

Root to shoot ratio of crops as influenced by CO₂

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Abstract

Crops of tomorrow are likely to grow under higher levels of atmospheric CO₂. 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 CO₂ concentration often stimulates the growth of both shoot and root, but the question remains whether elevated atmospheric CO₂ concentration will affect roots and shoots of crop plants proportionally. Since elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 com-

plex series of events leading from CO₂ 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 CO₂ in the atmosphere.

Our world of fossil power and hunger for land is forcing up the concentration of CO₂ in the atmosphere. Not only is the entire atmosphere affected, but so is the first molecular step that carries CO₂ 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; Witter, 1995). Carbon allocation determines plant health and yield under virtually all conditions and plays a pivotal role in the CO₂ response. In a recent review, Stulen and den Hertog (1993) conclude the assumption that a larger proportion of the extra dry matter produced under CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ concentration is readily explainable (Farrar and Gunn, 1996). However, unaltered allometry is not readily apparent from the CO₂ 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 CO₂, particularly when interacting with other environmental variables.

Raising the concentration of atmospheric CO₂ often results in dramatic increases in root growth. Root dry weight has been found to increase under elevated atmospheric CO₂ 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 CO₂ (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 CO₂ 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-

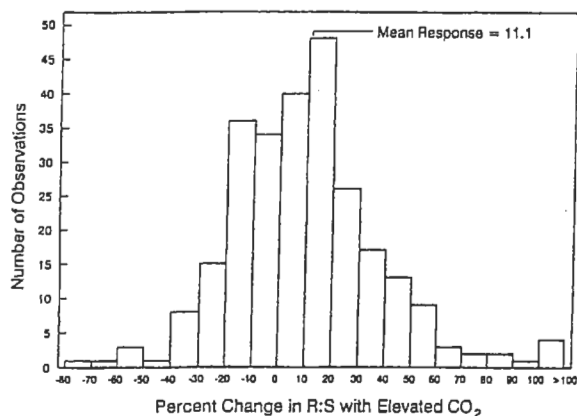


Figure 1. Frequency distribution of percent change in R:S (ambient to elevated CO₂) summarized for crop plants ($n=264$).

ic CO₂. The response of R:S to elevated atmospheric CO₂ 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 CO₂ while R:S of cotton (*Gossypium hirsutum*) grown under field conditions appeared to be unaffected by CO₂ concentration (Prior et al., 1994). In fact, the response of R:S to increased concentrations of atmospheric CO₂ 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 CO₂ 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 $\pm 30\%$) 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 CO₂ literature. In a discussion on natural ecosystem responses to rising CO₂ 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 CO₂ 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 (Wullschlegel 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 CO₂, 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. CO₂ 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 CO₂ (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 CO₂ response experiments can likely be attributed to crop species, so generalizations regarding R:S response to increasing CO₂ 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 C₃ plant species, but that R:S for C₄ plants tended to be unaffected by atmospheric CO₂ 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 CO₂) change in R:S for root and tuber crops (which have large sinks) was rarely negative and showed an overall increase with increasing CO₂ (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 CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Abelmoschus esculentus</i>	Phy	350	450	-2.3		Sionit et al. (1981c)
	Phy	350	675	-7.3		"
	Phy	350	1000	+15.7		"
<i>Asparagus officinalis</i>	GC	330	1650	-15.2	Light=80	Laforge et al. (1991)
	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	"
<i>Beta vulgaris</i>	GC	300	1000	0.0		Ford and Thorne (1967) ^b
	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)
<i>Brassica napus</i>	Phy	340	680	+21.9		Morison and Gifford (1984) ^b
<i>Brassica oleracea</i>	GC	300	1000	+15.9		Ford and Thorne (1967)
	GC	300	3300	+15.9		"
<i>Brassica oleracea</i> var. <i>gongylodes</i>	GC	300	900	+40.0	H ₂ O=25% of used	Sritharan and Lenz (1990)
	GC	300	900	+24.1	H ₂ O=50% of used	"
	GC	300	900	-11.0	H ₂ O=100% of used	"
<i>Citrus paradisi</i> × <i>Poncirus trifoliata</i>	SPAR	330	660	-7.3		Koch et al. (1983) ^c
<i>Citrus sinensis</i> × <i>P. trifoliata</i>	GC	395	795	-9.0		Downton et al. (1987)
	SPAR	330	660	-24.5		Koch et al. (1983) ^c
	SPAR	330	660	+3.2		Koch et al. (1987)
	SPAR	330	990	+15.5		"
<i>Cucumis sativus</i>	GC	345	1300	+7.4	Not grafted	Ito (1972) ^b
	GC	345	1300	-12.9	Grafted	"
	Phy	350	1000	-10.9	Day 0-16: 1 st 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	"
<i>Daucus carota</i> var. <i>sativus</i>	OTC	340	640	+36.0		Idso et al. (1988)

Table 1b. Percent change (ambient to elevated CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Echinochloa frumentacea</i>	GH	320	640	-35.2	N=2; Light=500	Wong and Osmond (1991) ^c
	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	"
<i>Fragaria × ananassa</i>	GH	330	900	+12.5		Desjardins et al. (1987) ^b
	GH	330	1500	+4.2		"
<i>Glycine max</i>	SPAR	330	450	+16.7		Allen et al. (1988)
	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 mM KH ₂ PO 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 μE m ⁻² s ⁻¹	Sionit et al. (1982) ^c
	Phy	350	675	-10.7	Light=1200 μE 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 CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Gossypium hirsutum</i>	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	"
<i>Helianthus annuus</i>	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	"
<i>Hordeum vulgare</i>	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
<i>Ipomoea batatas</i>	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	"
<i>Lactuca sativa</i>	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	"
<i>Lolium perenne</i>	Phy	340	680	+7.4		Morison and Gifford (1984) ^b
<i>Lycopersicon esculentum</i>	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 CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Macropitilium atropurpureum</i>	Phy	340	680	-38.1		Morison and Gifford (1984) ^b
<i>Medicago sativa</i>	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; + Rhizobium	"
	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
<i>Oryza sativa</i>	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
<i>Phalaris aquatica</i>	Phy	340	680	-3.9		Morison and Gifford (1984) ^b
<i>Phaseolus vulgaris</i>	GC	320	2500	+36.9	Salinity=0 mM NaCl	Schwarz and Gale (1984)
	GC	320	2500	+0.1	Salinity=40 mM 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 CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Pisum sativum</i>	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	"
<i>Raphanus sativus</i>	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 μE m ⁻² s ⁻¹	Sionit et al. (1982) ^c
	Phy	350	675	+42.6	Light=1200 μE m ⁻² s ⁻¹	"
<i>Rubus idaeus</i>	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	"
<i>Solanum tuberosum</i>	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	"	
<i>Sorghum bicolor</i>	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
<i>Trifolium repens</i>	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 CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Triticum</i>	GC	350	700	+3.0	No N added to soil	Billes et al. (1993)
<i>aestivum</i>	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	"
<i>Vicia faba</i>	Phy	340	680	+20.5		Morison and Gifford (1984) ^b
<i>Vigna</i>	Phy	340	680	+15.0		Morison and Gifford (1984) ^b
<i>unguiculata</i>	Phy	340	680	+17.9		"

Table 1g. Percent change (ambient to elevated CO₂) in root to shoot ratios for crop species

Species	Location	Ambient [CO ₂]	Elevated [CO ₂]	% Δ R:S	Interacting variables ^a	Reference
<i>Vitis vinifera</i>	GC	350	1200	+419.5		Kriedemann et al. (1976) ^c
<i>Zea mays</i>	GC	350	600	+25.7	H ₂ O=50% ET replaced	King and Greer (1986)
	GC	350	600	-6.3	H ₂ O=75% ET replaced	"
	GC	350	600	-12.9	H ₂ O=100% ET replaced	"
	GC	350	850	+14.6	H ₂ O=50% ET replaced	"
	GC	350	850	-12.7	H ₂ O=75% ET replaced	"
	GC	350	850	+8.6	H ₂ O=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 μE m ⁻² s ⁻¹	Sionit et al. (1982) ^c
	Phy	350	675	+13.3	Light=1200 μE m ⁻² s ⁻¹	"
	GC	320	2500	-14.1	Salinity=0 mM NaCl	Schwarz and Gale (1984)
	GC	320	2500	-8.1	Salinity=50 mM NaCl	"
	GC	400	550	+68.6		Whipps (1985) ^b
GC	400	800	+94.3		"	

Concentrations are in ppm CO₂. Locations: GC = growth chamber; GH = glasshouse; OTC = open top chamber; SPAR = soil-plant-atmosphere-research chamber; Phy = phytotron; FACE = free-air CO₂ enrichment system.

^aN is mM NO⁻³ and light is μmol m⁻² s⁻¹ unless otherwise stated.

^bStudy had multiple harvests; data presented are from final harvest only.

^cData estimated from graphs.

^dAbbreviations represent varieties: NY = New Yorker; BB = Better Boy.

^eNumbers (60, 125, 220, 380, and 550) refer to light levels in μE m⁻² s⁻¹.

^fAbbreviations represent varieties: N = Norland; RB = Russet Burbank; D = Denali.

average responses centered close to zero ($\pm 8\%$). The range in relative R:S change for fruit crops was large, but they also showed an overall positive effect of elevated CO₂ (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 CO₂ 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 grow-

ing 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 CO₂ 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 CO₂ 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 CO₂) in root to shoot ratios for various types of crops

Crop	Number of observations	Mean	Range	Interacting variables
<i>Fiber crops</i>				
Cotton	8	-5.6	-49.1 to +47.4	[CO ₂]; N
<i>Fruit crops</i>				
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 ₂ O; variety; hormones
Raspberry	6	+91.2	+55.6 to +137.5	[CO ₂]; light
All fruit crops	36	+16.0		
<i>Grain crops (C₃)</i>				
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 ₂ O; light; density
All C ₃ grain crops	56	+5.8		
<i>Grain crops (C₄)</i>				
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 ₂ O; light; salt
All C ₄ grain crops	26	+4.3		
<i>Leaf crops</i>				
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		
<i>Legume crops</i>				
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 ₂ O
All legume crops	53	+7.9		
<i>Seed crops</i>				
Oilseed rape	1	+21.9	NA	NA
Sunflower	3	-10.9	-12.5 to -8.0	temp.
All seed crops	4	-2.7		
<i>Forage crops</i>				
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; <i>Rhizobium</i>
White clover	3	+17.7	+7.9 to +29.3	[CO ₂]
All forage crops	27	+6.6		
<i>Root and tuber crops</i>				
Carrot	1	+36.0	NA	NA
Kohlrabi	3	+17.7	-11.0 to +40.0	H ₂ O
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 ₂ O
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 CO₂ 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 CO₂ 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 CO₂ with light, temperature, nitrogen, and water (Table 3) appears to be in general agreement with the influence these factors exert under ambient CO₂; 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 CO₂ experiments (Linder and McDonald, 1993) points to a need for more careful control of plant growth conditions in the design of CO₂ effects research.

Plants growing under high CO₂ 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 CO₂ 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 CO₂ level. Elevated CO₂ may interact with other nutrients in different ways. Under ambient levels of CO₂, 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 CO₂ compared to ambient (Table 1). Excessive starch accumulation in leaves under elevated CO₂ 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 elevat-

ed CO₂-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 CO₂. They point out that earlier papers emphasized that elevated CO₂ 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 CO₂-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 CO₂ concentration or pot size influenced R:S response. The differential in CO₂ 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 CO₂ tested increases. However, it is likely that optimal levels of CO₂ 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 CO₂) 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=250 μmol 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 CO₂) in root to shoot ratios for various interacting variables

Crop	Number of observations	Interacting variables	% Δ R:S
Japanese millet	2	N=2 mM NO ₃ ⁻	-43.9
"	2	N=12 mM NO ₃ ⁻	-49.8
Soybean	1	N=0.5 mM NO ₃ ⁻	+27.9
"	1	N=1.0 mM NO ₃ ⁻	-9.0
"	1	N=2.5 mM NO ₃ ⁻	-4.2
"	1	N=5.0 mM NO ₃ ⁻	+32.5
"	1	N=10.0 mM NO ₃ ⁻	-5.2
Cotton	1	N=0.6 mM NO ₃ ⁻	-20.9
"	1	N=4.0 mM NO ₃ ⁻	-32.5
"	1	N=12.0 mM NO ₃ ⁻	-49.1
"	1	N=24.0 mM NO ₃ ⁻	-28.7
Alfalfa	14	N=1.5 mM NO ₃ ⁻	+9.9
"	7	N=15 mM 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 mM NO ₃ ⁻	+14.3
"	2	N=12 mM NO ₃ ⁻	+11.0
Σ	27	N="low"	+2.5
Σ	20	N="high"	-4.4
Kohlrabi	1	H ₂ O=replace 25% of water used	+40.0
"	1	H ₂ O=replace 50% of water used	+24.1
"	1	H ₂ O=replace 100% of water used	-11.0
Sweet potato	2	H ₂ O=adequately watered	+19.1
"	2	H ₂ O=water stressed	+21.7
Tomato	2	H ₂ O=adequately watered	-27.8
"	2	H ₂ O=water stressed	-22.5
Pea	1	H ₂ O=adequately watered	-13.1
"	1	H ₂ O=water stressed	-21.8
Wheat	3	H ₂ O=adequately watered	-2.5
"	3	H ₂ O=water stressed	-10.3
"	1	H ₂ O=40 ml/pot/watering event	-19.4
"	1	H ₂ O=60 ml/pot/watering event	-27.7
"	1	H ₂ O=120 ml/pot/watering event	-16.0
"	1	H ₂ O=240 ml/pot/watering event	-29.1
"	2	H ₂ O=no drought cycles	-0.3
"	2	H ₂ O=1 drought cycle	+12.5
"	2	H ₂ O=2 drought cycles	+1.5
Corn	2	H ₂ O=replace 50% of evapotranspiration	+20.2
"	2	H ₂ O=replace 75% of evapotranspiration	-9.5
"	2	H ₂ O=replace 100% of evapotranspiration	-2.2
Σ	15	H ₂ O=adequately watered	-6.6
Σ	17	H ₂ O=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 photosyn-

thetic 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 CO₂ 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 CO₂ (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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ suggests that future allocation experiments, designed to study CO₂ 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 CO₂.
2. Work in the area of allocation response to multiple resource interactions including CO₂ enrichment.
3. Field studies of allocation which take the response of entire ecosystems to CO₂ 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 CO₂.
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 be factored into the whole plant carbon budget as influenced by elevated CO₂.
6. The interactions of atmospheric CO₂ concentration and the effects of soil properties (soil structure and function) on root to shoot allocation.
7. Response of soil processes to CO₂-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 CO₂ and other resources as they affect whole plant carbon and nitrogen allocation.

Conclusion

We examined the influence of atmospheric CO₂ 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 CO₂ may well depend on prevailing environmental conditions. To better understand how elevated CO₂ 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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