

IV. GENERAL DISCUSSION

IV-1. Facilities for studying effect of global warming on plant growth

The TGC and CTGC, constructed to study the effect of global warming on the growth of a plant population under field-like conditions, performed reliably with regards to the air temperature regulation in the TGC and the simultaneous air temperature and CO₂ concentration control in the CTGC. Dynamically stable CO₂ concentration and air temperature gradients were maintained, despite wide seasonal fluctuation in ambient air temperature and CO₂ concentration. This ability to highly regulate both chambers was achieved by the proportional-integral-differential (PID) algorithm (Hendrey *et al.*, 1993). The PID algorithm is a control action in which the output is proportional to a linear combination of the input, the time integral of the input and the time rate-of-change of the input. The control values to regulate the ventilation and CO₂ injection rates were calculated from a measured actual value and a desired value of air temperature and CO₂ concentration using the PID algorithm.

As a result, although the ambient air temperature changed seasonally (cf. Fig. 7) or even daily (cf. Fig. 8), a linear temperature gradient of 5°C from the air inlet to the outlet was consistently achieved in the TGC and CTGC; the temperature gradient was 1°C for every 5 m in both chambers with a precision of $\pm 0.2^{\circ}\text{C}$. In terms of the regulatory accuracy of the air temperature, both chambers were much superior to similar facilities previously developed by Horie *et al.* (1995) and Okada *et al.* (1995), because the analog control system employed here enabled us to set the various rates of ventilation and CO₂ release. In addition to the temperature gradient, the CO₂ concentration gradient was also created in the CTGC after 11 Feb., 1998; the mean CO₂

concentrations were 400 ppm at the air inlet and 799 ppm at the outlet (cf. Figs. 9 and 10). The CO₂ releasing system developed in this study was more helpful for maintaining elevated CO₂ in the CTGC than was the operation system employed by Horie *et al.* (1995) or Sinclair *et al.* (1995), because the CO₂ concentrations in the CTGC might be strongly influenced by biological processes such as photosynthesis in daytime, and plant and soil respirations all day.

The experiments conducted in the TGC and CTGC can provide tightly controlled temperature and CO₂ concentrations, and their relatively low cost per enclosure allows for a high degree of replication. In the CTGC, the annual CO₂ requirement was 156 kg m⁻². The total annual expense for the injected CO₂ was \$260 m⁻² at a cost of \$1,667 ton⁻¹ in which the consumption rate was greatly dependent on the ventilation rate, as demonstrated in Fig. 14. The amount of CO₂ required to enrich the same area of vegetation using the OTC or FACE systems would be at least an order of magnitude greater. Kimball (1992) calculated annual CO₂ requirements for operating the OTC and FACE systems as being 1.86 and 4.12 t m⁻² of enriched surface area, respectively, assuming a CO₂ enrichment of 300 µmol mol⁻¹ for 24 h day⁻¹ over 6 months. The FACE and OTC experiments cost about \$782 m⁻² and \$1,900 m⁻² (see Hendrey *et al.*, 1993), respectively, in spite of much cheaper CO₂ gas at \$70 ton⁻¹ in the USA.

Physiological and ecological studies under field conditions are rather easily conducted because the wide space also allows for direct measurements of leaf water potential, gas exchange, and soil respiration etc. In addition, when information on air flow rates is available, the water vapor can be calculated from the measurements of air dew-point and dry-bulb temperature that are taken at

the beginning and every 5-m away from air inlet (e.g. Polley *et al.*, 1993). The TGC and the CTGC thus fill a void in CO₂ research facilities by enabling the study of trends in partial and full ecosystem responses to temperature and CO₂. With this improvement, the chambers should also be capable of creating only those CO₂ concentration gradients that are above ambient values. Although the TGC and CTGC described here were designed for small-statured plants or vegetation such as grasses or tree saplings (< 2.5 m height), the space is sufficient for studying plant populations. Also, these facilities could be easily accessible to any plant at any location by using a long transparent greenhouse tunnel, a system already widely used in agriculture.

The chambers newly built for this study provided a highly reproducible regulation of temperature and CO₂ to create a gradient from the ambient conditions to the desired global warming conditions. A particular advantage of this approach is that it provides information on the recent and near future responses of ecosystems to temperature and CO₂ that is not available from any other field studies. To our knowledge, this is the only field facility available for controlling temperature and CO₂ on large field plots for extended periods (years). The physiological method used in laboratories and glasshouses to elevate CO₂ is not a viable option for extended field experiments in which massive quantities of air processing are required. Although temperature and CO₂ gradients were not replicated here, the approach described has the advantage of providing information on the shape of plant and ecosystem responses to a large gradient of CO₂ concentration and temperature. The paucity of experimental information on the response curve is a major hindrance to projecting the timing and nature of temperature and CO₂ effects (Körner, 1995). With the TGC and the CTGC

improvements, long-term studies can address this problem. These facilities can be more widely utilized with the most suitable conditions to obtain both parameterization and validation data sets for models contributing to plant growth, species composition, and global carbon flux analysis.

IV-2. Effect of elevated global warming on thermal condition and plant phenology

The most critical global warming effect in this study was the change in the thermal environment. The number of days with a daily mean temperature over 5°C were 282, 311, and 350, in the ambient, 2°C warmed condition, and 4°C warmed condition, respectively (cf. Figs. 7 and 15). The elongation of the periods available for plant growth resulted from extended summer-like thermal conditions and shortened winter-like thermal conditions. These results support the idea that increasing temperatures in cool seasons cause the advancement of phenological development, elongating the growth period for crops and natural species (e.g. Monteith, 1981), as most modeling studies have shown (Warrick *et al.*, 1986). Accordingly, global warming will potentially supply a longer photosynthetic period to plants. In particular, the total growth period will be lengthened in mid- and high-northern latitudes where plant growth is usually limited by low temperatures during the cool season. Also, the warming would contribute to an increase in the annual dry-matter production per unit ground area per year, since the growth period would surely be elongated. Indeed, Myneni *et al.* (1997) reported that the photosynthetic activity of terrestrial vegetation increased from 1981 to 1991 in a manner that was suggestive of an

increase in plant growth associated with a longer active growing season. Menzel and Fabian (1999) also analyzed data from more than 30 years of observation about change in phenology in Europe, and suggested that the longer growing season was likely to contribute to increased biomass formation, which is part of a global increase in biospheric activity. The region exhibiting the greatest increase lies between 45°N and 75°N, where marked warming has occurred in the springtime, due to the early disappearance of snow. Consequently, the current geographical distributions of most species will be altered as a result of the new weather conditions.

How will C3 and C4 species respond to altered atmospheric environmental conditions, particularly elevated temperatures due to elevated atmospheric CO₂ concentration? The data obtained in this study showed that the elevated-temperature and CO₂-concentration plots had a prominent effect on the phenological response of the three annual species, *C. album* (C3), *E. crus-galli* (C4), and *S. viridis* (C4) populations. As listed in Table 2, the seedling emergence times and the flowering times in the three species were significantly accelerated ($P < 0.05$) in all four warmed plots compared with those in the Control plot. The noteworthy fact is that the emergence times were much more accelerated in the two C4 species, while the flowering times were more accelerated in the C3 species. As a consequence of these different responses to warming, the vegetative growth periods were lengthened in the two C4 species and shortened in the C3 species. Further study of the alteration of such phenological responses among species will clarify the future species composition changes due to ongoing global warming.

Because earlier-emerging species might preempt resources, including

space, they may suppress later-emerging seedlings. In dense populations, the emergence time, number of emergents, and subsequent resource acquisition and growth are critical factors in determining the mortality and size variation of the survivors. For example, Morse and Bazzaz (1994) found that in the recruitment of C3 and C4 annuals, members of the first cohort had a significantly higher probability of surviving than those of the second cohort, which was only 4 d younger than the first. The difference in the neighboring plants' height may exert an essential influence upon their viability. Even a minor differences in height can result in a great difference in the amount of utilizable solar energy, which is of supreme importance for plants, as has been elucidated by Boysen Jensen (1932) and Monsi and Saeki (1953). For example, light is one of the most vital environmental factors for the growth of plants in the community through dry-matter production, especially under mesophytic conditions. So a slight difference in height will be progressively magnified with the mutual shading of leaves and consequently the competition for light with neighboring plants. Therefore, these late recruits are competitively inferior and can suffer from increased mortality because the early-recruited neighbors are already growing and using full sunlight (Bazzaz, 1996). The data obtained here will improve the predictability of such mechanistic terrestrial ecosystem models such as the Sim-CYCLE developed by Ito and Oikiawa (2000). In addition to the physiological difference between the C3 and C4 species of the photosynthetic pathway, these phenological differences will lead to changes in annual biomass and seed production and therefore determine superiority in species composition in the global warming world.

IV-3. Interactions between elevated temperature and CO₂ on plant growth

The vegetative stages for all experimental species were advanced to winter-like thermal conditions as the temperature was elevated (cf. Fig. 17 and Table 2). As a result, although the plants were grown in elevated-temperature plots, the mean temperatures during the vegetative stage of the three species were, unexpectedly, lower by 1.2°C in the 2°C warmed plot (T2 and CT2) and 1.0°C in the 4°C warmed plot (T4 and CT4) in comparison with the Control plot. As a result, the predicted high temperature due to global warming was offset by timely advanced phenology. These results indicate the possibility that the plants will be unaffected by high temperature due to global warming, at least during the spring to early-summer. Thus, although the temperature will be increased by global warming, advances in phenology will clearly ensure plant growth under moderate thermal conditions similar to current thermal conditions; this result may be seen particularly in mid- and high-latitude regions in which the plant growth is restricted by low temperatures during the winter season. In this study, although there were time-related differences, the growth during the vegetative stage for the *C. album* population showed almost the same tendency in all plots (cf. Fig. 17a).

On the other hand, the advanced plant phenology will have more favorable effects on the growth of the C3 species than on the C4 species because the C3 species do not prefer warmer and drier environments (Ehleringer and Björkman, 1977; Berry and Björkman, 1980; Pearcy *et al.*, 1981). However, as it entered the hot season, the growth rate of the *C. album* population, which has a long growth period, was clearly suppressed with the

increase in air temperature. The growth suppression due to high temperature supports the hypothesis that high temperatures in hot seasons will have a negative effect on the growth of C3 plants and that the high dominance of C3 species under the current atmospheric CO₂ concentration conditions is clearly related to low- temperature region or season (Teeri and Stowe, 1976; Hasegawa, 1979; de Jong *et al.*, 1982; Hattersley, 1983; Takeda, 1985; Kalapos, 1991). Therefore, if global warming progressed with no change in the current CO₂ concentration, the current dominance of C3 species in particular regions would be threatened (Epstein *et al.*, 1997). However, clearly, global warming comprises the simultaneous increase in atmospheric temperature and CO₂

Although the air temperature was raised, the *C. album* populations in the elevated-CO₂ plots did not show an abrupt decrease in the growth rate due to the high temperature, as shown in the CT2 and CT4 plots (cf. Figs. 7 and 17a). The sustained high growth rate of the *C. album* populations resulted from the positive effect of elevated CO₂ on the LAI and NAR. Elevated CO₂ has significant positive effects on the NAR of the *C. album* population and these effects were strongly dependent on temperature (cf. Fig. 19). The slope of the NAR's dependence on temperature suggested that the effect of elevated CO₂ was approximately 13.2%/°C in the range of 17-30°C. These results indicate that the effect of elevated CO₂ on plant growth may not occur fully by advanced phenology, at least in the vegetative stage, and that elevated CO₂ will compensate for the negative effect of high temperature (cf. Fig. 19). Similarly, these CO₂ fertilization effect dependencies on temperature were suggested in the other studies. Idso *et al.* (1989) studied the response of many plant species to elevated atmospheric CO₂ under various temperature regimes and concluded

that crops growing at cooler temperatures will be stimulated relatively less by elevated CO₂. There was no response or even a negative response from plants to elevated CO₂ at temperatures below 12°C. Coleman and Bazzaz (1991) also reported that the final biomass of *Amaranthus retroflexus* (C4) was enhanced at 28°C to the atmospheric CO₂ concentration of 700 ppm, but was depressed at 38°C. For *Abutilon theophrasti* (C3), elevated CO₂ increased initial plant relative growth rates at 28°C but not at 38°C, and had no significant effects on final biomass at either temperature. Oechel and Vourlitis (1996) suggested that the tundra ecosystem's lack of response to high CO₂ was due to low temperatures limiting the sink growth potential. In the warmer Chesapeake Bay salt marsh, Drake *et al.* (1996) attributed the large year-to-year variation in stimulation of net ecosystem CO₂ exchange to environmental interactions, in particular to the large stimulations from a very warm year when elevated CO₂ 'moderated the impact of stress on productivity'. This temperature interaction is consistent with the physiological expectation that a CO₂ stimulation of growth should be temperature dependent (Farrar and Williams, 1991; Long, 1991).

On the other hand, C3 species' advantage resulting from an advanced phenological response to high CO₂ concentrations may not occur adequately during the vegetative stage in low temperatures. In this study, the *C. album* population in the CT4 plot did not significantly stimulate plant growth during the early growth stage compared with the T4 plot until mid-April (cf. Fig. 17a and Table 2). These result resulted from low growth temperature. However, the late-growth stage, mainly the reproductive stage, of the *C. album* population experienced high temperatures which were not seen in the Control plot. After that, the relative effect of elevated CO₂ on the *NAR* of the *C. album* population

between the CT4 and T4 plots was highly increased (cf. Fig. 19). As the plants aged, the amount of accumulated dry matter between the CO₂-elevated plot and the non-elevated plot differed greatly (cf. Fig. 17a). As these results show the high CO₂ fertilization effect under the high temperature conditions that was explained in other studies. For example, one of the most important and most frequently observed CO₂ × temperature interactions is that the stimulation of C3 photosynthesis by elevated CO₂ increases as the temperature rises within the approximate temperature range of 20-35°C (Berry and Raison, 1981; Sage and Reid, 1994). One reason for the result is that at warm temperatures, the photorespiration of C3 plants is inhibited proportionally by increasing CO₂ (Jordan and Ogren, 1984). The second reason is that the magnitude of beneficial effects of elevated CO₂ on photosynthesis was greater in warm temperatures than in cool temperatures, because the metabolism and the sink demand for photosynthates are usually greater in warmer temperatures (Farrar and Williams, 1991). Consequently, there is a smaller accumulation of immediate photosynthetic products (triose and hexose phosphates, sucrose and starch) in the leaves in warmer temperatures than in cooler temperatures (Crawford and Wolfe, 1999).

As stated above, the CO₂ fertilizer effect on C3 species is dependent on the temperature. These results suggest that the magnitude of the CO₂ fertilizer effect on the dry-matter production would be largely increased by increasing temperatures. However, past experiments using the FACE or the OTC, in which plants are grown under ambient or near-ambient air temperature conditions, could have underestimated the CO₂ fertilizer effect on plants' dry matter production. For example, in the seven-year OTC experiment with normal

ambient and elevated CO₂ (= normal ambient + 340 ppm), Drake *et al.* (1996) found that stimulation of the net ecosystem CO₂ exchange of elevated CO₂ in the C3 and C4 communities increased by an average of 37% and 21% respectively. However, these results might underestimate the CO₂ fertilizer effect since the temperature factor was not taken into consideration. Drake *et al.* (1996) also showed that the stimulation of the net ecosystem CO₂ exchange by elevated CO₂ in the C3 species fluctuated proportionally to air temperature in the range of 27-35°C of the annual mean air temperature during the 7 years. These results suggest that the CO₂ fertilizer effect on dry-matter production would be highly accelerated in global warming. On the other hand, Hunt *et al.*, (1991) using a CO₂-enriched growth chamber showed that the dry-matter production of the *C. album* population was not stimulated by CO₂-enrichment. Such low fertilizer effects probably resulted from setting the growth temperature as low as 18°C. Thus to predict plant response to global warming, we must consider the effects of elevated CO₂ in combination with temperature.

High temperature stress may be expected to be alleviated by elevated CO₂, due to improved photosynthesis (Long, 1991). In addition to the CO₂ fertilizer effect on the *NAR*, the *LAI* and *RGR* of the *C. album* population in the CT4 plot also showed a higher value than that in the T4 plot throughout almost the full growth season (cf. Figs. 20 and 21). The higher *LAI*, *NAR*, and *RGR* in the CT4 plot resulted in an increase in the growth rate. The total final dry weight per unit ground area of the *C. album* population in the CT4 plot was significantly increased by about two folds (97.6%) compared with that in the T4 plot (cf. Fig. 18). Also, the *C. album* population grown in the T2 plot showed a significant decrease in total final dry weight per unit ground area compared with that in the

CT2 plot (cf. Fig. 18).

On the other hand, the two C4 species populations, the *E. crus-galli* and *S. viridis* populations, showed a different mean temperature during the vegetative stage (cf. Figs. 17b and c). These populations were not affected in terms of growth by high temperature except during the late-reproductive stage. This result was caused mainly by advanced phenology with increase of temperature and a relatively short growth period as compared to the C3 plant. In the case of the *E. crus-galli* populations, the mean air temperature during the vegetative stage was lower in the temperature-elevated plots than in the Control plot (cf. Table 3). For the C4 species, in general, low temperatures result in low photosynthetic activity, for some reason. For example, Potvin *et al.* (1986) also showed that C4 enzymes of the *E. crus-galli*, such NADP⁺-malate dehydrogenase and pyruvate *Pi* dikinase, are susceptible to being limited at low temperatures. The distribution of C3 and C4 grasses in North America showed that the percentage of C4 grasses in the flora dropped below 50% when the mean July minimum temperature dropped to below 18°C. The simulations of the productivity of C3 and C4 grasses along this same temperature gradient by Ehleringer (1978) reached similar conclusions, and suggested that the two groups should show equal net daily carbon gain at 45°N latitude in the Great Plains. This transitional latitude between the two types corresponds to a mean minimum July temperature of 15°C and a mean maximum July temperature of 29°C (Ehleringer, 1978). In the study on cold night treatments for *E. crus-galli*, Potvin *et al.* (1985) found that translocation of photosynthate was completely inhibited by exposure even to one night of low temperature. Similarly, Pearson and Derrick (1977) showed that, after exposure to low night temperatures,

export and photosynthetic rates were reduced in a C4 species, *Pennisetum americanum*. Therefore, considering the studies cited above, the lower temperature during the vegetative stage may result in a significant decrease in the total final dry weight per unit ground area of the *E. crus-galli* population in the T4 plot as well as in the CT4 plot compared with the Control plot.

Although the mean temperature during the reproductive stage for the *E. crus-galli* populations was slightly higher in the T4 and CT4 plots, the final dry matter production was not stimulated. The stimulation of the *NAR* and *RGR* due to elevated CO₂ was also low (cf. Figs. 19 and 20). It has been generally considered that because of the CO₂ concentrating mechanism in C4 plants they will show little CO₂ stimulation, irrespective of temperature (e.g. Gifford, 1992; Bowes, 1996).

The total final dry weights per unit ground area of the *E. crus-galli* and *S. viridis* populations decreased in the T4 plot, and the elevated CO₂ did not affect dry matter production compared with the Control plot.

IV-4. Effects of elevated temperature and CO₂ on size hierarchies

The significance of increasing levels of CO₂ on individual size and variation of the *C. album* population was highly temperature dependent (cf. Fig. 23). Wand *et al.* (1999) found that in meta-analytic tests of wild C4 and C3 grass species' responses to elevated atmospheric CO₂ concentrations, the tillering response was small. However, in this study the range of sizes dramatically increased in both the T4 and CT4 plots.

Because the regulation of the growth processes ultimately determines

the rate at which plants acquire resources, it was assumed that simultaneous changes in temperature and CO₂ would modify not only growth but the patterns of resource pre-emption (final population size and structure) among members within the population. In resource-rich environments, the growth rates may increase and result in more intense mutual interactions, higher mortality rate, and disproportionate growth of a few dominant individuals (Harper, 1977; Morris and Myerscough, 1984). The resources supplied from a single direction, e.g. light, are subject to pre-emption (asymmetric competition) and will drive dominance-suppression hierarchies as the leaf area index increases. The diffusible resources, however, are usually accessible to all individuals in proportion to their size (Weiner, 1990). Consequently, the increase in diffusible atmospheric resources such as CO₂ should affect only the mean size and not the extent of variation in size among individuals. Thus, the elevated CO₂ will increase the mean size of individuals in stands of C3 plants because CO₂ is a nonpre-emptable limiting resource. The models of plant-plant interaction suggest that for a constant density, the mean mass of an individual within the population will increase as resources (other than light) increase (see Weiner, 1990). The variation among individuals, however, is predicted not to change because the nonpre-emptable resources are used in proportion to an individual's size. Considering this theory it was assumed or predicted that, as CO₂ concentration increases, one should see an increase in the dry-matter production. For the *C. album* population (C3), this prediction was born out in the CT2 and CT4 plots. The resources affect not only the mean size and size distribution within populations but also the extent of mortality. In highly fertile plots, for example, the final densities were lower and mean sizes were larger

because of more intense self-thinning (Harper, 1977). The tendency for large size classes to exist in the *C. album* populations in the CT2 and CT4 plots suggests that CO₂ had a fertilizer effect (see also Bazzaz *et al.*, 1992; cf. Fig. 23a). The simultaneous change in both temperature and CO₂ will lead to different responses for C3 and C4 species because CO₂ is, at present, a limiting resource, particularly for C3 plants.

Interactive effects between temperature and CO₂ may give rise to complex patterns of population size and structure (including stand development) due to the differential effects of these factors on individual growth and development. Two important consequences of faster growth are that initial inequalities between individuals may diverge at a faster rate and that individuals will begin to compete with their neighbors sooner.

IV-5. Reproductive output under elevated temperature and CO₂

The advanced flowering time due to increasing temperature would also contribute to the reproductive output. High temperatures can greatly damage specific growth stages, particularly flowering and fertilization. For example, in rice (Yosida, 1981; Allen *et al.*, 1995; Horie *et al.*, 1995), very brief (≤ 1 h) exposures to high temperatures ($> 35^{\circ}\text{C}$) at anthesis can cause sterility. Wheat is similarly affected (Mitchell *et al.*, 1993; Wheeler *et al.*, 1996). Elevated temperature leads to loss of pollen viability in maize (Decker *et al.*, 1986), and reversal of vernalization in wheat (Evans., 1975). The mean temperature during the flowering time of the *E. crus-galli* and *S. viridis* populations was almost the same among the experimental plots, or it was lower in the temperature- elevated

plots. The high-temperature-induced injury in reproductive activity for mainly grass species would be circumvented by shifting the flowering time. Accordingly, the reproductive index (reproductive part dry weight/final total dry weight; e.g. harvest index in agronomy) of the C4 grass under the current weather conditions would be sustained (e.g. the *S. viridis* populations) or increased (e.g. the *E. crus-galli* populations) in a global warming environment (cf. Table 3). The reproductive index of the *E. crus-galli* populations in the CT4 plot was significantly increased by 23.5% compared with the Control plot. While the final total dry weight of the *E. crus-galli* population in the CT4 was significantly low compared with the Control plot, the total seed dry weight showed no significant difference (Table 4). Therefore, the simultaneous increases in temperature and CO₂ would have very little effect on the dry-matter production and the reproductive output of C4 species.

For the *C. album* populations, the mean temperature during flowering time did not show a great difference among the plots, except for the T4 plot, in which the mean temperature was slightly higher than in the other experimental plots. In the T4 plot, the reproductive index of the *C. album* population was significantly higher than that in the Control plot. Therefore, the flowering of the *C. album* population under optimum temperatures will be ensured by the advanced flowering phenology. However, the *C. album* population in the T4 plot showed a high reproductive index; the total seed dry weight did not increase because the total final dry matter was low. By contrast, the *C. album* population grown in the CT4 plot increased in the total seed dry weight by 2.1 times compared with the Control plot. The seed productivity of the *C. album* populations increased by 15.9% and 114.4% in the CT2 and CT4 plots, respectively, as compared to the

Control plot. This output resulted from a significant increase in the total dry weight due to elevated CO₂. Thus, at elevated CO₂, the reproductive output of C3 species would be greatly enhanced. C3 species in a warmer climate than occurs presently would have a competitive advantage over C4 species.

IV-6. Responses at the levels of the individual and population of C3 plant to elevated CO₂

In an experiment on an individual level, Garbutt *et al.* (1990) found that the *C. album* showed no significant effect in terms of total biomass in response to elevated CO₂ (500 and 700 ppm). Also, Hunt *et al.* (1991) showed that the total dry weight of the *C. album* in solitary conditions was not stimulated by CO₂ enrichments of 500, 650 and 800 ppm. Unlike the studies cited above, this study found that the dry matter production of the *C. album* population was greatly enhanced by elevated CO₂. Total final dry weight per ground area of the *C. album* population was enhanced by 23.2% and 97.5% to CO₂ enrichments of about 560 and 720 ppm, respectively. Total final dry weight per ground area of the two C4 plant populations also increased 20.8% for the *E. crus-galli* population and 18.2% for the *S. viridis* population to the elevated CO₂ of 560 and 720 ppm, respectively. One explanation would be that there might be a higher effect of CO₂ upon growth at the level of population than at the individual level. Supporting this argument, Morse and Bazzaz (1994) reported that the individual weights of *Abutilon theophrasti* (C3) at the population level were significantly increased by elevated CO₂ of 700 ppm. Yoder *et al.* (2000) reported

similar findings for C3 annual and perennial plants. Plants of *Achnatherum hymenoids* (C3 perennial) and *Bromus madritensis* spp. *Rubus* (C3 annual) had a larger response to CO₂ enrichment of 1000 ppm, 40 and 19%, respectively.

Plants growing in competitive arrays shade themselves and each other and create gradients of decreasing light availability from the top to the bottom of canopy. As the *LAI* increases, light transmittance in the stand decreases. These changes are known to have variable effects on different plant species, depending on their position in the community. Under the conditions of elevated CO₂, it has often been hypothesized that the *LAI*s would increase (e.g., Nijs *et al.*, 1989; Eamus and Jarvis, 1989). One reason that this could occur is through an increased production and retention of leaves in the understory that are disposed of in deep shade. Greater leaf retention under very low photon flux densities (PPFD) and elevated CO₂ could result from improved leaf carbon balance (Pearcy and Björkman, 1983) afforded by the CO₂-induced reductions in the light compensation point and by increases in the quantum use efficiency (e.g. Ehleringer and Bjorkmann, 1977). Similarly, an increase in the *LAI* and *NAR* of the *C. album*, *E. crus-galli*, and *S. viridis* populations in response to an elevated CO₂ condition is attributed to the enhanced dry matter production.

Species of the same community differed in their response to CO₂, and these differences may help explain the outcome of competitive interactions among these species above ambient CO₂ levels. Hogan *et al.* (1991) reviewed the results of the only three experiments to be concerned with individually grown (i.e. potted) tropical plants, and then speculated on the potential responses which might occur at the levels of the plant population, community, and ecosystem. These studies by Oberbauer *et al.* (1985), Reekie and Bazzaz

(1989), and Ziska *et al.* (1991) have shown that a variety of species from the moist tropics respond both physiologically and in terms of growth to elevated atmospheric CO₂. However, the results from these studies are far from consistent. The responses of six C₃, one C₄, and two CAM species observed by Ziska *et al.* (1991) were the most consistent with results typically reported for a wide range of agricultural plants and other temperate species growing under ample nutrient supply (cf. Strain and Cure, 1985). Oberbauer *et al.* (1985) reported a substantial increase in biomass accumulation under elevated CO₂ in seedlings of both species tested, but actually measured decreases in leaf-level photosynthesis. Reekie and Bazzaz (1989) observed no CO₂ effect on the biomass or photosynthesis of individually grown plants but did measure decreases in stomatal conductance.

Hogan *et al.* (1991) and Ziska *et al.* (1991) attributed the discrepancies among these studies to the negative effects of pot size on sink strength and the limited potential to respond to elevated CO₂ (Ziska *et al.* used relatively large pots, whereas Oberbauer *et al.* (1985) and Reekie and Bazzaz (1989) used relatively small pots) (cf. Thomas and Strain, 1991). Bernison *et al.* (1993) refuted this claim by showing that the effects of small pot size can be eliminated by increasing nutrient additions. Certainly both pot size and the actual amount of nutrients available to the plant can affect plant growth. Furthermore, all three of these experiments were conducted under unnaturally high nutrient conditions indicating that the species responses to elevated CO₂ observed may be quite untypical. Undoubtedly, the interpretation of potted individuals' CO₂ responses is confounded by extremes in pot size and the relatively large additions of fertilizer. Ground area, substrate depth, and average volume of substrate available per

individual plant were in some cases of different orders of magnitude. Planting density was also lower (6.6-11.6 versus 400 individuals per square meter), as was the amount of nutrients supplied/available in the Arnone and Körner experiments.