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NITROGEN MINERALIZATION: CHALLENGES OF A CHANGING PARADIGM

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Abstract. Until recently, the common view of the terrestrial nitrogen cycle had been driven by two core assumptions—plants use only inorganic N and they compete poorly against soil microbes for N. Thus, plants were thought to use N that microbes ''left over,'' allowing the N cycle to be divided cleanly into two pieces—the microbial decomposition side and the plant uptake and use side. These were linked by the process of net mineralization. Over the last decade, research has changed these views. N cycling is now seen as being driven by the depolymerization of N-containing polymers by microbial (including mycorrhizal) extracellular enzymes. This releases organic N-containing monomers that may be used by either plants or microbes. However, a complete new conceptual model of the soil N cycle needs to incorporate recent research on plant–microbe competition and microsite processes to explain the dynamics of N across the wide range of N availability found in terrestrial ecosystems. We discuss the evolution of thinking about the soil N cycle, propose a new integrated conceptual model that explains how N cycling changes as ecosystem N availability changes, and discuss methodological issues raised by the changing paradigm of terrestrial N cycling.

Key words: microsites; nitrogen availability; nitrogen mineralization; N-mineralization paradigm, evolving; plant uptake; soil N cycle.

DEVELOPMENT OF THE ''CLASSICAL'' PARADIGM OF N CYCLING

Since the late 1800s, N mineralization has been the perceived center point of the soil N cycle and the process that controls N availability to plants (Russell 1912, Waksman 1932, Harmsen and Van Schreven 1955, Aber and Melillo 2001). This view grew from two parallel and complimentary threads in the development of our understanding of plant–soil interactions. The first thread was the adoption of the mineral-nutrition theory of plant nutrition: with the writings of Liebig (1842), it became the widely accepted view that plants use only inorganic materials for their nutrition. Despite reports as early as the late 1800s that some plants actually can use organic N (Waksman 1932, Harmsen and Van Schreven 1955), the mineral nutrition theory remained effectively unchallenged for 150 years, as suggested by Black (1993:383):

> *A small amount of organic nitrogen is found in the soil solution, but plants are not known to take up any significant part of it, and must depend upon the inorganic forms that are released when microorganisms decompose the compounds containing the organic forms.*

The second key thread in developing the current view of the nitrogen cycle was the recognition that decomposition is a microbial process with NH_4^+ as a waste product, as described by Waksman (1932:444):

> *As long as there is free available energy, in excess of the available nutrients, there will be only a minimum accumulation of available plant food. When the energy approaches exhaustion ammonia (or nitrate) begins to accumulate. . . Since the microorganisms are unable to assimilate it, due to the absence of sufficient available energy material, it is left in the soil for the use of higher plants.*

These ideas framed the two core assumptions of N cycling studies that established mineralization as the perceived center point of the N cycle, and that most researchers have used for the last century when ex-

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amining soil N processes: (1) Plants only use inorganic N. (2) Plants are poor competitors for available soil N relative to microbes. They ''lose'' almost all competition events, and therefore effectively only have access to N that is left over after microbial N demands are met. More specifically and importantly, these assumptions established *net* mineralization as the key step in soil N cycling and as defining the amount of N available either for plant uptake or loss from the ecosystem (Vitousek et al. 1979). This tenet is repeatedly indicated by standard references of the 1970s and 1980s:

> *Part of the mineral nitrogen produced (Nmin), preferably ammonium, is consumed by the soil microorganisms (Jansson, 1958). As they are more successful than the higher plants in competing for Nmin (Bartholomew and Clark, 1950; Jansson, 1958; Zöttl, 1960a), of the total Nmin production (gross mineralization), the higher plants can use only that part (net mineralization) which exceeds the microbial demand.*
>
> —Runge (1971:191) (paraphrased in Melillo [1981:437])[4]

> *In unfertilized grasslands, uptake capabilities of microorganisms and plants together generally exceed the mineralization potentials of systems. . . . In such an environment, plants and microorganisms are in intense competition, often one or both classes of organisms will not meet their ''demands,'' and growth will be limited. During these periods of competition, microorganisms probably have the competitive advantage because of their intimate association with the substrate.*
>
> —Woodmansee et al. (1981:4491)

This thinking about the role of net mineralization naturally led to the development of net mineralization assays as the standard tool for measuring plant-available N. This was an important development in ecosystem science because developing theory saw nutrient availability and uptake as critical factors governing ecosystem development (Odum 1969, Vitousek and Reiners 1975), function (Chapin 1980, Gutschick 1981, Vitousek 1982), and response to disturbance (Vitousek et al. 1979). Further development was considered to be limited by the lack of an independent measurement of soil N availability: ''Ideally, nitrogen availability should be measured independently of the amount of nitrogen in litterfall, but direct measures of nitrogen availability in forest soils are not now possible'' (Vitousek 1982:564). Thus, the application of techniques such as the ''buried bag'' (Eno 1960) and the analogous but more sophisticated ''resin core'' (DiStefano and Gholz 1986) incubations became widely used, providing ecosystem ecologists with what was felt to be the best, broadly applicable, in situ assay of N available for plant uptake. For a number of years, such in situ net mineralization assays were considered an adequate measure of plant-available N:

> *Annual N uptake by vegetation at each site was assumed to be annual net mineralization in the 0–10 cm soil zone plus mineral N in precipitation minus mineral N leached from the rooting zone.*
>
> —Nadelhoffer et al. (1983:15)

> *An important feature of recent in situ methods [of measuring net mineralization] is that, with appropriate assumptions, uptake of inorganic-N by forests can be calculated.*
>
> —Adams et al. (1989:423)

Consequently, the main concerns with net mineralization assays were not focused on the underlying theory, but with artifacts associated with physically disrupting the soil, cutting roots and thereby changing C availability (Adams et al. 1989), and altering soil moisture (Tietema et al. 1992).

Over the course of the 1990s, however, thinking about net mineralization became more refined with the developing awareness of the technical limitations of the assays and of the complex dynamics of gross mineralization/immobilization reactions (Schimel et al. 1989, Tietema and Wessel 1992, Hart et al. 1994*a*). Studies showing substantial rates of gross mineralization and nitrification in systems where little NH_4^+ and NO_3^- accumulates during net mineralization assays particularly highlight the limitations of net rates as measures of N cycling dynamics (Davidson et al. 1992, Hart et al. 1994*b*, Neill et al. 1999). As a result, few papers now use net mineralization assays as a direct measure of plant-available N for whole-ecosystem budgeting purposes. Instead, net N mineralization is discussed as an ''index'' rather than as a ''measure'' of plant-available N:

> *Net N mineralization provides an index of plant available N in many systems (Nadelhoffer et al. 1983), but does not reflect the total amount of N cycling between organic matter and soil inorganic N.*
>
> —Neill et al. (1999:567)

> *The net accumulation of inorganic N in the absence of plant roots is thought to provide a good index of N availability to plants.*
>
> —Hart et al. (1994*a*:999)

The growing concern with net-mineralization assays that caused the shift in thought and language has not, however, eliminated its use as a measurement tool. Rather, net mineralization remains useful for some applications as a tool for assessing available N (e.g.,

[4] The citations within this quotation were not consulted by the authors in the preparation of this paper, but are included in the *Literature Cited* for the reader's convenience.

Reich et al. 1997, Evans et al. 1998, Piatek and Allen 2000).

Challenges to the ''Classical'' Paradigm

At the same time that the language of net-mineralization assays shifted from ''measurement'' to ''index,'' other studies were causing researchers to question the assay more deeply. Reports showing net immobilization during the entire growing season (Giblin et al. 1991), net immobilization during periods during the growing season when it would be likely that plants were taking up N (e.g., Nadelhoffer et al. 1984, Hill and Shackleton 1989, Polglase et al. 1992), and net mineralization rates well below estimates of plant uptake based on N accumulation in plants (e.g., Dyck et al. 1987, Chapin et al. 1988) suggested that in low-N ecosystems, at least, the core assumptions underlying the assay may be invalid. These concerns led to more focused research testing those assumptions. This research has led to two important conclusions that we develop in detail below. First, in low-N systems at least, plants appear to use organic N as a significant N source. Second, plants appear to compete effectively against soil microbes for available N; that is, they take up a portion of the N that would otherwise be absorbed by microbes and by doing so limit microbial growth or productivity.

Studies in a range of ecosystems have shown that plants may use amino acids and other organic N forms in situ. These studies started with Arctic tundra (Chapin et al. 1993, Kielland 1994, Schimel and Chapin 1996, Kielland 1997), but similar results have been found in boreal (Näsholm et al. 1998, Jones and Kielland 2002), alpine (Lipson and Monson 1998, Raab et al. 1999), wetland (Henry and Jefferies 2002), and even desert ecosystems (Schiller et al. 1998). Furthermore, studies show that some mycorrhizal plants are able to access amino acids (Finlay et al. 1992), amino sugars (Kerley and Read 1995), peptides (Bajwa and Read 1985, Abuzinadah and Read 1989), proteins (Abuzinadah and Read 1986, Finlay et al. 1992), and even chitin (Kerley and Read 1995) as N sources. Thus, it is becoming progressively more apparent that organic-N use by plants may be a common phenomenon, at least in systems where N supplies are limited. Despite these studies showing that plants in N-poor ecosystems access organic N, however, it is still unclear how much of a plant's N actually comes directly from organic sources (Hodge et al. 2000*a*); few studies have attempted to quantify the balance of organic vs. inorganic N forms taken up by plants (Leadley et al. 1997).

To overturn the argument that plants are fundamentally inferior to microbes as competitors for N, it must be shown that they can compete successfully for N in an N-limited environment and that plant N uptake can induce or exacerbate microbial N limitation. The direct evidence for this remains limited. The aforementioned papers that showed net-mineralization rates lower than plant uptake strongly suggest that plants do compete effectively against microbes under at least some circumstances. When plants are removed from the systems, as is the case during net-mineralization assays, the N that otherwise would have been taken up by plants is immobilized by the microbes, therefore resulting in low or negative net-mineralization estimates (Schmidt et al. 1999). Additional suggestive evidence comes from ^{15}N time-course studies. In studies in N-poor ecosystems where mineral N does not accumulate over the study, indicating that N availability remains limited, plants accumulate ^{15}N over time, suggesting they do ''win'' some of the competition events for N turning over in the soil (Marion et al. 1982, Johnson 1992, Yevdokimov and Blagodatsky 1994, Kaye and Hart 1997, Hodge et al. 2000*a*). Direct evidence that plants may outcompete microbes for N has also been demonstrated in a few studies. Jingguo and Bakken (1997) established microcosms with spatially variable N availability, using clover litter and straw to produce sites of high or low N availability. They showed that when the resources were spatially separated, root N uptake reduced microbial growth and activity in the areas of low N availability. A second study showed that under elevated CO_2, plants in a California annual grassland increased their N uptake at the direct expense of soil microbial activity and biomass N content (Hu et al. 2001). As we develop better approaches for identifying and understanding microbial N limitation (e.g., Schimel and Weintraub 2003), we expect that more such cases will be documented.

Research showing that plants can compete successfully with microbes for N at the whole-soil level presents a conundrum, as it still seems logical that soil microbes should win ''head-to-head'' competition events. Microbes have the advantage of higher substrate affinities, larger surface-area-to-volume ratios, and faster growth rates (Hodge et al. 2000*a*). They are also the organisms responsible for converting soil organic matter into bioavailable forms and so should have first access to newly available N. This being the case, one is forced to ask ''How can plants successfully compete with microbes for soil N?'' If they should be poor competitors at the individual, local scale, how do they succeed at the larger, whole-soil scale? There are two possible answers that may well work in parallel. The first is mycorrhizae, which act as ''microbial mercenaries.'' While their role in increasing the absorptive surface area of the plant roots and thereby increasing mineral-nutrient uptake has been known for decades, there is a growing appreciation for their direct role in decomposition and organic-nutrient uptake (Smith and Read 1997). Through both mechanisms, mycorrhizae allow the plant partner to be a more effective competitor against saprophytic microbes. The second answer stems from the improved understanding that has developed over the last few decades of microsite dynamics in soil (Sexstone et al. 1985, Parkin 1987, Jackson

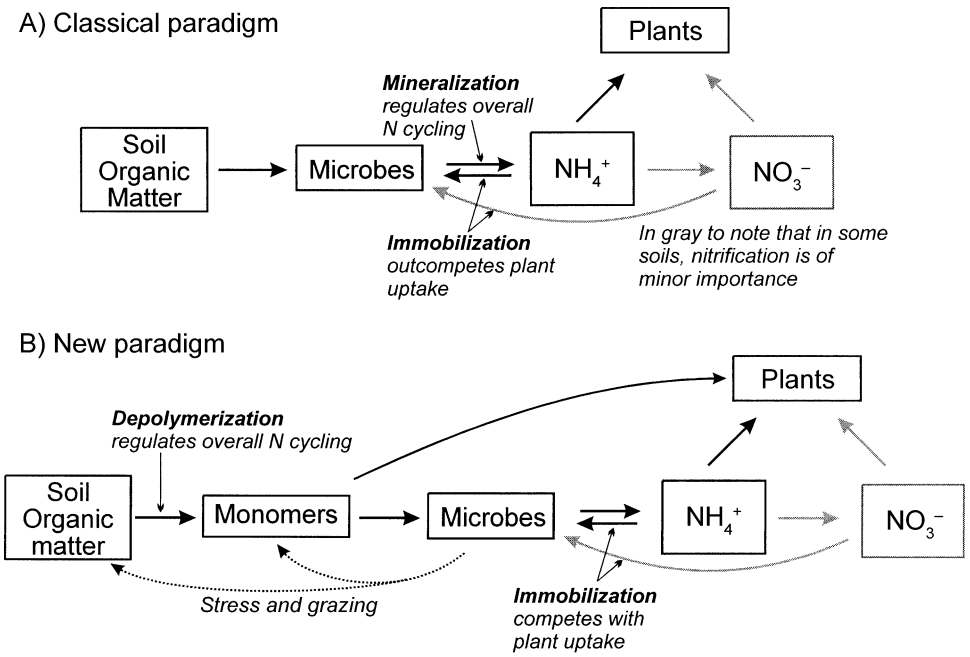

FIG. 1. The changing paradigm of the soil N cycle. (A) The dominant paradigm of N cycling up through the middle 1990s. (B) The paradigm as it developed in the late 1990s.

et al. 1989, Davidson and Hackler 1994, Norton and Firestone 1996, Jaeger et al. 1999, Chen and Stark 2000, Hodge et al. 2000*a*, *b*, Korsaeth et al. 2001, Ettema and Wardle 2002). Early researchers treated the soil as a homogenous medium and accepted measurements on soil samples as representative of whole-soil processes. This approach and perspective may have been adopted primarily due to limits in methodology. However, we now know that microsite processes may be important in regulating whole-soil phenomena. There are microsites where net N mineralization dominates and others where net N immobilization dominates (e.g., Jackson et al. 1989, Davidson et al. 1990, Chen and Stark 2000, Burger and Jackson 2003). Available N (inorganic or organic) diffuses between these sites (Jingguo and Bakken 1997, Chen and Stark 2000) and is available to the organism that first encounters it. This mechanism allows plant roots and mycorrhizae access to N that would otherwise be taken up by free-living microbes. Thus, some fraction of available N turning over through the soil solution is likely available to plants, even if in a head-to-head competition based on uptake kinetics, they would lose to soil microbes. In other words, at the micro-scale, plants may, in fact, be poor competitors for soil N. However, due to the differences in microsite conditions and the interception of N diffusing between sites, plants are able to ''win'' competition events when viewed at the macroscale or whole-soil level. Because plants retain N for extended periods of time, while microbial turnover is more rapid, even if plants only access a small fraction of the bioavailable N turning over through soil, integrated over time, they become more competitive (Kaye and Hart 1997).

DEVELOPMENT OF A NEW PARADIGM

As a result of the challenges to the classical paradigm, ecologists have been rethinking N mineralization as the center point in the N cycle (Fig. 1A). With the work on plant uptake of organic N in the mid-1990s, researchers initially discussed organic uptake as ''short circuiting'' the N cycle (Chapin 1995). However, such thinking was really transitional to a new perception of the ''circuit'' and the development of a new paradigm of N cycling that no longer places as much emphasis on mineralization as the driving process (Chapin et al. 2002; Fig. 1B).

The developing new paradigm recognizes that the critical point in the N cycle is the depolymerization of N-containing compounds. Polymers are not immediately bioavailable because they are too large (Chapin et al. 2002). They are cleaved by extracellular enzymes to release monomers (amino acids, amino sugars, nucleic acids, etc.) that are broadly bioavailable and may be used by either plants or microorganisms (Fig. 1B). Once N has entered the bioavailable DON (dissolved organic N) pool, it may be recycled and reused through the microbial system, either through (a) microbial metabolism via gross mineralization-immobilization (Fierer et al. 2001), (b) micro/meso-faunal grazing and the ''microbial loop'' (Elliott et al. 1980, Clarholm 1994, Coleman 1994), or (c) microbial death or damage due to stress (Birch 1958, Schimel and Clein 1996: Fig. 1). While grazing may directly cause N mineralization,

as some fauna excrete NH_4^+ (Lee and Atkinson 1977, Carefoot et al. 1992, Hassink et al. 1994), grazing also recycles some N into DON or polymeric SOM (soil organic matter) as undigested fecal material (Lee 1985, Woolley 1988, Ferrier-Pages et al. 1998). Stresses, such as drying–rewetting and freeze–thaw, can damage or kill microbes, returning microbial polymers (protein, cell walls) to the polymeric soil organic-matter pool, while releasing amino acids and other organic monomers into the DON pool (Kieft et al. 1987, DeLuca et al. 1992, Halverson et al. 2000). Plants also drive some of the recycle/reuse pathway as they exude amino acids into the rhizosphere (Jaeger et al. 1999). However, as all processes involving either plant or microbial N uptake, growth, and death ultimately involve returning N to polymeric forms, depolymerization is critical in maintaining an ongoing flow of new bioavailable N to the biotic system and maintaining an active cycle of N.

Since this new paradigm is now centered around depolymerization and also breaks the earlier organic–inorganic distinction in microbial vs. plant processes, its adoption can be viewed as a dramatic shift in thinking. Alternatively, as it leaves unchanged the core concept that microbes are responsible for breaking down complex organic materials to produce simple, plant-available nutrients, it can also be viewed as rather a more subtle shift in thinking essentially involving a broadening of the definition of ''mineralization.''

Regardless of how the paradigms are perceived conceptually, the new depolymerization-centered paradigm as reflected by Chapin et al. (2002) and shown in Fig. 1B better reflects the mechanics of soil N cycling. However, it is still incomplete. It does not fully incorporate new research on plant–microbe competition and the role of microsite phenomena to develop a full picture of how N cycling varies among terrestrial ecosystems. To accomplish this, it is necessary to incorporate all three of the major new threads of N cycling research (depolymerization, competition, and microsites) into a single integrated conceptual model that applies broadly across the wide range of soil N availability found in terrestrial ecosystems.

Integration of Soil Microsite Processes into the New Paradigm

The depolymerization step is critical in N cycling because it regulates the rate of N movement from litter and soil polymers into a bioavailable form. However, which process *appears* to dominate N cycling, and will determine the main form of N taken up by plants, is likely to vary across a gradient of increasing N availability (Fig. 2). We hypothesize that much of the observed variation in the nature of N cycling at the macroscale level likely results from the dynamics of microsite processes and how the relative importance of different processes changes with the amount of bioavailable N.

In extremely N-poor ecosystems, where litter inputs are low and decomposition and N cycling are slow (such as some boreal, arctic, and alpine ecosystems), plants and microbes probably compete primarily for N at the organic-monomer stage. Microbes would be N limited enough that they would retain absorbed amino acids (Schimel and Chapin 1996) and only rarely mineralize N. Such a phenomenon has been demonstrated in Arctic tussock tundra where net immobilization was measured over the entire growing season (Giblin et al. 1991). Thus, in such situations, both plants and microbes would rely on organic compounds for their N. While microbes would most likely win the majority of ''head-to-head'' competitions for amino acids, a small fraction of the amino acids would also probably diffuse to the roots, thus providing a small N flow to roots even under the most N-limited conditions (Fig. 2 case A; Schimel and Chapin 1996, Korsaeth et al. 2001).

Moving along the conceptual N-availability gradient diagramed in Fig. 2, decomposition, depolymerization, and the release of N containing monomers increase, partly as an increase in the proportion of N-rich microsites and partly as an increase in substrate N content. This leads to increasing N availability to the biota (Fig. 2: case B). Microbes would be less N limited and would begin to mineralize N. In this portion of the gradient (Fig. 2: case B), N mineralization would be restricted to particularly N-rich microsites, and the mineralized NH_4^+ would diffuse away from those microsites (Jingguo and Bakken 1997). If these N-rich sites last long enough, they might support the development of small populations of nitrifiers, causing some limited nitrification to occur, though the overall soil condition would not appear conducive to nitrification (Davidson et al. 1992, Hart et al. 1994*b*). The diffusing NH_4^+ (and NO_3^-) would be available to, and needed by, both plants and microbes in N-poor microsites (Fig. 2: case B). Thus, while plants might continue to have some access to organic-N compounds, the apparent dominance of NH_4^+ in the overall N cycle would increase, but plants and microbes would be actively competing for the limited amount of NH_4^+ diffusing away from mineralizing sites. The conditions described in case B might occur in some temperate forests, where litter is N poor and decomposition is slow, such as those where both net mineralization and immobilization are measured at various times in the same stand using in situ assays (Nadelhoffer et al. 1984, Polglase et al. 1992).

As overall N availability increases still further (Fig. 2: case C), a larger and larger fraction of the microbial community would meet their N needs from local organic sources, and would decrease their dependence on N diffusing in from N-rich microsites. That would reduce the competition between plants and microbes for the diffusing N, and plants would have access to the N that is mineralized after microbial demands are met, as assumed by the classical paradigm to always be the case. In this scenario, mineralization rates would in-

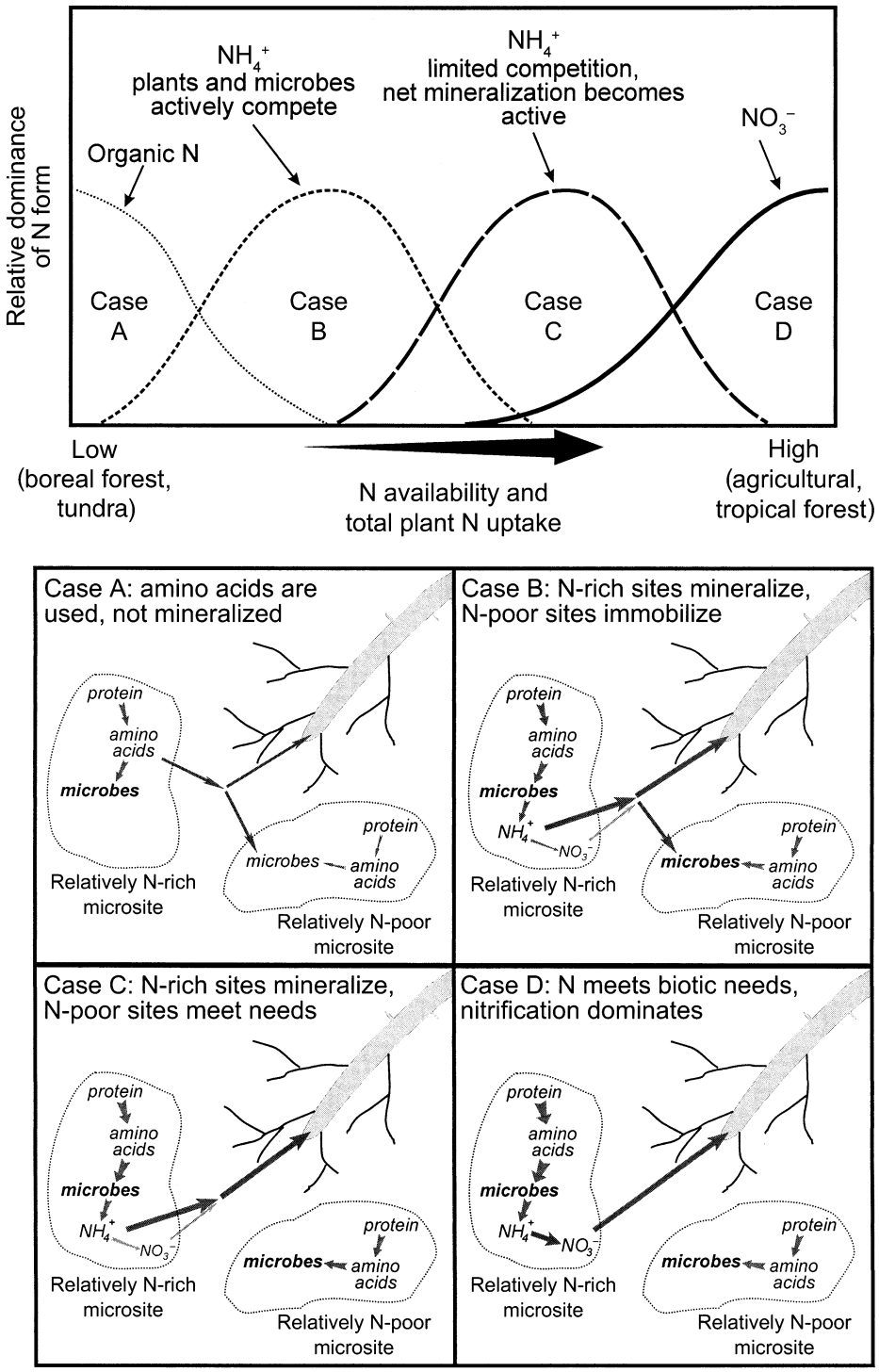

FIG. 2. The shifting dominance of N forms along a gradient of N availability and the soil processes that regulate N availability to plants under different N-availability regimes. Total N availability and plant uptake both increase along the hypothetical gradient. The diagrams specify that the polymers are protein, but only as a representative organic N-containing polymer. Cases A–D indicate the hypothesized soil processes that are regulating which N form is dominant in the soil. The width of the arrows indicates the relative magnitude of the flows. In cases B–D, flows from amino acids to roots have been dropped for clarity, not because they don't occur. Similarly in case D, some flow from NH_4^+ to roots likely occurs. It should be noted that mycorrhizal fungi may be the agents of depolymerization (by producing extracellular enzymes) in N-rich sites and thus the microbes that take up amino acids directly.

crease, and NH_4^+ would increasingly dominate soil N pools. In this mid-zone of N availability, the combined demands of microbial and plant uptake would still limit overall NH_4^+ supply to nitrifiers, thus maintaining an NH_4^+-dominated N economy in the ecosystem, though there would be progressively more NO_3^- production in N-rich microsites. These conditions likely occur in moderately fertile temperate forests (Pastor et al. 1984) and some grasslands (Woodmansee et al. 1981, Jackson et al. 1988).

At very high relative N availability, plant and heterotroph competition for NH_4^+ becomes low enough to allow nitrifiers to flourish and the N economy of the system becomes progressively more NO_3^- dominated (Fig. 2: case D). Nitrifiers would likely live in close-enough association with mineralizers so that NO_3^- becomes the dominant N form moving through the soil (Chen and Stark 2000) and plants would shift to relying on NO_3^- for their N. Such ecosystems might include agricultural systems and N-rich tropical forests (Hall and Matson 1999*b*).

Even in the very high N condition, depolymerization and the release of N-containing monomers still regulates the overall rate of N cycling, and microbes may still rely largely on organic-N compounds for their primary N supply (Fierer et al. 2001). However, the changing balance of supply and demand shifts the N forms that plants rely on, transitioning from organic forms to NH_4^+ to NO_3^- across the gradient (Nordin et al. 2001). Since the generation of organic-N-containing monomers increases along the gradient, it is quite possible that plant use of amino acids (and other organic sources) for N would continue even at high available-N levels. However, Persson and Näsholm (2002) showed that high cellular NH_4^+ concentrations inhibit amino-acid uptake, suggesting that organic-N use might decrease along the N-availability gradient. Regardless of whether organic-N uptake absolutely declines or not, it should become a progressively less important part of total plant uptake relative to inorganic N.

One additional factor that must be considered in this view of N cycling is the role of mycorrhizae. In all but the most N-rich conditions, they may be important in taking up N that is moving in the soil, simply by extending the root system (Smith and Read 1997). In low-N conditions, however, mycorrhizae may also be important in acting directly as decomposers. By producing the exoenzymes that break down organic polymers, a mycorrhizal fungus enhances the likelihood that it will capture the monomers released, and thus provide a more direct conduit between polymers and plants. A number of studies have shown that some mycorrhizal fungi have capabilities as decomposers (Abuzinadah and Read 1986, Haselwandter et al. 1990, Leake and Read 1990, Finlay et al. 1992, Kerley and Read 1995). However, with the exception of the ericaceaous mycorrhizae, mycorrhizal fungi generally appear to be poor decomposers relative to specialist fungi (Bending and Read 1996*a*, *b*, 1997), suggesting that in non-ericaceaous systems, direct decomposition and nutrient uptake may generally be a secondary function to competing for already-available N.

Methodological Challenges of the New Paradigm

One key step in the adoption of an intellectual paradigm is defining the tools that are needed to study the processes described by that paradigm. Thus it is important to consider the methodological implications of a change in the paradigm of N mineralization. The classical, mineralization-centered paradigm identified net-mineralization measurements as the fundamental tool of N-cycling research, and although the new paradigm does not invalidate that tool, it does put constraints on it. At low levels of available N (Fig. 2: cases A and B), net-mineralization assays are inadequate for evaluating plant N availability (as discussed above). For studies on systems on the high-N side of the schematic (Fig. 2: cases C and D), on the other hand, net mineralization should be an adequate measure of plant-available N. Also, for studies comparing systems across a wide gradient in N availability, net mineralization should correlate broadly (though possibly nonlinearly) with plant uptake and nutrient status, as has been observed (Pastor et al. 1984, Chapin et al. 1988, Kaye and Hart 1997, Bohlen et al. 2001). For studies evaluating other aspects of N cycling, net mineralization also remains a useful index of overall N availability. That will be particularly true for studying nitrification and processes that depend on it (e.g., NO_3^- leaching, denitrification, N_2O flux; Frank et al. 2000, Goodale and Aber 2001, Hall and Matson 1999*a*) because nitrifiers use only NH_4^+ and compete poorly against heterotrophic organisms for it (Gerards et al. 1998). For these reasons, net mineralization retains utility as an index of N availability but it is important to note that it is an *indirect* index, measuring something that is related to but is not actually the key step regulating N cycling. However, it still is necessary to answer the question ''How do we measure plant-available N in low-N ecosystems?''

For low-N systems where NH_4^+ represents a significant portion of the available soil N pool (Fig. 2: case B), the obvious answer would appear to be ^{15}N isotope-pool dilution techniques (Bjarnason 1988, Barraclough 1991, Davidson et al. 1991, Kirkham and Bartholomew 1954). By using such methods, net mineralization can be separated into gross N mineralization and immobilization measurements, thus allowing for an estimation of the actual rate at which NH_4^+ becomes available for plant–microbe competition. While such isotopic approaches clearly have power beyond that of net-mineralization assays (e.g., Myrold and Tiedje 1986, Schimel et al. 1989, Davidson et al. 1992), they have limitations as well. Based on the low ratio of C mineralization to gross N mineralization even in N-

poor soils, among other data, Fierer et al. (2001:1836) suggested that: ''Pool dilution may not measure the overall breakdown of soil organic matter and growth of microbial biomass but rather the microbial cycling and recycling of small pools of highly labile, N-rich compounds. Thus, pool dilution may be more of a measure of microbial cellular, rather than soil organic matter, processes.''

Given the apparent importance of microsite processes in regulating N dynamics (Jingguo and Bakken 1997, Chen and Stark 2000, Korsaeth et al. 2001), coupled to the suggestion that pool dilution measures processes tightly coupled to microbial cells, it raises the question of how effectively plants are able to access the N turnover measured by ^{15}N isotope-pool dilution. If the Fierer et al. (2001) hypothesis proves to be true, ^{15}N pool dilution may prove to be a powerful yet somewhat-limited tool in directly measuring plant-available N. In addition, in systems where organic-N uptake is a substantial fraction of plant uptake (Fig. 2: case A), any measure of N mineralization will be inadequate to assess plant-available N.

Given the limitations of inorganic-N-based approaches to assessing N availability, particularly in extremely N-limited systems (Fig. 2: case A), it would make sense to move toward a technique based on measuring depolymerization. Such approaches have been core to our understanding of C dynamics, in which models have always treated polymer breakdown as the rate-limiting step of overall decomposition and C flow to microorganisms. The monomers released are then rapidly consumed and largely respired (Schimel and Weintraub 2003). For C cycling, this has allowed both mass loss and CO_2 production to serve as accurate measures of the decomposition rate as they are so tightly coupled. For N cycling, there is not such a clean index of depolymerization, and that is one reason net mineralization has remained so widely used as an N-availability index—it is easy to measure. The most logical assay of depolymerization for N might be protease because that is the single enzyme that is most responsible for supplying bioavailable N (Paul and Clark 1996). However, even in assays without added protein substrate, protease activity is usually measured on disturbed samples and so is a ''potential'' assay at best (Alef and Nannipieri 1995). Additionally, it is necessary to eliminate microbial uptake of the produced amino acids to get an estimate of native protease activity, but that is hard to do without lysing cells and releasing both new protein substrates and new protease enzymes. Some studies have tried to estimate the turnover dynamics of amino acids directly by using isotopically labeled compounds (Jones and Kielland 2002). However, amino acids have small pool sizes and rapid turnover times, making their turnover dynamics difficult to measure reliably. Measuring the rate of depolymerization and the generation of bioavailable monomers remains a major challenge.

After going through the limitations of available soil analyses, we might be tempted to just throw our hands up and argue that the only way to measure plant-available N is to measure actual plant uptake. However, there are two challenges with that approach, one methodological, and one conceptual. The methodological challenge is simply the difficulty in accurately measuring N uptake. In forest and shrubland, the size of the plants makes measuring plant uptake difficult. In all ecosystems, measuring fine-root biomass and turnover is a major challenge (Ruess et al. 1996, Schimel and Chapin 1996, Dornbush et al. 2002), yet fine roots may retain a substantial amount of the ^{15}N usually used in estimating uptake kinetics (e.g., Schimel and Chapin 1996). The conceptual issue is grounded in the idea that plants and microbes compete for N. To use actual plant uptake as a measure of ''plant-available N'' implicitly accepts that plants compete poorly against microbes for N. It assumes there is a single pool of plant-available N and that plants get all of it. We have argued this is not necessarily the case. Rather, there is plant-available N turning over through the soil that plants miss. The partitioning of available N is somewhat plastic and so the proportion of available N that plants acquire may vary with conditions such as soil moisture or other environmental conditions. Thus, after two decades of intense research, we return in a way to the state described by Vitousek (1982): a new direct assay of potentially plant-available N would be a valuable tool for better understanding plant–microbe competition, the fate of N in terrestrial ecosystems, and overall ecosystem dynamics.

Conclusions

The late 1800s saw the dawn of modern thinking about N cycling and mineralization in terrestrial systems. The incorporation of mechanistic thinking about N mineralization led to important advances in the theory of ecosystem function, development, and response to perturbations. Over the last decade, however, the thinking about N mineralization has evolved. The concept of N mineralization as the driving process in the N cycle, is shifting to one where exoenzyme-driven depolymerization is seen as the rate-limiting step in the generation of bioavailable N (Chapin et al. 2002). That recognition has been critical in developing a new understanding of the terrestrial N cycle and is providing new perspectives on ecosystem dynamics. However, the appreciation of the importance of depolymerization is only one of several innovations that need to be incorporated into a new conceptual ''microsite model'' that adequately explains differences in N cycling across the range of terrestrial ecosystems (Fig. 2). The developing new paradigm frames several important questions that are receiving increasing research attention, but we are far from having full answers adequately integrated at the ecosystem scale:

1) How are the biotic process of depolymerization, mineralization, microbial uptake, and root uptake linked?
2) How important are physical and spatial processes occurring at the microsite scale in regulating macroscale characteristics of ecosystem N cycling?
3) How important are roots and mycorrhizae in creating high- or low-N microsites and in mediating the biochemical/biological processes and their linkages?

Adequately answering these questions requires a different set of tools than did studying N cycling within the framework of the ''classical'' paradigm. Some, perhaps many, of the necessary tools exist but we need to find better ways to use them in concert and we need to develop better tools for understanding depolymerization, how microsite dynamics work, and how they scale to the whole soil system.

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Literature Cited

Aber, J., and J. Melillo. 2001. Terrestrial ecosystems. Second edition. Harcourt Academic Press, San Diego, California, USA.

Abuzinadah, R. A., and D. J. Read. 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. III. Protein utilization by *Betula, Picea,* and *Pinus* in mycorrhizal association with *Hebeloma crustiliniforme*. New Phytologist **103**:507–514.

Abuzinadah, R. A., and D. J. Read. 1989. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants IV. The utilization of peptides by birch (*Betula pendula* L.) infected with different mycorrhizal fungi. New Phytologist **112**:55–60.

Adams, M. A., P. J. Polglase, P. M. Attiwill, and C. J. Weston. 1989. In situ studies of nitrogen mineralization and uptake in forest soils; some comments on methodology. Soil Biology and Biochemistry **21**:423–429.

Alef, K., and P. Nannipieri. 1995. Methods in applied soil microbiology and biochemistry. Academic Press, London, UK.

Bajwa, R., and D. J. Read. 1985. The biology of mycorrhizae in the Ericaceae IX. Peptides as nitrogen sources for the ericoid endophyte and for mycorrhizal and non-mycorrhizal plants. New Phytologist **101**:459–467.

Barraclough, D. 1991. The use of mean pool abundances to interpret ^{15}N tracer experiments. I. Theory. Plant and Soil **131**:89–96.

Bartholomew, W. V., and F. E. Clark. 1950. Nitrogen transformations in soil in relation to the rhizosphere microflora. Transactions of the Fourth International Congress of Soil Science **2**:112–113.

Bending, G. D., and D. J. Read. 1996*a*. Effects of the soluble polyphenol tannic acid on the activities of ericoid and ectomycorrhizal fungi. Soil Biology and Biochemistry **28**: 1595–1602.

Bending, G. D., and D. J. Read. 1996*b*. Nitrogen mobilization from protein–polyphenol complex by ericoid and ectomycorrhizal fungi. Soil Biology and Biochemistry **28**: 1603–1612.

Bending, G. D., and D. J. Read. 1997. Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. Mycological Research **101**:1348–1354.

Birch, H. 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil **10**:9–31.

Bjarnason, S. 1988. Calculation of gross nitrogen immobilization and mineralization in soil. Journal of Soil Science **39**:393–406.

Black, C. 1993. Soil fertility evaluation and control. Lewis, Boca Raton, Florida, USA.

Bohlen, P. J., P. M. Groffman, C. T. Driscoll, T. J. Fahey, and T. G. Siccama. 2001. Plant–soil–microbial interactions in a northern hardwood forest. Ecology **82**:965–978.

Burger, M., and L. E. Jackson. 2003. Microbial immobilization of ammonium and nitrate in relation to ammonification and nitrification rates in organic and conventional cropping systems. Soil Biology and Biochemistry **35**:29–36.

Carefoot, T., B. Taylor, S. Kalwa, G. Somogyi, and B. Hughes. 1992. Effect of dietary d-amino acids on growth, survival, ammonia excretion and specific dynamic action in the supralittoral isopod, *Liglia–Pallasii*. Comparative Biochemistry and Physiology A- Physiology **103**:559–563.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233–260.

Chapin, F. S., III. 1995. New cog in the nitrogen cycle. Nature **377**:199–200.

Chapin, F. S., III., N. Fetcher, K. Kielland, K. R. Everett, and A. E. Linkins. 1988. Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing water. Ecology **69**:693–702.

Chapin, F. S., III., P. Matson, and H. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag, New York, New York, USA.

Chapin, F. S., III, L. Moilanen, and K. Kielland. 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. Nature **361**:150–153.

Chen, J., and J. Stark. 2000. Plant species effects and carbon and nitrogen cycling in a sagebrush–crested wheatgrass soil. Soil Biology and Biochemistry **32**:47–57.

Clarholm, M. 1994. The microbial loop in soil. Pages 221–230 *in* K. Ritz, J. Dighton, and K. E. Giller, editors. Beyond the biomass. John Wiley and Sons, Chichester, UK.

Coleman, D. C. 1994. The microbial loop concept as used in terrestrial soil ecology studies. Microbial Ecology **28**: 245–250.

Davidson, E. A., and J. L. Hackler. 1994. Soil heterogeneity can mask the effects of ammonium availability on nitrification. Soil Biology and Biochemistry **26**:1449–1453.

Davidson, E. A., S. C. Hart, and M. K. Firestone. 1992. Internal cycling of nitrate in soils of a mature coniferous forest. Ecology **73**:1148–1156.

Davidson, E. A., S. C. Hart, C. A. Shanks, and M. K. Firestone. 1991. Measuring gross nitrogen mineralization, immobilization, and nitrification by ^{15}N isotopic pool dilution in intact soil cores. Journal of Soil Science **42**:335–349.

Davidson, E. A., J. M. Stark, and M. K. Firestone. 1990. Microbial production and consumption of nitrate in an annual grassland. Ecology **71**:1968–1975.

DeLuca, T. H., D. R. Keeney, and G. W. McCarty. 1992. Effect of freeze–thaw events on mineralization of soil nitrogen. Biology and Fertility Soils **14**:116–120.

DiStefano, J. F., and H. L. Gholz. 1986. A proposed use of ion exchange resins to measure nitrogen mineralization and nitrification in intact soil cores. Communications in Soil Science and Plant Analysis **17**:989–998.

Dornbush, M., T. Isenhart, and J. Raich. 2002. Quantifying fine-root decomposition: an alternative to buried litterbags. Ecology **83**:2985–2990.

Dyck, W., C. Mees, and P. Hodgkiss. 1987. Nitrogen availability and comparison to uptake in two New Zealand *Pinus radiata* forests. New Zealand Journal of Forest Science **17**: 338–352.

Elliott, E. T., R. V. Anderson, D. C. Coleman, and C. V. Cole. 1980. Habitable pore space and microbial trophic interactions. Oikos **35**:327–335.

Eno, C. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Science Society of America Proceedings **24**:277–279.

Ettema, C. H., and D. A. Wardle. 2002. Spatial soil ecology. Trends in Ecology and Evolution **17**:177–183.

Evans, C. A., E. K. Miller, and A. J. Friedland. 1998. Nitrogen mineralization associated with birch and fir under different soil moisture regimes. Canadian Journal of Forest Research **28**:1890–1898.

Ferrier-Pagès, C., M. Karner, and F. Rassoulzadegan. 1998. Release of dissolved amino acids by flagellates and ciliates grazing on bacteria. Oceanologica Acta **21**:485–494.

Fierer, N., J. Schimel, R. Cates, and J. Zou. 2001. The influence of balsam poplar tannin fractions on carbon and nitrogen dynamics in Alaskan taiga floodplain soils. Soil Biology and Biochemistry **33**:1827–1839.

Finlay, R. D., Å. Frostegård, and A. M. Sonnerfeldt. 1992. Utilization of organic and inorganic nitrgoen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contorta* Dougl. ex Loud. New Phytologist **120**:105–115.

Frank, D. A., P. M. Groffman, R. D. Evans, and B. F. Tracy. 2000. Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. Oecologia **123**:116–121.

Gerards, S., H. Duyts, and H. J. Laanbroek. 1998. Ammonium-induced inhibition of ammonium-starved *Nitrosomonas europaea* cells in soil and sand slurries. FEMS Microbiology Ecology **26**:269–280.

Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre, and A. J. McKerrow. 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecological Monographs **61**:415–435.

Goodale, C. L., and J. D. Aber. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. Ecological Applications **11**:253–267.

Gutschick, V. P. 1981. Evolved strategies in nitrogen acquisition by plants. American Naturalist **118**:607–637.

Hall, S. J., and P. A. Matson. 1999*a*. Nitrogen oxide emissions after nitrogen additions in tropical forests. Nature **400**:152–155.

Hall, S. J., and P. A. Matson. 1999*b*. Nutrient status of tropical rain forests influences soil N dynamics after N additions. Ecological Monographs **73**:107–129.

Halverson, L. J., T. M. Jones, and M. K. Firestone. 2000. Release of intracellular solutes by four soil bacteria exposed to dilution stress. Soil Science Society of America Journal **64**:1630–1637.

Harmsen, G., and D. Van Schreven. 1955. Mineralization of organic nitrogen in soil. Pages 299–398 *in* A. Norman, editor. Advances in agronomy. Academic Press, New York, New York, USA.

Hart, S., J. Stark, E. Davidson, and M. K. Firestone. 1994*a*. Nitrogen mineralization, immobilization, and nitrification. Pages 985–1018 *in* R. Weaver, S. Angle, P. Bottomley, D. Bezdicek, S. Smith, A. Tabatabai, and A. Wollum, editors. Methods of soil analysis. Part 2. Microbiological and biochemical properties. Soil Science Society of America, Madison, Wisconsin, USA.

Hart, S. C., G. E. Nason, D. D. Myrold, and D. A. Perry. 1994*b*. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology **75**:880–891.

Haselwandter, K., O. Bobleter, and D. J. Read. 1990. Degradation of ^{14}C-labelled lignin and dehydropolymer of coniferyl alcohol by ericoid and ectomycorrhizal fungi. Archives of Microbiology **153**:352–354.

Hassink, J., A. M. Neuth, and P. C. De Ruiter. 1994. C and N mineralization in sandy and loamy grassland soils: the role of microbes and microfauna. Soil Biology and Biochemistry **26**:1565–1571.

Henry, H., and R. Jefferies. 2002. Free amino acid, ammonium and nitrate concentrations in soil solutions of a grazed coastal marsh in relation to plant growth. Plant, Cell and Environment **25**:665–675.

Hill, A. R., and M. Shackleton. 1989. Soil N mineralization and nitrification in relation to nitrogen solution chemistry in a small forested watershed. Biogeochemistry **8**:167–184.

Hodge, A., D. Robinson, and A. Fitter. 2000*a*. Are microorganisms more effective than plants at competing for nitrogen? Trends in Plant Science **5**:304–308.

Hodge, A., J. Stewart, D. Robinson, B. S. Griffiths, and A. H. Fitter. 2000*b*. Competition between roots and soil micro-organisms for nutrients from nitrogen-rich patches of varying complexity. Journal of Ecology **88**:150–164.

Hu, S., F. S. Chapin III, M. K. Firestone, C. Field, and N. Chiarello. 2001. Nitrogen limitation of microbial decomposition in a grassland under elevated CO_2. Nature **409**: 188–191.

Jackson, L. E., J. P. Schimel, and M. K. Firestone. 1989. Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. Soil Biology and Biochemistry **21**:409–415.

Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1988. Plant and soil nitrogen dynamics in California annual grassland. Plant and Soil **110**:9–17.

Jaeger, C. I., S. Lindow, W. Miller, E. Clark, and M. K. Firestone. 1999. Mapping of sugar and amino acid availability in soil around roots with bacterial sensors of sucrose and tryptophan. Applied and Environmental Microbiology **65**: 2685–2690.

Jansson, S. L. 1958. Tracer studies on nitrogen transformations in soil with special attention to mineralisation/immobilisation relationships. Kungliga Lantbrukshögskolans Annaler **24**:101–361.

Jingguo, W., and L. Bakken. 1997. Competition for nitrogen during decomposition of plant residues in soil: effect of spatial placement of N-rich and N-poor plant residues. Soil Biology and Biochemistry **29**:153–162.

Johnson, D. 1992. Nitrogen retention in forest soils. Journal of Environmental Quality **21**:1–12.

Jones, D., and K. Kielland. 2002. Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. Soil Biology and Biochemistry **34**:209–219.

Kaye, J. P., and S. C. Hart. 1997. Competition for nitrogen between plants and soil microorganisms. Trends in Ecology and Evolution **12**:139–143.

Kerley, S. J., and D. J. Read. 1995. The biology of mycorrhizal in the Ericaceae. XVIII. Chitin degradation by *Hymenoscyphus ericae* and transfer of chitin-nitrogen to the host plant. New Phytologist **131**:369–375.

Kieft, T., E. Soroker, and M. Firestone. 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biology and Biochemistry **19**:119–126.

Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. Ecology **75**:2373–2383.

Kielland, K. 1997. Role of free amino acids in the nitrogen economy of arctic cryptogams. Écoscience **4**:75–79.
Kirkham, D., and W. V. Bartholomew. 1954. Equations for following nutrient transformations in soil, utilizing tracer data. Soil Science Society of America Proceedings **18**:33–34.
Korsaeth, A., L. Moldstad, and L. Bakken. 2001. Modelling the competition for nitrogen between plants and microflora as a function of soil heterogeneity. Soil Biology and Biochemistry **33**:215–226.
Leadley, P., J. Reynolds, and F. S. Chapin III. 1997. A model of nitrogen uptake by *Eriophorum vaginatum* roots in the field: ecological implications. Ecological Monographs **67**: 1–22.
Leake, J. R., and D. J. Read. 1990. Chitin as a nitrogen source for mycorrhizal fungi. Mycological Research **94**:993–1008.
Lee, D. L., and H. J. Atkinson. 1977. Physiology of nematodes. Second edition. Columbia University Press, New York, New York, USA.
Lee, K. E. 1985. Earthworms: their ecology and relationships with soil and land use. Academic Press, Sydney, New South Wales, Australia.
Liebig, J. 1842. Chemistry and its application to agriculture and physiology. Third American edition. John Owen, Boston, Massachusetts, USA.
Lipson, D., and R. Monson. 1998. Plant–microbe competition for soil amino acids in the alpine tundra: effects of freeze–thaw and dry–rewet events. Oecologia **113**:406–414.
Marion, G. M., P. C. Miller, J. Kummerow, and W. C. Oechel. 1982. Competition for nitrogen in a tussock tundra ecosystem. Plant and Soil **66**:317–327.
Melillo, J. M. 1981. Nitrogen cycling in deciduous forests. Ecological Bulletin **33**:427–442.
Myrold, D. D., and J. M. Tiedje. 1986. Simultaneous estimation of several nitrogen cycle rates using ^{15}N: theory and application. Soil Biology and Biochemistry **18**:559–568.
Nadelhoffer, K. J., J. D. Aber, and J. Melillo. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in Southern Wisconsin (USA). Canadian Journal of Forest Research **13**:12–21.
Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. Plant and Soil **80**:321–335.
Näsholm, T., A. Ekblad, A. Nordin, R. Giesler, M. Högberg, and P. Högberg. 1998. Boreal forest plants take up organic nitrogen. Nature **392**:914–916.
Neill, C., M. Piccolo, J. Melillo, P. Steudler, and C. Cerri. 1999. Nitrogen dynamics in Amazon forest and pasture soils measured by ^{15}N pool dilution. Soil Biology and Biochemistry **31**:567–572.
Nordin, A., P. Högberg, and T. Näsholm. 2001. Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. Oecologia **129**:125–132.
Norton, J., and M. Firestone. 1996. N dynamics in the rhizosphere of *Pinus ponderosa* seedlings. Soil Biology and Biochemistry **28**:351–362.
Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–270.
Parkin, T. B. 1987. Soil microsites as a source of denitrification variability. Soil Science Society of America Journal **51**:1194–1199.
Pastor, J., J. D. Aber, C. A. McClaugherty, and J. M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology **65**:256–268.
Paul, E. A., and F. E. Clark. 1996. Soil microbiology and biochemistry. Second edition. Academic Press, San Diego, California, USA.
Persson, J., and T. Näsholm. 2002. Regulation of amino acid uptake in conifers by exogenous and endogenous nitrogen. Planta **215**:639–644.
Piatek, K., and H. Allen. 2000. Site preparation effects on foliar N and P use, retranslocation, and transfer to litter in 15-years old *Pinus taeda*. Forest Ecology and Management **129**:143–152.
Polglase, P. J., P. M. Attiwill, and M. A. Adams. 1992. Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. II. N mineralization and nitrification. Plant and Soil **142**:167–176.
Raab, T., D. Lipson, and R. Monson. 1999. Soil amino acid utilization among species of the Cyperaceae: plant and soil processes. Ecology **80**:2408–2419.
Reich, P. B., D. F. Grigal, J. D. Aber, and S. T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. Ecology **78**:335–347.
Ruess, R. W., K. Van Cleve, J. Yarie, and L. A. Viereck. 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Canadian Journal of Forest Research **26**: 1326–1336.
Runge, M. 1971. Investigations of the content and the production of mineral nitrogen in soils. Pages 191–202 *in* H. Ellenberg, editor. Integrated experimental ecology: methods and results of ecosystem research in the German Solling project. Springer-Verlag, New York, New York, USA.
Russell, E. 1912. Soil conditions and plant growth. Longmans, Green and Company, London, UK.
Schiller, P., H. Heilmeier, and W. Hartung. 1998. Uptake of amino acids by the aquatic resurrection plant *Chamaegigas intrepidus* and its implication for N nutrition. Oecologia **117**:63–69.
Schimel, J. P., and F. S. Chapin III. 1996. Tundra plant uptake of amino acid and NH_4^+ nitrogen in situ: Plants compete well for amino acid N. Ecology **77**:2142–2147.
Schimel, J. P., and J. S. Clein. 1996. Microbial response to freeze–thaw cycles in tundra and taiga soils. Soil Biology and Biochemistry **28**:1061–1066.
Schimel, J. P., L. E. Jackson, and M. K. Firestone. 1989. Spatial and temporal effects of plant–microbial competition for inorganic nitrogen in a California annual grassland. Soil Biology and Biochemistry **21**:1059–1066.
Schimel, J. P., and M. N. Weintraub. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry **35**:549–563.
Schmidt, I. K., S. Jonasson, and A. Michelsen. 1999. Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. Applied Soil Ecology **11**:147–160.
Sexstone, A., N. Revsbech, T. Parkin, and J. Tiedje. 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Science Society of America Journal **49**:645–651.
Smith, S., and D. Read. 1997. Mycorrhizal symbiosis. Second edition. Academic Press, San Diego, California, USA.
Tietema, A., B. Warmerdam, E. Lenting, and L. Riemer. 1992. Abiotic factors regulating nitrogen transformations in the organic layer of acid forest soils: moisture and pH. Plant and Soil **147**:69–78.
Tietema, A., and W. W. Wessel. 1992. Gross nitrogen transformations in the organic layer of acid forest ecosystems subjected to incerased atmospheric nitrogen input. Soil Biology and Biochemistry **24**:943–950.
Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist **119**:553–572.
Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. Science **204**:469–474.
Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience **25**: 376–381.
Waksman, S. 1932. Principles of soil microbiology. Second

edition. Williams and Wilkins, Baltimore, Maryland, USA.
Woodmansee, R. G., I. Vallis, and J. J. Mott. 1981. Grassland nitrogen. Ecological Bulletin **33**:443–462.
Woolley, T. A. 1988. Acarology: mites and human welfare. Wiley Interscience, New York, New York, USA.
Yevdokimov, I. V., and S. A. Blagodatsky. 1994. Nitrogen immobilization and remineralization by microorganisms and nitrogen uptake by plants: interactions and rate calculations. Geomicrobiology Journal **11**:185–193.
Zöttl, H. 1960. Methodische Untersuchungen zür Bestimmung der Mineralstickstoffnachlieferung des Waldbodens. Forstwissenschaftliches Centralblatt **79**:72–90.