23 Increases in Atmospheric [CO_2] and the Soil Food Web

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23.1 Introduction

Organic matter deposited in soil by plants is the energy source for a complex web of functionally and nutritionally interconnected species. Bacteria and fungi, the initial consumers of soil organic matter, are themselves substrates for a multitude of tiny predators and grazers, including protozoa, nematodes, and arthropods, which comprise the soil food web (Brussaard et al. 1997). Dead plant tissue (i.e. litter), from both aboveground and belowground sources, is the dominant pathway by which plant carbon (C) moves to soil (Schlesinger and Lichter 2001), but living roots also transfer C to soil through turnover of fine roots (Jackson et al. 1997; Matamala et al. 2003) or living cells (Hawes 1990) and as soluble exudates (Rovira 1991). Direct herbivory of roots by certain nematodes (Ferris 1982) and other parasites constitutes another channel for C movement to soil. Plant C transferred to mycorrhizal fungi can be viewed as exudation because these organisms are separated from plant cells by membranes. Exuded compounds released from living roots may be more important than previously recognized because they are dynamically linked to plant growth (Farrar et al. 2003) and can be influenced both passively (Owen and Jones 2001; Jones et al. 2005) and actively (Phillips et al. 2004) by soil microorganisms. Thus, if either plant production of exudates or microbial pilfering of these compounds increases, one can foresee major effects on soil food web organisms and associated C storage. The importance of understanding how plant growth and microbial productivity are linked is widely recognized (Paterson 2003), but the specific mechanisms that control those connections are poorly understood.

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23.1.1 Soil Food Webs: The Concept

Soil food webs are assemblages of diverse, interdependent species. Although clear trophic levels often exist in aboveground ecosystems, the interdependence of microorganisms (bacteria and fungi), microfauna (protozoa and nematodes), mesofauna (mites, collembolans, and enchytraeids), and macrofauna (earthworms, ants, termites, and herbivorous insects) makes it difficult to distinguish trophic levels in belowground systems (Brussaard et al. 1997). As a result, soil organisms frequently are assigned to "functional" groups that share particular ecosystem roles, such as root colonization or predation (Fig. 23.1). Studies in which individual species have been removed show that not all species in a functional group are required for the basic operation of an ecosystem (Laakso and Setälä 1999). The exact niche of each species can be unclear, but temporal and spatial differences in species activity are often revealed by detailed observation (Gunapala et al. 1998; Ferris and Matute 2003).

One fundamental characteristic of soil food webs is that they are primarily heterotrophic assemblages which depend ultimately on autotrophic plants for a continuing supply of C resources. This fact suggests selection pressures may have favored survival of mutualistic interactions that stimulate plant growth while promoting an immediate or ultimate transfer of plant C to the soil organisms (Wall and Moore 1999). Existing ecological data support this idea.

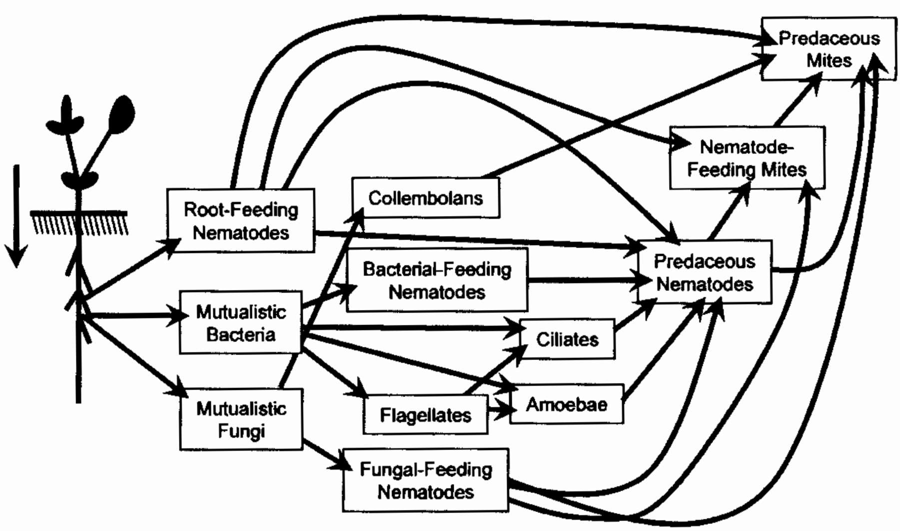

Fig. 23.1 Carbon flow in a soil food web associated with plant roots. Autotrophic plants supply C to root-colonizing organisms, which transfer C to various interconnected grazers and predators. (Moore and de Ruiter 1991)

eral nutrient status, undoubtedly influenced the results. One overall conclusion may be that elevated [CO_2] increases soil respiration, microbial respiration, and microbial biomass, if other factors are not limiting, but increases in any particular case will be difficult to predict and probably are a function of environmental conditions, the community structure, and metabolic rates of individual organisms.

Studies of elevated [CO_2] effects on soil food web structure show other incompletely explained changes. Data indicate that increased [CO_2] frequently stimulates mycorrhizal fungi (Langley et al. 2003; Rillig and Field 2003; Treseder et al. 2003; Olsrud et al. 2004); and such effects could alter soil food webs. In one study where fungal grazers were examined, the number of collembolans, which prefer non-mycorrhizal fungi, increased with additional N and elevated [CO_2] as their favored fungal food sources proliferated more than the mycorrhizal fungi (Klironomos et al. 1997). In other experiments, elevated [CO_2] altered the mixture of species present in assemblages of nematodes (Hoeksema et al. 2000; Yeates et al. 2003), protozoans (Treonis and Lussenhop 1997; Yeates et al. 2003), and collembolans (Jones et al. 1998). In most cases, the changes in species present occurred without altering the total abundance of organisms. Such changes may not always reflect varying availability of C resources because other parameters, such as soil moisture, could also have changed.

Soil food webs frequently are dominated by either bacteria or fungi, which are viewed as separate channels for energy flows (Moore and Hunt 1988; De Ruiter et al. 1993). Measurements at the ETH FACE site showed clear effects of elevated [CO_2] and N fertilization on these two energy channels (J.C. Moore and H. Ferris, unpublished data). Saprobic and mycorrhizal fungi declined with increased N, while protozoa feeding in the bacterial channel increased with N additions and decreased under elevated [CO_2]. Responses of bacterial-feeding, fungal-feeding, and plant-feeding nematodes were not definitive, but omnivorous nematodes, which are supported by both energy channels, declined with N fertilization, which is consistent with their sensitivity to mineral fertilizers (Tenuta and Ferris 2004). These changes are consistent with shifts toward the bacterial energy channel, which occur with increasing amounts of N derived from mineralization (Moore et al. 2003). They also suggest shifts toward the fungal energy channel under elevated [CO_2], in which case the potential for C storage and N immobilization may increase.

Given uncertainty over changes in total soil C under elevated [CO_2], attention has focused on how altered [CO_2] affect particular C inputs from plants. In forest ecosystems, elevated [CO_2] increased plant litter (Schlesinger and Lichter 2001) and living fine roots (Matamala and Schlesinger 2000). At the same time, however, the accumulation of both litter and dead fine roots was restricted by their turnover rates (Matamala and Schlesinger 2000; Schlesinger and Lichter 2001; Matamala et al. 2003). Such results suggest that the degradation capacity of soil food webs exceeded any incremental C inputs produced by elevated [CO_2]. A complete understanding of the forces operating in such experiments, however, requires an analysis of soluble root exudates.

Separating soluble root exudates from degradation of organic compounds in complex ecosystems is difficult; and for this reason data that assess changes in dissolved organic carbon under elevated [CO_2] (Jones et al. 1998; Uselman et al. 2000) cannot be interpreted as measures of root exudation. The possibility that root exudation rises with elevated [CO_2] is supported by an increase in oxalate outside the root under higher [CO_2] (Delucia et al. 1997), but data describing the effects of elevated [CO_2] on other key root exudates, such as amino acids and sugars (Fan et al. 2001), have not been reported. Because bacteria and fungi often stimulate root exudation (Meharg and Killham 1995), predators and grazers on these microorganisms could influence exudation and their interactions may affect soil C storage. For these reasons, a direct examination of how elevated [CO_2], microorganisms and the soil food web affect root exudation is justified.

23.3 Root Exudation and the Effects of Elevated [CO_2]

Root exudation of soluble compounds, such as amino acids, is a multi-faceted process involving both efflux and influx components (Fig. 23.2; Jones and Darrah 1994). Thus amino acid "exudation" is more properly viewed as a *net* efflux. Simple sugars move in and out of plant roots by mechanisms similar to those controlling amino acid fluxes (Jones and Darrah 1996), but dicarboxylic acids move primarily out of the root, and little influx has been detected at ecologically relevant concentrations (Jones and Darrah 1995). In biochemical terms, the passive efflux of amino acids is driven primarily by large differences in concentration between the inside (e.g. 10 mM) and the outside (e.g. 0.1–10 μM) of root cells, while influx involves proton-pumping ATPases that maintain an electrochemical potential difference across the plasma membrane to support uptake into the plant by proton-coupled amino acid transporters (Farrar et al. 2003). Other materials released from roots, such as proteins, complex carbohydrates, and insoluble cellular debris, are often mediated by physical processes, including herbivory by nematodes, enchytraeids, and insects, which are not addressed here.

Early work established that the presence of microorganisms around roots could increase photosynthate released by the plant into the soil (Meharg and Killham 1995). For amino acids, that increase occurs because amino acids present in soil at low concentrations, such as those coming from root exudation, are taken up more effectively by microorganisms than by roots (Jones et al. 2005). Obviously any amino acids used by microorganisms would not be available for reabsoprtion by the plant (Owen and Jones 2001). Though com-

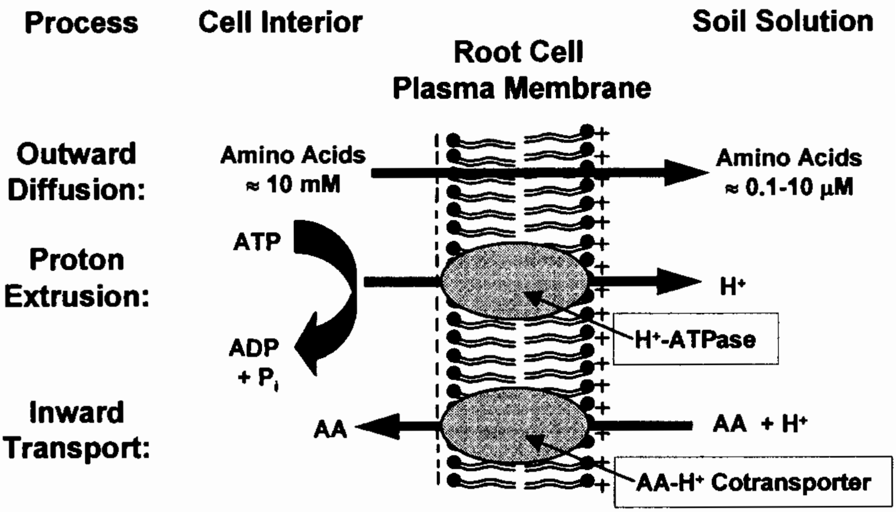

Fig. 23.2 Plant processes involved in amino acid (*AA*) exudation from roots. Amino acid exudation represents the net efflux resulting from separate efflux and influx processes (Jones and Darrah 1994). Exudation of most simple sugars also follows the principles shown here (Jones and Darrah 1996), but the dicarboxylic acid citrate is lost through efflux without being reabsorbed (Jones and Darrah 1995)

pletely correct, this traditional view of microorganisms as passive receptacles for amino acids lost from roots lacks the complexity suggested by data indicating that compounds produced by bacteria and fungi can actively increase the net efflux of amino acids (Phillips et al. 2004). That work, which quantified both efflux and influx components for 16 amino acids, showed that treating roots of four species of axenic plants with 100 μM 2,4-diacetylphloroglucinol (DAPG), increased net efflux 3- to 20-fold. DAPG is a common product of *Pseudomonas* bacteria (Cook et al. 1995), and 100 μM can be an ecologically relevant concentration (Bonsall et al. 1997). Other microbial compounds, including phenazine and phenazine-1-carboxylate from *Pseudomonas* (Taraz et al. 1990) and zearalenone from *Fusarium* fungi (Jimenez et al. 1996), also enhanced amino acid exudation in the absence of microorganisms (Phillips et al. 2004).

Additional experiments have now quantified influx and efflux of amino acids in maize, annual ryegrass, and medic seedlings treated with 425 ppm or 850 ppm [CO_2] (Phillips et al. 2006). Those results show that elevated [CO_2] probably can enhance rhizodeposition by two mechanisms. First, in C-3 wheat and medic, higher [CO_2] promoted root growth without altering amino acid efflux rate (nmol g^{-1} root fresh weight), and thus a larger root surface area would allow more exudation. Second, in C-4 maize elevated [CO_2] did not stimulate root or shoot growth, but there was a 44 % increase in the total efflux rate of 16 amino acids, which was associated with a significant (P=0.05) increase in efflux rates of six individual amino acids. These studies used axenic seedlings to examine the innate efflux and influx capacities of plants growing in the absence of culturable microorganisms. Roots of the three plant species studied, under both ambient and elevated [CO_2], took up the 16 amino acids at rates 94–374 % higher than they were effluxed, but in soil, adsorption of amino acids to soil particles before they were recovered through influx to the root should increase rhizodeposition under elevated [CO_2]. These striking results emphasizes the important role of microorganisms as both passive (Owen and Jones 2001; Jones et al. 2005) and active (Phillips et al. 2004) promoters of root exudation.

23.4 Linking Plants to Soil Food Webs under Changing [CO_2]

Soil food webs clearly can stimulate plant growth (Bonkowski 2004); and increased exudation under elevated [CO_2] has the potential to promote this effect by nurturing food web activities. Understanding these interactions and how they relate to progressive N limitations (Luo et al. 2004) are requirements for predicting the effects of climate change on soil food web functions. Predation of microorganisms by nematodes, protozoans, and/or arthropods contributes significantly to plant growth. In quantitative terms, predation can increase growth of a perennial grass by 145 % when nematodes feed on bacteria (Ingham et al. 1985). Mineralization of limiting nutrients (e.g. N) is one component of the growth stimulation (Ferris et al. 1997; Laakso and Setälä 1999; Wardle 1999; Wardle et al. 2004) but not a total explanation. For example, bacterial-feeding protozoa promoted biomass accumulation in woody tree seedlings by 55 % even when a complete, N-containing nutrient solution was supplied every 2 h (Jentschke et al. 1995). Other analyses suggest that additional benefits of predation, including the release of particular organic products (Phillips et al. 1999) and the promotion of root colonization by beneficial bacteria (Bonkowski and Brandt 2002), also contribute to plant growth. Thus two key processes underlying the promotion of plant growth by soil food webs must be explained: (1) root colonization by microorganisms and (2) predation of bacteria and fungi by nematodes, protozoa, and arthropods.

Root colonization reflects direct activities of microorganisms, as well as the indirect effects of their predators. Direct microbial interactions with roots through adhesion (Matthysse and McMahan 2001), biofilm formation (O'Toole et al. 2000), responses to their own quorum-sensing compounds (von Bodman et al. 2003) or plant-derived quorum-sensing mimics (Teplitski et al. 2000), and competitive exclusion of competing fungi (Cook et al. 1995) are topics of active investigation, but detailed connections to the soil food web are poorly understood. Indirect effects include the physical transport of bacteria to new resources by nematodes (Ingham et al. 1985; Brown et al. 2004). Some bacteria are transferred on the outer surface of nematodes, but many survive passage through the nematode intestine. Amoebae predators, in contrast, reduce the number of bacteria on roots while simultaneously increasing the proportion of auxin-producing bacteria (Bonkowski and Brandt 2002). One result of this population shift is an increase in lateral root length. Such plant-growth-promoting bacteria occur commonly on roots and may enhance growth through multiple mechanisms (Ryu et al. 2003). Any mechanism that promotes growth of the root or root-colonizing microorganisms obviously has the potential to benefit the larger soil food web.

Predation, the other key process involved with the soil food web promotion of plant growth, is well characterized at the organismic level, but molecular mechanisms are poorly understood (Phillips et al. 2003). Nematodes show preferences for certain bacterial species (Moens et al. 1999), which may be based on attraction, repellence or a combination of both, and the potential benefit of such preferences is evident in the fact that nematode growth rates differ as much as 12-fold when they are supplied with various bacterial species as food sources (Venette and Ferris 1998). Little is known about how nematodes locate bacteria, insect larvae, or other nematodes, but such complex behaviors clearly involve receptors and neurotransmissions (Chao et al. 2004). One can reasonably hypothesize that nematode selection of bacteria or detection of the root involves responses to particular compounds. Examining this hypothesis requires careful tests that measure two forms of nematode movement, kinesis and taxis (Young et al. 1998; Rodger et al. 2003). Chemotactic responses of nematodes are generally assumed to result from differences in signal perceived at the amphid neurons on either side of the head, although laser ablation of chemosensory neurons in one amphid does not prevent chemotaxis in *C. elegans* (Bargmann and Mori 1997). Studies of chemotactic behavior are often performed on agar surfaces on which many nematodes are oriented with their lateral surfaces at right angles to the agar and the signal source. In that case, the dorso-ventral movements of the nematode body probably do not expose the amphids to differences in signal strength. A three-dimensional matrix, although less tractable observationally, is probably a more realistic environment for studies of chemotactic behavior of soil nematodes (Perry and Aumann 1998; Lee 2002).

Nematodes move toward increasing [CO_2] (Klingler 1965; Robinson 1995; Lee 2002), but because they distinguish between CO_2-producing roots and insect larvae, they must sense additional factors (Ruhm et al. 2003). While they are attracted to plant roots (Prot 1977) and root exudates (Viglierchio 1961; Riddle and Bird 1985), no plant-specific compounds that specifically produce the response have been identified. We hypothesize that bacterial-feeding nematodes commonly found near plant roots respond positively to plant signature compounds and both positively and negatively to bacterial compounds, which they use to select particular bacterial species. Current experiments are testing these concepts.

Several regulatory molecules involved in communication between plants and soil food web organisms have been found in recent studies. For example, plant roots release chemical factors, which regulate bacterial quorum-sensing genes normally responding to *N*-acyl homoserine lactone (AHL) signals from other bacteria (Teplitski et al. 2000). These genes control key processes involved in root colonization, including motility, biofilm formation, and antibiotic production (von Bodman et al. 2003). Other examples include lumichrome, a riboflavin breakdown product, which increases plant growth at low concentrations (5–50 nM; Phillips et al. 1999), and homoserine lactone, an AHL degradation product that can increase stomatal opening and transpiration when supplied to roots at 10 nM (Joseph and Phillips 2003). Also, the bacterial product DAPG not only enhances amino acid exudation from roots (Phillips et al. 2004), but, in certain cases, it promotes plant growth (De Leij et al. 2002). Current experiments are detecting DAPG effects on gene transcription related to growth (T.C. Fox and D.A. Phillips, unpublished data). Other studies have already shown that treating roots with 10 nM AHLs alters the accumulation of over 150 plant proteins inside the treated region (Mathesius et al. 2003). Thus, there is mounting evidence that low external concentrations of key compounds produced by food web organisms have major effects on the functioning of both plants and the associated soil organisms. This evidence emphasizes that soil food webs have evolved to function in an environment with myriad active chemical factors. The processes of root colonization and predation undoubtedly reflect the effects of many such compounds, but whether elevated [CO_2] generally affects the production of secondary metabolites in plants that might reach soil food web organisms is unclear. For example, several phenolic compounds in roots and shoots of *Plantago maritima* increased under higher [CO_2] (Davey et al. 2004), but no changes in total phenolics were detected in several tree species exposed to elevated [CO_2] (Hamilton et al. 2004).

We doubt that a doubling of atmospheric [CO_2] will disrupt interactions between plants and the soil food web. Increases in plant litter and root exudation with rising [CO_2] may elevate soil food web activity until the autotrophic plant community restricts exudation for some reason, such as a progressive limitation of available mineral N (Luo et al. 2004). Atmospheric [CO_2] levels are currently approaching 400 ppm. When estimates of atmospheric [CO_2] levels based on stomatal abundance in fossils (Retallack 2001) are related to probable evolutionary interactions between terrestrial plants and soil organisms, it is evident that roots and soil food webs have co-evolved through multiple periods when atmospheric [CO_2] exceeded 2000 ppm (Fig. 23.3). It seems logical, therefore, that a natural balance or buffering of biochemical and physiological processes will help plants and their associated soil food webs survive [CO_2] much higher than current conditions.

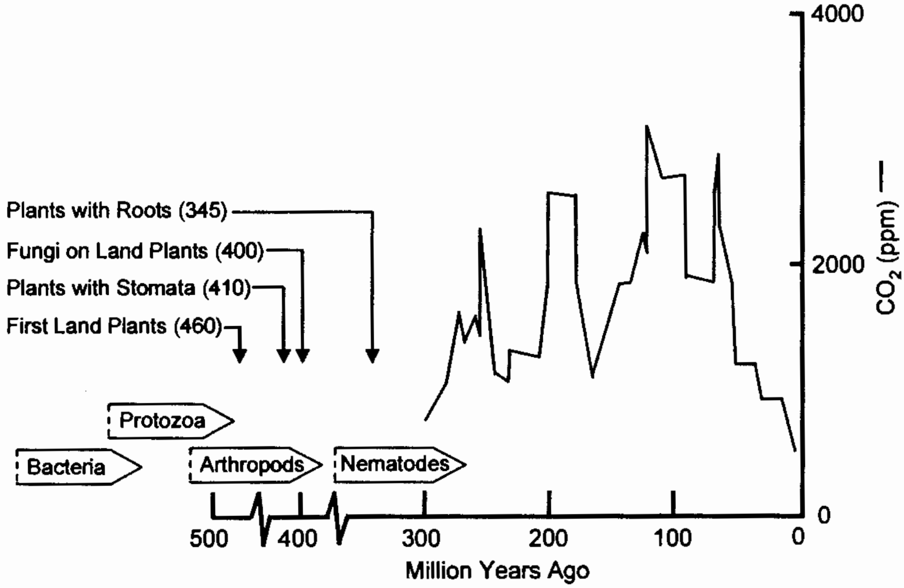

Fig. 23.3 Changes in estimated atmospheric [CO_2], based on stomatal abundance on leaf fossils (Retallack 2001) and their relationship to possible milestones in the evolution of soil food webs. Fossil evidence for many soft-bodied organisms present in soil food webs is limited (Poinar 1983), but numerous highly evolved individuals, morphologically similar to modern arthropods, are present in fossils from 400 million years ago

23.5 Conclusions

Organic inputs to soil are comprised largely of plant debris and root exudation, which is responsible for rhizodeposition. Increases in organic matter inputs from plants growing under elevated [CO_2] affect soil microorganisms and a limited set of conclusions can be drawn.

- Bacterial and fungal communities in soil ecosystems use such plant materials as resources to support multiple levels of tiny grazers and predators, which comprise soil food webs.
- Ten years of elevated [CO_2] at the ETH FACE site produced data on soil protozoa and nematodes that are consistent with adjustments predicted for availability of soil bacteria and fungi.
- Disparate changes in soil microorganisms and complex adjustments in food web structure reported under higher [CO_2] in a multitude of other experiments suggest that a better understanding of C resource availability is needed.
- Increases in living root mass under elevated [CO_2] could affect soil food webs through additional exudation, but limited information is available on

changes in root exudation under such conditions. We summarize here a new, more complex, understanding of root exudation that includes mechanisms by which microorganisms, and possibly their predators within the food web, can actively enhance root exudation. Initial experiments indicate that higher [CO_2] can increase root exudation of amino acids under axenic conditions by two separate mechanisms and these could result in more rhizodeposition.

- Little is known about how elevated [CO_2] levels alter predation, another key connection between the soil food web and the plant, but reductionist studies are beginning to support the concept that specific molecules affect predation and influence many organismic interactions in the root zone.
- Because the fossil record suggests soil food webs were exposed to widely varied levels of [CO_2] for long periods, a certain stability of these interactions should be expected as global atmospheric [CO_2] increases.

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