

## Commentary

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### Tomorrow's plant communities: different, but how?

Passively, plants everywhere sense the human influence on the environment. Most directly, immediately, and universally, plants respond to the rapid (> 0.5%) annual increase in the concentration of their carbon supply. But they also respond to changing climate patterns, deposition of acid and reactive nitrogen, the arrival and activity of new herbivores or competing species, and many other factors. With the environment changing so quickly, and in so many ways, there is an increasing demand for predictions of how ecosystems will look in the future, and an increasing challenge in making just those predictions.

Our understanding of how species will respond to environmental change has moved through several stages. Initial hypotheses based on first principles often gained credence from growth chamber studies that examined responses of single plants in pots to single environmental changes such as elevated CO<sub>2</sub>. However, some of these hypotheses were increasingly contradicted as researchers used more realistic settings: growing plants in nutrient-limited conditions or with competition, conducting studies outdoors in natural ecosystems, and discarding chamber-based studies for designs with less imposing infrastructure. Recently, several studies have examined responses of natural and managed ecosystems to multiple global changes, seeking to more closely and comprehensively simulate future conditions (Beier, 2004). In this issue, Williams *et al.* (pp. 365–374) provide an example of this 'multifactor' environmental change research, presenting the most comprehensive analysis to date of plant demographic responses in a natural ecosystem.

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*'results from these and similar studies suggest that photosynthetic pathways are not certain predictors of competitive outcomes in a future atmosphere'*

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### Winners and losers: testing an initial prediction for elevated CO<sub>2</sub>

How can we best predict 'winners' and 'losers' in a future environment? One approach has concentrated on grouping species by traits such as photosynthetic pathway. Decades ago, a straightforward working hypothesis suggested that C<sub>3</sub> plants, known to have strongly CO<sub>2</sub>-limited photosynthetic rates, would more commonly outcompete CO<sub>2</sub>-concentrating C<sub>4</sub> plants in a future, more CO<sub>2</sub>-rich atmosphere (e.g. Patterson & Flint, 1980). Growth chamber and glasshouse studies (typically measuring individual plants in pots) supported this hypothesis, as C<sub>3</sub> plants increased shoot mass by an average of 45% under elevated CO<sub>2</sub>, vs a smaller (but still positive) 12% increase in C<sub>4</sub> plants (Poorter & Navas, 2003). A strong C<sub>3</sub> advantage also emerged in competition experiments (again, typically in pots) that provided ample nutrients to the plants. However, C<sub>3</sub> species gained no advantage from elevated CO<sub>2</sub> in competition experiments with limited nutrient availability (Poorter & Navas, 2003). Relatively few experiments have studied responses of C<sub>3</sub> and C<sub>4</sub> plants in natural ecosystems. In those cases, however, the straightforward working hypothesis rarely triumphs. Two cases in which CO<sub>2</sub> preferentially benefited C<sub>3</sub> species were identified in eastern North America. In Maryland salt marshes, Erickson *et al.* (2007) found that elevated CO<sub>2</sub> increased growth of a C<sub>3</sub> sedge, and accelerated its replacement of a C<sub>4</sub> grass in a mixed C<sub>3</sub>–C<sub>4</sub> community. In the understory of a planted Tennessee forest, an invasive C<sub>3</sub> vine sometimes benefited from CO<sub>2</sub> enrichment while an invasive C<sub>4</sub> grass sometimes declined in these conditions (Belote *et al.*, 2003). The story is not always so straightforward; in North American shortgrass steppe, recruitment increased in one C<sub>3</sub> grass species and thus it produced more biomass in response to elevated CO<sub>2</sub>, while another C<sub>3</sub> grass and a C<sub>4</sub> grass did not respond (Morgan *et al.*, 2004). In the tallgrass prairie of the same continent, Owensby *et al.* (1993, 1999) found that C<sub>4</sub> plants sometimes benefited most from CO<sub>2</sub> enrichment, presumably via the water savings created when plants growing in elevated CO<sub>2</sub> narrow their stomatal openings. Together, results from these and similar studies suggest that photosynthetic pathways are not certain predictors of competitive outcomes in a future atmosphere – ecological processes such as competition for resources can complicate matters.

The changing climate also complicates predictions of C<sub>3</sub>–C<sub>4</sub> competition, as photosynthetic rates of C<sub>4</sub> plants typically respond more positively to warming. Before the experiment at the Tasmanian free-air CO<sub>2</sub> enrichment (TasFACE)

facility described by Williams *et al.*, no field studies had tested how competition among plants of these different photosynthetic types responds to both warming and CO<sub>2</sub>. Unlike previous studies that have examined responses of plant growth or (less often) reproduction, Williams *et al.* examined the entire life cycle of four common species in a temperate grassland on the Australian island state of Tasmania. While the dominant C<sub>4</sub> grass species was unaffected by CO<sub>2</sub> or warming, CO<sub>2</sub> unexpectedly reduced seed production of the dominant C<sub>3</sub> grass species, reducing population growth over 3 yr. Together, CO<sub>2</sub> and warming also reduced germination and establishment of the C<sub>3</sub> grass, triggering population decline. In addition to the responses of the two grass species, Williams *et al.* examined responses of two invasive C<sub>3</sub> weeds – both perennial members of the Asteraceae – with the intent of elucidating whether global changes will increase the abundance of these species over time.

### Will future conditions bring more 'unwelcome' plants?

A variety of 'unwelcome' species – such as agricultural weeds, plants with irritating oils or allergens, and invasive plants in wildland areas – benefit from CO<sub>2</sub> enrichment when grown in isolation in growth chambers or glasshouses (e.g. Ziska, 2003; McPeck & Wang, 2007; Ziska *et al.*, 2007). Although these studies can be informative on several fronts, the predictive value of plant responses in these settings is essentially zero; biomass responses of isolated plants are not correlated with responses of those same species in the context of a diverse plant community (Poorter & Navas, 2003). Furthermore, in these settings, the CO<sub>2</sub> responses of invasive species do not differ from those of noninvasive species (Dukes, 2000). Responses of species grown in monocultures better predict responses in mixed communities, but are far from perfect (Poorter & Navas, 2003). One example: above-ground biomass of the invasive annual forb *Centaurea solstitialis* increased by 70% in response to elevated CO<sub>2</sub> in monocultures, and by an almost identical amount when grown in competition with a native Californian serpentine grassland community – but, importantly, the response in diverse communities was not statistically significant (Dukes, 2002).

Relatively few experiments have examined the responses of problematic species to CO<sub>2</sub> or warming in more natural settings that include competition and realistic soil and environmental conditions. Results from these few studies highlight several cases where problem species benefit from elevated CO<sub>2</sub>. For instance, seedlings of an invasive broad-leaved evergreen tree grew faster in response to CO<sub>2</sub> in a Swiss forest, while seedlings of a similar native species did not, suggesting that the invasive may become more common over time (Hättenschwiler & Körner, 2003). Growth and

population biomass of poison ivy (*Toxicodendron radicans*), a native vine that produces an irritant to human skin, increased dramatically in North American forest exposed to elevated CO<sub>2</sub> (Mohan *et al.*, 2006). Adding to the problem, poison ivy grown in elevated CO<sub>2</sub> produced a more potent form of the irritant. Other studies suggest some caveats regarding the responses of invasive species. For instance, the aggressively invasive grass *Bromus madritensis* responded strongly to elevated CO<sub>2</sub> in a North American desert, but only in a wet year (Smith *et al.*, 2000). In the understory of an eastern North American forest, an invasive vine benefited from CO<sub>2</sub>, but an invasive C<sub>4</sub> grass declined – and each response was significant in only one of two years (Belote *et al.*, 2003).

The TasFACE study described by Williams *et al.* is one of the first to examine the responses of invasive species to two or more types of environmental change at a time. So what happened in the grasslands of Tasmania? Good news: population growth rates of the invasive forbs did not respond to elevated CO<sub>2</sub>, and were strongly suppressed by warming (via reduced germination), suggesting that these species may disappear from the grassland over time.

### Predicting community change

The study by Williams *et al.* highlights the utility of two approaches: first, a multifactor approach to the study of global change, which allows more comprehensive understanding of community and ecosystem responses, and secondly, a demographic approach to community change, in which responses of all life cycle stages are quantified for important species. This allows a more detailed and mechanistic understanding of why plant communities may change in future conditions, and may permit further extrapolation. For instance, if researchers determine individual life cycle effects of several separate factors, these may be combined to predict future population changes. However, one major obstacle remains: interactive effects.

Although Williams *et al.* identified cases where the response of a life cycle stage to combined CO<sub>2</sub> and warming did not match expectations based on the single treatments, they did not attempt to explain the mechanisms behind these interactive effects. A better understanding of when and why such interactions arise would greatly benefit the field of global change research, and may grow out of studies similar to this one.

As studies such as that of Williams *et al.* bring us closer to predicting the future composition of a plant community, we must keep in mind the bigger picture. Global change responses of diseases, herbivores, mutualists, and other species may have important effects that alter the community trajectory from that suggested by plot-scale

global change experiments, with important consequences for the eventual functioning of the ecosystem. The valuable approaches of Williams *et al.* are likely to be adopted by others, and should provide important clues to the future of other plant communities – but important challenges will remain.

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## References

- Beier C. 2004. Climate change and ecosystem function – full-scale manipulations of CO<sub>2</sub> and temperature. *New Phytologist* 162: 243–245.
- Belote RT, Weltzin JF, Norby RJ. 2003. Response of an understory plant community to elevated [CO<sub>2</sub>] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytologist* 161: 827–835.
- Dukes JS. 2000. Will the increasing atmospheric CO<sub>2</sub> concentration affect the success of invasive species? In: Mooney HA, Hobbs RJ, eds. *Invasive species in a changing world*. Washington, DC, USA: Island Press, 95–113.
- Dukes JS. 2002. Comparison of the effect of elevated CO<sub>2</sub> on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. *Plant Ecology* 160: 225–234.
- Erickson JE, Megonigal JP, Peresta G, Drake BG. 2007. Salinity and sea level mediate elevated CO<sub>2</sub> effects on C<sub>3</sub>–C<sub>4</sub> plant interactions and tissue nitrogen in a Chesapeake Bay tidal wetland. *Global Change Biology* 13: 202–215.
- Hättenschwiler S, Körner C. 2003. Does elevated CO<sub>2</sub> facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? *Functional Ecology* 17: 778–785.
- McPeck TM, Wang X. 2007. Reproduction of dandelion (*Taraxacum officinale*) in a higher CO<sub>2</sub> environment. *Weed Science* 55: 334–340.
- Mohan JE, Ziska LH, Schlesinger WH, Thomas RB, Sicher RC. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences, USA* 103: 9086–9089.
- Morgan JA, Mosier AR, Milchunas DG, LeCain DR, Nelson JA, Parton WJ. 2004. CO<sub>2</sub> enhances productivity, alters species composition, and reduces digestibility of shortgrass steppe vegetation. *Ecological Applications* 14: 208–219.
- Owensby CE, Coyne PI, Ham JM, Auen LM, Knapp AK. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO<sub>2</sub>. *Ecological Applications* 3: 644–653.
- Owensby CE, Ham JM, Knapp AK, Auen LM. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO<sub>2</sub>. *Global Change Biology* 5: 497–506.
- Patterson DT, Flint EP. 1980. Potential effects of global atmospheric CO<sub>2</sub> enrichment on the growth and competitiveness of C<sub>3</sub> and C<sub>4</sub> weed and crop plants. *Weed Science* 28: 71–75.
- Poorter H, Navas M-L. 2003. Plant growth and competition at elevated CO<sub>2</sub>: On winners, losers and functional groups. *New Phytologist* 157: 175–198.
- Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seemann JR, Nowak RS. 2000. Elevated CO<sub>2</sub> increases productivity and invasive species success in an arid ecosystem. *Nature* 408: 79–82.
- Williams AL, Wills KE, Janes JK, Vander Schoor JK, Newton PCD, Hovenden MJ. 2007. Warming and free-air CO<sub>2</sub> enrichment alter demographics in four co-occurring grassland species. *New Phytologist* 176: 365–374.
- Ziska LH. 2003. Evaluation of the growth response of six invasive species to past, present, and future atmospheric carbon dioxide. *Journal of Experimental Botany* 54: 395–404.
- Ziska LH, Sicher RC, George K, Mohan JE. 2007. Rising atmospheric carbon dioxide and potential impacts on the growth and toxicity of poison ivy (*Toxicodendron radicans*). *Weed Science* 55: 288–292.

**Key words:** C<sub>3</sub>, C<sub>4</sub>, climate change, elevated CO<sub>2</sub>, global change, invasive species, multifactor, weed.

## Spatial aspects of seed dispersal and seedling recruitment in orchids

Growing interest in spatial plant ecology is resulting in new approaches to the study of seed dispersal and seedling recruitment; two important processes determining population dynamics, genetic structure within and among plant populations and the colonization of new areas (Vekemans & Hardy, 2004). In general, seed dispersion patterns are determined by the spatial pattern of reproductive adults, their seed outputs and their seed shadows, while seedling recruitment mainly depends on the probability of seed arrival and the availability of a suitable microsite (Nathan & Muller-Landau, 2000). In the orchid family, successful germination and seedling establishment are crucial life history stages, as orchid seeds are unusual in being among the smallest seeds of all flowering plants, with an undifferentiated embryo that contains minimal reserves. Therefore, at germination, orchids are fully dependent on an interaction with a mycorrhizal fungus, which colonizes the seeds and provides all nutrients essential for seedling development. In the past decade, there have been several attempts to investigate the process of orchid seed germination in a spatial context (Perkins & McGee, 1995; McKendrick *et al.*, 2000; Batty *et al.*, 2001; Feuerherdt *et al.*, 2005; Diez, 2007); however, these studies have told us little about the extent to which seed dispersal and germination are associated with the spatial distribution of recruits. In this issue of *New Phytologist* (pp. 448–459), Jacquemyn *et al.* provide more insights into the within-population spatial genetic structure and recruitment potential of an orchid species, for which little is known regarding seed dispersal patterns and the successful establishment of mycorrhiza-dependent seedlings.