

**Will the increasing atmospheric CO<sub>2</sub> concentration affect the success of invasive species?**

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Over the last two centuries, accelerating rates of fossil fuel use and forest clearing by humans have led to increasing concentrations of carbon dioxide ( $[\text{CO}_2]$ ) in the atmosphere (Houghton et al. 1996). From a pre-industrial-era concentration of 280 parts per million (ppm), atmospheric  $[\text{CO}_2]$  rose to 364 ppm in 1997 (an increase of 30%), and is likely to reach 560 ppm, double the pre-industrial concentration, within the next century. Because the atmosphere is well-mixed, this increase is fairly uniform over the entire surface of the planet. Plants, which need  $\text{CO}_2$  to carry out photosynthesis, are directly affected. Animals, which are not directly dependent on  $\text{CO}_2$ , are primarily affected by changes in the plants that they use for food or shelter.

In this chapter, I explore how plant and animal responses to elevated atmospheric  $[\text{CO}_2]$  could affect the prevalence of invasive species. As  $[\text{CO}_2]$  continues to rise, will alien species that are currently benign become invasive? Will ecosystem properties change, permitting new invasions? Will problems that are currently caused by invaders become worse, or disappear? To address any of these questions, we must not only understand how different species and ecosystems respond to rising  $[\text{CO}_2]$ , but how these responses interact to favor one species over another - all in all, a complicated task.

Our understanding of the  $\text{CO}_2$  responses of natural systems has grown quickly over the last two decades, as a number of (generally small-statured) ecosystems have been studied in depth. However, many important ecosystems remain to be studied. In these unstudied systems, we still cannot confidently predict which species will benefit from the rise in  $[\text{CO}_2]$ . Furthermore, few of the ecosystem-level studies to date have focused attention on non-native species. Thus, the predictions about alien species in this chapter are necessarily speculative, but they are based on a broad and rapidly expanding foundation of knowledge about the effects of elevated  $[\text{CO}_2]$  on individual species and on ecosystems.

Because plant responses to rising  $[\text{CO}_2]$  mediate the responses of ecosystems and animals, they are covered first in this chapter. Ecosystem-level responses are covered next. Some of these responses may alter the susceptibility of communities to invasion. Responses of animal species are covered last.

## **Responses of Plants to Increasing $[\text{CO}_2]$**

The rise in  $\text{CO}_2$  availability directly impacts photosynthetic processes, evoking a wide range of physiological and morphological responses in plants. These vary among species, depending on differences in photosynthetic pathways, intrinsic growth rates, and other properties. Common responses include changes in growth rates (Poorter 1993, Poorter et al. 1996), allocation patterns (Bazzaz 1990), water use efficiency (Eamus 1991), and nutrient uptake rates (BassiriRad et al. 1996, Jackson and Reynolds 1996).

Without directly studying a plant species and the community in which it lives, it remains difficult to predict whether that species will benefit from elevated  $[\text{CO}_2]$ . We can, based on certain traits, usually predict whether an individually-grown plant will increase its growth in response to  $[\text{CO}_2]$  enrichment. Under these circumstances, most species that use the  $\text{C}_3$  photosynthetic pathway respond favorably to increased atmospheric  $[\text{CO}_2]$ . Species that use the  $\text{C}_4$  and CAM pathways are less predictable;

many respond positively, but in general the response is less vigorous than that of C<sub>3</sub> plants (Poorter 1993, Poorter et al. 1996). Two categories of C<sub>3</sub> species tend to respond most strongly to elevated [CO<sub>2</sub>]: fast-growing species and those that form symbioses with nitrogen-fixing microbes (Poorter 1993, Poorter et al. 1996). Although fast-growing species are responsive when they are grown individually in resource-rich conditions, few studies of plant communities have investigated whether these species are equally responsive in competitive conditions. Nitrogen-fixers generally respond strongly to elevated [CO<sub>2</sub>] when grown individually, and often respond in communities, as well (Newton et al. 1994, Stewart and Potvin 1996, Hebeisen et al. 1997, Vasseur and Potvin 1998, Thayer et al. 1999).

In competition-free environments, invasive species tend to respond strongly to elevated [CO<sub>2</sub>] (Table 1). However, these responses are statistically indistinguishable from the responses of non-invasive species of the same physiological type (Fig. 1, Table 2).

One must be careful not to extrapolate the biomass response of a species grown individually or in monoculture to its future success as a part of a community for two reasons: First, the long-term CO<sub>2</sub> response of populations will depend on changes in seed quality and output, which are rarely measured (but see the 1998 study of North American desert invader *Bromus rubens* by Travis Huxman and colleagues ). Second, a species that responds strongly to elevated [CO<sub>2</sub>] when grown individually or in monoculture may respond quite differently when grown in competition with other species of plants (Bazzaz and McConnaughay 1992). Whereas growth of a solitary plant might be limited by the availability of CO<sub>2</sub>, plants in communities are likely to be limited by the availability of light, water, and nutrients, for which they perceptibly compete with other plants. Thus, growth of plants in some communities might not directly respond to a rise in [CO<sub>2</sub>] availability (Reynolds 1996). Even in these situations, physiological responses of plants to elevated [CO<sub>2</sub>] might affect growth and competition by causing limitation of other resources to abate (or intensify). The species that best respond to the full suite of CO<sub>2</sub>-driven changes in resource availability are most likely to benefit from the [CO<sub>2</sub>] increase. Identifying these species without studying them in communities can be difficult, as is illustrated by the European annual *Chenopodium album*, a common weed throughout most of North America. While the species responds positively to elevated [CO<sub>2</sub>] when grown individually (see Table 1), it did not respond when grown in a Canadian pasture community, even in disturbed (and thus low-density) sites (Taylor and Potvin 1997).

Despite the difficulties, some general principles may yet emerge. Experimental results from the same Canadian pasture community suggest that the rise in [CO<sub>2</sub>] may slow succession, or the development of plant communities, allowing 'early-successional' species to persist in a community for longer than they do currently (Potvin and Vasseur 1997, Vasseur and Potvin 1998). If this turns out to be a general phenomenon, the abundance of invaders, many of which are considered early-successional species, could increase.

Certain traits may help to predict "winning" and "losing" species in community settings. Plants that use the C<sub>3</sub> photosynthetic pathway tend to respond more positively to elevated [CO<sub>2</sub>] than C<sub>4</sub> plants in communities such as salt marsh (Curtis et al. 1989)

and savanna (Johnson et al. 1993), as well as in experiments where C<sub>3</sub> crops are grown in competition with C<sub>4</sub> weeds (e.g., Alberto et al. 1996). However, results from mixed C<sub>3</sub>-C<sub>4</sub> communities are not entirely clear-cut. In an experiment on tallgrass prairie (Owensby et al. 1993), CO<sub>2</sub> enrichment favored C<sub>4</sub> plants. Dominant C<sub>4</sub> grasses responded to an increase in water availability under elevated [CO<sub>2</sub>], while the CO<sub>2</sub> response of shorter C<sub>3</sub> grasses was limited by nutrient and light availability. Carbon dioxide enrichment similarly benefited a C<sub>4</sub> annual more than a C<sub>3</sub> annual in a greenhouse-based competition experiment (Bazzaz et al. 1989). On the whole, results of competition experiments with C<sub>3</sub> and C<sub>4</sub> species suggest that, where both types of species co-occur, the rise in [CO<sub>2</sub>] is likely to favor C<sub>3</sub> species in most, but not all, cases. In natural communities, this could translate to increased success of C<sub>3</sub> shrubs, forbs and grasses that are invading C<sub>4</sub> grasslands, and decreased yield losses to C<sub>4</sub> weeds in fields of C<sub>3</sub> crops (Patterson 1995, Alberto et al. 1996). However, because high temperatures favor C<sub>4</sub> species over C<sub>3</sub> species, climate change may counteract these consequences of increasing [CO<sub>2</sub>].

In summary, research to date has not established a clear link between invasive and CO<sub>2</sub>-responsive plant species. We can identify with some confidence general categories of plant species that are likely to benefit from the [CO<sub>2</sub>] increase in community settings. Within these categories, it is still difficult to predict which species will benefit the most. However, knowledge about ecosystem-level responses can lead to the identification of plant traits that will confer advantages under elevated [CO<sub>2</sub>].

### **Ecosystem-level Responses to Increasing [CO<sub>2</sub>]**

Collectively, plant responses to CO<sub>2</sub> enrichment affect the availability of other resources, such as soil nutrients, water, and light, and could also alter fire regimes. These indirect changes will favor certain species over others (as was seen above with C<sub>4</sub> grasses in tallgrass prairie), and may increase the susceptibility of some ecosystems to invasion.

Most plants maintain a constant concentration of CO<sub>2</sub> in their stomata, the pores through which O<sub>2</sub> and CO<sub>2</sub> are exchanged and water vapor is lost to the atmosphere. Plants react to increased CO<sub>2</sub> availability by partially shutting their stomata, which increases the efficiency with which they use water. In some ecosystems, the increase in water-use efficiency leads to wetter soils (Bremer et al. 1996, Field et al. 1997, Fredeen et al. 1997). In plant communities such as these, alien species that are poised to take advantage of water availability increases could become more abundant.

Researchers working in California's sandstone annual grasslands have observed that the plants in this ecosystem deplete soil moisture reserves more slowly when they are exposed to elevated [CO<sub>2</sub>] (Field et al. 1997, Fredeen et al. 1997). In these grasslands, CO<sub>2</sub> enrichment can cause summer-active species such as *Hemizonia congesta* ssp. *luzulifolia* to more than double their annual biomass production (Field et al. 1996). The annual forb appears to respond to the wetter soil left after the senescence of the dominant grasses, rather than to the [CO<sub>2</sub>] itself. Although *Hemizonia* is native to these grasslands, alien species that are active in the summer might also take advantage of increased water availability. For instance, the Mediterranean annual *Centaurea solstitialis*, which is invasive in the western United States and other mediterranean-climate regions, is summer-

active. This species is also known to respond strongly to elevated [CO<sub>2</sub>] when grown in monoculture (J. Dukes, unpublished data).

Working on the same project in northern California, Nona Chiariello and Christopher Field (1996) studied the CO<sub>2</sub> response of serpentine grassland communities grown in microcosms with and without alien annual grasses. Non-native grasses are known to respond to increases in water availability in this ecosystem (Hobbs and Mooney 1991), but water availability in the field (at least at shallow depths) appears to be only minimally affected by elevated [CO<sub>2</sub>]. In the microcosm experiment, the annual grasses did not respond to increased [CO<sub>2</sub>], although one species responded strongly to fertilization. Interestingly, in this experiment and in the field, deep-rooted summer-active species did respond to CO<sub>2</sub> enrichment, indicating that deep reserves of soil moisture may be increased by elevated [CO<sub>2</sub>], or that the [CO<sub>2</sub>] increase allowed these species to grow root systems that more effectively exploited these deep water reserves.

Decreased water use by herbaceous dominants may allow invasions of woody species into some grassland ecosystems (Polley 1997). Grassland invaders mesquite (*Prosopis glandulosa*, Polley et al. 1996b) and huisache (*Acacia smallii*, Polley et al. 1997) both respond to elevated [CO<sub>2</sub>]. As [CO<sub>2</sub>] rises, invading species such as these may become more abundant in their native ecosystems, as well as in ecosystems where they are aliens (in South Africa, for instance - see Richardson et al., this volume).

Several North American ecosystems become susceptible to invasion when water is unusually plentiful. For instance, in Colorado shortgrass steppe communities, long-term irrigation facilitated the establishment of alien plants that persisted long after watering treatments were stopped (Milchunas and Lauenroth 1995). Heavy-rainfall years favor invasive grasses in many arid and semi-arid ecosystems, including Sonoran desert in Arizona (Burgess et al. 1991) and the transition between Great Basin and Mojave desert in Nevada (Hunter 1991). It is not known whether water availability will increase in these systems under elevated [CO<sub>2</sub>], or whether any increase would be large enough to facilitate invasions.

Invasive species can benefit from the addition of other resources to ecosystems, as well. In nutrient-poor ecosystems, fertilization often spurs success of faster-growing species. These species are mostly non-native in some North American ecosystems such as Minnesota grasslands (Wedin and Tilman 1996) and California's serpentine grasslands (Huenneke et al. 1990). In other ecosystems, including many in Europe, most of the responsive species are natives (Scherer et al., this volume). The rise in [CO<sub>2</sub>] will indirectly alter nutrient availability in many, if not all, ecosystems. At this time, no experimental studies have identified invaders that are likely to benefit from changes in nutrient availability associated with rising [CO<sub>2</sub>]. It is nonetheless worth briefly discussing the mechanisms by which increasing [CO<sub>2</sub>] alters nutrient availability.

A variety of plant responses to rising [CO<sub>2</sub>] can potentially lead to changes in nutrient availability. Increases in plant growth rates may increase competition for nutrients. Plant-mediated changes in soil moisture patterns may affect rates of litter and soil organic matter decomposition. Changes in litter chemistry can affect the rate at which nutrients that are bound in decomposing litter become accessible to plants and microbes. Some plant species respond to elevated [CO<sub>2</sub>] by increasing carbon inputs to soil from

roots, which can in turn increase the size of microbial populations, and thus alter nutrient availability (Díaz et al. 1993, Zak et al. 1993). Because plant species differ in their responses to CO<sub>2</sub>, changes in nutrient availability in a community may depend largely on the community's species composition (Hungate et al. 1996). Thus, CO<sub>2</sub>-driven shifts in species dominance can also affect nutrient availability. An example: if the rise in [CO<sub>2</sub>] causes legumes to become more abundant in a community, atmospheric N would be captured and made available to microbes and other plant species more quickly (Zanetti et al. 1997). It is too early to predict whether such CO<sub>2</sub>-driven changes in nutrient availability will alter the prevalence of biological invaders.

In ecosystems where the rise in [CO<sub>2</sub>] stimulates plant growth and litter accumulation, fire frequencies could increase. Because fire promotes biological invasion of many plant communities and can often increase the dominance of invasive species (D'Antonio and Vitousek 1992, D'Antonio et al. 1999, D'Antonio this volume), it is appropriate to discuss conditions in which the rise in [CO<sub>2</sub>] could affect fire regimes.

The degree to which fire regimes of different grassland communities are accelerated or depressed by rising [CO<sub>2</sub>] will depend in large part on the timing of plant growth and senescence in those communities. For instance, in annual grasslands where senescence of the dominant grasses precedes a summer dry season, any increase in litter buildup or continuity would persist through the dry season, heightening the risk of fires for many months of the year. In contrast, the rise in [CO<sub>2</sub>] improves water relations in some perennial grasslands (Bremer et al. 1996), which could delay senescence of the dominant grasses during mid-season droughts. This would decrease the flammability of the grasslands, and increase the length of droughts required for the grassland to become susceptible to fires. If this phenomenon slowed the fire cycle, less fire-tolerant species might invade. However, once the grasses did senesce, the increased litter buildup could trigger more intense fires (Sage 1996).

CO<sub>2</sub>-driven changes in species dominance could also alter fire frequencies, possibly leading to further changes in species composition. Some invasive plant species might have already benefited from the 30% increase in [CO<sub>2</sub>], and might have consequently triggered changes in fire regimes that facilitated further invasions. Although one can only speculate about such a scenario, there exists a candidate species. *Bromus tectorum*, which has invaded millions of acres of land in western North America, is known to respond to elevated [CO<sub>2</sub>] (Table 1). If the rise in [CO<sub>2</sub>] stimulated growth of this annual grass, it may have also contributed to the increase in fire frequency and subsequent increase in *Bromus* dominance in the intermountain west, the region between the Sierra Nevada and the Rocky Mountains (Mayeux et al. 1994). An increase in the water use efficiency of the grass that accompanied the rise in [CO<sub>2</sub>] may have also allowed *Bromus* to extend its range into regions that had previously been too arid to support its growth (Sage 1996).

### **Responses of Animals to Increasing [CO<sub>2</sub>]**

We expect that animal responses to the rise in [CO<sub>2</sub>] will be indirect, and based on the responses of plants. Changes in the tissue quality, phenology (timing of life stages),

physiology and distribution of plants are likely to have the most important consequences for animals (Cannon 1998). Responses of some animal species to CO<sub>2</sub>-driven changes in plants have been recorded, but no studies have examined how the responses of alien animal species differ from those of native species. Here, I briefly summarize the known impacts of elevated [CO<sub>2</sub>] on animal species, and speculate about possible consequences for native versus alien animals.

Most of the experiments that have examined animal responses to elevated [CO<sub>2</sub>] have focused on insect species. Insect herbivores are directly affected by changes in the quality of plant tissue that accompany elevated [CO<sub>2</sub>]. The nitrogen concentration of leaves generally decreases when plants are grown in elevated [CO<sub>2</sub>], and this reduces their nutritive value. To compensate, insect larvae of many species increase leaf consumption. In most cases, larvae that eat high-[CO<sub>2</sub>]-grown leaves nonetheless perform more poorly than larvae that eat leaves grown in ambient air (Cannon 1998). This is the case for gypsy moth (*Lymantria dispar*) larvae that are fed quaking aspen (*Populus tremuloides*) leaves. However, the response of these larvae to red oak (*Quercus rubra*) leaves illustrates that this phenomenon is dependent on the host plant species. Larvae that fed on oak leaves grown at elevated [CO<sub>2</sub>] performed better than larvae that consumed leaves grown in ambient air (Lindroth et al. 1993).

Some studies suggest that aphid populations could increase as [CO<sub>2</sub>] rises, as a consequence of increased fecundity (Awmack et al. 1996) and longer settling times (Smith 1996). As with insect larvae, this may depend on host plant species. The potato aphid, *Aulacorthum solani*, responds quite differently to elevated [CO<sub>2</sub>] when it is on bean (*Vicia faba*) than when it is on tansy (*Tanacetum vulgare*, Awmack et al. 1997).

When plants are grown under elevated [CO<sub>2</sub>], litter quality does not decline as consistently as tissue quality (Norby and Cotrufo 1998). When litter quality does decline, detritivores respond. Francesca Cotrufo and colleagues (1998) grew rooted cuttings of ash (*Fraxinus excelsior*) in ambient and CO<sub>2</sub>-enriched air and fed leaf litter from these plants to *Oniscus asellus* individuals. Elevated-[CO<sub>2</sub>]-grown litter had a higher lignin content and C:N ratio than ambient-grown litter, and the isopods consumed 16% less of the high-[CO<sub>2</sub>]-grown litter.

Animals that live in the soil may be affected by changes in soil moisture, and in the quality and growth of roots. For instance, earthworms living in plots of Swiss grassland exposed to elevated [CO<sub>2</sub>] produced 35% more surface cast mass than earthworms living in plots exposed to ambient air (Zaller and Arnone 1997). The increase in cast production was probably stimulated by an increase in soil moisture in the high-[CO<sub>2</sub>] plots.

As [CO<sub>2</sub>] rises, an accompanying decrease in forage quality is likely to affect eating habits of grazing and browsing animals, but little research has been done on this topic. Ranchers may be able to maintain growth of livestock at current levels by adding nutritional supplements to their animals' diet, but growth and reproduction of wild species is likely to decrease (Owensby et al. 1996).

Elevated [CO<sub>2</sub>] alters the development rates of some plant species, which will cause some species to flower and fruit at slightly different times of year (Reekie 1996). If these changes are extreme, the rise in [CO<sub>2</sub>] could lead some plant species to flower at a time when pollinators are not available. This could lead to a decline of both plant and

animal populations. Such a dissociation between flowering time and pollinator availability is less likely to occur between 'generalist' species than between 'specialist' species that rely on few species for pollination or for their food supply. Invasive insect species tend to be generalists, and thus are unlikely to encounter such problems.

It is not clear that elevated  $[\text{CO}_2]$  will affect the success of alien animal species. We can speculate that changes in the phenology of native plant species will adversely affect some native pollinators without substantially affecting alien pollinators, resulting in an increase in the relative abundance of the aliens. However, for most plant species, phenological changes under elevated  $[\text{CO}_2]$  appear to be slight. Changes in tissue and litter quality are likely to affect many herbivores and detritivores, but it is unclear that these changes would favor either natives or aliens. Similarly, changes in soil moisture may affect earthworms and other soil-living organisms, but will not necessarily alter the prevalence of invasive species.

### **Conclusions and Predictions**

The rise in  $[\text{CO}_2]$  will probably alter the prevalence of invasive species, but the nature of this change is difficult to predict. Whereas alien species may benefit from higher  $[\text{CO}_2]$  in some regions, native species may benefit in others. Plants with certain  $\text{CO}_2$ -responsive traits are likely to benefit from the rise in  $[\text{CO}_2]$ , especially if they are growing in ecosystems where those traits are rare. For instance,  $\text{C}_3$  species growing in  $\text{C}_4$ -dominated ecosystems are likely to benefit from the rise in  $[\text{CO}_2]$  (but under some circumstances may not). Invasiveness and  $\text{CO}_2$ -responsiveness are not clearly linked.

As with plants, ecosystems differ in their responses to elevated  $[\text{CO}_2]$ . In those ecosystems where the rise in  $[\text{CO}_2]$  increases the availability of other resources or causes a change in the fire regime, new, possibly alien species could take advantage of the novel conditions. Animal species will also be affected by the changes in plant and ecosystem qualities, but it is difficult to predict whether native and alien species will be affected differently.

Given the uncertainties, what specific changes might we expect to see in the future as  $[\text{CO}_2]$  continues to rise? It seems likely that increases in plant water use efficiency will allow some species, particularly annual grasses, to extend their ranges further into arid regions (as may already have happened). In some deserts that are dominated by widely-spaced, fire-intolerant perennial species, interactions of these invasions with fire could lead to the loss of the native perennials, as has already occurred in parts of North America.

In more mesic areas, increases in the water use efficiency of grassland dominants is likely to increase deep water percolation, which would benefit shrubs and other species with deep rooting patterns. Leguminous shrubs might become especially invasive as rising  $[\text{CO}_2]$  stimulates N fixation. In contrast,  $\text{C}_4$  grasses might become less competitive, rendering  $\text{C}_4$  grasslands especially invulnerable. Although  $\text{C}_4$  species benefit from increasing water availability, most do not respond strongly to elevated  $[\text{CO}_2]$  in wet conditions. Periodic droughts, which may currently limit some species from invading these grasslands, will become less frequent as  $[\text{CO}_2]$  rises. As a consequence, some of the species that are presently excluded may survive and invade (Polley et al. 1996a).

The future success of any single alien species depends on many factors other than the response of that species to elevated [CO<sub>2</sub>]. Other elements of global change, such as those discussed in this book, will also affect species' success. Interactions among the many elements of global change will undoubtedly be important in shaping the future composition of natural communities. Research projects that are designed to discover how these interactions will affect the earth's ecosystems are just getting underway.

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Table 1. Stimulation of growth of invasive plant species by elevated CO<sub>2</sub>. Data from Poorter (1993) and Poorter et al. (1996). A species was determined to be invasive if it appeared in the global natural area invaders data set compiled by Daehler (1998), was listed as not indigenous to, but common in North America by Whitson et al. (1996), or was one of the five most invasive pines listed by Rejmánek and Richardson (1996). Weight ratios are the dry weight of plants grown in elevated [CO<sub>2</sub>] divided by the dry weight of plants grown in the treatment closest to ambient [CO<sub>2</sub>].

Invasive species	Weight ratio	CO <sub>2</sub> Reference(s)
<b>Herbaceous C<sub>3</sub> species</b>		
<i>Abutilon theophrasti</i>	1.43	(Carlson and Bazzaz 1980, Patterson and Flint 1980, Patterson et al. 1988, Bazzaz et al. 1989, Dippery et al. 1995)
<i>Arrhenatherum elatius</i>	1.50	[Hunt, 1991 #459; 1993 #576], Gobin et al. unpub.
<i>Avena barbata</i>	1.21	Gobin et al. unpub.
<i>Bromus hordaceus</i>	3.60	Roumet et al. unpub.
<i>Bromus inermis</i>	1.03	Gobin et al. unpub.
<i>Bromus rigidus</i>	1.49	Gobin et al. unpub.
<i>Bromus tectorum</i>	1.72	(Smith et al. 1987), Roumet et al. unpub.
<i>Centaurea solstitialis</i>	1.51	Gobin et al. unpub.
<i>Chenopodium album</i>	1.26	(Carlson and Bazzaz 1982, Hunt et al. 1991)
<i>Dactylis glomerata</i>	1.39	(Hunt et al. 1993)
<i>Datura stramonium</i>	1.72	(Carlson and Bazzaz 1980, Carlson and Bazzaz 1982)
<i>Digitalis purpurea</i>	1.16	(Hunt et al. 1991)
<i>Elytrigia repens</i>	1.67	(Tremmel and Patterson 1993)
<i>Holcus lanatus</i>	1.68	(Hunt et al. 1991, Campbell et al. 1993)
<i>Lolium multiflorum</i>	1.61	(Campbell et al. 1993)
<i>Phalaris aquatica</i>	1.67	(Morison and Gifford 1984, Campbell et al. 1993)
<i>Phleum pratense</i>	2.09	(Campbell et al. 1993)
<i>Plantago lanceolata</i>	1.28	(Fajer et al. 1991, Hunt et al. 1991, Campbell et al. 1993)
<i>Plantago major</i>	1.48	(Poorter et al. 1988, Den Hertog et al. 1993, Poorter 1993)
<i>Rumex acetosella</i>	1.31	(Hunt et al. 1991)
<i>Taraxacum officinale</i>	2.30	(Poorter 1993)
<i>Trifolium subterraneum</i>	1.24	(Campbell et al. 1993)
<b>Woody C<sub>3</sub> species</b>		
<i>Acacia mangium</i>	1.40	(Ziska et al. 1991)
<i>Acacia melanoxylon</i>	1.21	Mathias et al. unpub.
<i>Alnus glutinosa</i>	1.44	(Norby 1987, Poorter 1993)

<i>Betula pendula</i>	1.76	(Petersson and McDonald 1992, Petersson et al. 1993, Mortensen 1994a, Silvola and Ahlholm 1995)
<i>Elaeagnus angustifolia</i>	1.61	(Norby 1987)
<i>Eucalyptus camaldulensis</i>	2.11	Wong et al. unpub.
<i>Eucalyptus globulus</i>	1.57	Mathias et al. unpub.
<i>Eucalyptus grandis</i>	2.03	(Conroy et al. 1992), Mathias et al. unpub.
<i>Lonicera japonica</i>	2.35	(Sasek and Strain 1991)
<i>Nerium oleander</i>	1.46	(Downton et al. 1980, Downton and Grant 1994)
<i>Pinus contorta</i>	1.02	(Mortensen 1994b)
<i>Pinus pinaster</i>	1.67	(Guehl et al. 1994)
<i>Pinus radiata</i>	1.35	(Conroy et al. 1986, Conroy et al. 1988, Conroy et al. 1990)
<i>Populus deltoides</i>	1.65	(Carlson and Bazzaz 1980)
<i>Prunus serotina</i>	1.33	(Bazzaz 1990)
<i>Pueraria lobata</i>	1.20	(Sasek and Strain 1988)
<i>Robinia pseudoacacia</i>	1.32	(Norby 1987)
<b>C<sub>4</sub> species</b>		
<i>Andropogon glomeratus</i>	0.63	(Bowman and Strain 1987)
<i>Andropogon virginicus</i>	1.14	(Wray and Strain 1986)
<i>Paspalum conjugatum</i>	1.22	(Ziska et al. 1991)
<i>Pennisetum clandestinum</i>	1.15	(Campbell et al. 1993)
<i>Sorghum halepense</i>	1.10	(Patterson et al. 1984, Tremmel and Patterson 1993)
<i>Spartina anglica</i>	0.88	(Campbell et al. 1993, Lenssen 1993, Lenssen et al. 1993)
<b>CAM species</b>		
<i>Opuntia ficus-indica</i>	1.22	(Nobel and Garcia de Cortazar 1991, Cui et al. 1993, Cui and Nobel 1994, Nobel et al. 1994)

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Table 2. Median weight ratios of invasive species from Table 1 and other species listed in Poorter et al. (1996), and *P*-values from Mann-Whitney U tests for differences between weight ratios of invasive and other species.

Species type	Invasives		Others		<i>P</i> -values
	median	<i>n</i>	median	<i>n</i>	
C <sub>3</sub> herbaceous	1.495	22	1.4	93	0.22
C <sub>3</sub> woody	1.46	17	1.4	80	0.30
C <sub>4</sub> herbaceous	1.12	6	1.16	18	0.24
CAM	1.22	1	1.14	5	0.55

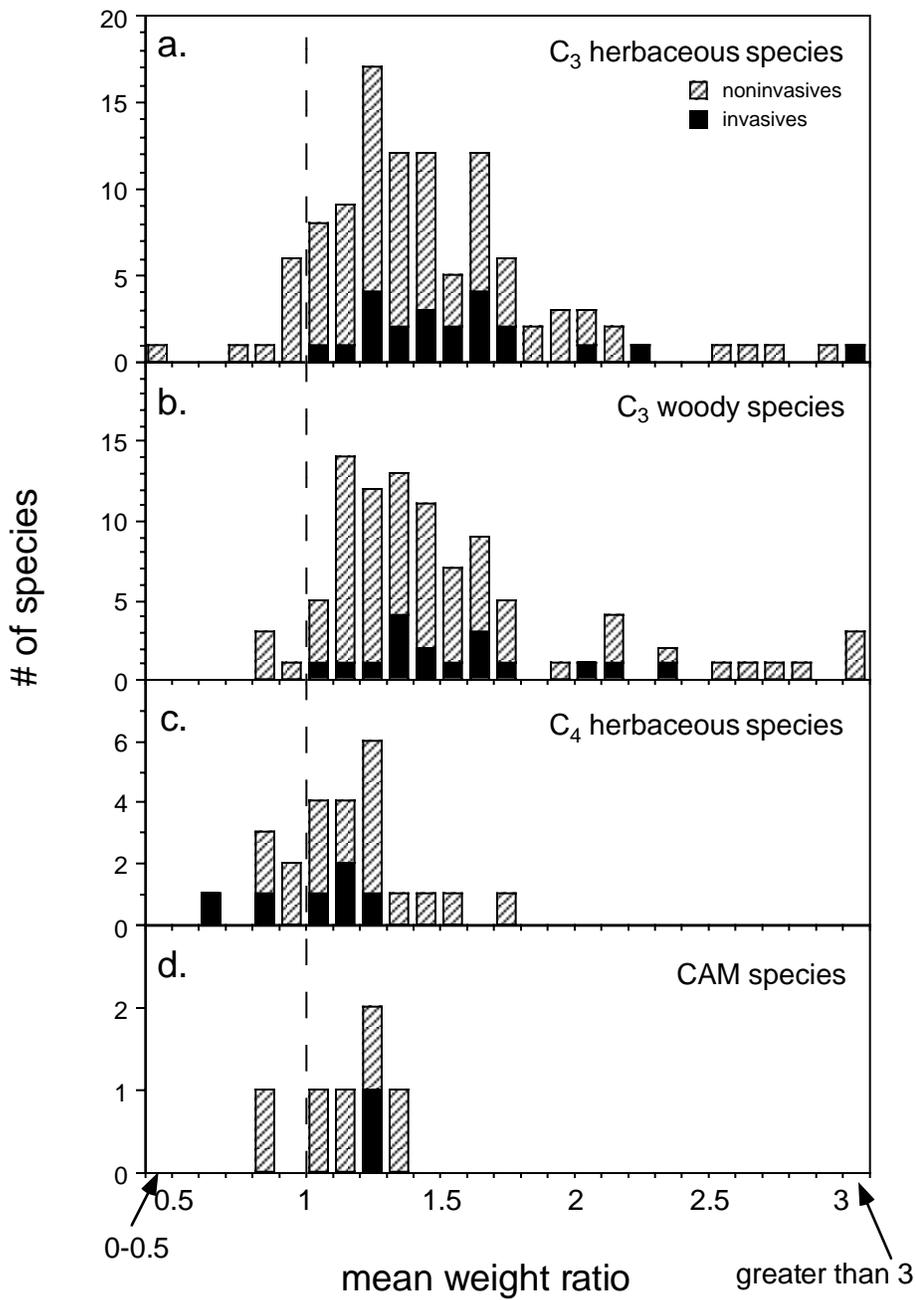


Figure 1. Distribution of mean weight ratios of species listed by Poorter and colleagues (1996), with species listed in Table 1 identified as invasive, and all other species identified as noninvasive. The dashed line represents the border between positive and negative CO<sub>2</sub> responses.