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7.5. Competition

Do higher levels of atmospheric CO_2 favor some plants over others? Could this result in ecological changes that could be judged "bad" because of their effects on wildlife or plants that are beneficial to mankind? This section seeks to answer these questions by surveying research on the effects of CO_2 enhancement on C_3 versus C_4 plants, and weeds versus crops.

Additional information on this topic, including reviews on competition not discussed here, can be found at http://www.co2science.org/ subject/c/subject _c.php under the heading Competition.

7.5.1. C_3 vs C_4 Plants

C_3 plants typically respond better to atmospheric CO_2 enrichment than do C_4 plants in terms of increasing their rates of photosynthesis and biomass production. Hence, it has periodically been suggested that in a world of rising atmospheric CO_2 concentration, C_3 plants may out-compete C_4 plants and displace them, thereby decreasing the biodiversity of certain ecosystems. However, the story is much more complex that what is suggested by this simple scenario.

Wilson *et al*. (1998) grew 36 species of perennial grass common to tallgrass prairie ecosystems with and without arbuscular mycorrhizal fungi, finding that the dry matter production of the C_3 species that were colonized by the fungi was the same as that of the non-inoculated C_3 species, but that the fungal-colonized C_4 species produced, on average, 85 percent *more* dry matter than the non-inoculated C_4 species. This finding is of pertinence to the relative responsiveness of C_3 and C_4 plants to atmospheric CO_2 enrichment; for elevated levels of atmospheric CO_2 tend to enhance the mycorrhizal colonization of plant roots, which is known to make soil minerals and water more available for plant growth. Hence, this CO_2-induced fungal-mediated growth advantage, which from this study appears to be more readily available to C_4 plants, could well counter the inherently greater biomass response of C_3 plants relative to that of C_4 plants, leveling the playing field relative to their competition for space in any given ecosystem.

Another advantage that may come to C_4 plants as a consequence of the ongoing rise in the air's CO_2 content was elucidated by BassiriRad *et al*. (1998), who found that elevated CO_2 enhanced the ability of the perennial C_4 grass *Bouteloua eriopoda* to increase its uptake of NO_3^- and PO_4^{3-} considerably more than the perennial C_3 shrubs *Larrea tridentata* and *Prosopis glandulosa*. In an eight-year study of the effects of twice-ambient atmospheric CO_2 concentrations on a pristine tallgrass prairie in Kansas, Owensby *et al*. (1999) found that the elevated CO_2 did not affect the basal coverage of its C_4 species or their relative contribution to the composition of the ecosystem.

The antitranspirant effect of atmospheric CO_2 enrichment (Pospisilova and Catsky, 1999) is often more strongly expressed in C_4 plants than in C_3 plants and typically allows C_4 plants to better cope with water stress. In a study of the C_3 dicot *Abutilon theophrasti* and the C_4 dicot *Amaranthus retroflexus*, for example, Ward *et al*. (1999) found that *Amaranthus retroflexus* exhibited a greater relative recovery from drought than did the C_3 species, which suggests, in their words, that "the C_4 species would continue to be more competitive than the C_3 species in regions receiving more frequent and severe droughts," which basically characterizes regions where C_4 plants currently exist.

Two years later, Morgan *et al*. (2001) published the results of an open-top chamber study of a native shortgrass steppe ecosystem in Colorado, USA, where they had exposed the enclosed ecosystems to atmospheric CO_2 concentrations of 360 and 720 ppm for two six-month growing seasons. In spite of an average air temperature increase of 2.6°C, which was caused by the presence of the open-top chambers, the elevated CO_2 increased above-ground biomass production by an average of 38 percent in both years of the study; and when 50 percent of the standing green plant biomass was defoliated to simulate grazing halfway through the growing season, atmospheric CO_2 enrichment still increased above-ground biomass by 36 percent. It was also found that the communities enriched with CO_2 tended to have greater amounts of moisture in their soils than communities exposed to ambient air; and this phenomenon likely contributed to the less negative and, therefore, less stressful plant water potentials that were measured in the CO_2-enriched plants. Last, the elevated CO_2 did not preferentially stimulate the growth of C_3 species over that of C_4 species in these communities. Elevated CO_2 did not significantly affect the percentage composition of C_3 and C_4 species in these grasslands; they maintained their original level of vegetative biodiversity.

This would also appear to be the conclusion of the study of Wand *et al*. (1999), who in a massive review of the scientific literature published between 1980 and 1997 analyzed nearly 120 individual responses of C_3 and C_4 grasses to elevated CO_2. On average, they found photosynthetic enhancements of 33 and 25 percent, respectively, for C_3 and C_4 plants, along with biomass enhancements of 44 and 33 percent, respectively, for a doubling of the air's CO_2 concentration. These larger-than-expected growth responses in the C_4 species led them to conclude that "it may be premature to predict that C_4 grass species will lose their competitive advantage over C_3 grass species in elevated CO_2."

Further support for this conclusion comes from the study of Campbell *et al*. (2000), who reviewed research work done between 1994 and 1999 by a worldwide network of 83 scientists associated with the Global Change and Terrestrial Ecosystems (GCTE) Pastures and Rangelands Core Research Project 1, which resulted in the publication of over 165 peer-reviewed scientific journal articles. After analyzing this body of research, they concluded that the "growth of C_4 species is about as responsive to CO_2 concentration as [is that of] C_3 species when water supply restricts growth, as is usual in grasslands containing C_4 species." The work of this group of scientists also provides no evidence for the suggestion that C_3 plants may out-compete C_4 plants and thereby replace them in a high-CO_2 world of the future.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/b/biodivc3vsc4.php.

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7.5.2. N-Fixers vs. Non-N-Fixers

Will nitrogen-fixing (N-fixing) plants benefit more from atmospheric CO_2 enrichment than non-N-fixers and thus obtain a competitive advantage over them that could lead to some non-N-fixers being excluded from certain plant communities, thereby decreasing the biodiversity of those ecosystems?

In a two-year glasshouse study of simulated low-fertility ecosystems composed of grassland species common to Switzerland, Stocklin and Korner (1999) found that atmospheric CO_2 enrichment gave nitrogen-fixing legumes an initial competitive advantage over non-N-fixers. However, it would be expected that, over time, a portion of the extra nitrogen fixed by these legumes would become available to neighboring non-N-fixing species, which would then be able to use it to their own advantage, thereby preserving the species richness of the ecosystem over the long haul. Indeed, in a four-year study of an established (non-simulated) high grassland ecosystem located in the Swiss Alps, Arnone (1999) found no difference between the minimal to non-existent growth responses of N-fixing and non-N-fixing species to elevated levels of atmospheric CO_2.

In a study of mixed plantings of the grass *Lolium perenne* and the legume *Medicago sativa*, Matthies and Egli (1999) found that elevated CO_2 did not influence the competition between the two plants, either directly or indirectly via its effects upon the root hemiparasite *Rhinanthus alectorolophus*. In a study of mixed plantings of two grasses and two legumes, Navas *et al*. (1999) observed that plant responses to atmospheric CO_2 enrichment are more dependent upon neighboring plant density than they are upon neighboring plant identity.

In the few studies of this question that have been conducted to date, therefore, it would appear that there is little evidence to suggest that N-fixing legumes will out-compete non-N-fixing plants.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/b/biodivnfixers.php.

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7.5.3. Weeds vs. Non-Weeds

Elevated CO_2 typically stimulates the growth of nearly all plant species in monoculture, including those deemed undesirable by humans, i.e., weeds. Consequently, it is important to determine how future increases in the air's CO_2 content may influence relationships between weeds and non-weeds when they grow competitively in mixed-species stands.

Dukes (2002) grew model serpentine grasslands common to California, USA, in competition with the invasive forb *Centaurea solstitiali*s at atmospheric CO_2 concentrations of 350 and 700 ppm for one year, determining that elevated CO_2 increased the biomass proportion of this weedy species in the community by a mere 1.2 percent, while total community biomass increased by 28 percent. Similarly, Gavazzi *et al*. (2000) grew loblolly pine seedlings for four months in competition with both C_3 and C_4 weeds at atmospheric CO_2 concentrations of 260 and 660 ppm, reporting that elevated CO_2 increased pine biomass by 22 percent while eliciting no response from either type of weed.

In a study of pasture ecosystems near Montreal, Canada, Taylor and Potvin (1997) found that elevated CO_2 concentrations did not influence the number of native species returning after their removal (to simulate disturbance), even in the face of the introduced presence of the C_3 weed *Chenopodium album*, which normally competes quite effectively with several slower-growing crops in ambient air. In fact, atmospheric CO_2 enrichment did not impact the growth of this weed in any measurable way.

Ziska *et al*. (1999) also studied the C_3 weed *C. album*, along with the C_4 weed *Amaranthus retroflexus*, in glasshouses maintained at atmospheric CO_2 concentrations of 360 and 720 ppm. They determined that elevated CO_2 significantly increased the photosynthetic rate and total dry weight of the C_3 weed, but that it had no effect on the C_4 weed. Also, they found that the growth response of the C_3 weed to a doubling of the air's CO_2 content was approximately 51 percent, which is about the same as the average 52 percent growth response tabulated by Idso (1992), and that obtained by Poorter (1993) for rapidly growing wild C_3 species (54 percent), which finding suggests there is no enhanced dominance of the C_3 weed over other C_3 plants in a CO_2-enriched environment.

Wayne *et al*. (1999) studied another agricultural weed, field mustard (*Brassica kaber*), which was sown in pots at six densities, placed in atmospheric CO_2 concentrations of 350 and 700 ppm, and sequentially harvested during the growing season. Early in stand development, elevated CO_2 increased above-ground weed biomass in a density-dependent manner, with the greatest stimulation of 141 percent occurring at the lowest density (corresponding to 20 plants per square meter) and the smallest stimulation of 59 percent occurring at the highest density (corresponding to 652 plants per square meter). However, as stands matured, the density-dependence of the CO_2-induced growth response disappeared, and CO_2-enriched plants exhibited an average above-ground biomass that was 34 percent greater than that of ambiently grown plants across a broad range of plant densities. This final growth stimulation was similar to that of most other herbaceous plants exposed to atmospheric CO_2 enrichment (30 to 50 percent biomass increases for a doubling of the air's CO_2 content), evidence once again that atmospheric CO_2 enrichment confers no undue advantage upon weeds at the expense of other plants.

In a study of a weed that affects both plants and animals, Caporn *et al*. (1999) examined bracken (*Pteridium aquilinum*), which poses a serious weed problem and potential threat to human health in the United Kingdom and other regions, growing specimens for 19 months in controlled environment chambers maintained at atmospheric CO_2 concentrations of 370 and 570 ppm and normal or high levels of soil fertility. They found that the high CO_2 treatment consistently increased rates of net photosynthesis by 30 to 70 percent, depending on soil fertility and time of year. However, elevated CO_2 did not increase total plant dry mass or the dry mass of any plant organ, including rhizomes, roots and fronds. In fact, the only significant effect of elevated CO_2 on bracken growth was observed in the normal nutrient regime, where elevated CO_2 reduced mean frond area.

Finally, in a study involving two parasitic species (*Striga hermonthica* and *Striga asiatica*), Watling and Press (1997) reported that total parasitic biomass per host plant at an atmospheric CO_2 concentration of 700 ppm was 65 percent less than it was in ambient air. And in a related study, Dale and Press (1999) observed that the presence of a parasitic plant (*Orobanche minor*) reduced its host's biomass by 47 percent in ambient air of 360 ppm CO_2, but by only 20 percent in air of 550 ppm CO_2.

These several studies suggest that, contrary to what is claimed by the IPCC, the ongoing rise in the air's CO_2 content will not favor the growth of weedy species over that of crops and native plants. In fact, it may provide non-weeds greater protection against weed-induced decreases in their productivity and growth. Future increases in the air's CO_2 content may actually increase the competitiveness of non-weeds over weeds.

Additional information on this topic, including reviews of newer publications as they become available, can be found at http://www.co2science.org/subject/b/weedsvsnonw.php.

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7.6. Respiration

Nearly all of earth's plants respond favorably to increases in the air's CO_2 concentration by exhibiting enhanced rates of net photosynthesis and biomass production during the light part of each day. In many cases, observed increases in these parameters (especially biomass production) are believed to be due, in part, to CO_2-induced reductions in carbon losses via respiration during the day and especially at night (called "dark respiration"). In this summary, we examine what has been learned about this subject from experiments conducted on various herbaceous and woody plants.

Additional information on this topic, including reviews on respiration not discussed here, can be found at http://www.co2science.org/subject/r/subject_r.php under the heading Respiration.

7.6.1. Herbaceous Plants

7.6.1.1. Crops

Baker *et al*. (2000) grew rice in Soil-Plant-Atmosphere Research (SPAR) units at atmospheric CO_2 concentrations of 350 and 700 ppm during daylight hours. Under these conditions, rates of dark respiration decreased in both CO_2 treatments with short-term increases in the air's CO_2 concentration at night. However, when dark respiration rates were measured at the CO_2 growth concentrations of the plants, they were not significantly different from each other.

Cousins *et al*. (2001) grew sorghum at atmospheric CO_2 concentrations of 370 and 570 ppm within a free-air CO_2 enrichment (FACE) facility near Phoenix, Arizona, USA. Within six days of planting, the photosynthetic rates of the second leaves of the CO_2-enriched plants were 37 percent greater than those of the second leaves of the ambiently grown plants. However, this CO_2-induced photosynthetic enhancement slowly declined with time, stabilizing at approximately 15 percent between 23 and 60 days after planting. In addition, when measuring photosynthetic rates at a reduced oxygen concentration of 2 percent, they observed 16 and 9 percent increases in photosynthesis for the ambient and CO_2-enriched plants, respectively. These observations suggest that the extra 200 ppm of CO_2 was reducing photorespiratory carbon losses, although this phenomenon did not account for all of the CO_2-induced stimulation of photosynthesis.

Das *et al*. (2002) grew tropical nitrogen-fixing mungbean plants in open-top chambers maintained at atmospheric CO_2 concentrations of either 350 or 600 ppm for two growing seasons, with the extra CO_2 being provided between either days 0 and 20 or days 21 and 40 after germination. This work revealed that the elevated CO_2 decreased rates of respiration by 54-62 percent, with the greatest declines occurring during the first 20 days after germination.

Wang *et al*. (2004) grew well-watered and fertilized South American tobacco plants from seed in 8.4-liter pots (one plant per pot) filled with sand and housed in controlled-environment growth chambers maintained at atmospheric CO_2 concentrations of either 365 or 730 ppm for a total of nine weeks. Over this period they found that the ratio of net photosynthesis per unit leaf area (A) to dark respiration per unit leaf area (Rd) "changed dramatically." Whereas A/Rd was the same in both treatments at the beginning of the measurement period, a month later it had doubled in the CO_2-enriched environment but had risen by only 58 percent in the ambient treatment. Speaking of this finding, the three researchers say that "if the dynamic relationship between A and Rd observed in *N. sylvestris* is applicable to other species, it will have important implications for carbon cycling in terrestrial ecosystems, since plants will assimilate CO_2 more efficiently as they mature."