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The Interactive Effects of Atmospheric Carbon Dioxide and Light on Stem Elongation in Seedlings of Four Species

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Four species, *Sinapis alba* L., *Medicago sativa* L., *Gypsophila paniculata* L. and *Picea abies* (L.) Karsten, were grown in three light regimes: darkness, low light (25 μmol m^{-2} s^{-1} for 10 min d^{-1}) and high light (120 μmol m^{-2} s^{-1} for 12 h d^{-1}) and four levels of carbon dioxide: 0, 350, 700 and 1400 ± 50 μl l^{-1}. Germination was not affected by any of the treatments. The effects of carbon dioxide on stem elongation were identical in low and high light: stem length increased at a decreasing rate with level of carbon dioxide in all species. Level of carbon dioxide also affected stem elongation in complete darkness, but the pattern was more complex and varied among species. Total weight did not vary with level of carbon dioxide to any significant extent in either darkness or low light, but increased with level of carbon dioxide at high light in all four species. Due to the absence of any effect of carbon dioxide on growth in darkness and low light, we suggest the effects of carbon dioxide on stem elongation are independent of effects on growth and may be due to a direct interaction with developmental processes. In contrast, level of carbon dioxide had little effect on allocation patterns in the dark and low light experiments, but had marked effects in high light. Therefore, the effect of carbon dioxide on allocation was probably due to the effects of carbon dioxide on growth rather than to any direct interaction between carbon dioxide and development. An understanding of the mechanisms by which carbon dioxide affects development may help us understand the often variable effects of carbon dioxide upon plants.

Key words: *Sinapis alba* L., *Medicago sativa* L., *Gypsophila paniculata* L. and *Picea abies* (L.) Karsten, elevated carbon dioxide, stem elongation, germination, allocation, phytochrome.

INTRODUCTION

Evidence from a large number of sources shows that the concentration of atmospheric carbon dioxide is steadily rising (Boden *et al*., 1994). The increasing levels are a result of an increase in global consumption of fossil fuels and land clearing practices. With increasing levels of carbon dioxide comes an enhancement in plant growth, though the degree of enhancement may vary widely depending upon species and environmental conditions (Bazzaz, 1990; Hunt *et al*., 1991; Bazzaz and Fajer, 1992; Poorter, 1993). This growth enhancement is generally thought to be a direct consequence of the effect of carbon dioxide on photosynthesis and stomatal conductance. Plants with the C_3 photosynthetic pathway often show marked increases in photosynthesis as carbon dioxide levels rise above ambient due to a decrease in photorespiration and increased carboxylation. Generally there is a decline in stomatal conductance with an increase in carbon dioxide concentration in both C_3 and C_4 plants (Pearcy and Bjorkman, 1983; Tolbert and Zelitch, 1983; Woodward, 1987; Mott, 1988; Bazzaz, 1990). This decline decreases transpiration per unit leaf area and increases instantaneous water use efficiency. It may also improve plant water status, and lower season-long water consumption leading to higher carbon gain and biomass accumulation (Rogers, Thomas and Bingham, 1983; Reekie and Bazzaz, 1989; Bazzaz, 1990). It has also been shown that elevated carbon dioxide can directly inhibit respiration (Gifford, Lambers and Morrison, 1985; Bunce, 1990; El-Kohen, Pontailler and Mousseau, 1991) and that the decrease in respiration can lead to enhanced growth, at least in the short term (Bunce, 1995).

Elevated carbon dioxide also has very significant effects on developmental patterns. Growth at high carbon dioxide changes stomatal density (Woodward, 1987), allocation patterns (Tolley and Strain, 1985; Luxmoore *et al*., 1986; Larigauderie, Hilbert and Oechel, 1988), specific leaf area (Garbutt, Williams and Bazzaz, 1990), branching patterns (Strain and Cure, 1985; Eamus and Jarvis, 1989; Bazzaz, 1990; Reekie, Hicklenton and Reekie, 1997), stem elongation (Reekie *et al*., 1997), leaf shape (Thomas and Bazzaz, 1996), phenology (Garbutt and Bazzaz, 1984), internal leaf anatomy (Madsen, 1968) and germination (Heichel and Jaynes, 1974; St. Omer and Horvath, 1983; Ziska and Bunce, 1993). These developmental effects, although often very marked, are not necessarily simple. In a study which examined the effect of elevated carbon dioxide on time of flowering in a group of forbs from an annual grassland (Reekie and Bazzaz, 1991), elevated carbon dioxide delayed, hastened or had no effect on time to flowering depending on species and environmental conditions. It is generally assumed that the effects of carbon dioxide on development are an indirect consequence of its effects on photosynthesis and stomatal conductance and therefore growth (Reekie, 1995). However in this study, differences among treatments in the effects of carbon dioxide

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on development were not correlated with the effect of carbon dioxide on plant size. This raises the question of how carbon dioxide affects developmental patterns, if not through growth?

One possible answer is provided by studies of the effects of carbon dioxide on flowering. Under short-day conditions, extremely high levels of carbon dioxide (10 000–50 000 μl l^{-1}) delayed or inhibited flowering in the short-day plants, *Pharbitus nil* and *Xanthium pennsylvanicum* and induced flowering in the normally long-day *Silene armeria* (Purohit and Tregunna, 1974). Hicklenton and Jolliffe (1980) confirmed these results. It seems that extremely high levels of carbon dioxide reverse the photoperiodic response, changing long-day plants into short-day plants and *vice versa*. More recently, it has been shown that lower levels of elevated carbon dioxide (1000 μl l^{-1}) similar to those predicted for the end of the next century, also appear to interact with daylength response. Elevated carbon dioxide uniformly hastened flowering in four long-day species and delayed flowering in four short-day species grown under identical experimental conditions except for daylength (Reekie, Hicklenton and Reekie, 1994). It has been suggested that the effects of carbon dioxide on flowering may be related to an interaction between carbon dioxide and phytochrome, the pigment responsible for sensing light in the photoperiodic response (Purohit and Tregunna, 1974; Hicklenton and Jolliffe, 1980; Reekie *et al*., 1994).

If elevated carbon dioxide interferes with the effects of phytochrome, it may affect other developmental processes besides flowering known to be controlled by phytochrome such as germination, stem elongation, branching patterns and leaf development (Morgan and Smith, 1981). As discussed above, elevated carbon dioxide is indeed known to affect many of these processes. Therefore effects of carbon dioxide on development may be related to a direct effect on phytochrome rather than an indirect effect mediated through the effect of carbon dioxide upon growth. The objective of this study was to determine if carbon dioxide could affect development in the absence of light and therefore the absence of any effect on photosynthesis and carbon gain. Plants were grown at four levels of carbon dioxide in either darkness or one of two levels of light availability. The low light treatment provided enough light to induce a phytochrome response but not enough to result in any significant photosynthesis, while the high light treatment provided enough light for photosynthesis and growth to occur. We examined the effect of these treatments on time of germination, stem elongation, allocation patterns and overall growth. To increase the scope of inference for the study, we examined these responses in four species of plants (*Picea abies* (L.) Karsten, *Sinapis alba* L., *Medicago sativa* L. and *Gypsophila paniculata* L.). These species were chosen on the basis of seed availability, and because they represent four very distinct taxa: Pinaceae, Brassicacea, Fabaceae and the Caryophyllacea.

MATERIALS AND METHODS

Experimental design and plant culture

Three different experiments were conducted with *Sinapis*, *Medicago* and *Gypsophila*: (1) complete darkness; (2) low light (25 μmol m^{-2} s^{-1}) for a period of 10 min each day; and (3) high light (120 μmol m^{-2} s^{-1}) for 12 h d^{-1}. In the low and high light experiments, a combination of cool white fluorescent and incandescent bulbs were used to supply light with a red/far red ratio of 1·8. Light levels were measured with a Li-Cor model LI-189 quantum sensor and red/far red ratio with a Skye SKR 100/110 sensor. In each experiment there were 20 fumigation chambers, five at each of four carbon dioxide levels (0, 350, 700 or 1400 μl l^{-1} carbon dioxide). All three experiments were conducted twice, randomly reassigning treatments to chambers each time. The low and high light experiments were also conducted once using *Picea*. All four species were grown from seed in 50 ml vials containing 0·6 % agar. To ensure the surface of the agar did not become dry over the course of the experiment, holes were drilled in the bottom of the vials and one end of a wick placed in the agar. The vials with the protruding wicks were placed in a reservoir of distilled water that was replenished as necessary. Ten seeds per vial were evenly spaced upon the agar surface. In the experiments involving *Sinapis*, *Medicago* and *Gypsophila*, there was one vial per species in each of the 20 fumigation chambers. Thus each fumigation chamber contained ten seeds of each species. In the *Picea* experiments, all three vials per fumigation chamber contained *Picea* and thus there were a total of 30 *Picea* seedlings per chamber. The *Sinapis*, *Medicago* and *Gypsophila* experiments lasted 6 d and the *Picea* experiments ran for 13 d.

Carbon dioxide fumigation system

A flow-through fumigation system was used to expose seedlings to the desired carbon dioxide concentrations ($\pm$ 50 μl l^{-1}). The fumigation chambers (0·75 l) consisted of an 11 cm length of a 10 cm diameter PVC pipe with an opaque cap on one end and a removable transparent plexiglass cover on the other. On one side of the fumigation chamber was a 0·5 cm diameter inlet tube and on the opposite side a 0·7 cm diameter outlet tube. The outlet tube was connected to a 30 cm length of 0·9 cm diameter Tygon tubing to minimize back diffusion into the chamber. The inlet tube of each fumigation chamber was connected to the humidified air supply system that provided a flow of 1 l min^{-1} per chamber. Air was obtained from a pressure regulated compressed air source that sampled air from outside the building at a height of $\sim$ 2 m above ground level. The 0 μl l^{-1} level was achieved by allowing the air to pass through a column of soda lime. The soda lime was changed as required to maintain the carbon dioxide level below 50 μl l^{-1}. The 350 μl l^{-1} level was unmodified ambient air. The 700 μl l^{-1} and 1400 μl l^{-1} levels were achieved by bleeding pure carbon dioxide into the atmospheric air source via needle valves. The level of carbon dioxide in the various airstreams was determined periodically using a Li-Cor model 6250 infrared gas analyser. All 20 fumigation

TABLE 1. *Percent final germination and level of significance for the effects of carbon dioxide in a one-way ANOVA*

Experiment	Species	CO_2 level ($\mu l\,l^{-1}$) 0	350	700	1400	Level of significance
Low light	*Sinapis*	89·2	92·4	93·7	89·9	NS
Low light	*Medicago*	87·5	89·4	86·4	87·7	NS
Low light	*Gypsophila*	87·8	91·2	90·5	89·3	NS
Low light	*Picea*	97·3	96·5	95·7	98·3	NS
High light	*Sinapis*	86·5	89·4	88·4	89·1	NS
High light	*Medicago*	85·4	86·7	87·2	86·4	NS
High light	*Gypsophila*	88·2	86·4	87·4	89·1	NS
High light	*Picea*	96·4	96·7	95·3	97·8	NS

Separate analyses were conducted for each species and light treatment.
** $P < 0{\cdot}01$; * $P < 0{\cdot}05$; NS, not significant.

TABLE 2. *Number of days required to reach 50% germination and level of significance for the effect of CO_2 in a one-way ANOVA*

Experiment	Species	CO_2 level ($\mu l\,l^{-1}$) 0	350	700	1400	Level of significance
Low light	*Sinapis*	2·2	2·3	2·2	2·2	NS
Low light	*Medicago*	2·7	2·7	2·7	2·7	NS
Low light	*Gypsophila*	2·5	2·5	2·4	2·6	NS
Low light	*Picea*	5·0	5·0	4·9	5·2	NS
High light	*Sinapis*	2·1	2·3	2·1	2·4	NS
High light	*Medicago*	2·4	2·4	2·4	2·4	NS
High light	*Gypsophila*	2·5	2·4	2·4	2·5	NS
High light	*Picea*	5·2	5·3	5·0	5·2	NS

Separate analyses were conducted for each species and light treatment.
** $P < 0{\cdot}01$; * $P < 0{\cdot}05$; NS, not significant.

chambers were placed in the same controlled environment chamber (Conviron model E15) which maintained a constant temperature of 20 °C.

Experimental measurements

Germination counts were made daily in the low and high light experiments. In the case of the dark experiments, final germination counts were taken on day 6. Stem height was measured at the end of the experiments. Plants were then harvested and the seedlings separated into stem, root and cotyledon. Plant material was dried for at least 48 h at 80 °C and dry mass determined.

Statistical analysis

Since germination is a binomial variate (i.e. a seed either germinates or does not), the germination data were transformed using the following equation (Sokal and Rohlf, 1969): $(P+1/n)/(1-P+1/n)$, where P is the proportion of seeds that germinated and n is the number of seeds per chamber. The transformed variable was then analysed by one-way ANOVA with carbon dioxide as the independent variable. Separate analyses were conducted for the various species and light experiments. To determine whether carbon dioxide had any effect on the time course of germination in the two light experiments, the time required to reach 50% germination was determined from linear interpolation between the two consecutive days that spanned 50% germination and analysed in a similar fashion. The mean height, weight and proportional allocation to root, stem and cotyledon were calculated for each species within each chamber. Seeds that did not germinate were not used in calculating the means. These data were then analysed by ANOVA as described above. As the proportional data were not normally distributed, they were transformed prior to analysis by taking the arcsine of the square root of the proportion (Sokal and Rohlf, 1969). In the *Sinapis*, *Medicago* and *Gypsophila* experiments, which were conducted twice, data for the two sets of experiments were first analysed separately and then pooled. There was no difference in the results regardless of how the data were analysed, so only the pooled data are presented here. Linear regression analysis was also used to describe the relationship between

TABLE 3. *The level of significance for differences among CO_2 treatments in height and weight*

Experiment	Species	Height	Total weight	Cotyledon Weight	Cotyledon Prop	Root Weight	Root Prop	Stem Weight	Stem Prop
Dark	*Medicago*	**	NS	NS	**	NS	NS	NS	NS
Dark	*Gypsophila*	**	NS	NS	NS	*	NS	*	NS
Dark	*Sinapis*	**	**	**	**	NS	**	NS	**
Low light	*Medicago*	**	NS	NS	NS	NS	NS	NS	NS
Low light	*Gypsophila*	**	NS	NS	NS	NS	NS	NS	NS
Low light	*Sinapis*	**	NS	NS	NS	NS	NS	NS	NS
Low light	*Picea*	**	NS	NS	NS	NS	NS	NS	*
High light	*Medicago*	**	**	**	**	**	**	**	**
High light	*Gypsophila*	**	*	NS	**	**	*	**	**
High light	*Sinapis*	**	**	**	**	**	**	**	**
High light	*Picea*	**	**	**	**	**	**	**	**

Separate analyses were conducted for each species and light treatment. Data for the component parts were analysed in terms of both the absolute weight and the proportion (prop) of total weight allocated to cotyledon, root and stem.
** $P < 0{\cdot}01$; * $P < 0{\cdot}05$; NS, not significant.

height and level of carbon dioxide. As the response to the 0 μl l^{-1} carbon dioxide treatment was very different from that observed at higher carbon dioxide levels, this treatment was excluded from this particular analysis. All analyses were done using SAS (Version 6·10) for a personal computer.

RESULTS

Neither final germination (Table 1) nor the time required to reach 50% germination (Table 2) was affected by carbon dioxide in any of the species or light treatments.

The level of carbon dioxide had a positive effect on plant height in both the low and high light regimes (Table 3). The effect of carbon dioxide on height was virtually identical in the two treatments (Figs 1 and 2). The greatest change in stem height was between the 0 and 350 μl l^{-1} CO_2 treatments. However, repression analyses excluding the 0 μl l^{-1} treatment found significant increases in height as the level of carbon dioxide increased from 350 to 1400 μl l^{-1} in *Sinapis*, *Gypsophila* and especially *Picea* (Table 4). The level of carbon dioxide also affected the height of plants grown in complete darkness, but the pattern of this effect was

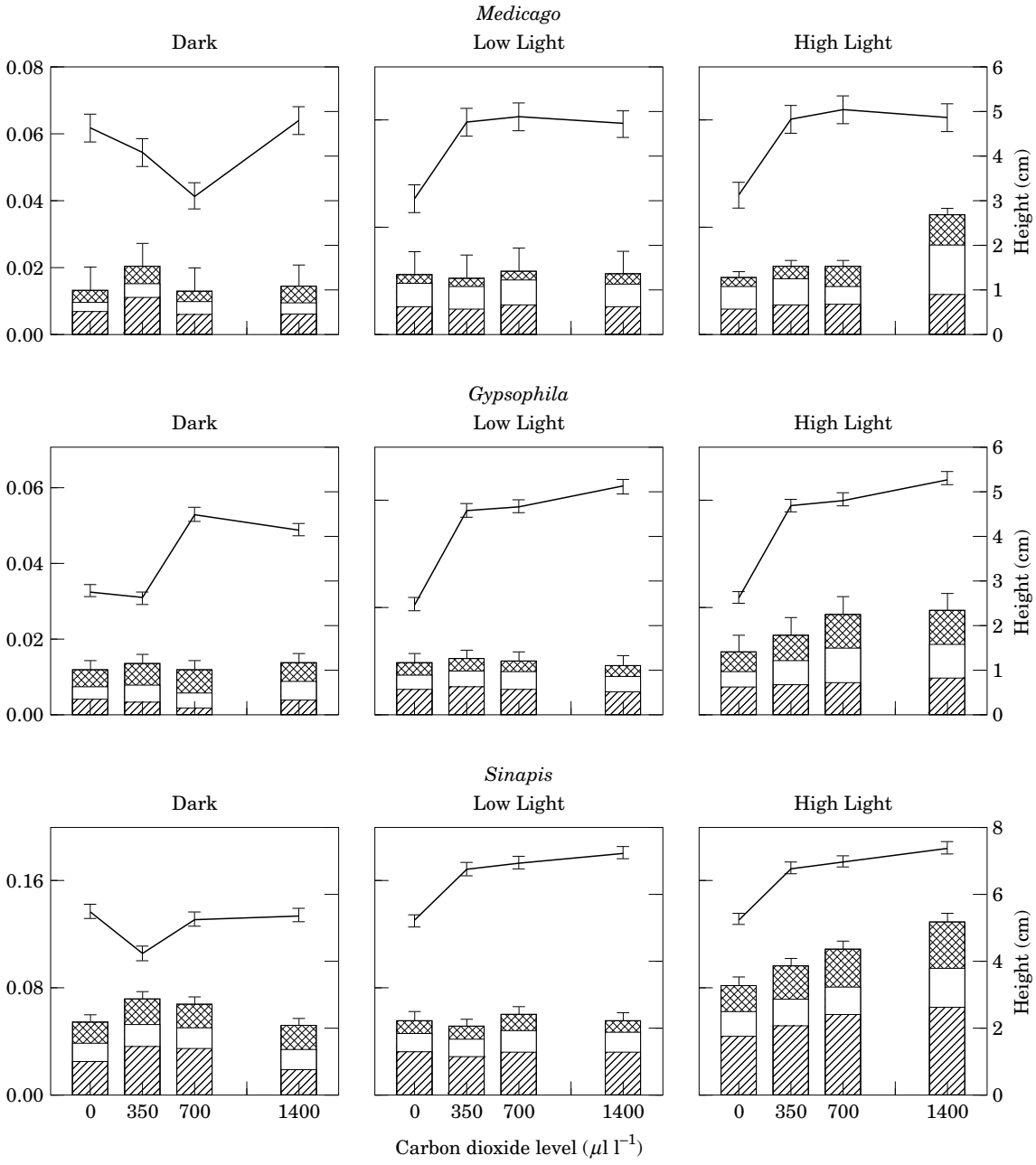

FIG. 1. Stem height (lines) and weight (bars) as affected by level of carbon dioxide in *Medicago*, *Gypsophila* and *Sinapis* grown in three different light regimes. The bars represent the weight of the root (▨), stem (□) and cotyledon (⊠). Error bars depict 2 s.e. and in the case of the bar graphs are for total weight.

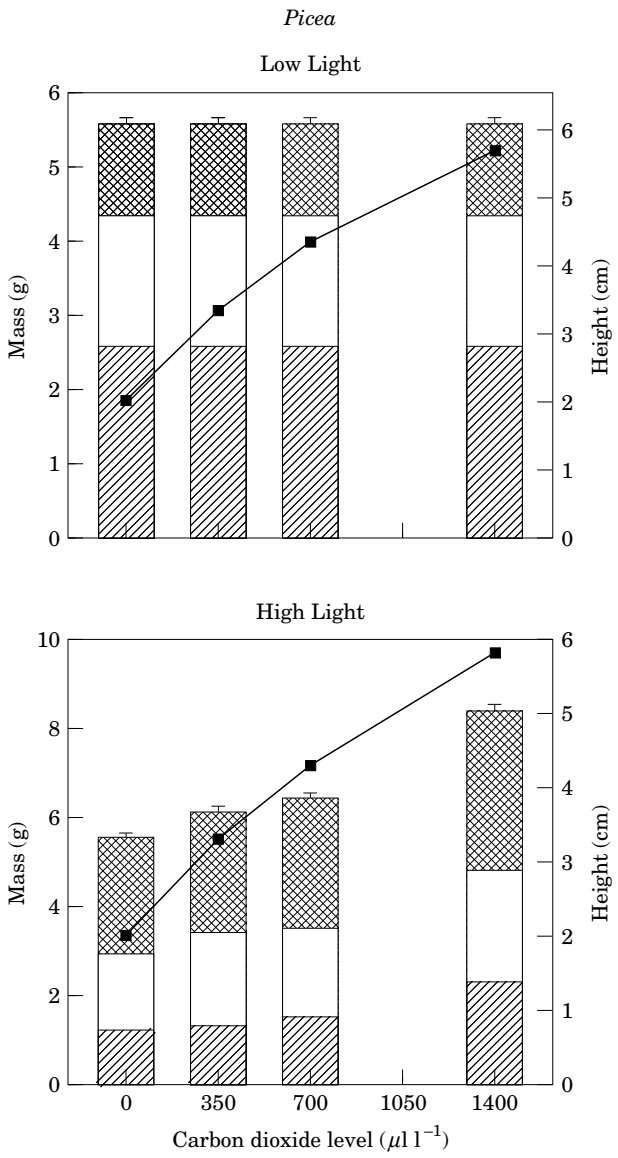

FIG. 2. Stem height (lines) and weight (bars) as affected by level of carbon dioxide in *Picea* grown in two different light regimes. The bars represent the weight of the root (▨), stem (□) and cotyledon (⊠). Error bars depict 2 s.e. and in the case of the bar graphs are for total weight.

different to that observed in the light (Fig. 1). The shortest plants were at intermediate levels of carbon dioxide: 350 μl l^{-1} for *Sinapis* and *Gypsophila* and 700 μl l^{-1} for *Medicago*.

The level of carbon dioxide had little or no effect on total weight in darkness and in the low light regime (Table 3). The only significant effect was a slight increase at intermediate carbon dioxide levels in *Sinapis* grown in complete darkness (Fig. 1). This increase in weight was largely in the roots and cotyledons; there was no significant change in the weight of the stem. In the high light regime, total dry weight increased with increasing carbon dioxide in all species. The weight of all component parts with the exception of cotyledons in *Gypsophila* also increased with carbon dioxide.

There was little effect of carbon dioxide upon allocation patterns in the dark and low light experiments (Table 3, Figs 3 and 4). The only case in which carbon dioxide had any substantial effect was for *Sinapis* grown in the dark where allocation to root, stem and cotyledon were all modified by carbon dioxide. Allocation to the root was highest, and allocation to the stem and cotyledon lowest, at intermediate levels of carbon dioxide (i.e. 350 and 700 μl l^{-1}). The only other effects of carbon dioxide in these two experiments were a slight increase in allocation to cotyledons in dark-grown *Medicago*, and a slight decrease in stem allocation in *Picea* grown in low light. In contrast to the dark and low light experiments, there were marked effects of carbon dioxide upon allocation in the high light experiments where allocation to all plant parts in all four species was modified (Table 3). The pattern of carbon dioxide effect was similar among the four species. Percent allocation to the root decreased as the level of carbon dioxide increased, while allocation to the stem and cotyledon generally increased. The only major difference among species was a decrease in stem allocation with increased carbon dioxide in *Medicago*.

DISCUSSION

Regardless of species or light treatment, the level of carbon dioxide had marked effects on plant height (Figs 1 and 2). One possible explanation for differences in height among carbon dioxide treatments is differences in time of germination, i.e. seeds which germinate late would be shorter than seeds that germinate early. This cannot explain differences in height among carbon dioxide levels in the

TABLE 4. *Results of the linear regression of height on level of carbon dioxide excluding the 0 μl l^{-1} treatment*

Experiment	Species	Intercept	Level of significance	Slope	Level of significance	R^2 (%)
Low light	*Medicago*	4·9	**	$-4{\cdot}6\times10^{-5}$	NS	0·19
Low light	*Gypsophila*	4·8	**	$5{\cdot}8\times10^{-4}$	**	67·0
Low light	*Sinapis*	6·7	**	$4{\cdot}9\times10^{-4}$	**	45·3
Low light	*Picea*	2·7	**	$2{\cdot}2\times10^{-3}$	**	69·1
High light	*Medicago*	5·0	**	$3{\cdot}6\times10^{-5}$	NS	0·10
High light	*Gypsophila*	4·9	**	$6{\cdot}4\times10^{-4}$	**	70·0
High light	*Sinapis*	6·7	**	$5{\cdot}7\times10^{-4}$	**	58·3
High light	*Picea*	2·6	**	$2{\cdot}3\times10^{-3}$	**	75·0

Separate analyses were conducted for each species and light treatment.
** $P < 0{\cdot}01$; * $P < 0{\cdot}05$; NS, not significant.

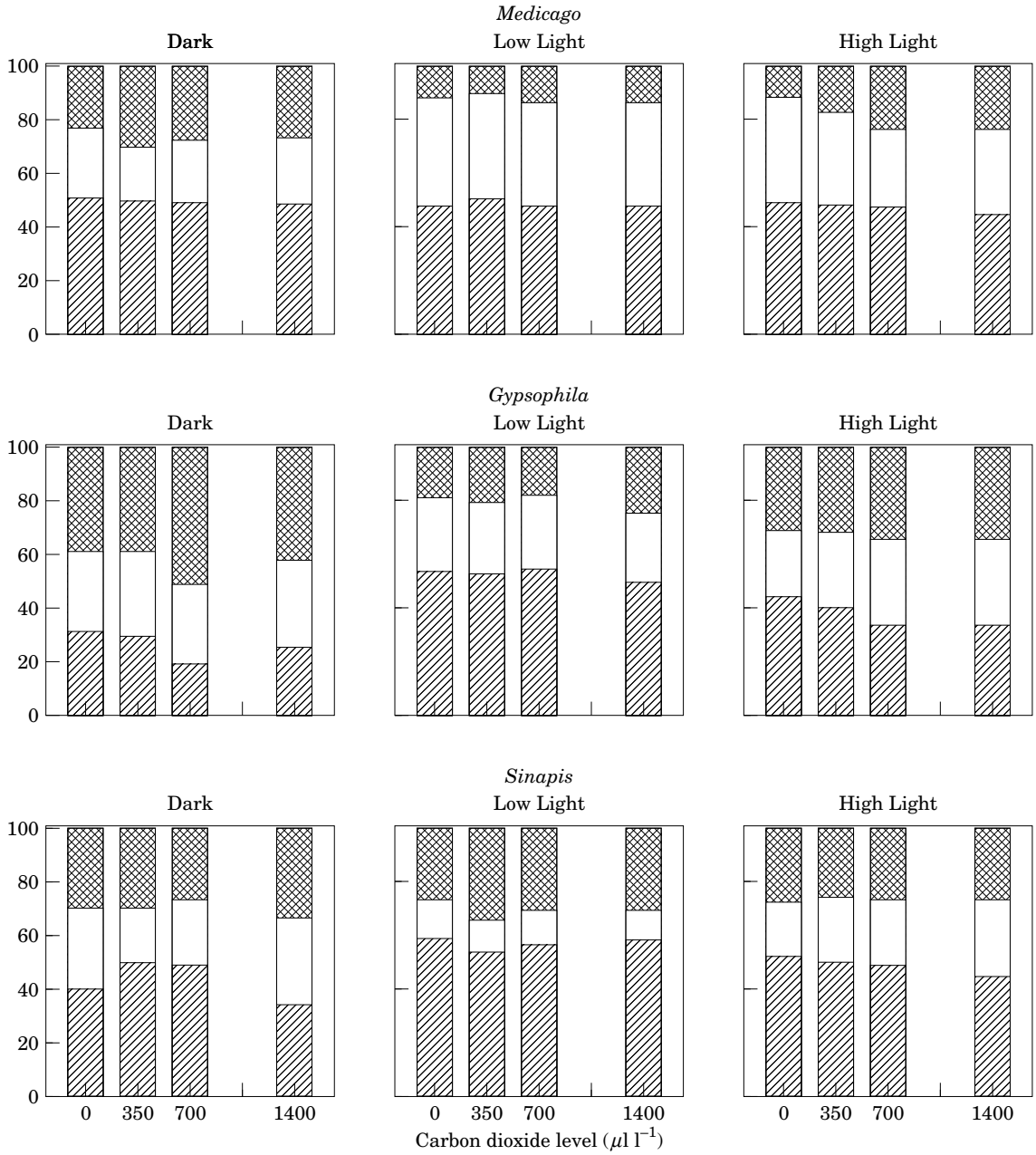

FIG. 3. Proportional allocation to root (▨), stem (□) and cotyledon (⊠) as affected by level of carbon dioxide for *Medicago*, *Gypsophila* and *Sinapis* grown in three different light regimes.

present case however, as the level of carbon dioxide had no effect on the timing of germination in any of the species (Table 2).

Elevated carbon dioxide had virtually identical effects on stem height in both the low and high light experiments (Figs 1 and 2). It may be concluded, therefore, that the increase in stem height was not dependent upon increases in growth resulting from carbon dioxide induced changes in photosynthesis, water use efficiency or respiration. Although carbon dioxide increased plant weight in the high light treatment, in the low light treatment weight was the same regardless of carbon dioxide level. The fact that carbon dioxide affected stem elongation in total darkness (Fig. 1) confirms that the carbon dioxide effect on growth is not necessarily related to its effect on development. It also demonstrates that light has an impact on the effects of carbon dioxide, aside from its role in photosynthesis, as the effect of carbon dioxide in darkness differed from that in light.

The above observations raise the question of how carbon dioxide affects stem elongation if not through effects on growth. A survey of the literature offers two possible explanations: (1) effects of carbon dioxide on ethylene synthesis; and (2) a possible interaction between carbon dioxide and phytochrome action. Although, our data do not allow us to determine conclusively the mechanism by which

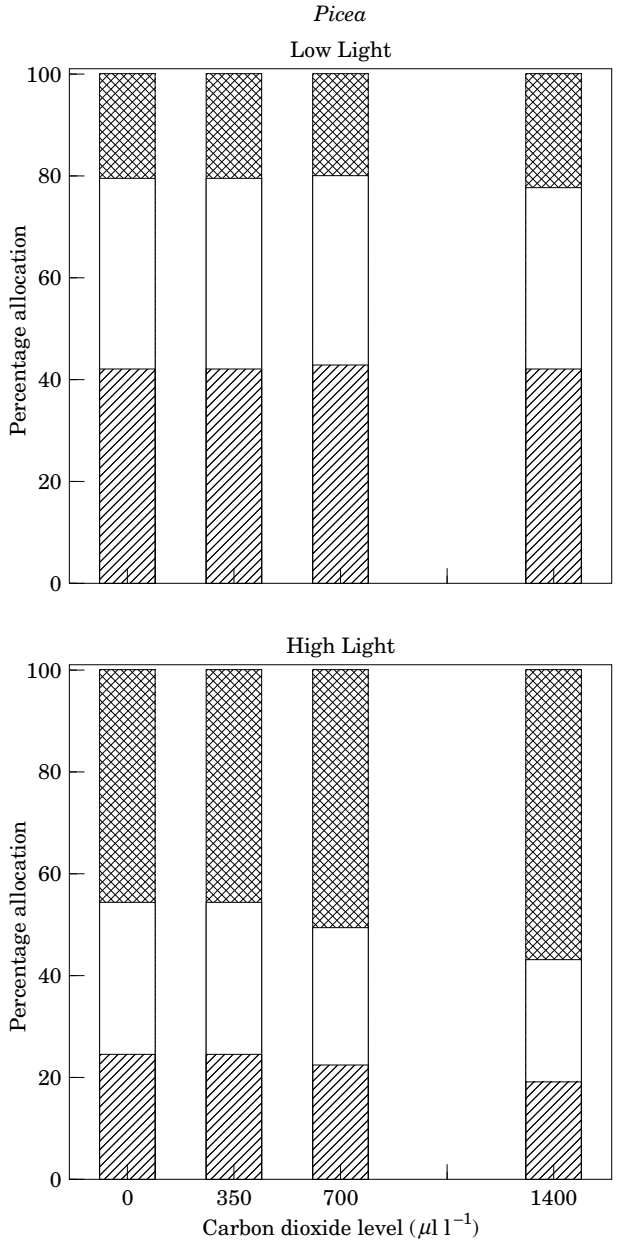

FIG. 4. Proportional allocation to root (▨), stem (□) and cotyledon (⊠) as affected by level of carbon dioxide in *Picea* grown in two different light regimes.

carbon dioxide affects stem elongation, it does provide some indication as to which of these two possibilities is more likely.

Ethylene is known to affect many developmental processes in plants including flowering, fruit ripening, senescence, seed germination and stem elongation (MacMillan, 1980). At high concentrations (50000–100000 μl l^{-1}) carbon dioxide interferes with the role of ethylene by affecting its synthesis. According to Cheverry *et al.* (1988), high levels of carbon dioxide decrease the conversion of ACC (1-aminocyclopropan-1-carboxylic acid) to ethylene by acting as a competitive inhibitor. If the levels of carbon dioxide used in our study decreased ethylene production this could explain the increased stem elongation at high carbon dioxide levels as ethylene inhibits stem elongation (Camp and Wickliff, 1981; Eisinger, 1983). Although the levels of carbon dioxide used in our study were much lower than those commonly reported to inhibit ethylene production, at least one study has shown that a doubling of ambient carbon dioxide levels can affect ethylene production in some species (Lu and Kirkham, 1992). However, it is difficult to explain how an effect of carbon dioxide on ethylene synthesis could account for the contrasting effects of carbon dioxide on stem elongation in the light *vs.* dark experiments (Figs 1 and 2). There is no *a priori* reason to suggest that the presence or absence of light would have any effect on the role of carbon dioxide as a competitive inhibitor of ACC conversion to ethylene.

As discussed earlier, studies of the effect of carbon dioxide upon flowering suggest that carbon dioxide interferes with phytochrome action (Purohit and Tregunna, 1974; Hicklenton and Jolliffe, 1980; Reekie *et al.*, 1994). In addition to controlling time of flowering by sensing daylength, phytochrome is also involved in the etiolation and de-etiolation response of seedlings. The role of phytochrome in controlling the growth of seedlings is complex and known to involve at least two types of phytochrome (Smith, 1995). When an etiolated (i.e. dark grown) seedling is first exposed to light, its extension growth is inhibited. This response is extremely sensitive to light even at very low fluence rates, but far red light at high irradiances can exert an additional inhibitory effect. The inhibition is mediated through phytochrome A which is present in large concentrations in dark-grown seedlings. This response is thought to be the system used to detect whether or not a seedling has reached the soil surface and therefore should decrease the rate of stem elongation. Phytochrome A is light labile and upon exposure to light is rapidly broken down to low steady state levels. Subsequent regulation of the de-etiolation process and stem elongation is controlled by phytochrome B. The inhibitory effect of far red radiation disappears as phytochrome A is replaced by phytochrome B. Instead, stem elongation is enhanced by far red radiation and inhibited by red radiation. This response is thought to be a shade avoidance mechanism which allows the seedling to detect whether it is in the shade of other plants (i.e. a low red: far red ratio), or in the open (i.e. a high red: far red ratio). Given these differences in the type of phytochrome and the contrasting effects of far-red light on stem elongation in dark- *vs.* light-grown seedlings, it is to be expected that the effect of carbon dioxide on stem elongation would also differ between dark- and light-grown seedlings (Fig. 1) if carbon dioxide does indeed interact with the phytochrome system. In this regard, it would be useful to compare the effect of carbon dioxide on stem elongation in the various phytochrome mutants of *Arabidopsis thaliana*; both phytochrome A (Whitelam *et al.*, 1993) and phytochrome B (Reed *et al.*, 1993) deficient mutants have been described in this species.

Although the effect of carbon dioxide on stem elongation appears to be due to a direct effect on developmental processes, this is not necessarily true of other effects of carbon dioxide on development. Allocation to cotyledon,

stem and root was not affected by carbon dioxide to any extent in the low light and dark treatments (Figs 3 and 4). However, allocation patterns did change markedly with carbon dioxide in the high light treatment. This can be attributed to the effect of carbon dioxide on photosynthesis and therefore on the availability of assimilates for allocation to various plant organs.

Ecological implications

There is a marked carbon dioxide gradient at the soil-atmosphere interface. Beneath the soil surface, carbon dioxide concentrations range between 2500–45 000 μl l^{-1} (Greenwood, 1970; Wood and Greenwood, 1971). Above the soil surface, the carbon dioxide concentration declines sharply but can still reach levels as high as 1800 μl l^{-1} within a few centimeters of the surface depending upon wind conditions, thickness of the litter layer and the surrounding plant canopy (Bazzaz and Williams, 1991). Germinating seedlings must elongate quickly to get above the soil and the layer of litter in order to photosynthesize as soon as possible. The role of light and light quality (e.g. red : far red ratio) in controlling the elongation of the stem has been well documented. Our study suggests that the level of carbon dioxide also plays an important role, with the decrease in carbon dioxide above the soil surface signalling that the seedling is above the soil and litter and that rate of stem elongation should be reduced.

Our results are also relevant to understanding how changes in atmospheric carbon dioxide may affect plant communities in the future. The effect of increases in carbon dioxide above current ambient levels on stem elongation varied tremendously among the four species examined (Table 4). The magnitude of this effect ranged from no significant increase in *Medicago* to an approximate doubling of plant height in *Picea* as carbon dioxide level increased from 350 to 1400 μl l^{-1}. This variation has significant ecological consequences. Reekie and Bazzaz (1989), found that the height at which leaves were displayed in five tropical tree species either increased or decreased with carbon dioxide depending upon the particular species and demonstrated that it caused a marked shift in community composition due to competition for light. It is clear that changes in stem elongation associated with rising atmospheric carbon dioxide concentrations have the potential to significantly alter competitive processes. Plant height is probably the single most important determinant of competitive success in many communities (Gaudet and Keddy, 1988). Therefore, it is important that we understand the mechanism by which carbon dioxide affects plant height so that we may better predict how communities may respond to increases in atmospheric carbon dioxide.

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