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Effects of elevated [CO_2] at the community level mediated by root symbionts

Sandra Díaz
Instituto Multidisciplinario de Biología Vegetal (CONICET Universidad Nacional de Córdoba). Casilla de Correo 495. 5000 Córdoba, Argentina[*]

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Abstract

This review examines the effects of elevated [CO_2] on plant symbioses with mycorrhizal fungi and root nodule bacteria, with emphasis on community and ecosystem processes. The effects of elevated [CO_2] on the relationships between single plant species and root symbionts are considered first. There is some evidence that plant infection by and/or biomass of root symbionts are stimulated by elevated [CO_2], but growth enhancement of the host seemingly depends on its degree of dependence on symbiosis and on soil nutrient availability. Second, the effects of elevated [CO_2] on the relationships between plant multispecies assemblages and soil, and likely impacts on above-ground and belowground diversity, are analysed. Experimental and modelling work have suggested the existence of complex feedbacks in the responses of plants and the rhizosphere to CO_2 enrichment. By modifying C inputs from plants to soil, elevated [CO_2] may affect the biomass, the infectivity, and the species/isolate composition of root symbionts. This has the potential to alter community structure and ecosystem functioning. Finally, the incorporation of type and degree of symbiotic dependence into the definition of plant functional types, and into experimental work within the context of global change research, are discussed. More experimental work on the effects of elevated [CO_2] at the community/ecosystem level, explicitly considering the role of root symbioses, is urgently needed.

Introduction

The atmospheric concentration of CO_2 has increased by 25% in the last two centuries and its steady rise throughout the next century is the most certain prediction related with global change (Houghton et al., 1992). Accordingly, a large body of research has been devoted in the last few decades to the effects of elevated [CO_2] on plants. The interest on the effects of CO_2 enrichment on plant-soil processes, however, is much more recent. Although the existence of complex feedbacks involving root symbionts and other rhizospheric organisms was suggested in the early '80s (Lamborgh et al., 1983; Luxmoore, 1981), experimental initiatives aimed at exploring them were rare before the '90s. At present, there is a growing interest in the effects of elevated [CO_2] on root symbionts. This is probably related to the realisation that responses of whole communities cannot be predicted from single species experiments (Bazzaz and McConnaughay, 1992; Körner, 1993), and to the idea that the "missing carbon sink" (i.e. an amount of 1.8±1.4 Pg. per year not accounted for by the global C budgets; Houghton et al., 1992) could be connected with biotic below-ground processes (Dyson, 1992).

Probably one of the most important influences of elevated [CO_2] at the ecosystem level is the modification of plant carbon allocation patterns. Altered amount and quality of substrate made available to other trophic levels may produce changes in the whole cycling of materials through food webs. Root symbionts are a constituent part of most natural terrestrial communities, thus these changes may have major implications for their responses to the changing environmental conditions expected for the next century. Most of the research effort in this field has been focused on simple systems, typically involving one plant species and one or very few root symbiont species/isolates. Very recently, however, the role of root symbionts within

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[*] FAX No.: + 5451332104. E-mail: sandra@imbiv.edu.ar

more complex systems has begun to receive increasing attention.

The main objective of this article is to review what is known to date about the effects of elevated [CO_2] on plant associations with mycorrhizal and root nodule symbionts, with emphasis on community and ecosystem processes. It also aims at identifying areas in which critical information is needed in order to increase our understanding of likely responses of natural systems to global environmental change. The effects of elevated [CO_2] are considered at three levels. Firstly, a review is presented on the relationships between single plant species and root symbionts. Symbioses with AM and EM mycorrhizal fungi, root nodule bacteria and to a lesser extent ericoid mycorrhizal fungi and N-fixing actinomycetes, are considered. Secondly, more complex interactions between plant multispecies assemblages and soil, and impacts on aboveground and below-ground diversity, are analysed. Finally, the incorporation of symbiotic relationships into the definition of plant functional types, and into experimental work within the context of global change research, are discussed.

Effects of elevated [CO_2] on the interactions between single plants and root symbionts

The most important effects of mycorrhizal fungi and root nodule bacteria on plants include increased nutrient and water status, increased protection from pathogens and toxicity, and stimulation of photosynthesis due to enhanced sink strength for carbon (Table 1). There are several thorough reviews on the topic, and probably the most general conclusion from them is that in many plants the presence of root symbiosis tends to enhance host-plant performance, at least at some life stages, and particularly when growing under low nutrient supply (Allen, 1991; Fitter, 1985; Harley and Smith, 1983; Read, 1991).

Elevated [CO_2] may influence root growth, activity and/or concentration of non-structural carbohydrate, and thus has the potential to alter plant-symbiont relationships. This section summarises reported effects of CO_2 enrichment on below-ground processes, with emphasis on mycorrhizal and nodulating plants.

Effects of elevated [CO_2] on plant carbon allocation below ground

The amount and quality of living roots and root-derived compounds (exudates, sloughed-off cells and dead roots) are extremely important for below-ground processes (Van Veen et al., 1989). Mycorrhizas (Clarkson, 1985; Jakobsen and Rosendahl, 1990) and nodulated legume roots (Kucey and Paul, 1982) represent high demands for C and therefore stimulate the transport of carbohydrate through the root system and the C fixation at the whole-plant level. Accordingly, several authors have reported stimulated photosynthesis in the presence of mycorrhizal and root nodule bacteria as compared with uninfected plants (Allen et al., 1981; Paul and Kucey, 1981; Reid et al., 1983). Within a single plant, individual EM- (Reid et al., 1983) and AM-infected roots (Pearson, 1993; Snellgrove et al., 1982) act as greater sinks for photosynthate than non-mycorrhizal roots, at least at early stages of development. The presence of AM fungi decreases exudation (Graham et al., 1981; Ratnayake et al., 1978) and the concentration of soluble carbohydrate in the roots, affecting the amount of C available for root growth and for colonisation by other symbiotic fungi (Pearson, 1993). Increased biomass and C:N ratios of roots should therefore stimulate symbioses betweeen plants and nodule bacteria and/or mycorrhizal fungi.

There is evidence that this happens in some plants growing under elevated [CO_2], although this response is by no means universal (Table 2). Root mass consistently increases under elevated [CO_2] (Bazzaz, 1990; Eamus and Harvis, 1989; Rogers et al., 1994; Stulen and den Hertog, 1993), despite the fact that root-to-shoot ratio on average seems to change little (Norby, 1994). The effect of CO_2 enrichment on root C:N ratio is not consistent across species and experimental conditions. Although it increases in many cases, it remains unchanged in others. The same is true for exudation from roots to the rhizosphere.

Effects on mycorrhizal and nodulating plants

Conclusions from recent reviews (O'Neill, 1994; Rogers et al., 1995; Stulen and den Hertog, 1993) seem to support the idea that elevated [CO_2] may enhance the growth of root symbionts through altered C allocation patterns of host plants. Under CO_2 enrichment, more mycorrhizal tissue per plant is usually reported. This is a result of greater root mass with unchanged percent root colonised in some studies, and of net increase of

Table 1. Summary of the most important effects of root symbioses on host plants

Effect	Type of symbiont	Source
Enhacement of nutritional status		
Nitrogen	EM fungi	Abuzinadah and Read (1986a, b)
	Ericoid mycorrhizal fungi	Bajwa and Read (1985)
Phosphorus	AM fungi	Bolan et al. (1987)
		Graham et al. (1981)
	EM fungi	Finlay and Read (1986)
Potassium	AM fungi	Bethlenfalvay et al. (1989)
	EM fungi	Rygiewicz and Bledsoe (1984)
Calcium	AM fungi	Rhodes and Gerdeman (1978)
	Ericoid mycorrhizal fungi	Leake and Read (1989)
Sulphur	AM fungi	Cooper and Tinker (1978)
Nitrogen and Phosphorus	AM fungi and root nodule bacteria	Bethenfalvay et al. (1989)
		Kucey and Paul (1982)
Enhancement of water status	AM fungi	Allen and Allen (1986)[a]
		Sanders and Tinker (1973)[a]
		Trent et al. (1989)
	EM fungi	Bowen (1973)
Increased sink strength for C	AM fungi	Snellgrove et al. (1982)
		Trent et al. (1989)
	EM fungi	Reid et al. (1983)
	Root nodule bacteria	Paul and Kucey (1981)
Protection from pathogens	AM fungi	Newsham et al. (1995)
	EM fungi	Marx (1969)
		Sylvia and Sinclair (1983)
Protection from toxicity	Ericoid mycorrhizal fungi	Jalal and Read (1983)

[a]Only during periods of water stress.

colonisation per unit root mass in some others (Table 2). According to O'Neill (1994), the second situation seems more common among EM-mycorrhizal plants). Total N-fixation in nodulating plants also tends to increase under CO_2 enrichment due to increased nodule weight and/or to enhanced specific nodule activity (Table 2).

It is not very clear, however, whether the enhanced symbiont biomass and/or activity is reflected in enhanced plant performance. Sustained sink strengh for C seems necessary for plant growth enhancement by elevated [CO_2] for extended periods (Arp, 1991; Stitt, 1991). Larger or more numerous root nodules or larger mycorrhizal hyphae may act as extra sinks for carbohydrate, and thus suppress or retard downregulation effects on photosynthesis (Lewis et al., 1994). Most infected plants show increased dry weight and/or better nutritional status under elevated [CO_2], but in a small number of cases no significant change was found (see O'Neill, 1994; Rogers et al., 1995; Stulen and den Hertog, 1993 for detailed discussion and references). The extra benefits that plants could obtain from symbionts under CO_2 enrichment are likely to depend on their degree of reliance on symbiosis and on resource availability from the soil. Experimental studies on symbiotic and non-symbiotic species

Table 2. Effects of elevated [CO_2] on plant carbon allocation below ground and root symbioses. -: root symbionts absent or not addressed in the study

	Response to elevated CO_2	Plant species	Type of symbiont	Source
Root mass	Increased	*Alnus rubra*	*Frankia*	Amone and Gordon (1990)
		Citrus aurantium	-	Idso and Kimball (1991)
		Liriodendron tulipifera	-	O'Neill et al. (1987b)
		Pinus echinata	EM fungi	O'Neill et al. (1987a)
		Pinus taeda	EM fungi	Lewis et al. (1994)
		Pinus taeda	-	Tschanplinsky et al. (1993)
		Populus grandidentata	-	Zak et al. (1993)
		Quercus alba	EM fungi	O'Neill et al. (1987a)
		Triticum aestivum	-	Billès et al. (1993)
	Unchanged	*Artemisia tridentata*	-	Johnson and Licoln (1991)
		Betula nana	-	Oberbauer et al. (1986)
		Bouteloua gracilis	-	Riechers and Strain (1988)
Root C:N ratio	Increased	*Betula pendula*	-	Cotrufo and Ineson (1995)
		Castanea sativa	-	Côuteaux et al. (1991)
		Picea sitchensis	-	Cotrufo and Ineson (1995)
		Pinus echinata	EM fungi	Norby et al. (1987)
		Pinus taeda	EM fungi	Lewis et al. (1994)
		Pinus taeda	-	Tschanplinsky et al. (1993)
		Scirpus olneyi	-	Curtis et al. (1990)
	Unchanged	*Glycine max*	-	Vessey et al. (1990)
		Spartina patens	-	Curtis et al. (1990)
		Triticum aestivum	-	Billès et al. (1993)
Exudation	Increased	*Castanea sativa*	-	Rouhier et al. (1994)
		Triticum aestivum	-	Lekkerkerk et al. (1990)
	Increased only at early stages	*Pinus echinata*	EM fungi	Norby et al. (1987)
	Unchanged	*Triticum aestivum*	-	Billès et al. (1993)
		Zea mays	-	Whipps (1985)
Mycorrhizal biomass	Increased	*Liriodendron tupilifera*	AM fungi	O'Neill et al. (1991)
		Pinus echinata	EM fungi	O'Neill et al. (1987a)
		Pinus taeda	EM fungi	Lewis et al. (1994)
		Quercus alba	EM fungi	O'Neill et al. (1987a)
	Increased only at early stages	*Pinus echinata*	EM fungi	Norby et al. (1987)
Mycorrhizal colonisation	Increased	*Bouteloua gracilis*	AM fungi	Monz et al. (1994)
		Pinus echinata	EM fungi	Norby et al. (1987)
		Quercus alba	EM fungi	O'Neill et al. (1987a)
	Increased only at early stages	*Pinus echinata*	EM fungi	O'Neill et al. (1987a)
	Unchanged	*Liriodendron tupilifera*	AM fungi	O'Neill et al. (1991)
		Pascopyrum smithii	AM fungi	Monz et al. (1994)
		Pinus taeda	EM fungi	Lewis et al. (1994)

Table 2. Continued.

Nodule weight	Increased	*Alnus rubra*	*Frankia*	Amone and Gordon (1990)
		Eleagnus angustifolia	*Frankia*	Norby (1987)
		Glycine max	*Rhizobium*	Finn and Brun (1982)
		Glycine max	*Rhizobium*	Shivashankar and Vlassak (1978)
		Robinia pseudoacacia	*Rhizobium*	Norby (1987)
		Trifolium repens	*Rhizobium*	Masterson and Sherwood (1978)
Specific nodule activity	Increased	*Alnus rubra*	*Frankia*	Amone and Gordon (1990)
		Glycine max	*Rhizobium*	Shivashankar and Vlassak (1978)
		Trifolium repens	*Rhizobium*	Masterson and Sherwood (1978)
	Unchanged	*Eleagnus angustifolia*	*Frankia*	Norby (1987)
		Glycine max	*Rhizobium*	Finn and Brun (1982)
		Robinia pseudoacacia	*Rhizobium*	Norby (1987)

often involve different nutritional conditions. Therefore direct comparisons of plant growth enhancement under elevated [CO_2] accross a wide range of symbiotic and non-symbiotic species are difficult. However, recent reviews suggest that the growth of mycorrhizal and nodulating plant species may be more stimulated by high [CO_2] than that of non-symbiotic species (Poorter, 1993; Rogers et al., 1995; Stulen and den Hertog, 1993).

Symbiotic interactions: a missing link in ecosystem studies?

The previous section focused on the effects of elevated [CO_2] on interactions between individual plants and their symbionts. Recent studies on more complex assemblages, however, indicate the existence of various feedbacks between soil microbiota and different kinds of plants. Therefore the responses of natural systems may not be predictable from the results observed in experiments on single plant species growing under highly artifcial conditions (Bazzaz and McConnawghay, 1992; Körner, 1993; O'Neill and Norby, 1996). The effects of elevated [CO_2] on the relationships between plants, soil, and belowground organisms are poorly understood, in part because of methodological difficulties. Net nutrient mineralization (Hungate, 1995; Körner and Amone, 1992; Norby et al., 1986; Zak et al., 1993) or immobilisation (Díaz et al., 1993; Owensby et al., 1994; Rouhier et al., 1994; Whitford, 1992) in the soil have been proposed as likely outcomes under atmospheric CO_2 enrichment. These studies have in common that they either ignored root symbionts, or considered them as a "black box" (Klironomos et al., 1995). Although its potential importance was highlighted in early models (Luxmoore, 1981), the role of root symbionts has been also overlooked in most of the subsequent modelling developments (see Andersen et al., 1992 for review). This may seriously mislead attempts to predict the responses of natural communities to a changing environment, because of two reasons: (1) elevated [CO_2] may differentially enhance the growth of mycorrhizal and nodulating plants and alter rhizospheric processes involving free-living microorganisms, therefore the balance between symbiotic and non-symbiotic plants in mixed stands may shift; and (2) mycorrhizal fungi are known to have considerable influence at the community and ecosystem levels; these effects may be altered if fungal biomass or composition changes.

Elevated [CO_2] may tip the balance between symbiotic and non-symbiotic plants

In mixed communities involving symbiotic and non-symbiotic species, elevated [CO_2] may be expected to differentially promote the growth of symbiotic species by the concurrence of two mechanisms. First, as reported from experiments on individual plants, atmospheric CO_2 enrichment tends to enhance mycorrhizal and nodule biomass and/or activity. Second, as suggested by Díaz et al. (1993), non-symbiotic species, lacking the sinks for C represented by symbiotic fungi and/or bacteria, may release increased amounts of carbonaceous substrate into the rhizosphere, stimulating the competition for nutrients between roots and free-living microbes surrounding them. This process may be particularly important for fast-growing, nonmycorrhizal species from disturbed habitats, which tend to have high nutritional requirements (e.g. Brassicaceae, Caryophyllaceae, Chenopodiaceae, Polygonaceae; Francis and Read, 1994; Grime et al., 1988; Read, 1991). Mycorrhizal or nodulating roots, on the other hand, may experience decreased competition by surrounding free-living microbes due to their decreased release of carbonaceous exudates to the rhizosphere, as well as the benefits from enhanced symbiosis,. Although this last suggestion still awaits specific testing, there is some circumstantial evidence that C exudation to soil is lower in mycorrhizal roots than in nonmycorrhizal roots (Graham et al., 1981; Ratnayake et al., 1978). Higher sink strength of mycorrhizas for C is invoked as the most likely explanation (Pearson, 1993; Reid et al., 1983; Snellgrove et al., 1982).

Very little experimental work has been published on the impacts of CO_2 enrichment on the interaction between symbiotic and non-symbiotic plant species. Some of the few available examples seem to support the idea that elevated [CO_2] would differentially affect symbiotic and non-symbiotic species in mixed communities. Díaz et al. (1993), working with microcosms from a productive tall herb community and an acidic grassland, found that increase in leaf C:N ratio under elevated [CO_2] was much greater in nonmycorrhizal than in mycorrhizal plants (30% and 10%, respectively). Spring et al. (1996) subjected calcareous grasslands to elevated [CO_2] and temperature in the field, and found ca. 60% total biomass decrease of nonmycorrhizal species, and approximately 50% of increase of mycorrhizal species.

Information on the responses of plants associated with N-fixing bacteria to elevated [CO_2] in mixed communities is also scant. Newton et al. (1994) and Ross et al. (1995), working with turves of *Trifolium repens* and *Lolium perenne*, found that elevated [CO_2] differentially promoted the growth of nodulating *T. repens*. On the other hand, preliminary results reported by Rötzel et al. (1995) suggest no differential responses of nodulating legumes to elevated [CO_2] in calcareous grasslands, as compared with non-nodulating plants. It is obvious that the evidence is still too scarce to draw generalisations, and new insights should be gained from medium- to long-term experiments.

Elevated [CO_2] may affect diversity and succession

Root symbionts can play a substantial role in the structure and functioning of natural ecosystems, by influencing the diversity and succession of plants communities and also affecting the diversity of other trophic levels. Mycorrhizal fungi are known to transfer resources between plants of different species (see Newman, 1988 for review). AM fungi contribute to plant diversity (Grime et al., 1987), even in highly disturbed early-successional communities (Gange et al., 1990), by transference of resources from dominant to subordinate individuals (Grime et al., 1987) and/or direct antagonistic effect of the AM fungal mycelium on the growth of nonmycorrhizal species (Francis and Read, 1994). EM fungi and AM fungi influence plant diversity and secondary succession in forests (Amaranthus and Perry, 1994; Janos, 1983). It seems obvious that root symbionts can hardly be overlooked when trying to investigate vegetation responses to global change. However, to my knowledge no experiment has been published specifically addressing their role in secondary succession or resource transfer between plant species under elevated [CO_2].

Responses not only of biomass and activity, but also of genetic and functional diversity of root symbionts are worth considering in global change research. Mycorrhizal fungi and N-fixing symbiotic bacteria show considerable diversity, which does not necessarily follow pattems of plant diversity (Allen et al., 1995; Young and Johnston, 1989). Higher atmospheric [CO_2] may result in shifts in fungal community composition (Klironomos et al., 1995; Lewis et al.,1994; O'Neill, 1994). Given the wide differences in the ability of mycorrhizal fungi to enhance the growth of the host (Abbot and Robson, 1985; Sanders et al., 1977), this in turn may affect vegetation composition. For example, results from Klironomos et al. (1995) and Lewis et al. (1994) suggest shifts from mutualistic to opportunistic/parasitic interactions under CO_2 enrichment, involving AM and EM fungi, respectively.

Very few experiments on the effects of elevated [CO_2] on diversity of non-symbiotic below ground organisms have been carried out, with mixed and sometimes opposite results (Côuteaux et al., 1991; Freckman et al., 1991; Runion et al., 1994; J Lawton, pers. comm.). Mycorrhizal composition influences the diversity of other belowground microorganisms (fixing- and non-fixing bacteria, protozoa, collembola) through altered exudation, and also because grazers tend to have preferences for specifc fungal species/isolates (Fitter and Garbaye, 1994; Ingham and Massicotte, 1994). Altered patterns of C allocation to mycorrhizas under high [CO_2] thus may modify interactions across the whole rhizosphere.

The lack of information about the effects of elevated [CO_2] on the complex community/ecosystem processes discussed in this section seriously precludes our capacity to predict the responses of natural systems to global change. It is imperative to design ecosystem-level experiments in which specific hypothesis on the role of root symbioses are tested.

Root symbioses, elevated-CO_2 responsiveness, and plant functional types

In view of the complexity of organisms and interactions which make up most natural systems, it is clear that studying the responses of every single (or even dominant) species is not a reasonable way for global change research to proceed. Some authors have put forward the concept of functional types as a possible way to tackle this problem (e.g. Smith et al., 1996). Functional types are sets of organisms showing similar responses to environmental conditions and similar effects on dominant ecosystem processes. Some research groups have taken the approach of identifying key traits associated with plant response to major environmental factors, and constructing plant functional types on that basis (Díaz and Cabido, 1995; Grime et al., 1996; Leishman and Westoby, 1992). Plant responsiveness to elevated [CO_2] is undoubtedly to be taken into account in this task. The challenge here is to predict whether a plant will show enhanced growth under CO_2 enrichment on the basis of its morphological and functional traits. At the individual level, there is a large body of literature pointing to photosynthetic pathway and assimilate demands (determined in turn by relative growth rate, size, presence of non-photosynthetic organs, and longevity) associated with enhanced plant growth under elevated [CO_2]. Plants with high relative growth rate and high sink strength capacity tend to be more responsive than those which are either slow-growing or fast growing, short-lived, and small (Hunt et al., 1991, 1993; Poorter, 1993). However, performance in communities is usually not predictable from behaviour in short-term physiological experiments in which plants are grown in isolation (Körner, 1993; O'Neill and Norby, 1996). Díaz (1995) has recently advocated the inclusion of other traits, which can be measured on individual plants, but, at the same time, are relevant to interactions within multispecies assemblages. Examples of those traits are canopy display and phenology, mode of acquisition of mineral nutrients, and interactions with aboveground and belowground organisms.

The presence and nature of root symbionts is a good example of these kind of trait. The occurrence of root symbioses, and especially mycorrhizal status, is often related with plant traits and habitat characteristics in a predictable way. A preliminary model of these recurrent patterns and their likely association with plant responsiveness to elevated [CO_2] is presented in Table 3. There are well-established trade-offs between plant traits that lead to low nutrient loss rate in resource-poor habitats, and those that lead to high dry matter production in productive habitats (Chapin et al., 1993; Grime et al., 1988). Plants in the first group tend to be more dependent on mycorrhizal symbioses than those in the second group (Grime et al., 1988; Read, 1991). Very few plant families are composed mostly of nonmycorrhizal species (Newman and Reddell, 1987). Their members tend to be fast-growing, short-lived plants, with high seed output and strong nutritional demands, which typically thrive on highly disturbed, early successional habitats and are excluded from most closed plant communities (Francis and Read, 1994; Grime et al., 1988; Read, 1991). Notable exceptions to this general pattern are members of the Proteaceae and Cyperacea, which are typically nonmycorrhizal slow-growing plants of nutrient poor, nondisturbed habitats. However, they show specialised roots structures (swollen portions of lateral roots, bearing dense clusters of root hairs) that are usually interpreted as playing a role in soil resource capture (Torrey and Clarkson, 1975). Although there are examples of plants associated with N-fixing bacteria among both the fast-growing, long-lived perennials and fast-growing "pionner" species, N-fixing symbiosis is probably disadvantageous for both plants with very short lifespan, and those growing under severe water, temperature or pH stress (Pate, 1986).

Some recurrent patterns linking symbiotic interactions, plant physiological and morphogenetic traits, and responsiveness to elevated [CO_2] are starting to emerge. However, clearly more exploration is needed in order to assess the validity of the model sketched in Table 3. These likely associations need sharper definition, in order to be explicitly tested. Major obstacles are the low comparability of studies on plant responses to elevated [CO_2], and the limited range of plant families and functional types involved in these studies. Further integration of possible effects of [CO_2] into theories of C allocation at the whole-plant and plant-soil levels is also required. However, the incorporation of type and

Table 3. A preliminary model of recurrent association patterns among habitat characteristics, plant traits, symbiotic status, and expected plant responses to atmospheric high [CO_2]. See text for further explanation, and references indicated by superscript letters for description of mechanisms and examples

Habitat[a,g,n]	Nutrient availability chronically low High C:N ratio in soil Low disturbance	Intermediate or seasonally high nutrient availability Disturbance low to intermediate	High nutrient availability Low C:N ration in soil High disturbance
Plant traits[c,d,e,g,h,n]	Slow-growing perennials	Perennials with intermediate to high growth rates	Fast-growing annuals and ephemerals
	Investment in long-term resource storage	Investment in long-term resource capture and growth	Investment in short-term growth and reproduction
	High investment in C-based defence	Various defence strategies	Low investment in C-based defence
	Low litter decomposition rate	Litter decomposition rates intermediate to high	High litter decomposition rate
Symbiotic associations[a,j,k,l,n]	High mycorrhizal dependence (ericoid, EM, AM)	High to intermediate mycorrhizal dependence (EM, AM)	Nonmycorrhizal or faculative AM mycorrhizal
	Association with root nodule bacteria infrequent	Tripartite association with root nodule bacteria common	Association with root nodule bacteria infrequent
Predicted growth enhancement by high [CO_2][b,f,h,l,m]	Nil to moderate, sustained in time	High, sustained in time	Nil to low, after an initial high pulse
	Chronic source limitation of photosynthesis associated with intrinsically low growth rate	Symbiotic associations may help to maintain high sink strength for C during unfavourable season Most likely to sustain adequate source:sink balance	Early down regulation of photosynthesis associated with lack of sink organs

[a] Allen (1991); [b]Bazzaz (1990); [c]Bryant et al. (1983); [d]Chapin et al. (1993); [e]Cornelissen (1996); [f]Díaz (1995); [g]Grime et al. (1988); [h]Hunt et al. (1991, 1993); [i]Körner (1993); [j]Janos (1983);[k]Newman and Reddell (1987); [l]Pate (1986); [m]Poorter (1993); [n]Read (1991).

degree of symbiotic associations seems both desirable and feasible in the search for functional types within the framework of climate change research.

Concluding remarks

Root symbionts play an important role in many natural systems. The evidence to date indicates that elevated [CO_2] is likely to have an effect on them, mediated by altered C inputs from plants. This in turn is expected to modify community structure and ecosystem functioning in various and perhaps unexpected ways. Therefore, these factors should not be underestimated in experimental or modelling studies aimed at predicting the responses of natural systems to global change.

Two ways can be mentioned to incorporate the role of root symbionts into global change research. Firstly, in community experiments (both in the field and in micro- or mesocosms) root symbioses can be deliberately manipulated, or at least explicitly taken into account in the design. Secondly, the so-called "big-leaf" approach, namely extrapolating directly from short-term physiological responses of leaves to vegetation, which is then treated as a black (or green) box, is unlikely to produce reliable predictions of the responses of natural communities to rising atmospheric [CO_2]. An alternative or complementary way is to consider the concept of plant functional types. Responsiveness to elevated [CO_2] is an obvious criterion to incorporate into them, and in doing so the degree and nature of symbiotic associations should not be ignored.

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