

# The influence of the forest canopy on nutrient cycling

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**Summary** Rates of key soil processes involved in recycling of nutrients in forests are governed by temperature and moisture conditions and by the chemical and physical nature of the litter. The forest canopy influences all of these factors and thus has a large influence on nutrient cycling. The increased availability of nutrients in soil in clearcuts illustrates how the canopy retains nutrients (especially N) on site, both by storing nutrients in foliage and through the steady input of available C in litter. The idea that faster decomposition is responsible for the flush of nitrate in clearcuts has not been supported by experimental evidence. Soil N availability increases in canopy gaps as small as 0.1 ha, so natural disturbances or partial harvesting practices that increase the complexity of the canopy by creating gaps will similarly increase the spatial variability in soil N cycling and availability within the forest.

Canopy characteristics affect the amount and composition of leaf litter produced, which largely determines the amount of nutrients to be recycled and the resulting nutrient availability. Although effects of tree species on soil nutrient availability were thought to be brought about largely through differences in the decomposition rate of their foliar litter, recent studies indicate that the effect of tree species can be better predicted from the mass and nutrient content of litter produced, hence total nutrient return, than from litter decay rate. The greater canopy complexity in mixed species forests creates similar heterogeneity in nutritional characteristics of the forest floor.

Site differences in slope position, parent material and soil texture lead to variation in species composition and productivity of forests, and thus in the nature and amount of litter produced. Through this positive feedback, the canopy accentuates inherent differences in site fertility.

*Keywords:* canopy gaps, clearcut, decomposition, litterfall, nitrification, nitrogen mineralization, site fertility, species influences, species mixtures.

## Introduction

The availability of nutrients in forest ecosystems depends on efficient recycling of nutrients within the ecosystem. Through this cycle, nutrients are returned to the soil in litter following the death of plant tissues, released from the litter through decomposition and mineralization, recycled through soil organisms and taken up by vegetation. Rates of decomposition and nutrient mineralization are governed by temperature and

moisture conditions, and by the chemical and physical nature of the litter. The forest canopy influences all of these factors and thus has a large influence on nutrient cycling. The shading and insulation afforded by the canopy buffer temperature extremes at the ground surface. The canopy also alters hydrological conditions by redirecting precipitation, reducing snow accumulation, and removing soil water through transpiration. These hydrological alterations reduce the magnitude of nutrient losses through leaching or overland flow. The canopy also alters the chemical composition of precipitation; as rain passes through the canopy, concentrations of nutrients such as N, P, K and Ca may increase or decrease (Sollins et al. 1980, Lovett and Lindberg 1993). The foliage and branches of the canopy are a major nutrient sink, which retains nutrients on site. Although branches and foliage comprise only a small portion of total tree biomass, these tissues are relatively nutrient-rich, and so may contain up to half of the N, P, Mg, K and Ca immobilized in tree biomass (Alban et al. 1978 as cited by Perry 1984).

The most important aspect of the canopy in terms of its influence on nutrient cycling is its role as the source of leaf litter. Characteristics of the canopy determine the amount and composition of leaf litter produced, which largely determines the amount of nutrients to be recycled, the composition of the soil microbial and faunal communities and the resulting availability of nutrients. Although up to half the mass of litter produced annually in forests may originate below ground (Vogt et al. 1986), the canopy is a key source of nutrients in mature forests. In three Rocky Mountain forests, canopy litter (foliage, reproductive tissue and fine woody debris) accounted for 66 to 86% of the mass, 63 to 90% of the N, and 49 to 92% of the P returned annually in aboveground litter (Laiho and Prescott 1999, Figure 1). Extrapolation of input and decomposition rate data from these forests demonstrates the overriding importance of canopy litter in the recycling of N and P (Laiho and Prescott 1999, Figure 2).

Here I discuss ways in which the canopy, primarily through its role as litter producer, influences the availability of nutrients in the forest floor and soil. I largely focus on N, the most frequently limiting nutrient in many forests, and thus the nutrient that has received the most research attention. I also examine ways in which increasing canopy complexity, either by creating gaps or by increasing the number of species present, may affect the cycling of nutrients in the forest.

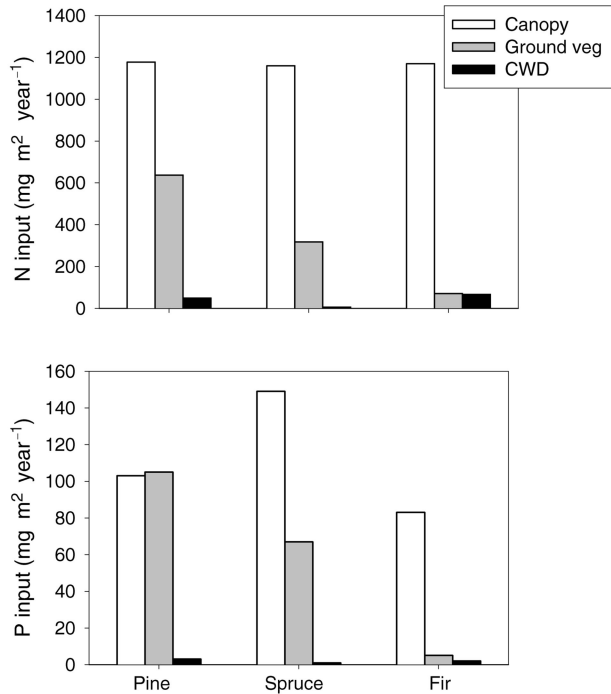


Figure 1. Average inputs of N and P from canopy litter, ground vegetation and coarse woody debris (CWD) in three Rocky Mountain forests. Each value is the mean of 5 years for canopy litter, 1 year for ground vegetation and 10 years for CWD. Adapted from Laiho and Prescott (1999).

### The canopy retains nutrients on site

Removal of the canopy during forest harvest is associated with several changes in nutrient cycling. Some, such as death and decay of roots (Fahey et al. 1988), changes in ground vegetation (Hannerz and Hanell 1997), or disruption of surface soil (Ryan et al. 1992), may be indirect effects of canopy removal, but they nonetheless indicate the role of an intact canopy in nutrient cycling. Clearcut harvesting is usually followed by a period of increased availability of most nutrients in soil, which may be associated with greater losses of nutrients through leaching and denitrification (Keenan and Kimmins 1993). Increased rates of N mineralization and nitrification have been reported in forest floors and soils following clearcut harvesting of forests (Frazer et al. 1990, Smethurst and Nambiar 1990, Dahlgren and Driscoll 1994), as have elevated nitrate concentrations in soils and drainage waters (Bormann and Likens 1979, Vitousek et al. 1979, Sollins et al. 1981, Hendrickson et al. 1989, Fisk and Fahey 1990, Feller et al. 2000). The effect usually begins within 1 year of clearcutting and lasts 3–5 years (C.E. Prescott et al., unpublished data), although the intensity and period of the effect vary according to site fertility (Vitousek et al. 1979). This phenomenon is attributed to: (1) the decline in nutrient uptake by vegetation (Bormann and Likens 1979); (2) increased rates of decomposition of residual organic matter resulting from the warmer and moister conditions in openings (Stone 1973, Bormann et al.

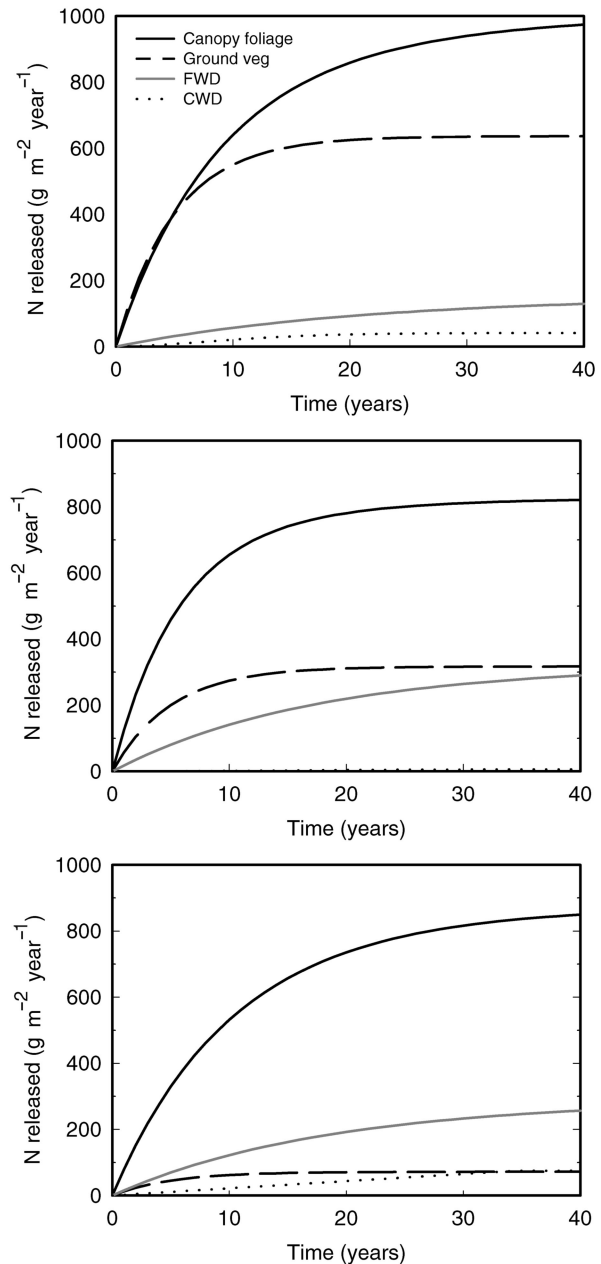


Figure 2. Contributions of canopy foliage, ground vegetation, fine woody debris (FWD) and coarse woody debris (CWD) to annual N release from decomposing organic matter in three Rocky Mountain forests, during a 40-year simulation period (Laiho and Prescott 1999).

1974); (3) reduction in C inputs from litter and root exudation, leading to a decline in N assimilation by microbial biomass (Hart et al. 1994, Bradley et al. 2000); and (4) decay of logging debris including foliage, woody materials and root systems (Smethurst and Nambiar 1990, Emmet et al. 1991). The relative importance of each of these causative factors has not been determined.

The idea that faster decomposition is responsible for the flush of nitrate in clearcuts has not been supported by experi-

mental evidence (Prescott et al. 2000a). Rather, the idea that reduced concentrations of available C may result in increased nitrate availability in clearcuts has gained momentum. This follows the discovery of high rates of gross nitrification in mature forests (Davidson et al. 1992, Stark and Hart 1997), and the microcosm study of Hart et al. (1994) that linked the onset of net nitrification with the decline in C availability to microbes. It has been hypothesized that the cessation of annual input of litter from the canopy and the resulting reduction in labile C sources causes the microbial biomass to be C-limited rather than N-limited, leading to reduced assimilation of nitrate and the flush of available nitrate characteristic of clearcuts (Prescott 1997, Bradley et al. 2000). Thus, it could be argued that the canopy plays an important role in retaining nutrients (especially N) on site both by storing nutrients in foliage and through the steady input of available C in litter.

### Canopy gaps create patches of higher nutrient availability

Gaps in the canopy can create changes in N cycling reminiscent of the effects of forest removal. Elevated N mineralization rates and nitrate availability have been observed in openings of 0.25 ha (Prescott et al. 1992), 0.1 ha (C.E. Prescott et al., unpublished data; Figure 3), a 30-m-diameter, 0.07 ha patch (Bauhus and Barthel 1995), and in a gap created by the removal of 15 trees (Parsons et al. 1994). Removal of the same proportion of trees by single-tree thinning does not have the same effect (Parsons et al. 1994), indicating that canopy gaps larger than single trees are needed to induce changes in N cycling. This suggests that natural disturbances or partial harvesting practices that increase canopy complexity by creating gaps will similarly increase the spatial variability in soil N cycling and availability within the forest.

### Canopy species composition influences litter quality and nutrient availability

Because of differences in the chemical quality of leaf litter among tree species, the species composition of the canopy would be expected to have a substantial effect on nutrient cycling. Some distinct differences in nutrient availability have been reported in the forest floor and soil beneath stands of different tree species. For example: greater N concentration, content and mineralization rate under N-fixing species such as *Alnus* (Binkley 1983, J.M. Lavery et al., Forest Research Institute, Rotorua, New Zealand, unpublished data) and *Albizia* (Binkley 1997, Kaye et al. 2000); high pH and Ca concentrations in forest floors of cedar (*Thuja plicata* Donn ex D. Don) (Alban 1969, Turner and Franz 1985, Kiilsgaard et al. 1988, Prescott et al. 2000c) and sugar maple (*Acer saccharum* Marsh) (Finzi et al. 1998); high rates of net N mineralization and nitrification in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest floors (Prescott and Preston 1994, Prescott 1996, Thomas and Prescott 2000, Prescott et al. 2000c); low nutrient concentrations in pine litter and low nutrient availability in pine forest floors (Prescott et al. 1992, Stump and Binkley 1993, Prescott 1996), with the exception of white

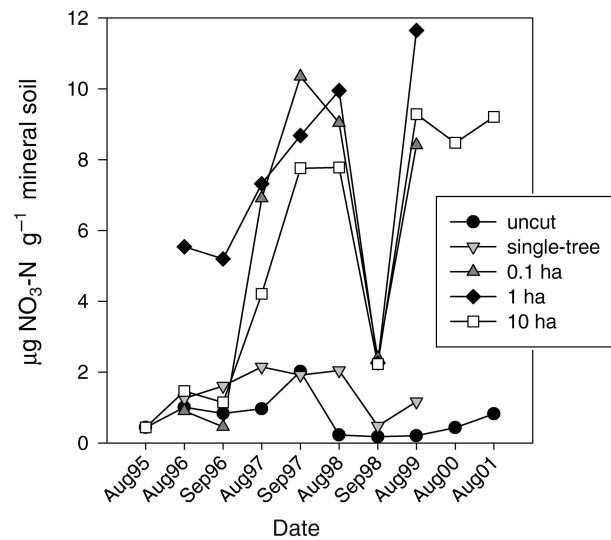


Figure 3. Concentrations of NO<sub>3</sub>-N in mineral soil samples following incubation in openings of 0 to 10 ha in a high-elevation spruce–fir forest in B.C. (C.E. Prescott et al., unpublished data).

pine (*Pinus strobus* L.) (Binkley and Giardina 1998); high nutrient concentrations in spruce litter, compared with that of pines (Perala and Alban 1982, Fyles and McGill 1987, Fyles and Côté 1994, Johansson 1995); and low pH and base cations in hemlock forest floors (Turner and Franz 1985, Finzi et al. 1998).

Differences in nutrient availability in stands of different tree species may be brought about largely through differences in the decomposability of their foliar litter. The lignin/N ratio of foliar litter has been significantly correlated with rates of decomposition (Melillo et al. 1982, Taylor et al. 1991, Figure 4) and net N mineralization in forests of different species (Gower and Son 1992, Stump and Binkley 1993, Prescott and Preston 1994, Scott and Binkley 1997, Ferrari 1999) (Figure 5). However, in other studies, no relationship has been observed between the lignin/N ratio of litter and its rate of decay or N mineralization, or between the rates of litter decomposition and N mineralization (Prescott et al. 2000c, Thomas and Prescott 2000). Rates of litter decomposition, particularly in the early stages, appear less closely associated with rates of turnover and nutrient release than was earlier thought. Species with rapid initial litter decomposition rates reach a stage of slow decay sooner and in some cases with a greater proportion of their original mass remaining than do species with slower initial decomposition rates (Berg et al. 1995). This observation refutes the presumed close relationship between initial rates of litter decay and nutrient availability in different forest types. Thus, although nutrient availability differs in forests of differing species composition, these differences cannot be predicted from the initial chemistry or decay rate of the litter.

The effect of tree species on nutrient availability can be better predicted from the litter mass and nutrient content, i.e., total nutrient return, than from litter decay rate. The amount of nutrients returned in the litter will determine the amount avail-

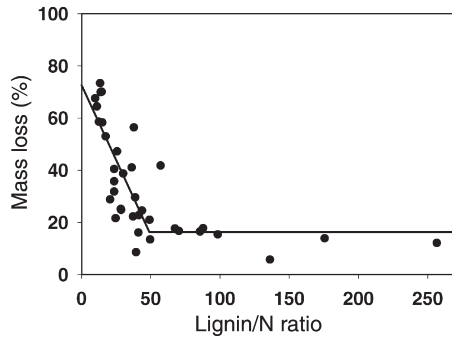


Figure 4. Mass loss after 3 years as a function of the initial lignin/N ratio of 19 litter types decomposing in three Rocky Mountain forests (Taylor et al. 1991).

able for recycling, and feedbacks between nutrient availability and litter nutrient content (Gosz 1981) promote this relationship. Strong positive relationships between the initial concentrations of N or P and the rate of release of nutrients during the initial stages of decay have been reported in several studies (MacLean and Wein 1978, Edmonds 1980, Berg and Ekbohm 1983, Yavitt and Fahey 1986, Stohlgren 1988). Positive correlations between the N content of litter and N availability in the forest floor or soil have also been demonstrated (Pastor et al. 1984, Reich et al. 1997). Cole et al. (1995) concluded that the higher N availability under red alder (*Alnus rubra* Bong.) stands compared with Douglas-fir stands was attributable to the greater amount and higher N content of the litter than to its more rapid decay.

Despite the long-standing belief in effects of tree species on nutrient availability, differences among tree species are not consistent among studies, making it difficult to generalize about the species effect (Binkley and Giardina 1998). Even the long-held belief that nutrient cycling and availability is higher under broad-leaved than needle-leaved trees is not consistently supported by experimental evidence. Higher rates of litter

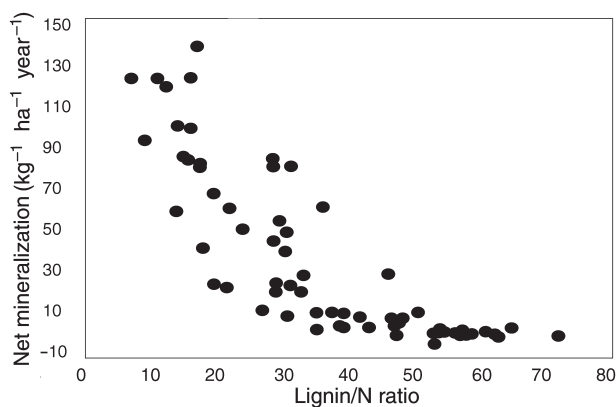


Figure 5. Net soil N mineralization as a function of the lignin/N ratio of aboveground litter from nine common-garden experiments with temperate forest species (Scott and Binkley 1997).

decomposition and N mineralization in forest floors of aspen (*Populus tremuloides* Michx.) relative to conifers have been reported in some studies (Flanagan and Van Cleve 1983, Stump and Binkley 1993), but in other studies rates of N mineralization in birch forests have been the same (Priha and Smolander 1997), or lower (Saetre et al. 1999, Thomas and Prescott 2002) than those in coniferous forests. Similarly, faster decomposition of broadleaf litter than needle litter has been reported in many studies (Flanagan and Van Cleve 1983, Fried et al. 1990, Klemmedson 1992, Cornelissen 1996), whereas others have reported no difference (McLaugherty et al. 1985, Gower and Son 1992). Long-term incubation of broadleaf and needle litter suggests that the faster decay of broadleaf litter was short-lived (Cole et al. 1995, Prescott et al. 2000d: Figure 6). However, the litter of many broadleaf species has a higher base cation concentration and usually creates forest floors higher in base cations and pH (Binkley and Valentine 1991, Brantberg et al. 2000).

#### Nutrient availability is altered in some mixed species canopies

Species diversity may affect nutrient cycling, but this appears to depend on the species present. Nutritional interactions in mixed species forests have recently been reviewed by Rothe and Binkley (2001). As expected, the largest and most consistent effects on nutrient cycling attributable to mixtures occur with N-fixing species; other consistent effects relate to the nurse species phenomenon with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on nutrient-poor sites in the U.K. and Ireland. Greater contents of N and P have been reported in mixtures with N-fixing species compared with pure conifer stands, whereas mixing of broad-leaved species that do not fix N increases cycling of base cations but not N and P. Faster decay of mixed litter of different species has been reported in some studies (Rustad and Cronan 1988, Taylor et al. 1989, Fyles and Fyles 1993), whereas others have reported no effects (Thomas 1968, Klemmedson 1992, Rustad 1994, Prescott et al. 2000d, Figure 6). Comprehensive experiments with litter mixtures (McTiernan et al. 1997, Wardle et al. 1997) indicate that the effects of mixing on decomposition rate are highly species-specific and not a general consequence of mixing species. Thus, there is little evidence of a consistent effect of mixing in terms of synergistic or antagonistic interactions that alter nutrient cycling, indicating that the influence of species mixtures on nutrient cycling can be simply predicted by the nutrient content of litter returned by each component species. Finally, investigations of nutrient availability under trees in mixed forests (Alban 1969, Ferrari 1999) have demonstrated that the greater canopy complexity in mixed species forests creates similar heterogeneity in nutritional characteristics of the forest floor.

#### The canopy accentuates differences in site fertility

Some of the variability in effects of species may be related to the ability of site factors other than tree species to influence

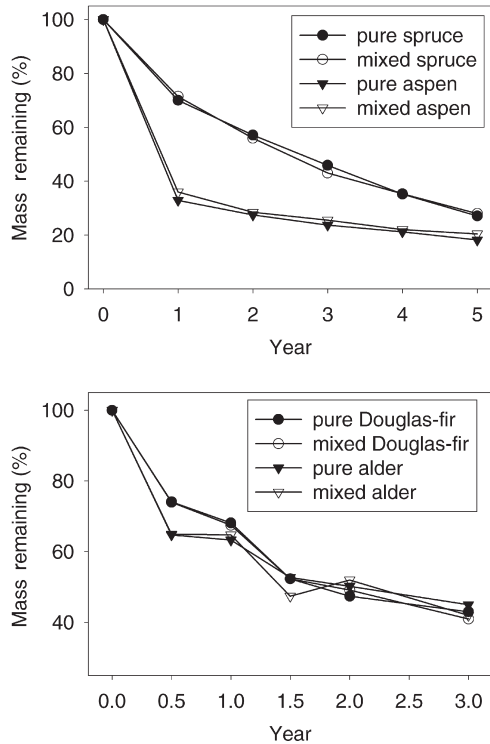


Figure 6. Mass remaining of pure and mixed foliar litters of white spruce and trembling aspen (a) and Douglas-fir and red alder (b) during incubation in boreal and coastal B.C. forests, respectively (Prescott et al. 2000d).

nutrient availability. For example, comparing pure plantations of four conifer species on four sites, Prescott et al. (2000c) found greater differences in forest floor net N mineralization rates among sites than among species (Figure 7). Differences in slope position and associated differences in ground vegeta-

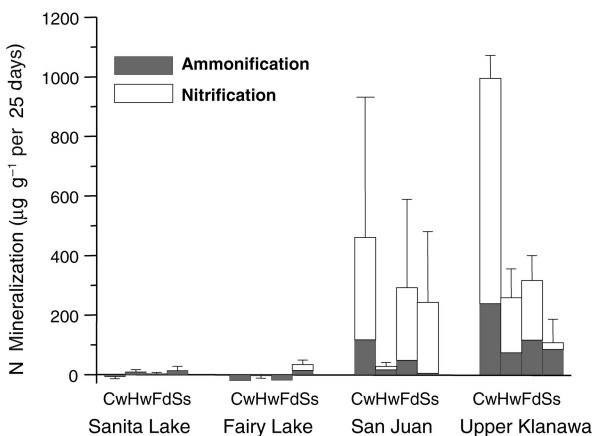


Figure 7. Rates of N mineralization and proportion of ammonium and nitrate produced during a 25-day laboratory incubation of forest floors beneath stands of four tree species at four sites in coastal B.C. (Prescott et al. 2000c). Abbreviations: Cw = western red cedar; Hw = western hemlock; Fd = Douglas-fir; and Ss = Sitka spruce.

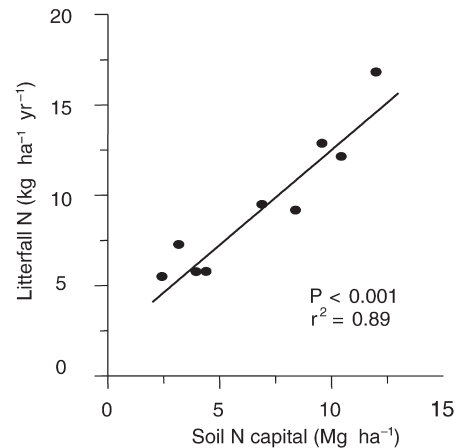


Figure 8. Nitrogen content of aboveground litter in nine Douglas-fir stands in relation to soil N capital (Prescott et al. 2000b).

tion had a much greater influence than tree species (Prescott et al. 2000c). Fyles and Cote (1994) also found that the influence of species was confounded by site factors. Thus, although the quality of leaf litter produced by the tree species occupying a site influences nutrient cycling, it may not be the dominant factor.

The role of inherent site factors such as slope position, parent material and soil texture in influencing the species composition of forests has been demonstrated in several studies (Whitney 1991, Host and Pregitzer 1992, van Breeman et al. 1997). Investigations that have compared nutrient cycling in different forest types along soil fertility gradients (Pastor et al. 1984, Reich et al. 1997) have indicated that litterfall N content is an important feedback that accentuates inherent differences in site fertility. This was also apparent in a comparison of N cycling in Douglas-fir forests along a gradient of soil N capital (Prescott et al. 2000b). On sites with higher N capital, there was more N returned in canopy litterfall, as a result of greater mass and greater N concentrations (Figure 8). This positive feedback perpetuated greater N cycling and N availability on sites that had a high N capital, which in turn appeared to be related to soil texture. Thus, by determining both the quantity and quality of litter returned to the soil, the canopy species composition can intensify differences in site fertility.

These examples illustrate several ways in which the forest canopy, primarily through the production of foliar litter, influences key processes associated with the recycling of nutrients in the ecosystem. In addition to the many other functions of the canopy discussed in this special issue, the canopy should be recognized as a key source of the "dead stuff" critical to ecosystem functioning.

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