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Root to shoot ratio of crops as influenced by CO_2

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Abstract

Crops of tomorrow are likely to grow under higher levels of atmospheric CO_2. Fundamental crop growth processes will be affected and chief among these is carbon allocation. The root to shoot ratio (R:S, defined as dry weight of root biomass divided by dry weight of shoot biomass) depends upon the partitioning of photosynthate which may be influenced by environmental stimuli. Exposure of plant canopies to high CO_2 concentration often stimulates the growth of both shoot and root, but the question remains whether elevated atmospheric CO_2 concentration will affect roots and shoots of crop plants proportionally. Since elevated CO_2 can induce changes in plant structure and function, there may be differences in allocation between root and shoot, at least under some conditions. The effect of elevated atmospheric CO_2 on carbon allocation has yet to be fully elucidated, especially in the context of changing resource availability. Herein we review root to shoot allocation as affected by increased concentrations of atmospheric CO_2 and provide recommendations for further research. Review of the available literature shows substantial variation in R:S response for crop plants. In many cases (59.5%) R:S increased, in a very few (3.0%) remained unchanged, and in others (37.5%) decreased. The explanation for these differences probably resides in crop type, resource supply, and other experimental factors. Efforts to understand allocation under CO_2 enrichment will add substantially to the global change response data base.

Abbreviations: R:S – root to shoot ratio, dry weight basis

Introduction

Carbon allocation in plants is regulated by source-sink relationships which are balanced by conditions both internal and external to the plant. As dynamic functions within plants modulate inputs from the environment, the various plant organs receive photosynthetically derived products according to their various demands and the availability of these products. The plant must integrate incoming stimuli from both above and below the ground in order to optimize its functions either to survive if there are resource limitations, or to flourish if there are not. Madore and Lucas (1995) briefly summarize allocation processes by stating, "Plant productivity is determined by a complex series of events leading from CO_2 fixation in the chloroplasts, formation of phloem-mobile and storage metabolites, and delivery of these to sink tissues. We are only just beginning to understand the extent of these complexities." This statement is particularly relevant to potential shifts in plant carbon balance due to increasing levels of CO_2 in the atmosphere.

Our world of fossil power and hunger for land is forcing up the concentration of CO_2 in the atmosphere. Not only is the entire atmosphere affected, but so is the first molecular step that carries CO_2 back into the biosphere. This change in photosynthetic reaction is magnified in a ripple effect across fundamental plant processes. Carbon dioxide enhances some processes and attenuates others. Water and nutrient use efficiency, growth and development, response to stress, and plant

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productivity can all be affected (Bowes, 1993; Wittwer, 1995). Carbon allocation determines plant health and yield under virtually all conditions and plays a pivotal role in the CO_2 response. In a recent review, Stulen and den Hertog (1993) conclude the assumption that a larger proportion of the extra dry matter produced under CO_2 enrichment is allocated to roots needs critical reexamination, which has been echoed by other researchers (Norby, 1994; Rogers et al., 1994). It has been further suggested that any reconsideration of R:S should include thought about why the parameter is of interest (Norby, 1994). In this review, we attempt to outline the importance of alterations in carbon allocation and then critically examine the extant data on the response of root to shoot allocation to changing atmospheric CO_2 for agronomic crops.

Allocation in crops

Carbon allocation is of critical importance to all plants and it has been suggested that differences in carbon allocation leads to the wide diversity of flora that inhabit Earth's biomes (Schulze, 1983). For crop plants, genetic improvement of yield has come mainly through selection for better carbon partitioning and it appears to be the most promising path for continued crop increases (Daie, 1985).

Plant growth is essentially the accretion of carbon metabolites (Farrar, 1992). The fundamental value of R:S shifts, for plant growth and survival, lies in resource acquisition. It has been suggested that source leaf and root tissue must increase in a coordinated way, even if the ability of each unit of tissue to acquire resources changes, in order for plants to sustain growth (Farrar and Gunn, 1996). However, coordinated growth does not necessarily imply equal partitioning of carbon among plant tissues. Sink-source relationships within a plant control partitioning so that, in general, the partitioning of more carbon assimilate to the plant part with the greatest need for sorptive capacity helps ensure survival, i.e. the enlargement of the interface through which the limited resource must pass is favored. Storage allows demands to be met even when source products are attenuated. This carbon balance hypothesis dictates that plants maintain the ability to unequally alter, while still maintaining homeostasis, carbon partitioning in response to changing environmental conditions.

The allocation of photosynthetically derived materials between roots and shoots depends on plant species, environmental conditions, and plant phenology (Klepper, 1991). It is generally known that R:S usually responds to deficits in light (Boote, 1976), water (Kramer and Boyer, 1995), and major mineral nutrients (Cakmak et al., 1994; Gutschick, 1993) with the R:S response to a given factor usually diverting dry weight to the plant part that is the most limiting to growth under prevailing environmental conditions (Wilson, 1988). However, the effects of elevated atmospheric CO_2 on R:S are much less clear and have only recently begun to receive pronounced attention.

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A major consequence of increased atmospheric CO_2 is an increased rate of photosynthesis and, thus, increased concentration of soluble and storage carbohydrates (Farrar and Gunn, 1996). Uncertainty remains with regard to partitioning of these carbohydrates among various plant tissues. It has been suggested, since there is no reason to assume that shoots will increase or decrease more than roots, that the unaltered allometry of growth seen in high CO_2 concentration is readily explainable (Farrar and Gunn, 1996). However, unaltered allometry is not readily apparent from the CO_2 literature and there are several reasons (given improvement in water (Rogers et al., 1983) and/or nutrient (Cure et al., 1988a, b) use efficiency) why shoot and root growth might increase unequally under high CO_2, particularly when interacting with other environmental variables.

Raising the concentration of atmospheric CO_2 often results in dramatic increases in root growth. Root dry weight has been found to increase under elevated atmospheric CO_2 in most investigations regardless of species or study conditions (see Rogers et al., 1994). In many instances roots exhibit the greatest relative dry weight gain among plant organs under high CO_2 (Hocking and Meyer, 1991; Imai and Murata, 1976; Imai et al., 1985; Norby et al., 1992; Rogers et al., 1983). A majority of studies have also found that elevated CO_2 resulted in more and/or longer plant roots or faster root growth, possibly leading to increased penetration of the soil profile (Baker et al., 1990; Chaudhuri et al., 1990; Rogers et al., 1992a) and/or spread (Idso and Kimball, 1991). Despite consistent results with these root measures, R:S responses have been more variable.

We have identified 264 determinations of R:S response in crop species under elevated atmospher-

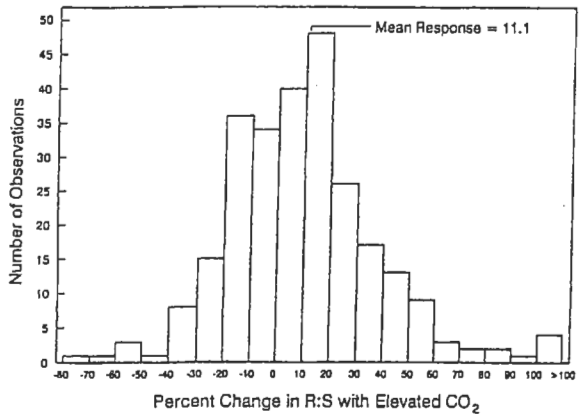

Figure 1. Frequency distribution of percent change in R:S (ambient to elevated CO_2) summarized for crop plants (n=264).

ic CO_2. The response of R:S to elevated atmospheric CO_2 is highly variable among crop species and experimental conditions (Table 1). For example, Rogers et al. (1992a) demonstrated significant increases in R:S for soybean (*Glycine max*) exposed to elevated CO_2 while R:S of cotton (*Gossypium hirsutum*) grown under field conditions appeared to be unaffected by CO_2 concentration (Prior et al., 1994). In fact, the response of R:S to increased concentrations of atmospheric CO_2 approximates a normal distribution (Shapiro-Wilk statistic, W=0.76, Pr< W=0.0001; Figure 1). Analysis of available data for crops shows that positive responses in R:S to elevated CO_2 occurred in 59.5% of 264 observations from 62 reports; negative responses occurred 37.5% and no response occurred 3.0% of the time. Further analysis demonstrated that most of these observations were clustered close to zero (75.4% occurred between ±30%) with a mean response of +11.1% (Figure 1), which is significantly greater than zero (centered signed rank statistic, S=5769, Pr>S=0.0001).

In general, this increase in R:S is in agreement with other reviews in the CO_2 literature. In a discussion on natural ecosystem responses to rising CO_2 concentration, Bazzaz (1990) points out that most studies have shown that there is generally an increase in allocation to roots especially when nutrients and water are limiting. Acock and Allen (1985), in a review of 184 crop studies, found a general increase in R:S. According to Enoch and Zieslin (1988), R:S goes up when CO_2 concentration is elevated; this was found both in crops with large storage organs (e.g. tuber crops) and in species without large storage organs (e.g. grain crops). Norby et al. (1995) using a subset of data covering 73 tree species (Wullschleger et al., 1995) reported a 6% increase in R:S as the mean response of log-transformed data. Although there appears to be a fairly consistent trend for R:S to increase (albeit small) under conditions of elevated CO_2, exceptions have been observed (Table 1). Variability in R:S among plant responses may be the result of differences in measurement of R:S, plant species and developmental age, and other experimental conditions (e.g. CO_2 exposure system and concentration, nutrients, water, light, temperature, pot size, soil medium, and duration of study).

Stulen and den Hertog (1993) caution that results must be interpreted with care as uncertainty in the measurement of R:S may arise for several reasons: the morphological boundary between root and shoot in a given plant can be unclear and thus cause experimental error; the retrieval of roots from soil in extrication procedures may not be complete; and root materials may be washed or leached away in preparation for measurement. Such procedures are notoriously costly, labor intensive, and time consuming, so better methodology is often sought. The existence of other belowground carbon sinks besides root systems may be another possible source of experimental error (Milchunas et al., 1985). In wheat (*Triticum aestivum*), for example, three or four times as much carbon is translocated below ground as is recoverable as roots per se due to rhizodeposition, i.e. exudation and sloughing (Gifford, 1986). Root growth and turnover may be increased under elevated CO_2 (Pregitzer et al., 1995) and so root mortality (Gifford, 1979) and respiratory losses (Wardlaw, 1980) must so be considered.

Some variation in R:S encountered in CO_2 response experiments can likely be attributed to crop species, so generalizations regarding R:S response to increasing CO_2 for an individual plant species should be avoided. However, summarizing data by crop type affords slightly more flexibility in making generalizations or extrapolations from existing data. Patterson and Flint (1980) found that R:S increased for C_3 plant species, but that R:S for C_4 plants tended to be unaffected by atmospheric CO_2 concentration. This conclusion is not supported from our summary of R:S data by crop type (Table 2) which shows large amounts of variability in R:S regardless of photosynthetic pathway. As was expected, the relative (ambient to elevated CO_2) change in R:S for root and tuber crops (which have large sinks) was rarely negative and showed an overall increase with increasing CO_2 (Table 2). With the exception of fruit crops, the remaining crop types showed large ranges in relative change in R:S, with

Table 1a. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Abelmoschus	Phy	350	450	-2.3		Sionit et al. (1981c)
esculentus	Phy	350	675	-7.3		"
	Phy	350	1000	+15.7		"
Asparagus	GC	330	1650	-15.2	Light=80	Laforge et al. (1991)
officinalis	GC	330	1650	-15.6	Light=125	"
	GC	330	1650	+51.5	Light=250	"
	GC	330	3000	-15.2	Light=80	"
	GC	330	3000	-8.2	Light=125	"
	GC	330	3000	+43.8	Light=250	"
Beta	GC	300	1000	0.0		Ford and Thorne (1967)[b]
vulgaris	GC	300	3300	0.0		"
	GC	300	1000	+46.2	Light=3.7 cal dm^{-2} min^{-1}	"
	GC	300	1000	+52.0	Light=7.7 cal dm^{-2} min^{-1}	"
	GC	300	3300	+31.6	Light=3.7 cal dm^{-2} min^{-1}	"
	GC	300	3300	+38.9	Light=7.7 cal dm^{-2} min^{-1}	"
	Phy	350	675	+25.9	Light=600 μE m^{-2} s^{-1}	Sionit et al. (1982)[c]
	Phy	350	675	+78.6	Light=1200 μE m^{-2} s^{-1}	"
	GC	300	1000	+31.5		Wyse (1980)
Brassica napus	Phy	340	680	+21.9		Morison and Gifford (1984)[b]
Brassica	GC	300	1000	+15.9		Ford and Thorne (1967)
oleracea	GC	300	3300	+15.9		"
Brassica	GC	300	900	+40.0	H_2O=25% of used	Sritharan and Lenz (1990)
oleracea	GC	300	900	+24.1	H_2O=50% of used	"
var. *gongylodes*	GC	300	900	-11.0	H_2O=100% of used	"
Citrus paradisi × *Poncirus trifoliata*	SPAR	330	660	-7.3		Koch et al. (1983)[c]
Citrus sinensis	GC	395	795	-9.0		Downton et al. (1987)
× *P. trifoliata*	SPAR	330	660	-24.5		Koch et al. (1983)[c]
	SPAR	330	660	+3.2		Koch et al. (1987)
	SPAR	330	990	+15.5		"
Cucumis	GC	345	1300	+7.4	Not grafted	Ito (1972)[b]
sativus	GC	345	1300	-12.9	Grafted	"
	Phy	350	1000	-10.9	Day 0-16: 1st true leaf	Peet (1986)
	Phy	350	1000	+46.5	Day 16-36: vegetative	"
	Phy	350	1000	-1.3	Day 36-43: flowering	"
	Phy	350	1000	+3.0	Day 43-60: fruiting	"
Daucus carota var. *sativus*	OTC	340	640	+36.0		Idso et al. (1988)

Table 1b. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Echinochloa	GH	320	640	-35.2	N=2; Light=500	Wong and Osmond (1991)[c]
frumentacea	GH	320	640	-52.5	N=2; Light=2000	"
	GH	320	640	-70.9	N=12; Light = 500	"
	GH	320	640	-28.7	N=12; Light=2000	"
Fragaria	GH	330	900	+12.5		Desjardins et al. (1987)[b]
× *ananassa*	GH	330	1500	+4.2		"
Glycine	SPAR	330	450	+16.7		Allen et al. (1988)
max	SPAR	330	600	+15.9		"
	SPAR	330	800	+9.7		"
	SPAR	330	660	+19.0		Allen et al. (1991)[b]
	SPAR	330	990	+3.5		"
	Phy	350	1000	0.0	Continuous CO_2	Clough and Peet (1981)
	Phy	350	1000	+4.3	2 day alternating exposure	"
	Phy	350	1000	-4.3	4 day alternating exposure	"
	Phy	350	1000	+8.7	6 day alternating exposure	"
	Phy	350	700	+27.9	N=0.5	Cure et al. (1988a)[c]
	Phy	350	700	-9.0	N=1.0	"
	Phy	350	700	-4.2	N=2.5	"
	Phy	350	700	+32.5	N=5.0	"
	Phy	350	700	-5.2	N=10.0	"
	Phy	350	700	-13.8	P=0.005 m*M* KH_2PO_4	Cure et al. (1988b)[c]
	Phy	350	700	+10.7	P=0.100	"
	Phy	350	700	+22.6	P=0.250	"
	Phy	350	700	+13.5	P=0.500	"
	Phy	350	700	+11.8	P=1.000	"
	GC	350	1000	-23.2		Finn and Brun (1982)[b]
	OTC	340	640	0.0		Idso et al. (1988)
	GC	350	600	+15.4		Patterson and Flint (1980)
	GC	350	1000	+15.4		"
	OTC	340	520	+29.4		Rogers et al. (1983)
	OTC	340	718	+17.7		"
	OTC	340	910	+41.2		"
	Phy	350	700	+30.4		Rogers et al. (1992a)
	Phy	350	675	-20.0	Light=600 $\mu E\ m^{-2}\ s^{-1}$	Sionit et al. (1982)[c]
	Phy	350	675	-10.7	Light=1200 $\mu E\ m^{-2}\ s^{-1}$	"
	Phy	350	675	-6.2	Temperature=18/12	Sionit et al. (1987)[b,c]
	Phy	350	675	+17.4	Temperature=22/16	"
	Phy	350	675	-14.3	Temperature=26/20	"
	Phy	350	1000	-27.2	Temperature=18/12	"
	Phy	350	1000	+6.5	Temperature=22/16	"
	Phy	350	1000	-23.8	Temperature=26/20	"
	Phy	400	650	-0.6		Vessey et al. (1990)[b]
	Phy	400	900	-13.5		"

Table 1c. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Gossypium hirsutum	Phy	340	680	+25.7		Morison and Gifford (1984)[b]
	OTC	340	640	0.0		Idso et al. (1988)
	FACE	360	550	+13.4	1988, Yazoo City, MS	Rogers et al. (1992b)
	FACE	360	550	+47.4	1989, Maricopa, AZ	"
	GH	320	640	-20.9	N=0.6	Wong (1990)[c]
	GH	320	640	-32.5	N=4.0	"
	GH	320	640	-49.1	N=12.0	"
	GH	320	640	-28.7	N=24.0	"
Helianthus annuus	Phy	340	680	-12.5	Temperature=19/14	Morison and Gifford (1984)[b]
	Phy	340	680	-8.0	Temperature=28/23	"
	Phy	340	680	-12.1	Temperature=30/24	"
Hordeum vulgare	GC	300	1000	+11.1		Ford and Thorne (1967)[b]
	GC	300	3300	+39.4		"
	GC	300	1000	+2.1	Light=3.7 cal dm^{-2} min^{-1}	"
	GC	300	1000	+18.2	Light=7.7 cal dm^{-2} min^{-1}	"
	GC	300	3300	+18.1	Light=3.7 cal dm^{-2} min^{-1}	"
	GC	300	3300	+51.0	Light=7.7 cal dm^{-2} min^{-1}	"
	Phy	340	680	-17.4		Morison and Gifford (1984)[b]
Ipomoea batatas	Phy	350	675	+18.2	Roots only	Bhattacharya et al. (1985)[b]
	Phy	350	675	+30.0	Roots and tubers	"
	Phy	350	1000	-9.1	Roots only	"
	Phy	350	1000	+60.0	Roots and tubers	"
	OTC	364	438	+4.4	Adequately watered	Bhattacharya et al. (1990)
	OTC	364	438	+24.4	Water stressed	"
	OTC	364	666	+33.8	Adequately watered	"
	OTC	364	666	+19.0	Water stressed	"
Lactuca sativa	GH	380	1200	-25.7	NO_x=0	Caporn (1989)
	GH	380	1200	-18.0	NO_x=0.5	"
	GH	380	1200	-17.6	NO_x=2.0	"
Lolium perenne	Phy	340	680	+7.4		Morison and Gifford (1984)[b]
Lycopersicon esculentum	GC	350	1000	+10.8		Hurd (1968)
	GC	345	1300	+1.1		Ito (1972)[b]
	Phy	350	675	-18.9	NY[d]-adequately watered	Paez et al. (1984)
	Phy	350	675	-11.5	NY-water stressed	"
	Phy	350	675	-36.6	BB-adequately watered	"
	Phy	350	675	-33.5	BB-water stressed	"
	GH	300	1000	+10.5	no root hormones	Tognoni et al. (1967)
	GH	300	1000	0.0	GA root hormones	"
	GH	300	1000	+4.0	CCC root hormones	"
	GH	300	1000	-1.2	BA root hormones	"
	GH	300	1000	-9.7	NAA root hormones	"
	GH	300	1000	+8.5		Wittwer (1966)
	GH	300	1000	+10.5		Wittwer (1970)

Table 1d. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Macroptilium atropurpureum	Phy	340	680	-38.1		Morison and Gifford (1984)[b]
Medicago sativa	GC	350	1325	+27.8	N=15; 60[e]; - Rhizobium	MacDowall (1982)
	GC	350	1325	-2.7	N=15; 125; -Rhizobium	"
	GC	350	1325	-8.3	N=15; 220; - Rhizobium	"
	GC	350	1325	+45.7	N=15; 380; - Rhizobium	"
	GC	350	1325	+87.5	N=1.5; 60; - Rhizobium	"
	GC	350	1325	+20.0	N=1.5; 125; - Rhizobium	"
	GC	350	1325	0.0	N=1.5; 220; - Rhizobium	"
	GC	350	1325	-21.9	N=1.5; 380; - Rhizobium	"
	GC	350	1325	+56.8	N=1.5; 60; + Rhizobium	"
	GC	350	1325	+32.4	N=1.5; 125; + Rhizobium	"
	GC	350	1325	+7.3	N=1.5; 220; + Rhizobium	"
	GC	350	1325	+5.6	N=1.5; 380; + Rhizobium	"
	GC	350	720	-8.8	N=15; 550; - Rhizobium	"
	GC	350	720	-36.4	N=1.5; 550; - Rhizobium	"
	GC	350	720	+57.1	N=1.5; 550; + Rhizobium	"
	GC	350	1325	-22.5	N=15; 550; - Rhizobium	"
	GC	350	1325	-19.2	N=1.5; 550; - Rhizobium	"
	GC	350	1325	-2.9	N=1.5; 550; + Rhizabium	"
	GC	350	2400	-32.6	N=15; 550; - Rhizobium	"
	GC	350	2400	-51.2	N=1.5; 550; - Rhizobium	"
	GC	350	2400	+3.1	N=1.5; 550; + Rhizobium	"
	Phy	340	680	-14.8		Morison and Gifford (1984)[b]
Oryza sativa	SPAR	330	500	+5.9		Baker et al. (1990)[b]
	SPAR	330	660	+50.0		"
	SPAR	330	900	+23.5		"
	GH	350	700	+13.4	110 days at 28/21 - 1981	Imai et al. (1985)
	GH	350	700	+38.4	110 days at 33/26 - 1981	"
	GH	350	700	+34.6	40 days at 33/26 - 1982	"
	GH	350	700	+35.2	100 days at 33/26 - 1982	"
	Phy	340	680	-13.5		Morison and Gifford (1984)[b]
Phalaris aquatica	Phy	340	680	-3.9		Morison and Gifford (1984)[b]
Phaseolus vulgaris	GC	320	2500	+36.9	Salinity=0 m*M* NaCl	Schwarz and Gale (1984)
	GC	320	2500	+0.1	Salinity=40 m*M* NaCl	"
	GH	300	1000	+38.9	No root hormones	Tognoni et al. (1967)
	GH	300	1000	+12.5	GA root hormones	"
	GH	300	1000	+48.9	BA root hormones	"
	GH	300	1000	+34.8	NAA root hormones	"
	GH	300	1000	+14.7		Wittwer (1966)
	GH	300	1000	+38.9		Wittwer (1970)

Table 1e. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Pisum sativum	Phy	340	680	+13.3		Morison and Gifford (1984)[b]
	Phy	350	1000	+7.4		Paez et al. (1980)
	Phy	350	675	-13.1	Adequately watered	Paez et al. (1983)
	Phy	350	675	-21.8	Water stressed	"
Raphanus sativus	OTC	340	640	+36.0		Idso et al. (1988)
	GC	400	1200	+118.2		Knecht (1975)
	Phy	340	680	+21.2		Morison and Gifford (1984)[b]
	Phy	350	675	+41.2	Light=600 $\mu E\ m^{-2}\ s^{-1}$	Sionit et al. (1982)[c]
	Phy	350	675	+42.6	Light=1200 $\mu E\ m^{-2}\ s^{-1}$	"
Rubus idaeus	GC	330	1650	+66.7	Light=80	Laforge et al. (1991)
	GC	330	1650	+75.0	Light=125	"
	GC	330	1650	+87.5	Light=250	"
	GC	330	3000	+55.6	Light=80	"
	GC	330	3000	+125.0	Light=125	"
	GC	330	3000	+137.5	Light=250	"
Solanum tuberosum	GH	350	700	+12.0		Goudriaan and de Ruiter (1983)
	GC	350	750	-0.8	Light=320 W m^{-2}	Hayashi et al. (1990)[b]
	GC	350	750	-17.3	Light=582 W m^{-2}	"
	GC	365	1000	-11.8	Variety=Norland	Wheeler and Tibbitts (1989)
	GC	365	1000	+19.2	Variety=Russet Burbank	"
	GC	350	1000	+13.2	N[f]; Light=400 for 12 h	Wheeler et al. (1991)
	GC	350	1000	-11.7	N; Light=400 for 24 h	"
	GC	350	1000	+22.4	N; Light=800 for 12 h	"
	GC	350	1000	-12.8	N; Light=800 for 24 h	"
	GC	350	1000	+12.6	RB[f]; Light=400 for 12 h	"
	GC	350	1000	+23.4	RB; Light=400 for 24 h	"
	GC	350	1000	+43.5	RB; Light=800 for 12 h	"
	GC	350	1000	+10.6	RB; Light=800 for 24 h	"
	GC	350	1000	+14.1	D[f]; Light=400 for 12 h	"
	GC	350	1000	+9.0	D; Light=400 for 24 h	"
	GC	350	1000	+42.8	D; Light=800 for 12 h	"
	GC	350	1000	-7.4	D; Light=800 for 24 h	"
Sorghum bicolor	GC	330	485	-11.1		Chaudhuri et al. (1986)
	GC	330	660	0.0		"
	GC	330	795	+11.1		"
	Phy	340	680	-18.0		Morison and Gifford (1984)[b]
Trifolium repens	Phy	340	680	+15.9		Morison and Gifford (1984)[b]
	GC	200	1000	+29. 3	After first growth	Scheidegger and
	GC	200	1000	+7.9	After regrowth	Nösberger (1984)

Table 1f. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Triticum aestivum	GC	350	700	+3.0	No N added to soil	Billes et al. (1993)
	GC	350	700	-13.1	32 mg N/pot added	"
	GC	340	485	+2.6	Adequately watered	Chaudhuri et al. (1990)[b,c]
	GC	340	485	-5.5	Water stressed	"
	GC	340	660	+10.7	Adequately watered	"
	GC	340	660	-9.9	Water stressed	"
	GC	340	825	-20.8	Adequately watered	"
	GC	340	825	-15.6	Water stressed	"
	GC	330	660	+3.8	Density=40 plants m^{-2}	Du Cloux et al. (1987)[b]
	GC	330	660	+60.8	Density=200 plants m^{-2}	"
	Phy	340	590	-19.4	Water=40 mL watering^{-1}	Gifford (1979)[c]
	Phy	340	590	-27.7	Water=60 mL watering^{-1}	"
	Phy	340	590	-16.0	Water=120 mL watering^{-1}	"
	Phy	340	590	-29.1	Water=240 mL watering^{-1}	"
	GH	340	1500	-6.5	N=0.5 mol m^{-3}	Hocking and Meyer (1991)
	GH	340	1500	-3.3	N=2.5 mol m^{-3}	"
	GH	340	1500	+18.2	N=6.0 mol m^{-3}	"
	GH	340	1500	+16.2	N=12.0 mol m^{-3}	"
	GH	340	1500	+20.5	N=25.0 mol m^{-3}	"
	GH	350	700	-24.0		Lekkerkerk et al. (1990)[b]
	GH	350	1300	-64.2		MacDowall (1972)[b]
	GH	350	2200	-52.7		"
	GC	220	500	+13.3	In "loose" soil	Masle et al (1990)[b,c]
	GC	220	500	+22.7	In "compact" soil	"
	Phy	340	680	-9.7		Morison and Gifford (1984)[b]
	Phy	350	1000	+5.8	No drought cycles	Sionit et al. (1980)
	Phy	350	1000	+23.3	1 drought cycle	"
	Phy	350	1000	+7.5	2 drought cycles	"
	Phy	350	675	+27.5	N=1/16 Hoagland's	Sionit et al. (1981b)
	Phy	350	675	+1.0	N=1/8 Hoagland's	"
	Phy	350	675	-1.4	N=1/2 Hoagland's	"
	Phy	350	675	+18.8	N=1/1 Hoagland's	"
	Phy	350	675	+23.2		Sionit et al. (1981a)
	Phy	350	1000	+13.4		"
	Phy	350	1000	-6.3	No drought cycles	Sionit et al. (1981d)
	Phy	350	1000	+1.7	1 drought cycle	"
	Phy	350	1000	-4.6	2 drought cycles	"
	GH	320	640	+7.6	N=2; Light=500	Wong and Osmond (1991)[b]
	GH	320	640	+20.9	N=2; Light=2000	"
	GH	320	640	-34.6	N=12; Light=500	"
	GH	320	640	+56.5	N=12; Light=2000	"
Vicia faba	Phy	340	680	+20.5		Morison and Gifford (1984)[b]
Vigna unguiculata	Phy	340	680	+15.0		Morison and Gifford (1984)[b]
	Phy	340	680	+17.9		"

Table 1g. Percent change (ambient to elevated CO_2) in root to shoot ratios for crop species

Species	Location	Ambient [CO_2]	Elevated [CO_2]	% Δ R:S	Interacting variables[a]	Reference
Vitis vinifera	GC	350	1200	+419.5		Kriedemann et al. (1976)[c]
Zea mays	GC	350	600	+25.7	H_2O=50% ET replaced	King and Greer (1986)
	GC	350	600	-6.3	H_2O=75% ET replaced	"
	GC	350	600	-12.9	H_2O=100% ET replaced	"
	GC	350	850	+14.6	H_2O=50% ET replaced	"
	GC	350	850	-12.7	H_2O=75% ET replaced	"
	GC	350	850	+8.6	H_2O=100% ET replaced	"
	Phy	340	680	-13.2		Morison and Gifford (1984)[b]
	GC	350	600	+12.0		Patterson and Flint (1980)
	GC	350	1000	-8.0		"
	OTC	340	520	+59.3		Rogers et al. (1983)
	OTC	340	718	+25.4		"
	OTC	340	910	+47.0		"
	Phy	350	675	+23.5	Light=600 $\mu E\ m^{-2}\ s^{-1}$	Sionit et al. (1982)[c]
	Phy	350	675	+13.3	Light=1200 $\mu E\ m^{-2}\ s^{-1}$	"
	GC	320	2500	-14.1	Salinity=0 m*M* NaCl	Schwarz and Gale (1984)
	GC	320	2500	-8.1	Salinity=50 m*M* NaCl	"
	GC	400	550	+68.6		Whipps (1985)[b]
	GC	400	800	+94.3		"

Concentrations are in ppm CO_2. Locations: GC = growth chamber; GH = glasshouse; OTC = open top chamber; SPAR = soil-plant-atmosphere-research chamber; Phy = phytotron; FACE = free-air CO_2 enrichment system.
[a]N is m*M* NO^{-3} and light is μmol $m^{-2}\ s^{-1}$ unless otherwise stated.
[b]Study had multiple harvests; data presented are from final harvest only.
[c]Data estimated from graphs.
[d]Abbreviations represent varieties : NY = New Yorker; BB = Better Boy.
[e]Numbers (60, 125, 220, 380, and 550) refer to light levels in $\mu E\ m^{-2}\ s^{-1}$.
[f]Abbreviations represent varieties: N = Norland; RB = Russet Burbank; D = Denali.

average responses centered close to zero (±8%). The range in relative R:S change for fruit crops was large, but they also showed an overall positive effect of elevated CO_2 (Table 2). This overall positive (+16.0%) response was primarily due to large positive responses of raspberry (*Rubus idaeus*) plantlets (Laforge et al., 1991) and may have been an artifact of the young age of the plantlets and of experimental conditions specifically designed to study in vitro rooting of these young plantlets. If data for the raspberry plantlets are omitted, the overall average response for fruit crops becomes +1.0% which is more in line with the other crop types.

Plant age (ontogenic and/or phenologic), in addition to plant type or species, is a major factor affecting R:S. Since elevated CO_2 can affect plant development and its rate (Prior and Rogers, 1995; Rogers et al., 1984), this further confuses interpretations of altered R:S. For most crop plants, R:S is high early in the growing season (during vegetative growth) and decreases with increasing plant development (see for example Baker et al., 1990; Desjardins et al., 1987; Sionit et al., 1987; Vessey et al., 1990). However, the opposite often occurs for root and tuber crops (Bhattacharya et al., 1985; Sionit et al., 1982). Idso et al. (1988) confirm that R:S for root and tuber crops differs substantially from that for other types of crops; however, they suggest that the relative response of R:S to elevated CO_2 is independent of plant size and plant growth stage. Since so few studies exist, further experimentation is definitely required to verify this conclusion; however, it does not appear to be supported from our review of the available literature. Also, it seems logical that elevated CO_2 may increase R:S in crops with aboveground yield components by altering carbon allocation to favor roots during vegetative growth for improved acquisition of soil resources, while at reproductive maturity alloca-

Table 2. Percent change (ambient to elevated CO_2) in root to shoot ratios for various types of crops

Crop	Number of observations	Mean	Range	Interacting variables
Fiber crops				
Cotton	8	-5.6	-49.1 to +47.4	[CO_2]; N
Fruit crops				
Okra	3	+2.0	-7.3 to +15.7	[CO_2]
Asparagus	6	+6.9	-15.6 to +51.5	[CO_2]; light
Cucumber	6	+5.3	-12.9 to +46.5	Phenology; grafting
Strawberry	2	+8.4	+4.2 to +12.5	
Tomato	13	-5.1	-36.6 to +10.8	H_2O; variety; hormones
Raspberry	6	+91.2	+55.6 to +137.5	[CO_2]; light
All fruit crops	**36**	**+16.0**		
Grain crops (C_3)				
Barley	7	+17.5	-17.4 to +51.0	[CO_2] ; light
Rice	8	+23.5	-13.5 to +50.0	[CO_2] ; temp.
Wheat	41	+0.4	-64.2 to +60.8	[CO_2]; N; H_2O; light; density
All C_3 grain crops	**56**	**+5.8**		
Grain crops (C_4)				
Japanese millet	4	-46.8	-70.9 to -28.7	N; light
Sorghum	4	-4.5	-18.0 to +11.1	[CO_2]
Corn (maize)	18	+17.6	-14.1 to +94.3	[CO_2]; H_2O; light; salt
All C_4 grain crops	**26**	**+4.3**		
Leaf crops				
Kale	2	+15.9	+15.9 to +15.9	[CO_2]
Lettuce	3	-20.4	-25.7 to -17.6	[NO_x]
All leaf crops	**5**	**-5.9**		
Legume crops				
Soybean	37	+5.2	-27.2 to +41.2	[CO_2]; light; N; P; temp.
Beans	10	+20.8	-38.1 to +48.9	hormones; salt
Peas	6	+3.1	-21.8 to +17.9	H_2O
All legume crops	**53**	**+7.9**		
Seed crops				
Oilseed rape	1	+21.9	NA	NA
Sunflower	3	-10.9	-12.5 to -8.0	temp.
All seed crops	**4**	**-2.7**		
Forage crops				
Ryegrass	1	+7.4	NA	NA
Canarygrass	1	-3.9	NA	NA
Alfalfa	22	+5.5	-51.2 to +87.5	[CO_2]; N; light; *Rhizobium*
White clover	3	+17.7	+7.9 to +29.3	[CO_2]
All forage crops	**27**	**+6.6**		
Root and tuber crops				
Carrot	1	+36.0	NA	NA
Kohlrabi	3	+17.7	-11.0 to +40.0	H_2O
Sugar beet	9	+33.9	0.0 to +78.6	[CO_2] ; light
Sweet potato	8	+22.6	-9.1 to +60.0	[CO_2]; H_2O
Radish	5	+51.8	+21.2 to +118.2	[CO_2]; light
Potato	17	+9.5	-17.3 to +43.5	Light; variety
All root tuber crops	**43**	**+23.1**		

tion should be altered to favor aboveground reproductive tissues. Since CO_2 stimulates growth and resource use efficiency, control plants and treated plants may quickly diverge in terms of their respective rates of development and resource requirements, making morphological comparison valid only at the same growth stage (Farrar and Gunn, 1996).

In addition to variability resulting from differences in plant species and developmental age, other environmental factors and experimental procedures can affect R:S. Atmospheric CO_2 concentration often interacts with environmental factors (i.e. water, temperature, light, nutrition, salinity, air pollutants, and competition) to affect plant growth (Rogers and Dahlman, 1993). These interactions complicate interpretation of R:S data. A summary of interacting effects of CO_2 with light, temperature, nitrogen, and water (Table 3) appears to be in general agreement with the influence these factors exert under ambient CO_2; i.e. reduced light or adequate levels of N and water tend to result in decreased R:S. The lack of regulation (or standardization) of procedures used during CO_2 experiments (Linder and McDonald, 1993) points to a need for more careful control of plant growth conditions in the design of CO_2 effects research.

Plants growing under high CO_2 appear to be able to produce more biomass with available nutrients (Rogers et al., 1996), a majority of which may be located belowground (Rogers et al., 1994). For spring wheat the influence of doubling the CO_2 concentration was to reduce R:S with nitrogen fertilization but to increase it somewhat when nitrogen was not added (Billes et al., 1993). Also, plant characteristics (nitrogen productivity and the relationship of photosynthetic rate to internal nitrogen concentration) which control R:S (Ågren and Ingestad, 1987) can certainly be influenced by CO_2 level. Elevated CO_2 may interact with other nutrients in different ways. Under ambient levels of CO_2, Cakmak et al. (1994) found that R:S increased in phosphorous-deficient plants, which could be due to the buildup of sucrose and starch in leaves resulting in higher photosynthate transport to the roots or to increased carbohydrate utilization efficiency (Qiu and Israel, 1992). However, data from Cure et al. (1988b) indicate that R:S is decreased under low levels of phosphorus in elevated CO_2 compared to ambient (Table 1). Excessive starch accumulation in leaves under elevated CO_2 has been shown to distort or damage chloroplasts and thylakoids (Goudriaan and de Ruiter, 1983; Yelle et al., 1989). Under phosphorus-limited conditions, it is possible that the accumulation of starch in elevated CO_2-grown plants may damage leaves to a point which inhibits carbohydrate transport to the roots, thus reducing R:S.

Lambers et al. (1995) have considered the effects of temperature and water supply on carbon partitioning in wheat and closely related species as influenced by elevated CO_2. They point out that earlier papers emphasized that elevated CO_2 favors investment of biomass in roots relative to leaves, but that it has now become clear that these are indirect effects due to more rapid depletion of nutrients in the root environment as a consequence of enhanced growth. However, if nutrients cannot be absorbed in proportion to enhanced growth, then CO_2-enriched plants show an increased allocation to roots, at the expense of that to leaves. The effect of temperature on allocation in the vegetative stage is that relative investment of dry matter of roots is lowest at a certain optimum temperature and increases with either rise or fall in temperature. Temperature affects allocation mainly through its impact on the capacity of roots to transport water. Effects of water deficit on carbon partitioning are unambiguous; roots receive relatively more carbon.

In addition to the environmental variables previously discussed, we analyzed data from the extant literature (Table 1) to determine if CO_2 concentration or pot size influenced R:S response. The differential in CO_2 test concentrations used (elevated minus ambient) exhibited a significant positive relationship with percent change in R:S (Pearson's correlation; $n = 264$, R=0.15, Pr>R=0.01). This indicates, not surprisingly, that the relative responsiveness of R:S increases as the level of high CO_2 tested increases. However, it is likely that optimal levels of CO_2 exist for various plant species under specific sets of environmental conditions, above which this correlation would no longer hold.

Pot size was found to be unrelated to percent change in R:S (Pearson's correlation; $n = 231$ after removal of field data and those of Laforge et al. (1991), R=0.03, Pr>R=0.65). It would seem logical that root restriction, due to small pot volume, would result in altered allocation patterns and reduced R:S, as was reported by Arp (1991) using substantially fewer data points from agronomic species as well as other plant types. It appears that the large variation in the literature precludes support of this logical assumption. However, if we restricted variability by examining a single plant species with a large number of observations (e.g. soybean) we were able to detect the expected positive

Table 3a. Percent change (ambient to elevated CO_2) in root to shoot ratios for various interacting variables

Crop	Number of observations	Interacting variables	% Δ R:S
Asparagus	2	Light=80 μmol m^{-2} s^{-1}	-15.2
"	2	Light=125 μmol m^{-2} s^{-1}	-11.9
"	2	Light=250μmol m^{-2} s^{-1}	+47.7
Sugar beet	2	Light=3.7 cal dm^{-2} min^{-1}	+38.9
"	2	Light=7.7 cal dm^{-2} min^{-1}	+45.5
"	1	Light=600 μE m^{-2} s^{-1}	+25.9
"	1	Light=1200 μE m^{-2} s^{-1}	+78.6
Japanese millet	2	Light=500 μmol m^{-2} s^{-1}	-53.1
"	2	Light=2000 μmol m^{-2} s^{-1}	-40.6
Soybean	1	Light=600 μE m^{-2} s^{-1}	-20.0
"	1	Light=1200 μE m^{-2} s^{-1}	-10.7
Barley	2	Light=3.7 cal dm^{-2} min^{-1}	+10.1
"	2	Light=7.7 cal dm^{-2} min^{-1}	+34.6
Alfalfa	3	Light=60 μE m^{-2} s^{-1}	+57.4
"	3	Light=125 μE m^{-2} s^{-1}	+16.6
"	3	Light=220 μE m^{-2} s^{-1}	-0.3
"	3	Light=380 μE m^{-2} s^{-1}	+9.8
"	9	Light=550 μE m^{-2} s^{-1}	-12.6
Radish	1	Light=600 μE m^{-2} s^{-1}	+41.2
"	1	Light=1200 μE m^{-2} s^{-1}	+42.6
Raspberry	2	Light=80 μmol m^{-2} s^{-1}	+61.2
"	2	Light=125 μmol m^{-2} s^{-1}	+100.2
"	2	Light=250 μmol m^{-2} s^{-1}	+112.5
Potato	1	Light=320 W m^{-2}	-0.8
"	1	Light=582 W m^{-2}	-17.3
"	3	Light=400 μmol m^{-2} s^{-1} for 12hr	+13.3
"	3	Light=400 μmol m^{-2} s^{-1} for 24hr	+6.9
"	3	Light=800 μmol m^{-2} s^{-1} for 12hr	+36.2
"	3	Light=800 μmol m^{-2} s^{-1} for 24hr	-3.2
Wheat	2	Light=500 μmol m^{-2} s^{-1}	-13.5
"	2	Light=2000 μmol m^{-2} s^{-1}	+38.7
Corn	1	Light=600 μE m^{-2} s^{-1}	+23.5
"	1	Light =1200 μE m^{-2} s^{-1}	+13.3
Σ	26	Light="low"	+13.8
Σ	13	Light="medium"	+19.6
Σ	32	Light="high"	+17.8
Soybean	2	Temperature=18/12 °C (day/night)	-16.7
"	2	Temperature=22/ 16 °C (day/night)	+12.0
"	2	Temperature=26/20 °C (day/night)	-19.1
Sunflower	1	Temperature=19/14 °C (day/night)	-12.5
"	1	Temperature=28/23 °C (day/night)	-8.0
"	1	Temperature=30/24 °C (day/night)	-12.1
Rice	1	Temperature=28/21 °C (day/night)	+13.4
"	1	Temperature=33/26 °C (day/night)	+38.4
Σ	4	Temperature="low"	-8.1
Σ	3	Temperature="Medium"	+5.3
Σ	4	Temperature="high"	-3.0

Table 3b. Percent change (ambient to elevated CO_2) in root to shoot ratios for various interacting variables

Crop	Number of observations	Interacting variables	% Δ R:S
Japanese millet	2	N=2 m*M* NO_3^-	-43.9
"	2	N=12 m*M* NO_3^-	-49.8
Soybean	1	N=0.5 m*M* NO_3^-	+27.9
"	1	N=1.0 m*M* NO_3^-	-9.0
"	1	N=2.5 m*M* NO_3^-	-4.2
"	1	N=5.0 m*M* NO_3^-	+32.5
"	1	N=10.0 m*M* NO_3^-	-5.2
Cotton	1	N=0.6 m*M* NO_3^-	-20.9
"	1	N=4.0 m*M* NO_3^-	-32.5
"	1	N=12.0 m*M* NO_3^-	-49.1
"	1	N=24.0 m*M* NO_3^-	-28.7
Alfalfa	14	N=1.5 m*M* NO_3^-	+9.9
"	7	N=15 m*M* NO_3^-	-0.2
Wheat	1	N=no N added	+3.0
"	1	N=32 mg N/pot as NH_4-NO_3	-13.1
"	1	N=0.5 mol m^{-3}	-6.5
"	1	N=2.5 mol m^{-3}	-3.3
"	1	N=6.0 mol m^{-3}	+18.2
"	1	N=12.0 mol m^{-3}	+16.2
"	1	N=25.0 mol m^{-3}	+20.5
"	1	N=1/16 strength Hoagland's	+27.5
"	1	N=1/8 strength Hoagland's	+1.0
"	1	N=1/2 strength Hoagland's	-1.4
"	1	N =1/1 strength Hoagland's	+18.8
"	2	N=2 m*M* NO_3^-	+14.3
"	2	N=12 m*M* NO_3^-	+11.0
Σ	27	N="low"	+2.5
Σ	20	N="high"	-4.4
Kohlrabi	1	H_2O=replace 25% of water used	+40.0
"	1	H_2O=replace 50% of water used	+24.1
"	1	H_2O=replace 100% of water used	-11.0
Sweet potato	2	H_2O=adequately watered	+19.1
"	2	H_2O=water stressed	+21.7
Tomato	2	H_2O=adequately watered	-27.8
"	2	H_2O=water stressed	-22.5
Pea	1	H_2O=adequately watered	-13.1
"	1	H_2O=water stressed	-21.8
Wheat	3	H_2O=adequately watered	-2.5
"	3	H_2O=water stressed	-10.3
"	1	H_2O=40 ml/pot/watering event	-19.4
"	1	H_2O=60 ml/pot/watering event	-27.7
"	1	H_2O=120 ml/pot/watering event	-16.0
"	1	H_2O=240 ml/pot/watering event	-29.1
"	2	H_2O=no drought cycles	-0.3
"	2	H_2O=1 drought cycle	+12.5
"	2	H_2O=2 drought cycles	+1.5
Corn	2	H_2O=replace 50% of evapotranspiration	+20.2
"	2	H_2O=replace 75% of evapotranspiration	-9.5
"	2	H_2O=replace 100% of evapotranspiration	-2.2
Σ	15	H_2O=adequately watered	-6.6
Σ	17	H_2O=water stressed	+0.4

correlation of R:S with pot size (Pearson's correlation; n=236, R=0.36, Pr>R=0.03).

Many factors influence R:S and lead to the wide range of values reported in the literature and to the large variability in our analyses. In addition to those previously discussed, duration of study likely had a strong influence on the lack of correlation of R:S with pot size; that is, if studies are of a short duration (several days to a few weeks), root restriction may not occur or may not exert sufficient influence to affect carbon partitioning. Interpolating graphed data from Thomas and Strain (1991) reveals reduced R:S for 4-wk-old cotton plants under elevated CO_2 in both small (0.38 L) and large (1.75 L) pots, with the relative reduction being greater in the large pots. It is possible the influence of the small pot size would have been greater had the study extended throughout the entire vegetative growth phase. McConnaughay et al. (1996) reported little effect of pot size (0.3 - 3.0 L) on growth of three tree species for 12 weeks. They did find reduced R:S in the smaller pots, but this reduction was not affected by CO_2 concentration.

Some insight into the source-sink and CO_2 relationship has been gleaned from investigations of root restriction. Grodzinski (1992) points out that during CO_2 enrichment the source-to-sink balance within plants changes more rapidly than under ambient CO_2 levels. Farrar and Gunn (1996) suggest that carbon transport and partitioning under elevated CO_2 is most likely sink controlled, due to increased activity often resulting in buildup of carbohydrates in source leaves. They further suggest that plant growth, while enhanced under elevated CO_2, may be limited (possibly genetically) beyond the plant's ability to utilize the quantity of carbohydrates produced by the increased source activity; this buildup of carbohydrates in source leaves should then downregulate photosynthetic rate. This would seem to be particularly relevant under environmental conditions which limit sink activity, such as reduced pot size. Considerations of sink activity (i.e. carbon partitioning among the various plant organs) may help interpret divergent findings with regard to photosynthetic capacity (Cure et al., 1987, 1991; Drake, 1992; Geiger, 1986; Herold, 1980).

Sionit et al. (1984), comparing the response of container and field grown soybeans, concluded that stress imposed on plants by confining the roots may appreciably decrease the magnitude of their photosynthetic response to atmospheric CO_2 enrichment. This potential decrease in photosynthetic capacity is supported by the strong correlation between pot size and photosynthetic capacity reported by Arp (1991). He found that R:S increased with lack of restriction and decreased as pot size got smaller. This appeared to be related to the impact to the imbalance in source-sink relations brought about by the spatial restriction of root growth. Thomas and Strain (1991) have also shown that inadequate rooting volume reduced the photosynthetic capacity of cotton. These data emphasize the need to consider rooting volume in both CO_2 response and carbon allocation experiments. Progressive reduction of photosynthetic capacity as root growth space became smaller indicated a possible sink-limited feedback inhibition of net photosynthesis. However, McConnaughay et al. (1996) summarize the interacting effects of environmental variables (nutrients and water) on root restriction and photosynthetic capacity and conclude, "...the link between root restriction and reduced photosynthetic capacity remains ambiguous." This also appears to be the case for allocation of photosynthetically derived products and R:S.

Norby (1994) suggests, "...we may find that root to shoot ratio of small, potted plants provides little useful information for addressing the larger-scale issues concerning the integrated responses of plants and ecosystems to elevated CO_2." While this is indeed true, it should not be taken as a negation of the usefulness of CO_2 research conducted in pots. Soil volume is limiting not only in greenhouse pots, but it can also be a restricting factor in farm fields. Masle (1992a) considered the possible improvement of plant performance under atmospheric CO_2 enrichment on soils prone to dry conditions or with high mechanical impedance. While improvement of plant performance is probable, sink limitations induced by root signals need to be investigated to help understand the role of elevated CO_2 in such situations (hard, dry edaphic conditions). There is limited evidence to suggest a role of carbohydrates in root signalling (Atwell, 1993; Farrar and Gunn, 1996; Masle et al., 1990). Masle (1992b) further suggested that signals regulating plant performance may also be triggered by soil impedance to roots. Such direct communication (Tardieu, 1994) could be pivotal to understanding CO_2 effects on partitioning.

Root response of plants exposed to elevated CO_2 suggests that measures of root biomass may need to be accompanied by structural information that better describes the geometry of roots as they occupy the soil profile. Taylor et al. (1994) indicate that the effects of elevated atmospheric CO_2 on root and root system structure (e.g. root length and branching) and function need to be emphasized in future research. They indicate

that both cell production and cell expansion appear to be promoted in the roots of plants exposed to elevated levels of CO_2 and further suggest that additional carbon may affect production of root primordia and root branches. This notion of measuring root architecture is supported by Van Noordwijk and de Willigen (1987) in that the concept of 'functional equilibrium' suggests the most relevant way to relate root and shoot may be on the basis of the size of their interfaces with the environment (e.g. root area to leaf area ratio). This seems logical since the location and density of roots within the soil profile determine nutrient (Barber, 1995) and water acquisition and it has also been suggested that this measure could possibly provide better insight into root function (i.e. water and nutrient absorption) than R:S (Stulen and den Hertog, 1993). Others have indicated that measures in addition to R:S may be helpful in understanding resource acquisition in the context of elevated CO_2 (Norby, 1994), and have suggested compartment (leaf, stem, and root) weights given as a fraction of plant total (Lambers et al., 1995).

The potential for increasing levels of CO_2 to alter root architecture indicates that better measures of root growth and exploration as well as root activity are needed, including determinations of root length and branching, periodicity in root growth and turnover, distribution among root size and type classes, and nutrient absorption rates. Beyond this is the need to know how much carbon has been allocated to the roots in total, not just what quantity of roots could be recovered. Roots that have died, root respiration, rhizodeposition (sloughing, grazing by soil biota, and exudation), and carbon allocated to roots for symbiotic activity represent important carbon losses which must be included in the belowground carbon budget. Not only is this work essential for a more complete understanding of CO_2 response, but also for developing a better picture of plant reaction to soil stresses. Elucidation of mechanisms controlling carbon partitioning (and thus R:S) under increasing levels of atmospheric CO_2 requires substantially more research specifically designed toward this end. Conventional techniques for the experimental measurement of root production may overlook these important parameters. In order to meet future research goals regarding belowground plant processes and carbon allocation, new experimental approaches will be needed (Rogers et al., 1994).

Research recommendations

Our survey of R:S in crops under elevated atmospheric CO_2 suggests that future allocation experiments, designed to study CO_2 response, focus on the following:

1. A clearer understanding of the biochemistry of carbon allocation (including the intricacies of source-sink relationships) as affected by elevated atmospheric CO_2.
2. Work in the area of allocation response to multiple resource interactions including CO_2 enrichment.
3. Field studies of allocation which take the response of entire ecosystems to CO_2 into account.
4. In addition to root-shoot biomass measurements, quantitative descriptions of root and shoot configuration (i.e. architecture) and effective surface (i.e. more accurate measurement of their interfaces to the environment) as affected by CO_2.
5. In plant carbon balance, root losses due to mortality, rhizodeposition, respiration, and experimental protocols and shoot losses due to leaching or volatilization need to factored into the whole plant carbon budget as influenced by elevated CO_2.
6. The interactions of atmospheric CO_2 concentration and the effects of soil properties (soil structure and function) on root to shoot allocation.
7. Response of soil processes to CO_2-induced changes in plant allocation patterns, with respect to carbon and nutrient dynamics, and soil quality.
8. Development of crop models that are sensitive to CO_2 and other resources as they affect whole plant carbon and nitrogen allocation.

Conclusion

We examined the influence of atmospheric CO_2 concentration on root to shoot allocation. It is clear that much remains to be done and evident from the highly variable data base that additional parameters will need to be controlled or recorded in future experiments. With regard to root-shoot allocation, we do know that it is highly dynamic in nature and its response to elevated atmospheric CO_2 may well depend on prevailing environmental conditions. To better understand how elevated CO_2 will impact the biosphere, we need to amplify our understanding of the mechanisms that regulate partitioning, how they work, and how they are controlled (by genes and other exogenous factors, and by atmospheric and edaphic resources). The flow of

carbon within the crop plant is key to our predictions of how global change will affect future agroecosystems. A greater knowledge of crop carbon dynamics will better enable us to feed ourselves and six billion fellow inhabitants.

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