Effect of sink size on growth response to elevated atmospheric CO_2 within the genus *Brassica*

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Abstract: Many plants grown at elevated CO_2 concentrations exhibit enhanced photosynthetic rates. However, this increase in photosynthesis is often reduced after prolonged exposure to elevated CO_2. This reduction may be related to the capacity of plants to utilize the extra photosynthate produced at elevated CO_2. This study examined the effect of source to sink ratio on the capacity of plants to respond to elevated CO_2. Seven species or cultivars within the genus *Brassica* were germinated and grown at either 350 or 1000 ppm CO_2. Broccoli (*Brassica oleracea* L.) and cauliflower (*B. oleracea* L.) have large carbon sinks in the reproductive structures; Chinese broccoli (*Brassica campestris* L.) and marrow stem kale (*B. oleracea*) have carbon sinks in the stem; turnip (*B. campestris*) stores carbon in the root; rape (*Brassica napus* L.) and white mustard (*Brassica alba* (L.) Rabenh.) have no obvious carbon storage structures and were assumed to have a lower sink strength relative to the above cultivars. Plants were harvested at three stages of development and total plant weight, leaf area ratio, and allocation to leaf, root, and stem determined. As young seedlings, all cultivars responded positively to elevated CO_2. The long-term growth response of different cultivars to CO_2 was independent of sink location, but was dependent on sink size. Cultivars with no obvious carbon storage structures showed no significant growth enhancement by elevated CO_2 by the end of the experiment. However, neither leaf area ratio nor biomass allocation pattern were reliable predictors of response to CO_2 suggesting that assessing differences in source to sink ratio is not necessarily straightforward.

Key words: biomass allocation, sink strength, functional groups, elevated carbon dioxide, leaf area ratio.

Résumé : Plusieurs plantes montrent une augmentation des taux de photosynthèse lorsque cultivées en présence de teneurs en CO_2 élevées. Cependant, cette augmentation de la photosynthèse diminue souvent après une exposition prolongée aux CO_2 élevé. Cette réduction pourrait être reliée à la capacité des plantes d'utiliser le surplus de photosynthétats produit en présence de CO_2 élevé. Les auteurs examinent l'effet du rapport source à puit sur la capacité des plantes à réagir au CO_2 élevé. Ils ont fait germer et cultivé sept espèces ou cultivars provenant du genre *Brassica* en présence de 350 ou 1000 ppm de CO_2. Le broccoli (*Brassica oleracea* L.) et le choux-fleur (*B. oleracea* L.) ont d'importants puits de carbone dans leurs structures de reproduction. Le broccoli chinois (*Brassica campestris* L.) et le choux chinois (*B. oleracea*) ont des puits de carbone dans leurs feuilles; le navet (*B. campestris*) emmagasine le carbone dans sa racine; le colza (*Brassica napus* L.) et la moutarde blanche (*Brassica alba* L.) Rabenh.) n'ont pas de structures évidentes pouvant servir de puit de carbone et les auteurs ont assumé qu'ils ont un puit moins important que les cultivars pré-mentionnés. Ils ont récolté les plantes à trois stades du développement et ils ont déterminé le poids total du plant, le rapport de la surface foliaire ainsi que l'allocation à la feuille, à la racine et à la tige. À l'état de plantules, tous les cultivars réagissent positivement au CO_2 élevé. La réaction de croissance à long terme des différents cultivars au CO_2 élevé est indépendante de la localisation du puit, mais dépend de la dimension du puit. Les cultivars sans structures évidentes pour l'accumulation de carbone ne montrent aucune augmentation significative de croissance sous l'influence de CO_2 élevé vers la fin de l'expérience. Cependant, ni le rapport de surface foliaire, ni le patron d'allocation de la biomasse ne constituent des éléments de prédiction de la réaction au CO_2, ce qui suggère que l'évaluation des différences des rapports sources aux puits n'est pas nécessairement simple.

Mots clés : allocation de la biomasse, importance du puit, groupes fonctionnels, bioxyde de carbone élevé, rapport de la surface foliaire.

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Introduction

Because of the current rise in atmospheric CO_2, there has been a great deal of interest in the effect of elevated CO_2 on plant communities (see references cited in Bazzaz 1990). These studies have shown that when grown as individuals without competition, most species respond favorably to elevated CO_2 though the magnitude of this response varies significantly. When grown in competition, the overall biomass of the community may still increase, but the growth of some individual

species may be reduced, substantially altering community composition. Although a number of factors are probably involved (Reekie 1996), simple differences in the magnitude of the CO_2 effect on individual growth may explain these community shifts (Bolker et al. 1995). Those species that respond more favorably to elevated CO_2 as individuals out compete and reduce the growth of those species whose growth may be only marginally enhanced by CO_2. Therefore, the first step in trying to understand how changes in atmospheric CO_2 will modify community composition is to be able to predict how elevated CO_2 will affect the growth of individual species when grown without competition. However, due to the large number of species found in most natural communities, experimentally determining the effect of CO_2 on each species is logistically impossible. Some have tried to overcome this obstacle by classifying species into categories on the basis of their photosynthetic pathway, growth strategy, developmental patterns, mechanism of sugar transport, etc., and then examining the CO_2-induced differences in growth among these functional groups (e.g., Hunt et al. 1991; Korner et al. 1995; Poorter et al. 1996). Providing the chosen classification scheme explains most of the variation among species in response to CO_2, this approach may allow us to predict how communities will change without detailed knowledge of the response of individual species to elevated CO_2.

One method of classifying plants into functional groups is on the basis of source to sink ratio. Species can differ widely in their capacity to photosynthesize relative to their capacity to utilize the fixed carbon in growth. This is reflected in differences in leaf area ratio, root:shoot ratio and allocation to reproductive or storage structures. Studies that artificially manipulate the size of the carbon source relative to the size of the carbon sink by removing leaves or developing fruits (Clough et al. 1981; Peet 1984) find that plants with a low source to sink ratio respond more positively to elevated CO_2. Presumably, plants with a high source to sink ratio exhibit either direct or indirect feedback inhibition that prevents photosynthesis from responding to elevated CO_2 to the same extent as in plants with a lower source to sink ratio (Arp 1991).

Manipulative studies with single species clearly suggest that source to sink ratio affects response to elevated CO_2. However, this does not necessarily mean that differences in source to sink ratio among species can explain differences in the extent of their response to CO_2. In manipulative studies, wounding effects are confounded with differences in source to sink ratio. This is not the case when one compares innate differences in source to sink ratio among species. Review studies that compare the response of a variety of species to elevated CO_2 offer an alternative means of addressing this question that avoids the problem of wounding effects. This approach presents its own difficulties however, in that differences in source to sink ratio are confounded with differences in environmental conditions among studies and with other differences among species that are unrelated to source to sink ratio. Nevertheless, a review of the published literature does indicate that species with large carbon storage sinks (e.g., potatoes and sugar beets) respond more positively to elevated CO_2 than species lacking well developed carbon storage organs (Cure and Acock 1986).

The present study examines the response to elevated CO_2 of seven cultivars or species within the genus *Brassica*: broccoli (*B. oleracea* L.), cauliflower (*B. oleracea*), marrow stem kale (*B. oleracea*), Chinese broccoli (*B. campestris* L.), turnip (*B. campestris*), rape (*B. napus* L.) and white mustard (*B. alba* L.). These cultivars or species are the end result of selection by crop breeders for different allocation patterns, and differ markedly in both the size and location of their carbon sinks. Broccoli and cauliflower have large carbon sinks in the reproductive structures; Chinese broccoli and marrow stem kale have carbon sinks in the stem; turnip stores carbon in the root; rape and white mustard on the other hand, lack well developed carbon storage organs. Assuming that the presence of carbon storage organs is indicative a low source to sink ratio, this group of cultivars allows us to address the hypothesis that innate differences in source to sink ratio among plants influences their response to elevated CO_2. This study avoids the potential problems associated with artificial manipulation of source to sink ratio by surgery and minimizes differences among plants being compared that are not associated with differences in source to sink ratio (i.e., the plants are all closely related and grown within a common environment). Further, this study allows us to address the question of whether location of the sink in root, stem or reproductive structures has any influence on response to elevated CO_2.

Materials and methods

All plants were grown from seed in 15-cm pots (2 L) containing one part perlite to four parts ASB grower mix (Greenworld Ltd., Waterloo, Ont.). Plants were watered daily and fertilized weekly with 15:15:18 general purpose fertilizer (Plant Products Co. Ltd., Brampton, Ont.) containing 200 $\mu L \cdot L^{-1}$ nitrogen, 200 $\mu L \cdot L^{-1}$ P_2O_5, and 240 $\mu L \cdot L^{-1}$ K_2O. The experiments were conducted in four controlled-environment growth cabinets (model GR-36, Enconaire Systems Ltd., Winnipeg, Man.) maintained at either 350 or 1000 $\mu L \cdot L^{-1}$ CO_2 (i.e., two cabinets at each CO_2 level). Carbon dioxide was injected into the growth cabinets from a liquid source and its concentration monitored by an infrared gas analyzer (Nova Model 421P, Hamilton, Ont.) by drawing a 45-s air sample from each growth cabinet on a 180-s cycle (Lander Control Systems Inc., Orangeville, Ont.). Plants were exposed to their assigned CO_2 level continuously throughout the entire experiment. All plants received a photosynthetic photon flux (PPF) of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (400–700 nm) supplied by a mixture of cool-white fluorescent and incandescent lamps (62.5 and 37.5% input wattage, respectively) for a 16 h light : 8 h dark photoperiod. To minimize PPF variability within the growth cabinets, the area within 20 cm of the growth cabinet wall was not used. Plants with their respective CO_2 treatments were switched between growth cabinets on a weekly basis. At the same time, position of plants within cabinets was rearranged. Day and night air temperatures within the growth cabinets were 20 and 15°C, respectively.

For all cultivars except Chinese broccoli there were 36 plants at each of the two CO_2 levels (i.e., 18 in each cabinet) for a total of 72 plants per cultivar. Because of poor germination, there were only 48 plants in the case of Chinese broccoli. The size of the growth cabinets (3.3 m^2) allowed the plants to be spaced such that at no time were the canopies of adjacent plants overlapping ensuring similar levels of light availability over the course of the experiment. To assess the time course of their response to CO_2, plants were harvested at three points in their development (two in the case of Chinese broccoli) with 12 plants per harvest for each cultivar and CO_2 level. For marrow stem kale, turnip, rape, and mustard, plants were harvested 16, 30, and 43 days after planting. Chinese broccoli was only harvested on days 16 and 43. By the final harvest, all of these cultivars had developed their characteristic growth habits: marrow stem kale and Chinese broccoli had enlarged stems: turnip, an enlarged storage root; and rape and mustard had more or less balanced allocation patterns with

Fig. 1. Total weight of broccoli (B), cauliflower (C), Chinese broccoli (CB), marrow stem kale (MK), turnip (T), rape (R), and white mustard (WM) grown at either 330 μL·L^{-1} (open bars) or 1000 μL·L^{-1} CO$_2$ (solid bars). Plants were harvested at three different developmental stages. Error bars are 1 SE. The level of significance for the difference between CO$_2$ levels is given separately for each cultivar. Cultivars with the same letter above the bars are not different from each other at the 0.05 level of significance.
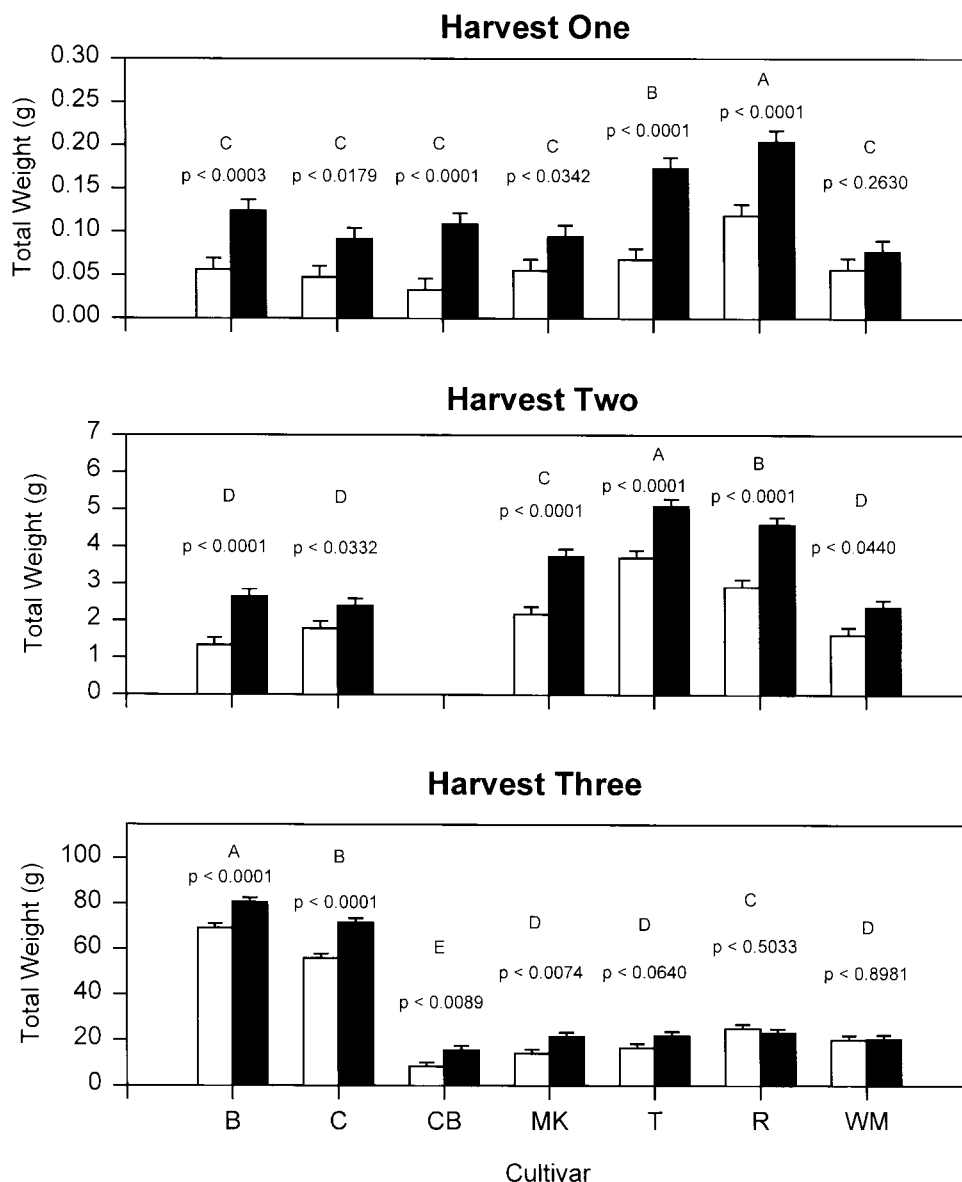

roughly equal amounts allocated to root, leaf, and stem. White mustard was the only species that had initiated flowering by day 43. In the case of broccoli and cauliflower, the first two harvests were on days 16 and 30, but the third harvest was delayed to day 83 to allow these cultivars sufficient time to flower and develop significant reproductive sinks. At the final harvest, plants were divided into roots, leaves, and stem. Because of the difficulty of objectively separating stems from reproductive structures in broccoli and cauliflower, reproductive structures were included with the stems. Plant material was dried at 60°C for more than 48 h prior to weighing. Total plant leaf area was measured by means of a leaf area meter (LI-COR model 3100, Lincoln, Neb.) and leaf area ratio (leaf area per unit total dry weight) calculated.

Total dry weight and leaf area ratio data were analyzed by two-way factorial analysis of variance. The two independent variables were cultivar and level of CO$_2$. Preliminary analyses included growth cabinet as a blocking factor, but as there was no significant effect of cabinet within CO$_2$ level, this term was pooled with the error term to test treatment effects (Carmer et al. 1969). Separate analyses were conducted for each harvest. A priori paired comparisons were used to compare the two levels of CO$_2$ for each cultivar and Student–Newman–Keuls multiple comparison procedure was used to compare all possible combinations of the various cultivars. The allocation data for all cultivars except turnip were analysed by multivariate analysis of variance. The dependent variables were proportional allocation to roots, leaves and stem (plus reproductive structures) and the independent variables were cultivar and CO$_2$. Turnip was excluded from this analysis because it was acaulescent and did not allocate any biomass to stems. A separate one-way analysis of variance was used to determine the effect of CO$_2$ upon allocation in this cultivar.

Fig. 2. Biomass allocation to root (solid bars), leaf (open bars), and stem plus reproductive structures (shaded bars) in broccoli (B), cauliflower (C), Chinese broccoli (CB), marrow stem kale (MK), turnip (T), rape (R), and white mustard (WM) grown at either 330 $\mu L \cdot L^{-1}$ (ambient) or 1000 $\mu L \cdot L^{-1}$ (elevated) CO_2. Cultivars with the same letter above the bars are not different from each other at the 0.05 level of significance.
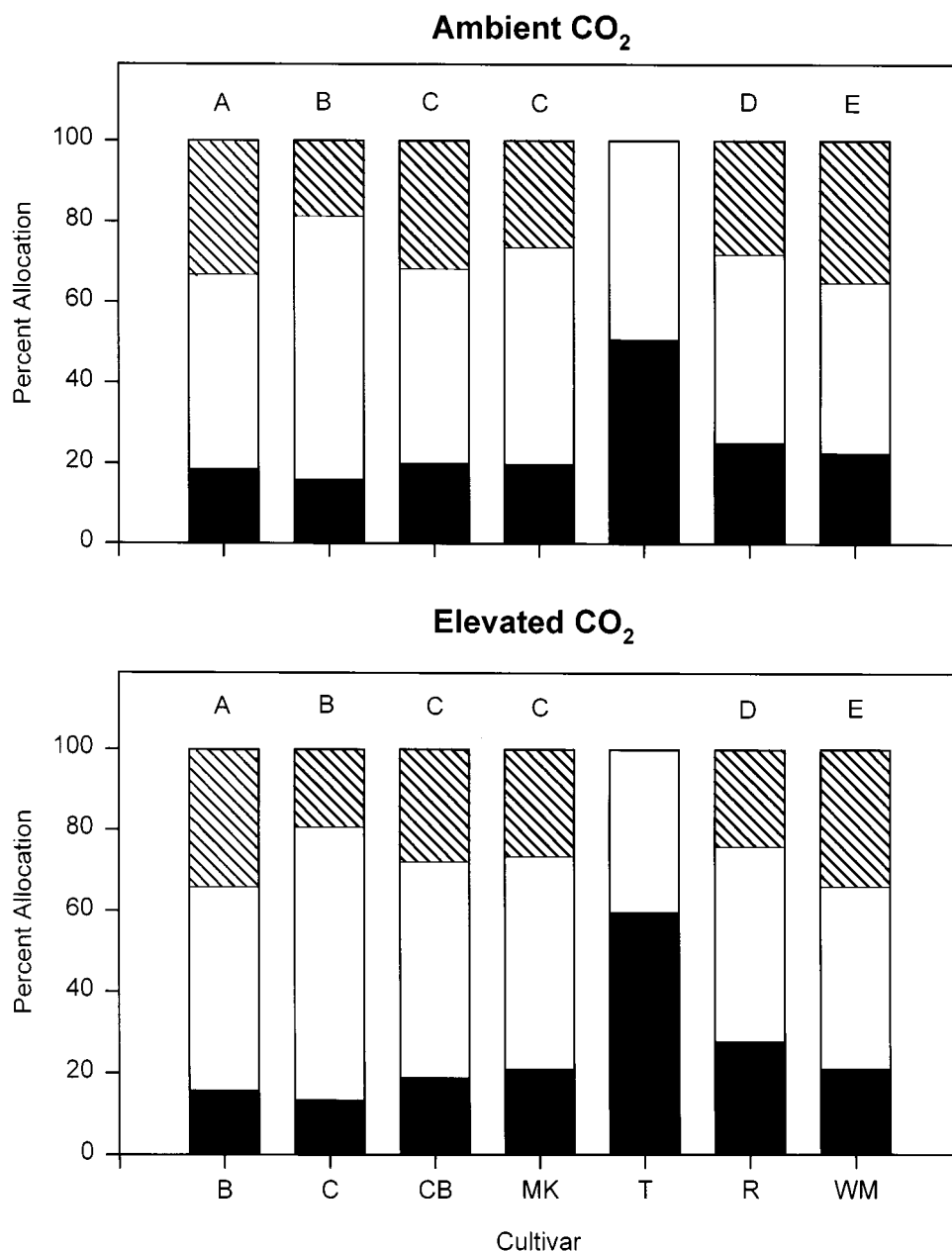

Results

Total weight

There were marked differences in total weight among species at all three harvests ($p < 0.0001$; Fig. 1). Generally similar patterns were observed at harvests one and two. Rape and turnip were the largest plants, with rape being larger than turnip at harvest one and turnip larger at harvest two. There were no differences among the remaining species at harvest one while at harvest two, marrow stem kale was larger than the remaining species. At harvest three, broccoli and to a lesser extent cauliflower, were substantially larger than the other species, but this difference was an artifact resulting from the fact

that these two species were harvested later than the others. Among the species harvested on day 43, differences among species were roughly similar to those observed at the earlier harvests. Rape was the largest, Chinese broccoli was the smallest and the remaining species were intermediate in size.

In general, elevated CO_2 increased growth ($p < 0.0001$ for the main effect of CO_2 at all three harvests; Fig. 1), but there was variation among species in this response ($p < 0.05$ for the $CO_2 \times$ species interaction at all three harvests). At harvest one, the CO_2 enhancement ratios (i.e., weight of plants at elevated CO_2 divided by weight at ambient CO_2) for the seven species were: broccoli (2.2), cauliflower (1.8), Chinese broccoli (3.1), marrow stem kale (1.5), turnip (2.6), rape (1.6), and white

Fig. 3. Leaf area ratio of broccoli (B), cauliflower (C), Chinese broccoli (CB), marrow stem kale (MK), turnip (T), rape (R), and white mustard (WM) grown at either 330 $\mu L \cdot L^{-1}$ (open bars) or 1000 $\mu L \cdot L^{-1}$ CO_2 (solid bars). Plants were harvested at three different developmental stages. Error bars are 1 SE. The level of significance for the difference between CO_2 levels is given separately for each cultivar. Cultivars with the same letter above the bars are not different from each other at the 0.05 level of significance.
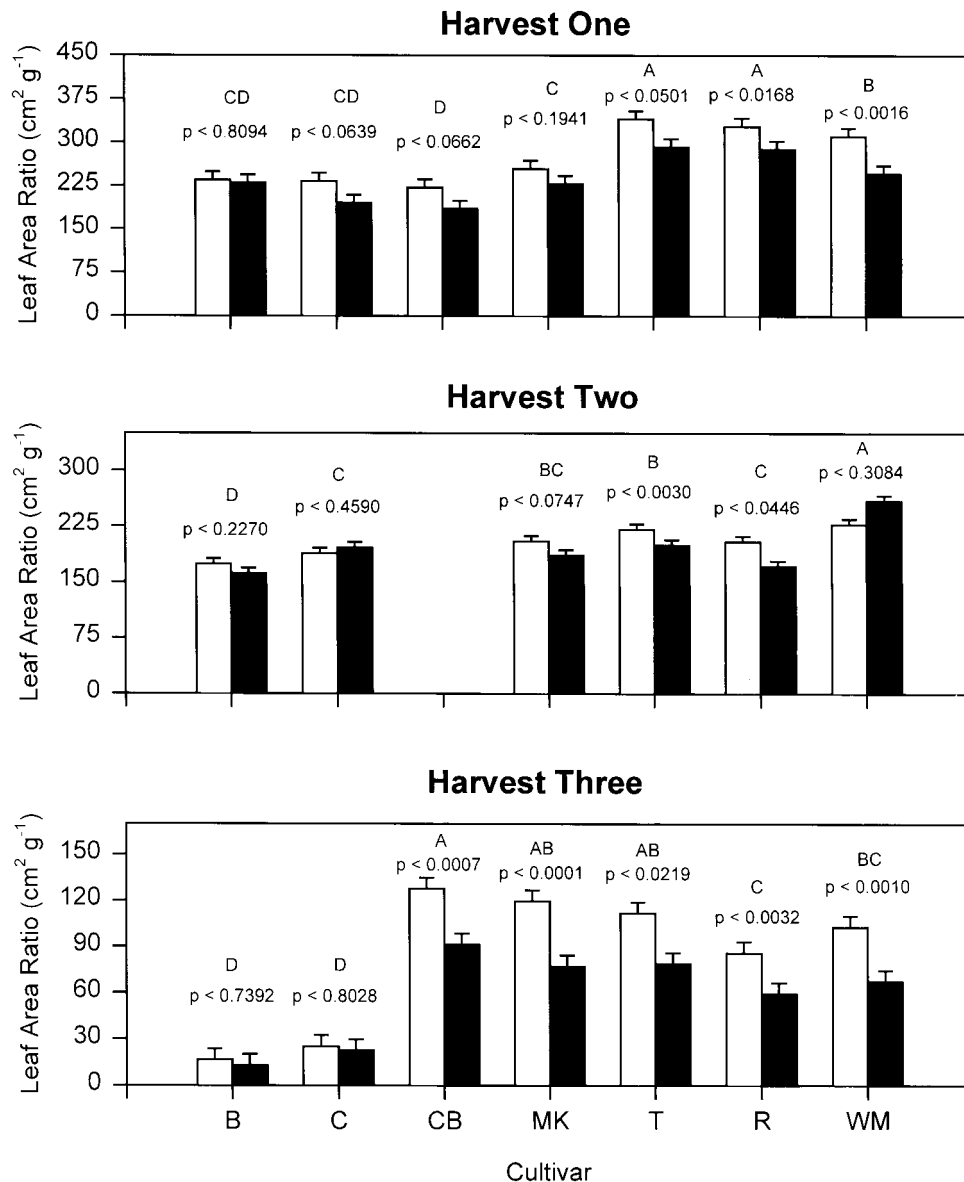
mustard (1.4). White mustard, the species with the lowest ratio, in fact, showed no significant increase in growth with elevated CO_2. At harvest two, CO_2 enhanced growth in all species, but the magnitude of this effect was relatively small in the case of white mustard and cauliflower, both of which had an enhancement ratio of 1.3. The enhancement ratios of the remaining species were: broccoli (2.3), marrow stem kale (1.8), turnip (1.3), and rape (1.6). At harvest three, neither white mustard (1.0) nor rape (1.0) showed any significant enhancement of growth with elevated CO_2, and there was only a marginally significant increase in growth for turnip (1.3). The enhancement ratios for the remaining species were: broccoli (1.2), cauliflower (1.3), Chinese broccoli (1.7), and marrow stem kale (1.4).

Allocation to root, stem, and leaves

There were marked differences among species in their allocation patterns ($p < 0.0001$ for the main effect of species in a MANOVA). Rape and white mustard allocated roughly equal proportions of biomass to root, leaf and stem (Fig. 2). White mustard was different from rape however, in that it allocated slightly more to stem and reproductive tissues. Turnip produced no stem at all and allocated over half of its biomass to root tissue. Chinese broccoli and marrow stem kale had virtually identical allocation patterns and were similar to rape except less was allocated to roots and more to leaves. Of all the species, cauliflower had the largest allocation to leaves and the least to root and stem. Broccoli, like white mustard, allocated a relatively large proportion of its biomass to stem and repro-

ductive tissue, but it had a low root allocation relative to white mustard.

Level of CO_2 had no effect on allocation patterns in broccoli, cauliflower, Chinese broccoli, marrow stem kale, rape, or white mustard ($p < 0.6498$ for the main effect of CO_2 and $p < 0.1371$ for the $CO_2 \times$ species interaction in a MANOVA). Level of CO_2 did affect allocation in turnip however, increasing allocation to root (Fig. 2, $p < 0.0048$).

Leaf area ratio

There were marked differences among species in LAR at all three harvests ($p < 0.0001$ for the main effect of species). At harvest one, turnip and rape had the highest LAR followed by white mustard, then marrow stem kale, cauliflower, broccoli, and finally Chinese broccoli. At harvest two, white mustard had the highest value followed by turnip and marrow stem kale, then rape, cauliflower, and finally broccoli. At the final harvest, Chinese broccoli, marrow stem kale, and turnip had a relatively high LAR; white mustard and rape had intermediate values; and broccoli and cauliflower had the lowest values.

Elevated CO_2 tended to decrease LAR ($p < 0.05$ for the main effect of CO_2 at all three harvests), but there were differences among species in the extent of this effect (Fig. 3). In the case of broccoli and cauliflower, the effect was never significant at the 0.05 level, in Chinese broccoli and marrow stem kale there was little effect until the final harvest, while the most pronounced effects were observed in turnip, rape and to a lesser extent, white mustard.

Discussion

Source to sink ratio clearly has an impact on the response of plants to elevated CO_2. Plants with obvious carbon storage structures responded positively to CO_2 throughout the experiment, whereas rape and white mustard, which lack well developed carbon storage structures, did not (Fig. 1). This was most apparent at the final harvest where all plants except rape and white mustard displayed at least a marginally significant increase in growth at elevated CO_2. It should be noted however, that rape and to lesser extent white mustard, did respond positively to elevated CO_2 early in the experiment. Decreases in response to CO_2 with plant age have been reported in many other species (Wulf and Strain 1982; Jolliffe and Ehret 1985; Bazzaz et al. 1989). This decrease is correlated with a number of changes in physiology, morphology, and anatomy including: decreases in stomatal density (Woodward 1987), formation of large starch granules in the chloroplasts (Madsen 1968; Cove et al. 1981; Wulf and Strain 1982), decreased rubisco activity (Downton et al. 1980), increases in leaf thickness due to the formation of additional mesophyll cell layers (Thomas and Harvey 1983) and decreased leaf area ratio (Bazzaz et al. 1989). All of these changes and perhaps others may contribute to the long term decrease in response to elevated CO_2. The present study suggests maintenance of a low source to sink ratio minimizes such effects, allowing plants to continue to respond to elevated CO_2 even when mature.

It has been suggested that pot size limitation and the consequences this has for resource availability may contribute to the decrease in response of plants to elevated CO_2 over time (e.g., Arp 1991, but see also McConnaughay et al. 1993). However, it is unlikely that differences among cultivars in the ex-

tent to which pot size may have limited growth could account for the present results. One would expect that pot size would be most limiting for the largest plants and least limiting for the smallest. In reality, the two cultivars with the weakest response to elevated CO_2 by the end of the experiment (i.e., rape and white mustard) were intermediate in size (Fig. 1, harvest 3). Cultivars that were both larger and smaller than rape and white mustard were more responsive to CO_2.

Given that source to sink ratio is important in determining the responsiveness of plants to elevated CO_2, it would be useful to have an objective measure of source to sink ratio in order to classify plants into response categories. This would be preferable to subjectively grouping plants into categories on the basis of whether or not they have obvious carbon storage structures. Biomass allocation to photosynthetic versus non-photosynthetic tissues and leaf area ratio (leaf area per unit total plant weight) are two potential measures of source to sink ratio. Our data, however, suggest that neither of these measures adequately reflect differences in source to sink ratio within the genus *Brassica*.

Biomass allocation to photosynthetic versus non-photosynthetic structures suggest that cauliflower should have poorest response to CO_2 since it has the highest leaf allocation and turnip, with its low leaf allocation, should have the best response (Fig. 2). Rape and white mustard were in fact intermediate between these two extremes. Furthermore, the allocation patterns of rape and white mustard were not particularly distinct from those of the other cultivars. Broccoli and white mustard, for example, were probably more similar in terms of allocation patterns than rape and white mustard. Thus, biomass allocation by itself is not a good indicator of source to sink ratio.

Rape and white mustard do tend to have a high LAR, but at each of the three harvests, there are other species with a LAR as high as those of rape and white mustard (Fig. 3). Since these other species display obvious carbon sinks, it is apparent that high LAR by itself does not always mean a high source to sink ratio. Further, at harvest one, rape had a higher LAR than white mustard but responded to CO_2 while white mustard did not. Also, LAR in general was high in all species early in the experiment and declined over time while response to CO_2 decreased rather than increased.

One reason why LAR and biomass allocation may not be good measures of sink strength are differences in respiratory rates among tissues. For example, the stem of rape or white mustard is primarily composed of structural material that has a low respiratory cost for maintenance (Penning de Vries 1975). Other species such as marrow stem kale and Chinese broccoli also allocate a large proportion of their biomass to stems, but the stems in this case are used for carbohydrate storage. The carbohydrates are stored in metabolically active cells that have a higher maintenance cost (Penning de Vries 1975), and consequently a higher respiration rate. A true measure of source to sink ratio would not only take into consideration the relative sizes of photosynthetic versus non-photosynthetic organs, but also their metabolic activity.

Differences in rates of respiration may help explain why response to CO_2 declines over time (Fig. 1). The proportion of structural tissue will increase as plants mature so even though LAR may decline with age, the respiratory demand of the tissue will also decline and it is possible that the source to sink ratio may actually increase. In this regard, it may also be

necessary to consider the possible effects of CO_2 on respiration. Although various effects have been reported, long-term exposure to elevated CO_2 often depresses respiration rate (e.g., Ziska and Bunce 1993; Callaway et al. 1994; Wang et al. 1995). This would tend to decrease sink demand and therefore, response to elevated CO_2. Finally, it should be noted that any sink, and particularly the relatively small sinks of plants that lack specialized storage organs, will eventually mature and stop importing carbon. This will also tend to increase the source to sink ratio over time.

Although the presence of obvious carbon sinks has an influence on response to elevated CO_2, it is clearly not the only important factor. It can not for example, explain why white mustard and rape differ in their response early in the experiment, nor why turnip is not as responsive as Chinese broccoli and marrow stem kale (Fig. 1). Further work will be necessary to obtain better measures of source to sink ratio and elucidate the other factors responsible for controlling response to CO_2 before we can accurately assign species to functional groups that differ in their response to elevated CO_2.

Acknowledgements

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