a population of five competing genotypes in which (1) the fitness of genotype *i* competing with genotype *j* is a linear function of the frequency of *j* and (2) the complex competitive interaction of genotype *i* with all the five genotypes is equal to the sum of the interactions of *i* with each genotype:

Genotype	Frequency	Fitness
A	P_A	$W_A = \sum_j P_j W_{A_j}$
B	P_B	W_B
C	P_C	W_C
D	P_D	W_D
E	P_E	W_E

W_{ij} is defined as above and P_j is the proportion of genotype *j* in the population. The mean fitness of the population is

$$\bar{W} = P_A W_A + \cdots + P_E W_E = \sum_i P_i W_i$$

$$= \sum_i \left(P_i \sum_j P_j W_{ij} \right).$$

The frequency of *i* in the $t + 1$ generation is $P_i^{(t+1)} = P_i^{(t)} W_i / \bar{W}$. For each CO_2 concentration, simulations were performed with the data from the two harvests up to equilibrium.

RESULTS

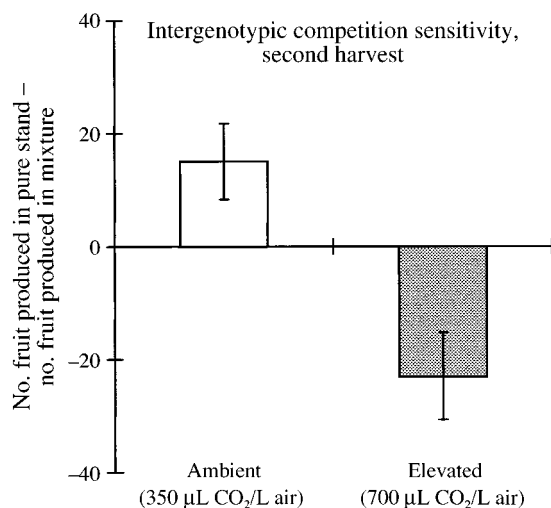The correlation between fruit number and seed number per fruit was positive and significant ($r = 0.296$;

FIG. 2. Mean difference in production of *Arabidopsis thaliana* fruits between a culture in a pure stand and a culture in a mixture, in the two CO$_2$ treatments and for the second harvest (under ambient CO$_2$, $\bar{X}$ = 15.08, 1 SE = 6.74, n = 146; under elevated CO$_2$, $\bar{X}$ = −23.03, 1 SE = 7.73, n = 143). The data used for a particular genotype were either production of fruits when its relative frequency was 100% (pure stand), or a 20% (mixture) with one of each of the other four genotypes.

n = 91 plants; P = 0.0043). The plants that produced the most fruits also produced the highest seed number per fruit, and therefore the highest total seed number.

CO$_2$ modified significantly the sensitivity of genotypes to intergenotypic competition (Table 1). At the second harvest, in the ambient CO$_2$ treatment, genotypes performed better in pure stands than in a mixtures (Fig. 2). The reverse was true in the high-CO$_2$ treatment (Fig. 2). Two types of responses could explain such a result: an increase in fruit production with increasing CO$_2$ when plants are cultivated in a mixture (genotypes C and D) or a decrease when plants are cultivated in a pure stand (genotypes E and A) (Fig. 3). The five genotypes influenced differently the neighbor's yield (Table 1: GenoN effect). The effect of the genotype of the neighbor and the effect of the genotype of the plant itself were complex as they both interacted significantly with CO$_2$ treatment (Table 1).

At the first harvest, irrespective of the CO$_2$ treatment, the fruit production of pure stands was not significantly different from that of mixtures.

The simulations allowed us to understand the direction of the selective process with complex intergenotypic relationships and frequency-dependent selection. In the two CO$_2$ concentrations, intergenotypic competition did not maintain all the genotypes (Fig. 4). From the reaction norms, at the second harvest, genotypes C and D greatly increased fruit production in elevated CO$_2$ (Fig. 3). In this high-CO$_2$ concentration, the simulation shows a stable equilibrium between these two strong competitor genotypes (Fig. 4), where-

as genotype E will not survive. At the first harvest, when there was no effect of competition on fecundity, only the genotype with the shortest life cycle (genotype D) was selected. Under elevated CO$_2$, we observed an equilibrium between this genotype D and the genotype B, which displayed the largest CO$_2$ response.

DISCUSSION

In our experiment, we show that in ambient CO$_2$ the fitness of a genotype was greater when surrounded by the same genotype than when surrounded by individuals of a different genotype. In this situation, intergenotypic competition generates positive frequency-dependent selection and thus is unable to maintain genetic variation. This result is in total disagreement with the classical multiple-niche selection view, where the competitive environment of a genotype is more intense when the habitat is occupied by individuals of the same
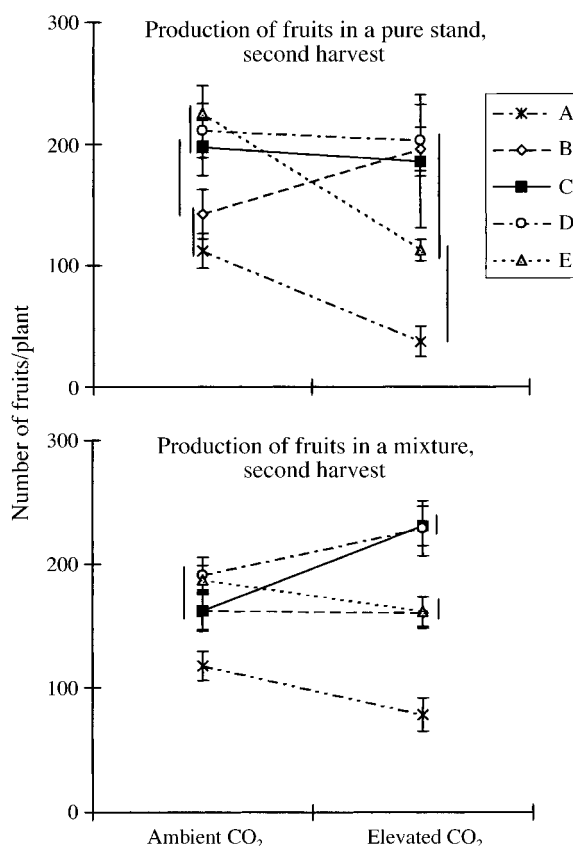

FIG. 3. Reaction norms for the five *Arabidopsis thaliana* genotypes (A–E) in the two CO$_2$ treatments. Only the production of fruits at the second harvest has been plotted. In mixed culture, the data used for a particular genotype were its production of fruits when its relative frequency was 20% with one of each of the other four genotypes. Vertical bars group means that were not significantly different ($P > 0.05$) by a Duncan's test (SAS Institute 1990). For the pure stands and the mixtures, in each CO$_2$ treatment, the Duncan's test was performed after a simple ANOVA where genotype effect was tested.
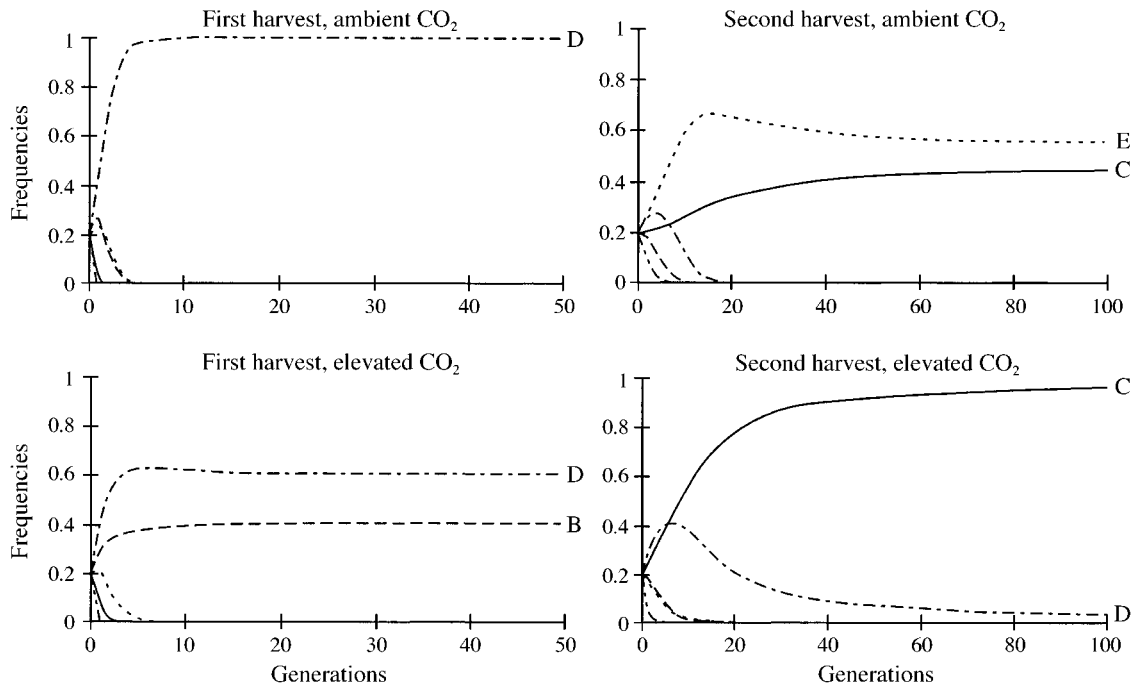
FIG. 4. Simulated frequencies of the five genotypes (A–E) of *Arabidopis thaliana* based on production of fruits measured at the two harvests at ambient and elevated CO_2 (350 and 700 μL CO_2/L air, respectively) in mixture and pure stand cultures. Surviving genotypes are designated by capital letters.

genotype within the same niche. Such a reduction in competition resulting from genetic differences between neighbors has been demonstrated by Allard and Adams (1969), who showed that inbred lines of barley often interact positively with each other and that stable multi-genotypic associations in populations seem to be possible. If inter-genotypic competition with frequency-dependent selection is potentially very important in maintaining genetic diversity, especially for a species growing at a high density and in single-species stands (Ennos 1983), it is necessary to invoke other mechanisms for explaining the maintenance of genetic variation in *Arabidopsis thaliana.* How can we explain the apparently positive responses among plants having the same genotype? *A. thaliana* is a highly autogamous species (Abbott and Gomes 1989, Krannitz et al. 1991) with low seed dispersal (Harper 1977). In natural populations, individuals are very often surrounded by plants arising from the same parent plant and thus having the same (or similar) genotype. By kin selection, genotypes reducing the degree to which they repress the growth of their neighbors could be selected (Bell 1997). This has been reported by Goodnight (1985), who showed that group selection on leaf area occurs in *A. thaliana.* Such a process of group selection in viscous populations (where the migration rate is limited and individuals interact mainly with their relatives) is believed to be a possible cause of altruistic evolution in a wide range of organisms (Stevens and Wiley 1995)

and has been studied theoretically (Ferrière and Michod 1995).

Interestingly, this result does not hold true in elevated CO_2, in which plants performed better in mixtures than in pure stands. The increase in intragenotypic competitive interactions in high CO_2 and the differences among genotypes in morphological and physiological response to CO_2 (see *Introduction*) could explain this result. In *A. thaliana,* Zhang and Lechowicz (1995) found, for example, the opposite response for the shoot/root ratio between two genotypes. As a consequence, the increase in competition resulting from CO_2 enrichment will cause two plants with the same physiological response (e.g., relative increase in the shoots) to interact negatively more strongly than two plants with divergent responses. By this mechanism, the fitness in a pure stand may decrease (as shown for genotypes A and E in our experiment) or the fitness in a mixture may increase (genotypes C and D).

Griffing (1989) found that one highly successful genotype of *A. thaliana* was also the best competitor across the range of environments tested, which did not include CO_2. With only five genotypes it was impossible for us to test the relationship between competitiveness and overall mean productivity. However, we found a tendency for the most productive genotypes to be the most competitive, reducing the fitness of their partner genotypes under ambient CO_2 conditions. This relationship disappeared completely under the elevat-

ed-CO$_2$ environment. The difference in the relationship between overall performance and competitiveness in the two environments is contrary to the finding of Griffing (1989).

Since negative frequency-dependent selection leads more easily to the maintenance of genetic diversity, the evolutionary consequences of these results could be important. However, despite a certain level of negative frequency-dependent selection in high CO$_2$, our simulations show that only two genotypes could be maintained in these conditions. Independent of the intensity of competition, the genotypes that showed the strongest positive response to the CO$_2$ treatment (genotypes C and D) were always selected. Among those genotypes that produced more seeds in elevated CO$_2$, kin selection should favor those that grow better in pure stands. Through the simulations we showed that there may be a shift in population genetic composition in elevated CO$_2$. The general level of interactions among plants will increase, and the competitive characteristics of genotypes within species may change. To be selected, genotypes must have two characteristics: first, be a good competitor in mixture, and second, be able to grow in a pure stand (genotypes C and D).

Our model and our experiment consider interactions between only two genotypes at a time. Clearly, in the field higher order interactions certainly occur, as well as interspecific competition and complex environmental effects. In addition, the increase of CO$_2$ concentration will be progressive and many others important environmental parameters (temperature, pattern of precipitation) are expected to change (IPCC 1990). Considering the scale of our study, our models and experiments are not able to consider all these parameters at once. Nonetheless, addressing this simple situation permits insights into the changing interactions that might be expected under changing environmental conditions.

Our simulations predict that only one or two genotypes will be maintained, even though negative frequency-dependent selection under high CO$_2$ should increase, at least temporarily, genetic diversity in *A. thaliana* populations. The consequences of increasing CO$_2$ level on genetic diversity is actually poorly documented. One hypothesis is that high CO$_2$ constitutes a novel environment (Thomas and Jasienski 1996) that may allow expression of new gene combinations. Neutral genetic diversity under ambient CO$_2$ concentration could become selected genetic diversity for fitness-related traits under high CO$_2$. From this hypothesis, as from our results, genetic diversity in a high-CO$_2$ world could increase in several species. However, this increase should be temporary because, first, individual selection would remove genetic variance for these fitness-related traits, and, second, group selection in viscous populations would favor genotypes that make the transition from negative frequency-dependent selection that we found in *A. thaliana* into positive frequency-dependent selection, which cannot maintain genetic

variation. Furthermore, there is another hypothesis that predicts a decrease in genetic diversity under elevated CO$_2$ because small-scale environmental sources of variation in plant fitness may increase via an increase in the competitive interactions in this rich environment (Thomas and Jasienski 1996).

To really predict the long-term consequences of elevated CO$_2$ on genetic diversity it seems more interesting to characterize the CO$_2$ selective pressure. From our experiment, in disturbed habitats, a genotype (not selected in undisturbed habitats) that enhances its fitness in elevated CO$_2$ more rapidly (genotype B) will be favored. Other studies showed that the CO$_2$–genotype interaction depends on the general level of competition (Bazzaz et al. 1995, Steinger et al. 1997). All these results point to the changeable characteristics of selective pressures exerted by the new CO$_2$ environment. Even though there may be uniform change in CO$_2$ level all over the globe, for a particular species this does not mean that the same genotype will be selected in different areas. Local selection will depend on other environmental conditions, both biotic and abiotic.

Literature Cited

Abbott, R. J., and M. F. Gomes. 1989. Population genetic structure and outcrossing rate of *Arabidopsis thaliana* (L.) Heynh. Heredity **62**:411–418.

Allard, R. W., and J. Adams. 1969. Population studies in predominantly self-pollinating species. XIII. Intergenotypic competition and population structure in barley and wheat. American Naturalist **103**:621–645.

Andalo, C., B. Godelle, M. LeFranc, M. Mousseau, and I. Till-Bottraud. 1996. Elevated CO$_2$ decreases seed germination in *Arabidopsis thaliana*. Global Change Biology **2**:129–135.

Andalo, C., C. Raquin, N. Machon, B. Godelle, and M. Mousseau. 1998. Direct and maternal effects of elevated CO$_2$ on early root growth of germinating *Arabidopsis thaliana* seedlings. Annals of Botany **81**:405–411.

Baskin, J. M., and C. C. Baskin. 1971. Ecological life cycle and physiological ecology of seed germination of *Arabidopsis thaliana*. Canadian Journal of Botany **50**:353–360.

Bazzaz, F. A., D. D. Ackerly, F. I. Woodward, and L. Rochefort. 1992. CO$_2$ enrichment and dependence of reproduction on density in an annual plant and a simulation of its population dynamics. Journal of Ecology **80**:643–651.

Bazzaz, F. A., and R. W. Carlson. 1984. The response of plants to elevated CO$_2$. I. Competition among an assemblage of annuals at two levels of soil moisture. Oecologia **62**:196–198.

Bazzaz, F. A., and K. Garbutt. 1988. The response of annuals in competitive neighborhoods: effects of elevated CO$_2$. Ecology **69**:937–946.

Bazzaz, F. A., M. Jasienski, S. C. Thomas, and P. Wayne.

1995. Microevolutionary response in experimental populations of plants to CO_2-enriched environments: parallel results from two model systems. Proceedings of National Academy of Sciences (USA) **92**:8161–8165.

Bazzaz, F. A., and K. D. M. McConnaughay. 1992. Plant–plant interactions in elevated CO_2 environments. Australian Journal of Botany **40**:547–563.

Bell, G. 1997. The basics of selection. Chapman & Hall, New York, New York, USA.

Ennos, R. A. 1983. Maintenance of genetic variation in plant populations. Evolutionary Biology **16**:129–155.

Ferrière, R., and R. E. Michod. 1995. Invading wave of cooperation in a spatial iterated prisoner's dilemma. Proceedings of the Royal Society of London **259**:77–83.

Goldringer, I., P. Brabant, and R. A. Kempton. 1994. Adjustment for competition between genotypes in single-row-plot trials of winter wheat (*Triticum aestivum*). Plant Breeding **112**:294–300.

Goodnight, C. J. 1985. The influence of environmental variation on group and individual selection in a cress. Evolution **39**:545–558.

Griffing, B. 1989. Genetic analysis of plant mixtures. Genetics **122**:943–956.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

IPCC [Intergovernmental Panel on Climate Change]. 1990. Policymakers summary. Pages xii–xxxiii *in* J. T. Houghton, G. J. Jenkins, and J. J. Ephraums, editors. Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, UK.

Keeling, C. D., R. B. Bacastow, A. F. Carter, S. C. Piper, T. P. Whorf, M. Heimann, W. G. Mook, and H. Roeloffzen. 1989. A 3-dimensional model of atmospheric CO_2 transport based on observed winds. 1. Analysis of observational data. Pages 165–236 *in* D. H. Peterson, editor. Aspects of climate variability in the Pacific and the western Americas. Geophysical Monograph 55. American Geophysical Union, Washington, D.C., USA.

Krannitz, P. G., L. W. Aarssen, and J. M. Dow. 1991. The effect of genetically based differences in seed size on seedling survival in *Arabidopsis thaliana* (Brassicaceae). American Journal of Botany **78**:446–450.

Kuittinen, H., A. Mattila, and O. Savolainen. 1997. Genetic variation at marker loci and in quantitative traits in natural populations of *Arabidopsis thaliana*. Heredity **79**:144–152.

Leadley, P. W., and J. Stöcklin. 1996. Effects of elevated CO_2 on model calcareous grasslands: community, species, and genotype level responses. Global Change Biology **2**:389–397.

Norton, L. R., L. G. Firbank, and A. R. Watkinson. 1995. Ecotypic differentiation of response to enhanced CO_2 and temperature levels in *Arabidopsis thaliana*. Oecologia **104**:394–396.

Potvin, C., and L. Vasseur. 1997. Long-term CO_2 enrichment of a pasture community: species richness, dominance, and succession. Ecology **78**:666–677.

Ratcliffe, D. 1961. Adaptation to habitat in a group of annual plants. The Journal of Ecology **49**:187–203.

SAS Institute. 1990. SAS/STAT user's guide. Release 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Schutz, W. M., C. A. Brim, and S. A. Usanis. 1968. Intergenotypic competition I. Feedback system with stable equilibria in population of autogamous homozygous lines. Crop Science **8**:61–66.

Steinger, T., C. Lavigne, A. Birrer, K. Groppe, and B. Schmid. 1997. Genetic variation in response to elevated CO_2 in three grassland perennials—a field experiment with two competition regimes. Acta Oecologia **18**:263–268.

Stevens, E. E., and R. H. Wiley. 1995. Genetic consequences of restricted dispersal and incest avoidance in a cooperatively breeding wren. Journal of Theoretical Biology **175**:423–436.

Thomas, S. C., and M. Jasienski. 1996. Genetic variability and the nature of microevolutionary responses to elevated CO_2. Pages 51–81 *in* C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations, and communities. Academic Press, San Diego, California, USA.

Ward, J. K., and B. R. Strain. 1997. Effects of low and elevated CO_2 partial pressure on growth and reproduction of *Arabidopsis thaliana* from different elevations. Plant Cell and Environment **20**:254–260.

Wray, S. M., and B. S. Strain. 1987. Competition in old-field perennials under CO_2 enrichment. Ecology **68**:1116–1120.

Zhang, J., and M. J. Lechowicz. 1995. Response to CO_2 enrichment by two genotypes of *Arabidopsis thaliana* differing in their sensitivity to nutrient availability. Annals of Botany **75**:491–499.