

Breaks in the cycle: dissolved organic nitrogen in terrestrial ecosystems

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Dissolved organic nitrogen (DON) is present in soils and streams around the world. We are only now beginning to explore the important roles this chemically heterogeneous mixture of compounds plays in terrestrial nitrogen (N) cycling. Over centuries, DON leaching may represent a significant "leak" of N, which occurs because plants and microbes cannot prevent DON losses, even in times of high N demand. However, in many ecosystems, plants may "short-circuit" the terrestrial N cycle by direct uptake of amino acid DON without microbial mineralization of organic N to ammonium (NH₄⁺). These apparently contradictory roles for DON in N cycling are due to the biological and physical factors that regulate DON loss, and the fact that there are many biochemical forms of organic N in solution. Recognition of these processes complicates the standard conceptual view of terrestrial N cycling. Here we focus on the dual roles of DON as a nutrient-loss pathway and as an N source for plants.

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Dissolved organic nitrogen (DON) is an increasingly important focus of ecological studies that seek to understand the controls over nitrogen (N) cycling within, and N losses from, ecosystems. Until recently, experimental studies and biogeochemical theory concentrated on inorganic N cycling and loss, perhaps reflecting the agricultural roots of biogeochemistry. In addition, most ecological research has been clustered in Europe and the northeastern US, where some of the highest rates of anthropogenic N input occur, and where inorganic N dominates both deposition and stream chemistry (Hedin *et al.* 1995). In these settings, the critical determinant of N nutrition in plants and the status of N in ecosystems is the concentration and turnover of inorganic N in soil solution.

While most research has looked at inorganic N, the element occurs most often in organic form in terrestrial ecosystems. If mobilized, the organic N pool in most ecosystems could satisfy plant demand for many years. Nevertheless, plant productivity remains N-limited in most temperate and northern regions (Vitousek and Howarth 1991), which raises questions about what limits the conversion of organic to inorganic N, and what regulates its overall availability (Eviner and Chapin 1997). Consequently, microbial N mineralization and immobilization have been considered as both ends of an axis, along which microbes can either compete with plants for scarce N resources, or make them available (to plants or the surrounding environment) through mineralization. Described as both the plant–soil–microbe bottleneck (Hobbie and Vitousek 2000) and the plant–microbe competition (Kaye and Hart 1997), the processes that partition N between plants and microorganisms are a central feature of biogeochemical theory and study.

Recent work on DON in ecosystems suggests that the traditional view of terrestrial N cycling misses two important processes. First, there is increasing evidence that DON can leach from ecosystems, despite high biotic demand for N (Hedin *et al.* 1995; Perakis and Hedin 2002). Second, several studies have now shown that plants can take up amino acid forms of N without relying on microbial mineralization (reviewed by Lipson and Näsholm 2001). These new observations of DON cycling challenge our standard concept of the terrestrial N cycle, suggesting new hypotheses that include both "leaks" and "short circuits" (Figure 1). Our discussion centers on reconciling two emerging hypotheses.

Hypothesis 1 (leaks of N): DON leaching can occur despite biological demand for N. Over time, the limited capacity of biotic systems to retain DON contributes to

In a nutshell:

- Dissolved organic nitrogen (DON) is found in almost every terrestrial and aquatic ecosystem around the world
- DON can be a "short circuit" in the terrestrial N cycle when plants take up some organic forms of N directly from solution, without the need for microbial mineralization
- DON can "leak" from ecosystems, despite high demand for N in plants and microbes, when some forms of DON are flushed from ecosystems due to their recalcitrance or during rapid rates of leaching
- DON's role as both a "leak" and a "short circuit" is possible because DON contains multiple forms of organic N, including both labile and recalcitrant forms prone to different types of behavior

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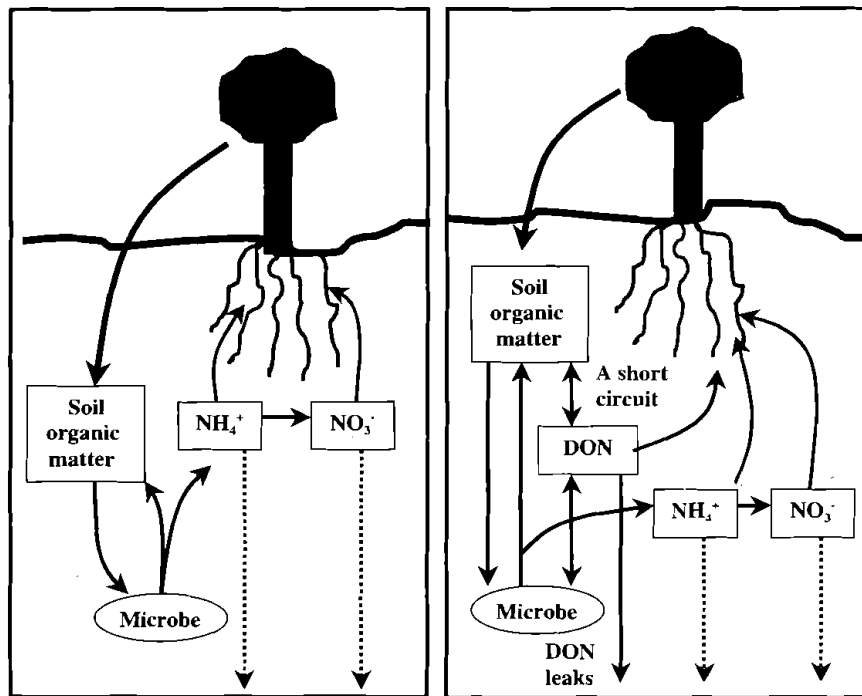


Figure 1. Standard (left) and developing (right) views of the terrestrial N cycle. Dashed blue lines indicate losses that can be regulated by plant demand. Black lines indicate biological transformations of N where microbes control the conversion of solid soil organic N to inorganic N. Purple lines indicate a mixture of biological and physical processes involved in DON cycling. Note the possibility of direct plant uptake of DON without microbial intervention. DON may also leach from ecosystems despite high plant demand for N.

the development and persistence of terrestrial N limitation.

Hypothesis 2 (short circuits in the N cycle): direct DON uptake allows plants to compete with microbes where microbial mineralization of N is limited by physical or biological factors.

These hypotheses appear contradictory at first glance. Hypothesis 1 seems possible only if biotic systems lose DON, despite N demand, whereas hypothesis 2 is possible only when there is direct biotic uptake of DON. We suggest that DON can play multiple roles in ecosystems, in part because it contains compounds that are both labile (easily degraded by plants or microorganisms) and recalcitrant (not easily utilized by plants or microorganisms), which behave in fundamentally different ways.

■ The terrestrial organic N cycle

DON enters ecosystems through precipitation (Neff *et al.* 2002) and is produced during the contact of water with soils and vegetation. It ultimately leaves ecosystems through leaching into streams or groundwater (Hedin *et al.* 1995; Lajtha *et al.* 1995; Currie *et al.* 1996; Perakis and Hedin 2002). As DON moves from plant canopies through layers of soil, some forms are consumed, while others are generated. In general, the largest DON fluxes and concentrations occur in throughfall and in the sur-

face layers of soil solution (Michalzik *et al.* 2001). Unlike the inorganic forms of N in solution, DON is not a single compound or even a single class of compounds. Instead, it is an operational definition for a structurally complex mixture of materials, ranging from simple compounds that are readily used by plants and microbes to polyphenols or tannins that are not easily metabolized (Smolander and Kitunen 2002). This point is often lost in discussions of DON's role in ecosystems.

Another point that is often forgotten is that the mechanisms responsible for generating DON include a complex mix of biotic and abiotic processes. DON is produced directly from microbial turnover (Seely and Lajtha 1997) and indirectly through microbial generation of extracellular enzymes (Trasar-Cepeda *et al.* 2000). High organic matter content typically results in a high potential for the generation of DON or dissolved organic carbon (DOC), as a result of physical dissolution or desorption of organic matter from litter or soils (reviewed in Aitkenhead-Peterson *et al.* 2000). Finally, DON can be

formed from the physical and/or biologically mediated association of dissolved organic matter (DOM) with nitrate (NO_3^-) in soils (Perakis *et al.* 2001; Davidson *et al.* 2003).

There is evidence that DON inputs in precipitation are relatively labile, (easily degraded by microorganisms) (Seitzinger and Sanders 1999). Similarly, the DON that leaches from fresh and senesced plant tissues also appears to be highly labile, with average microbial decomposability approaching 70% across a range of species (Cleveland *et al.* in press). In soils, there is limited information available on the decomposability of DON. For DOC, which can serve as a rough proxy for DON, there appear to be variable, but sizable, labile, and recalcitrant fractions (Zsolnay and Steindl 1991; Coore *et al.* 1999). The presence of a large labile and recalcitrant DOC fraction in soil may help explain the tendency of some DON to leak from ecosystems (assuming it decomposes in a manner similar to DOC), despite microbial or plant demand for N, while other forms of DON are taken up by plants and microbes.

Both dissolved organic elements are subject to the development of strong mineral-organic matter associations, which are in turn influenced by factors such as soil mineralogy, surface reactivity, and organic matter content (Moore *et al.* 1992; Kaiser and Zeck 2000). In general, fluxes of DOC and DON tend to be higher in sandy soils than in more heavily textured soils (Dosskey and Bertsch 1994; McClain *et al.* 1997; Campbell *et al.* 2000). These

differences become apparent at the watershed scale, when “blackwater” rivers are formed. In many parts of the world, the combination of high levels of rainfall, high organic matter content, and the presence of sandy soils lead to dark, DOM-rich rivers, such as the Rio Negro and other tributaries to the Amazon River (Figure 2).

■ Nitrogen leaks

Fluxes of N into and out of ecosystems are typically an order of magnitude lower than the N fluxes associated with productivity and soil organic matter turnover (Chapin *et al.* 2002; Van Breemen *et al.* 2002). However, persistent but small N losses can eventually lead to a reduction in accumulation of N stores in an ecosystem, and limitations to productivity (Vitousek *et al.* 1998). Most ecologists are familiar with the concept that C-sequestering systems exhibit net retention of incoming N. This idea, which is part of the nutrient-retention hypothesis, argues that ecosystems that are accumulating C will also show highly efficient biotic retention of incoming N (Vitousek and Reiners 1975). The corollary to the hypothesis is that a system that exhibits no net growth will have N outputs that equal N inputs. In other words, a system at steady state with respect to C will also be at steady state with respect to N. At the heart of the nutrient-retention hypothesis is the simple but crucial argument that N losses are controlled by biology and, as long as demand is high, losses are minimal.

An N leak is fundamentally different from an N loss that can be controlled by biological demand. Leaks occur where biotic systems cannot fully prevent N losses, despite an overall system demand for N. Over time, nutrient leaks need to be replaced by new N, or they will constrain the accumulation of N capital (the sum of N in plants and soils) in an ecosystem. Eventually, such processes can contribute to N limitation of productivity. The hypothesis that DON may function as a leak of N from ecosystems was first developed by Hedin *et al.* (1995), and based on observations that DON fluxes dominate stream N fluxes in Chilean ecosystems characterized by very low atmospheric inputs of N and high rates of precipitation. Multiple studies have now shown that DON can account for a significant fraction of N losses to streams, despite ecosystem demand for N (Sollins and McCorrison 1981; Hedin *et al.* 1995; Lajtha *et al.* 1995; Perakis and Hedin 2002). DON losses are sometimes described as biologically



Figure 2. The confluence of the silt-laden Amazon and organic-rich Manacapuru rivers just west of Manaus, Brazil. Image taken with the Earth Observing-1 Advanced Land Imager. The dark color of the Manacapuru results from the high concentrations of dissolved organic matter in the water.

independent (eg Hedin *et al.* 1995) because they do not vary with biological activity, fertility, or season, as much as inorganic N (Campbell *et al.* 2000; Goodale *et al.* 2000; Neff *et al.* 2000; Qualls 2000). This is not to say that all forms of DON are controlled by physical rather than biological mechanisms and always function independently of N status in the ecosystem. However, the importance of abiotic production mechanisms, and the potential to leach recalcitrant fractions of DON from soils before decomposition or uptake can occur, both contribute to the potential for DON losses, even during periods of substantial ecosystem demand for N.

Many factors contribute to DON leaks, including the physical factors, such as soil texture, described above. Taken as a whole, however, DON losses are a simple consequence of life in a semi-aqueous environment. Organisms must produce molecules that resist chemical or biological breakdown during their lifetimes, but at a molecular level, these same properties increase the likelihood of DON loss after microbial death. Complex dissolved organic compounds are often too large to cross membranes, and too complex for decomposition by a single extracellular enzyme (Carreiro *et al.* 2000). As a result,

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the decomposition of these structurally complex materials takes time, and may not be possible when water fluxes carry dissolved compounds rapidly out of soils.

■ Short circuits in the N cycle

Microbial mineralization of organic N in soils is traditionally considered the bottleneck in the internal cycling of this element in ecosystems, because it is an essential intermediate step between the transfer of organic N to the soil and the availability of inorganic N for subsequent plant growth (Zak *et al.* 1990; Chapin *et al.* 2002). From a plant perspective, microbial control of N mineralization has the potential to create a feedback loop in which low inorganic N availability results in the creation of biomass with high C:N ratios. This leads to increased microbial immobilization of N and yet lower inorganic N availability, higher plant C:N ratios, and so on. This plant–soil–microbe loop is commonly represented in ecological models and discussed in theoretical evaluations of ecosystem nutrient dynamics (Hobbie 1992; Aber and Melillo 2001).

If plants were able to access the organic N in soils directly, without depending on microbial mineralization to produce inorganic N, they could have a potential competitive advantage over other plants, as well as over microbial competitors for soil N. There is now strong evidence that plants in boreal (Näsholm *et al.* 1994, 1998; Kielland 2001), arctic (Chapin *et al.* 1993; Schimel and Chapin 1996; Jones and Kielland 2002), and alpine (Lipson and Monson 1998; Lipson *et al.* 1999; Raab *et al.*

1999) ecosystems directly absorb, and generally prefer, amino acids over inorganic N. Amino acid uptake by plants occurs in many species, including non-mycorrhizal, vesicular–arbuscular mycorrhizal, and ericoid and ectomycorrhizal plants (reviewed in Lipson and Näsholm 2001). Taken together, these studies represent a growing body of evidence that direct organic N uptake by plants plays an important role in plant nutrient use. There have even been suggestions that plant–mycorrhizal associations, and the associated facilitation of plant polyphenol decomposition, is a coevolved strategy to increase plant N acquisition (Northup *et al.* 1995).

Many of the in situ observations of amino acid uptake by plants have been in northern or alpine ecosystems (Chapin *et al.* 1993; Kielland, 1994, 1997; Näsholm *et al.* 1998). Outside of these environments, evidence for amino acid use by plants is mixed, and there is evidence that plants are poor competitors for amino acids in agricultural ecosystems (Owen and Jones 2001). The amino acid pool is only a small portion of the total DON pool, which generally contains less than 10% free amino acids in temperate ecosystems (Qualls and Haines 1991; Yu *et al.* 2002). Boreal soils may contain larger amounts (10–20%) of amino acids in the soil DON pool, and this may be one of the reasons why amino acid use is so prevalent in northern ecosystems (Jones and Kielland 2002). The use of amino acids to satisfy a substantial proportion of plant N demand in northern-latitude and alpine systems may also be related to the frequent presence of relatively wet soils and low rates of microbial activity. In northern regions, there is a considerable flush of bioavailable DON to streams during snowmelt (Whalen and Cornwell 1985; MacLean *et al.* 1999; Stepanauskas *et al.* 2000) (Figure 4). In terms of plant adaptation, it would be surprising if plants were not able to take advantage of the confluence of wet soils, high organic matter content, and slow microbial turnover (Atkin 1996). In areas with high concentrations of DON and low microbial activity in the soil, the ability to take up highly labile forms of DON, such as amino acids, may offer plants a competitive advantage in regions with short growing seasons (Lipson and Monson 1998).

The mechanisms involved in plant uptake of organic N and implications for plant N uptake are reviewed elsewhere (Lipson and Näsholm 2001). From the standpoint of plant–microbe competition and the short-circuit hypothesis, Kielland (2001) argues that plant competition for amino acids in soil solutions is important to N acquisition, particularly in those envi-

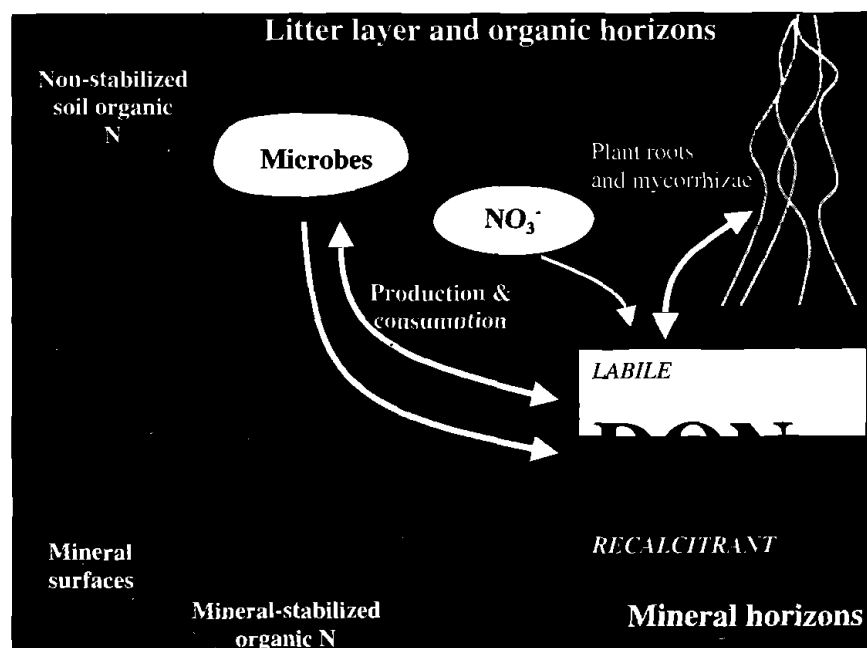


Figure 3. Mechanistic controls over the soil DON cycle. Solid yellow arrows and text show fluxes dominated by biological processes; blue dashed lines and blue text indicate physically controlled processes. Note that only DON cycling processes are shown. The arrow from NO_3^- to DON shows the possibility of a biotic or abiotic incorporation of NO_3^- into dissolved organic matter.



Figure 4. An ephemeral stream with high concentrations of dissolved organic N runs over permafrost near Delta Junction, Alaska. The dark color of the water is caused by dissolved organic compounds produced during the movement of water through organic-rich surface horizons. The movement of DON in streams such as this one represents a potentially significant loss of N from terrestrial ecosystems.

ronments where decomposition is slow. Plant uptake of organic N is an active area of research, and more work is needed to evaluate the relative importance of plant organic N use across ecosystems. There are also important questions about the role of mycorrhizal associations in the process (including the potential for uptake of more complex forms of DON) and persistent difficulties in quantifying the benefits to individual plants of organic N uptake. However, the process of organic N uptake does appear to have important implications for plant–microbe competition, and is likely to act, at least for some ecosystems, as a short circuit in the N cycle.

At one level, the role of DON in the N cycle seems contradictory. In the case of N leaks, DON is important because the biota cannot regulate its loss, and in the case of plant–microbe N competition, DON is important because it allows a short circuit in the competitive feedback loop between plants and microbes. This apparent contradiction arises out of the grouping of several organic compounds into one operational definition – DON. Amino acids are one small fraction of a larger pool of DON that contains more complex and biologically recalcitrant compounds, and the same conditions that may favor plant amino acid uptake (such as those shown in Figure 4) may also lead to the loss of other forms of DON through leaching. While it is important to understand the dynamics of utilization of all forms of dissolved N by plants, it is equally important to differentiate between the use of amino acids and DON as a whole.

DON should be considered as at least two pools of material: one characterized by high biological lability, and the

other by its biological recalcitrance. This distinction would place labile DON – largely soluble amino acids – in the same general class of terrestrial N as NH_4^+ and NO_3^- , while the recalcitrant DON would function in a manner similar to bulk soil organic matter. If, as Northup *et al.* (1995) suggest, there has been some coevolution of plant–mycorrhizal associations to facilitate the decomposition of structurally complex DON, then this simple separation of DON would require reevaluation. In general, however, it is clear that, on a time scale of days to seasons, plant and microbial competition for amino acids, NH_4^+ , and NO_3^- plays an important role in meeting the nutrient requirements of plants, even while the slow loss of more recalcitrant forms of DON helps lead to, or maintain, overall ecosystem N limitation.

■ Conclusions

While there is mounting support for the two hypotheses presented above, considerable uncertainty remains. From the standpoint of DON leaks and the development of nutrient limitation (hypothesis 1), it is still difficult to close the N budget of most terrestrial ecosystems. Until N budgets can be measured with high precision, the long-term trajectory of nutrient balance will be difficult to predict. For this reason, the development of N limitation remains an important biogeochemical puzzle, with persistent questions about the controls over the balance between inputs and losses.

For plant N acquisition and hypothesis 2, the relative importance of direct amino acid uptake across a variety of ecosystems requires additional research, but the potential importance of the process as a short circuit of the N cycle is clear. However, the mechanisms that generate amino acids (plant vs microbial), and the processes responsible for maintaining the full diversity of compounds present in the soil DON pool, are less clear. One exciting new avenue of inquiry lies in the exploration of the evolutionary mechanisms that structure plant–microbial competition for N, which could help explain the variations in the dynamics of plant N use across ecosystems and species. Research into these areas will help us fully understand the partitioning of mineral resources within ecosystems.

Nutrient use and nutrient balance are central themes in ecosystem ecology. Traditionally, the N cycle is viewed as a balance between plant and microbial use of inorganic N (Harte and Kinzig 1993). It is now clear that DON also plays important roles in terrestrial N cycling. As new studies examine the implications of DON in both nutrient leaks and short circuits, it will be increasingly important

to develop a more complex view of DON as a mixture of both labile and recalcitrant compounds that have substantial – and very different – roles in terrestrial biogeochemistry.

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