

Research review

The potential effects of nitrogen deposition on fine-root production in forest ecosystems

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SUMMARY

Temperate forests are recipients of anthropogenic nitrogen (N) deposition. Because growth in these ecosystems is often limited by N availability, elevated N inputs from the atmosphere can influence above- and belowground production in forests. Although fine-root production is the largest component of belowground production in forests, it is unclear whether or how increases in N availability to forest trees accompanying increased N deposition might influence fine-root growth. Uncertainties as to how fine-root dynamics (i.e. production and turnover) vary in relation to soil N availability contribute to this problem. Although fine-root biomass typically decreases along soil N availability gradients in forests, it is unclear whether fine-root production and turnover also decrease along these gradients. Here, four possible relationships between fine-root turnover, fine-root production, and forest soil N availability are evaluated to develop a general hypothesis about changes in rooting dynamics that might accompany increases in N deposition. The four possible relationships are as follows. (1) Fine-root turnover rates do not systematically change with N availability in forest soils. If this is true, then fine-root production rates decrease with fine-root biomass in relation to soil N availability, and increased N deposition could lead to decreased fine-root production in forests. (2) Decreases in photosynthate allocation belowground along N availability gradients will function to slow fine-root turnover (or increase life span) as N availability increases with N deposition, thereby dramatically decreasing fine-root production. (3) Fine-root production might increase with N availability even though fine-root biomass typically decreases with N availability. This could occur if fine-root metabolism and turnover increase (life span decreases) with soil N supply. Increases in fine-root production accompanying increases in N availability, if large enough, could result in constant proportions of forest production being allocated to fine roots as soil N availability increases with N deposition. (4) Although fine-root turnover and production might both increase as N becomes more available to tree roots, the proportional allocation of total primary production to fine roots could decrease. Identifying the most likely of these four possibilities requires intersite comparisons of forest root dynamics along gradients of soil N availability and N deposition. Collective results of studies that use sequential sampling of fine-root biomass to estimate production suggest that fine-root turnover and production either; do not vary systematically, or that they decrease as N availability increases. By contrast, studies using ecosystem C or N budgets suggest that fine-root turnover and production both increase with N availability and that similar increases might be expected with elevated N deposition. It is argued here that assumptions underlying most biomass-based estimates of fine-root production are more suspect than are assumptions underlying element budget-based estimates. If so, it is likely that N deposition will function to decrease forest fine-root biomass but to stimulate fine-root turnover and production. However, increases in fine-root turnover and production could eventually decrease if chronically elevated N deposition leads to forest stand mortality.

Key words: fine roots, nitrogen deposition, root turnover, belowground production, N saturation, forest ecosystems.

INTRODUCTION

'In questions of science the authority of a thousand is not worth the humble reasoning of a single individual.' Galileo Galilei (1564–1642)

Before the twentieth century, rates of nitrogen (N) deposition on the Earth's surface were low (Logan, 1983), and annual N inputs to forests from the atmosphere were miniscule compared with rates of N uptake by tree roots. However, atmospheric deposition of biologically available N (mainly NH_x and NO_y) on landscapes is increasing together with use of fossil fuel and N fertilizer (Galloway *et al.*, 1995). Although N deposition is highest in temperate industrialized regions of eastern North America and Europe, rates are likely to increase dramatically in other regions as industrial development and agricultural activities increase N emissions to the atmosphere in lower latitudes (Galloway *et al.*, 1994).

Recognition that high rates of N deposition could damage forest trees (Friedland *et al.*, 1984; Nihlgård, 1985; Schulze, 1989) led to the development of various 'N saturation' hypotheses (Ågren & Bosatta, 1988; Skeffington & Wilson, 1988; Aber *et al.*, 1989). These hypotheses describe forest responses to chronically elevated N deposition as a progression from 'pristine' conditions in which growth is N-limited and ecosystem N losses are small, to a 'saturated' stage characterized by nutrient imbalances in plant tissues and high rates of tree mortality and nitrate leaching. N saturation hypotheses have been tested in a number of multiple-site experiments (Burton *et al.*, 1993; Wright *et al.*, 1994; Emmett *et al.*, 1998; Tietema *et al.*, 1998) and decade or longer manipulations of N inputs (Magill *et al.*, 1997; Chappell *et al.*, 1999; Fernandez *et al.*, 1999). Studies of the effects of N deposition on forests have focused mainly on aboveground plant responses, soil N dynamics and ecosystem N losses. As a result, much has been learned about how aboveground plant growth, plant species competition, nutrient cycling and nutrient input and/or output balances respond to N deposition (Stoddard, 1994; Aber *et al.*, 1998; Gundersen *et al.*, 1998).

Responses of belowground plant processes, such as fine-root growth and mortality, have been less extensively studied than have soil microbial and aboveground processes (but see Pregitzer *et al.*, 1995). As a result, there is a great deal of uncertainty regarding the possible effects of N deposition on fine-root production and turnover (the inverse of life span). In this review, I evaluate hypotheses about how fine-root dynamics might vary in relation to changes in N uptake by forest trees that will be likely to accompany increased N deposition. The possible implications of chronically elevated N deposition on fine-root dynamics in forest ecosystems are then explored.

IS THERE A RELATIONSHIP BETWEEN FINE-ROOT PRODUCTION AND ABOVEGROUND PRIMARY PRODUCTION?

Aboveground primary production and N cycling rates are often correlated both within and across ecosystem types and regions (Reich *et al.*, 1997). This is because plant growth is often limited by N availability. Moreover, annual rates of foliar production, N inputs to soils in litterfall and N uptake into aboveground plant tissues are correlated in many forests worldwide (Vitousek, 1982; Vogt *et al.*, 1986), presumably reflecting the importance of N limitation in regulating aboveground growth. Foliage turnover increases with N availability, both because of changes in functional group composition and changes within functional groups. Deciduous species often dominate over evergreen species in temperate forests that have higher N-cycling rates (Gower *et al.*, 1993). Also, foliar turnover times in evergreen trees are typically shorter on nutrient-rich than on nutrient-poor sites (Mooney & Gulmon, 1982).

Observed increases in foliar metabolism (e.g. photosynthesis and respiration) and turnover along forest soil N gradients have led to the hypothesis that fine roots might respond to N concentrations in a similar manner to aboveground production, respiration rates and turnover rates increasing with N availability across sites (Hendricks *et al.*, 1993). Increases in fine-root turnover (or decreases in mean root life span) across N availability gradients, if large enough, could allow for increases in fine-root production even though fine-root biomass typically decreases along such gradients (Nadelhoffer *et al.*, 1985; Vogt *et al.*, 1986). The hypothesis that fine-root production increases with N availability contrasts with a number of studies (Grier *et al.*, 1981; Vogt *et al.*, 1986; Gower *et al.*, 1992) suggesting that fine-root production decreases as aboveground production and N availability increase.

Consistent observations of greater fine-root biomass at N-poor than at N-rich sites, together with reports of negative correlations between fine-root biomass and aboveground forest production, suggest that fine-root production might vary systematically with the more easily measured processes of aboveground growth and net N mineralization in forest soils. Most researchers, concerned with the nature of the relationship between fine-root production and N availability to forest trees, have largely discounted the possibility that there is not a general relationship between root production and N availability in forest soils. However, given the paucity of reliable estimates of fine-root production, we cannot as yet unequivocally reject the null hypothesis.

POSSIBLE RELATIONSHIPS BETWEEN FINE-ROOT PRODUCTION AND N AVAILABILITY

Unless fine-root production is unrelated to either N availability or aboveground production in forests, four possible relationships between fine-root turnover (the inverse of mean root life span) and N availability exist (Fig. 1). It is well established that fine-root (including mycorrhizal) biomass declines with increasing N availability. If fine-root turnover either does not vary (Fig. 1a) or decreases along N-availability gradients (Fig. 1b), then annual fine-root production rates (the product of mean fine-root biomass and turnover) must decrease. It follows that such decreases would be absolute (as less fine-root biomass is produced in N-rich than in N-poor sites). Therefore, progressively smaller proportions of total above- plus belowground production would be allocated to fine roots along N availability gradients. Alternatively, more rapid fine-root turnover could serve to increase fine-root production along N availability gradients. If turnover increased sufficiently along such gradients, the proportion of total net primary production allocated to fine roots could be relatively constant (Fig. 1c). Also, lower fine-root biomass together with increasing turnover rates could increase fine-root production in absolute terms even if fine-root production were to decrease relative to total above- plus belowground production (Fig. 1d).

Which of these four possible relationships (Fig. 1) is best supported by data? Unfortunately, the level of understanding of the way in which soil N availability influences fine-root dynamics is insufficiently developed to allow for a definitive answer. This is mainly because methods have not yet been developed for directly measuring root production in ecosystems. Reported 'measurements' of fine-root production (Gower *et al.*, 1996; Vogt *et al.*, 1998) are, in fact, estimates. Most of these estimates of fine-root production are derived from intensively sampling fine-root biomass across one or more growing seasons. Estimates have also been derived from the assumption that N used in fine-root production is the difference between annual net N mineralization and annual N uptake into aboveground biomass (Aber *et al.*, 1985; Nadelhoffer *et al.*, 1985). The 'root ingrowth' method in which root growth into *in situ* incubations of root-free material is assumed to equal root production in the surrounding soil (Raich *et al.*, 1994; Majdi, 1996) is also occasionally used to estimate fine-root production.

Where relationships between fine-root production and aboveground production or nutrient availability have been identified, however, conclusions as to the nature of the relationship are strongly method-dependent. For example, Nadelhoffer & Raich (1992) analyzed fine-root-production estimates based on one of three basic methods; fine-root biomass

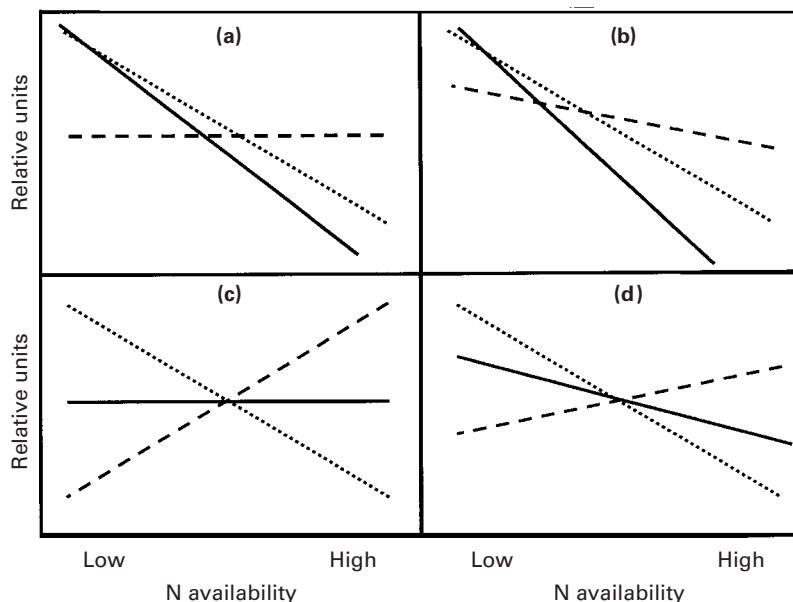


Fig. 1. Four possible patterns of fine-root turnover and proportional production along N-availability gradients in forests. Fine root biomass declines in relation to N availability in all scenarios. Biomass, dotted line; turnover, broken line; percentage of net primary production (NPP), solid line. If fine-root turnover (the inverse of mean fine-root life span) is assumed constant (a), then the proportion of total NPP allocated to fine roots declines dramatically as soil N availability increases. If fine root turnover decreases with fine-root biomass (b), then the proportion of total NPP allocated to fine roots decreases even more than when fine-root turnover is constant. If fine-root turnover rates increase sufficiently as fine-root biomass declines (c), then the proportion of NPP allocated to fine roots could remain constant. However, slower increases in fine-root turnover and production along N availability gradients (d) would result in a declining proportion of NPP being allocated to roots as N availability increases.

sampling, ingrowth and N budget techniques. Fine-root production and aboveground production were not correlated in the data set that included all three techniques ($r^2 = 0.05$, $n = 54$). Yet fine-root and aboveground production were strongly correlated ($r^2 = 0.63$, $P < 0.0002$, $n = 16$) using the subset of data from forests where N budgets were used to estimate fine-root production. For the 32 sites at which sequential sampling of fine-root biomass was used to estimate fine-root production neither 'sequential coring' nor 'maximum–minimum' techniques (Aber *et al.*, 1985) yielded significant correlations with aboveground production. Fine-root production estimates derived from 'ingrowth core' studies showed a trend of increasing root production with aboveground production, but the number of studies employing this technique ($n = 6$) were too few for a robust statistical analysis (Nadelhoffer & Raich, 1992).

PROBLEMS AND PROGRESS IN ESTIMATING FINE-ROOT PRODUCTION

Summaries of results based on different techniques lead to strikingly different conclusions about whether, and how, fine-root production varies with N availability. Therefore, it is necessary to evaluate whether inherent weaknesses in the various methods used to estimate fine-root production seriously compromise conclusions derived from their use.

Sequential sampling of fine-root biomass is the most common means of estimating fine-root production. This technique has been strongly criticized on statistical grounds (Singh *et al.*, 1984; Lauenroth *et al.*, 1986; Sala *et al.*, 1988). The primary criticism is that repeated sampling of fine-root biomass confounds spatial and temporal variation in root biomass and often leads to overestimating fine-root production rates. In addition, these critics point out that repeated sampling can also lead to underestimates, particularly if fine-root growth and mortality rates are synchronous. As such, statistical and sampling artefacts inherent in sequential sampling can lead to either underestimates or overestimates of fine-root production. Furthermore, the simultaneous growth and death of fine roots between sampling events can lead to underestimating production. Various means of improving biomass-based estimates have been developed, including the use of 'compartment flow' techniques (Santantonio & Grace, 1987). However, compartment flow analyses require information about fine-root decomposition which is difficult to acquire (Publicover & Vogt, 1993; Fahey *et al.*, 1999). Moreover, compartment flow-based estimates are highly sensitive to variations in values of the decay constants used to characterize fine-root decomposition. The statistical flaws and uncertain assumptions underlying biomass-based estimates are sufficiently serious that

the value of cross-site comparisons based on these estimates is questionable.

The less commonly used N-budget technique also suffers from uncertainties. Here, N used annually in fine-root production is assumed to be the difference between annual net N mineralization and net N uptake into aboveground production. Other fluxes are typically ignored. The inclusion of smaller N fluxes, such as N leaching below the rooting zone or N inputs via atmospheric deposition in the budgets is useful, but is not necessary if N inputs (deposition) and outputs (leaching, denitrification) largely offset one another or if these fluxes are small relative to annual net N mineralization and tree N uptake. This is normally the case for N saturated forests (*sensu* Ågren & Bosatta, 1988; Aber *et al.*, 1989). Most importantly, this method assumes that net N mineralization (the release of ammonium and nitrate from decomposing organic matter to plant roots) estimates derived using *in situ* soil incubations (using methods similar to Robertson *et al.*, 1999) provide reliable estimates of annual N uptake by forest vegetation (above- and belowground). Opinion varies as to the accuracy of *in situ* net N mineralization estimates in forests. Strong correlations between *in situ* measurements of annual net N mineralization and measurements of annual N uptake into aboveground production in forests (Aber *et al.*, 1985; Pastor *et al.*, 1993) and agricultural crops (Westermann & Crothers, 1980) provide indirect evidence that measurements of net N mineralization provide ecological insights.

Analysis of soil C budgets also suggests that fine-root production increases along N availability gradients in forests. This method assumes that annual changes in forest soil C content are small relative to C inputs (owing to litterfall and root death) and to C exports (owing to litter and root decomposition and to respiration of live roots). Analysis of soil respiration and litterfall data from forests along a global gradient of aboveground production suggested that total C allocation to roots (i.e. C used in root production + root respiration) increases linearly with N availability to forest trees (Nadelhoffer & Raich, 1992). Thus, independent analyses of forest ecosystem N and C budgets both suggest that fine-root production increases with aboveground production and N availability, even though fine-root biomass decreases.

FINE-ROOT DYNAMICS AND N AVAILABILITY IN FORESTS: LIKELY SCENARIOS

Which of the possible relationships linking fine-root turnover and production to forest N availability (Fig. 1) is the most likely? This question is best answered in the context of multiple-site comparisons in which methods used for estimating fine-root production are specified and evaluated.

As already stated, decreasing fine-root production with increasing N availability requires that root turnover either remains nearly constant (Fig. 1a) or decreases along N availability gradients (Fig 1b). If either of these patterns reflects reality, then the proportion of total primary production attributable to fine roots varies dramatically with N availability to forest vegetation. The possible extent of such variation is described by Vogt *et al.* (1986), who concluded from sequential sampling data that root inputs could be about four times greater than leaf litter inputs to temperate forest floors at nutrient-poor sites, whereas root inputs could be three times less than leaf inputs at nutrient-rich sites. Comparative studies of small numbers of sites (2–5) using repeated sampling of fine-root biomass to estimate production have suggested that fine-root production decreases with fine-root biomass as N availability and aboveground production increase (Grier *et al.*, 1981; Gower *et al.*, 1992). At face value, therefore, these studies support hypotheses depicted in Fig. 1a,b. However, it is likely that serious statistical problems (Singh *et al.*, 1984; Lauenroth *et al.*, 1986; Sala *et al.*, 1988) and violations of assumptions (e.g. that fine-root growth and death are largely asynchronous) implicit in biomass-based estimates of fine-root production underlie these conclusions.

Furthermore, many reports of fine-root production based solely on repeated root sampling either approach or exceed constraints on total belowground C allocation (Nadelhoffer & Raich, 1992). This casts additional doubt on the reliability of such measures given that total belowground C allocation (*sensu* Raich & Nadelhoffer, 1989) includes C allocated to live-root respiration as well as to root-biomass production. Clearly root respiration is a major portion of total belowground C allocation by forest trees. The evidence in support of either constant (Fig. 1a) or decreasing (Fig. 1b) fine-root turnover along N availability gradients is derived from studies using statistically flawed methods and small numbers of sites, and I consider both of these patterns to be unlikely.

Carbon budgets provide compelling evidence that the absolute amount of C allocated to roots increases with forest-site fertility. For example, annual soil respiration rates were 2–3 times greater than annual aboveground litter inputs to soils in the 30 forests analyzed by Raich & Nadelhoffer (1989). Clearly, most C respired from forest floors at all these sites was root-derived, released from the root decomposition and live-root respiration. Results of N-budget studies (summarized by Nadelhoffer & Raich, 1992) conducted at sites other than those used in C-budget studies, provide corroborating evidence that fine-root turnover along with aboveground production increases with N availability in forests. As with C budgets, estimates of the amount of N available for supporting fine-root production increased linearly

with both net N mineralization and aboveground primary production.

Analyses of forest C and N budgets suggest that fine-root turnover increases with N availability across forest sites (Fig. 1c,d). Early N-budget analysis (Nadelhoffer *et al.*, 1985) suggested that fine-root turnover increased sufficiently with N availability such that the proportion of total primary production attributable to fine roots remained constant along N availability gradients even though mean fine-root biomass decreased (Fig. 1c). Subsequent and more comprehensive C and N analyses (Nadelhoffer & Raich, 1992) suggested that although fine-root production is likely to increase in absolute terms because of increased turnover with N availability, fine-root production does not increase as much as aboveground production along N-availability gradients. Therefore, although root turnover and production are likely to increase with N availability and aboveground production in forests, the proportion of total production accounted for by fine roots probably declines (Fig 1d).

The overall pattern of fine-root turnover and production increasing with N availability, accompanied by a decline in fine-root production as a proportion of total above- plus belowground production (Fig 1d), appears to be the most likely of the scenarios proposed here. This conclusion, while not definitive, reflects the alternative which is best supported by comparative studies using data derived from methods which are the least problematic and which conform to realistic constraints imposed by ecosystem element fluxes. It is also consistent with increases in fine-root N concentrations in fine-root tissues collected from temperate forests along a nitrate-availability gradient (Fig. 2) as reported by Hendricks *et al.* (2000). The gradual increase in fine-root N concentrations with increasing N availability suggests that root metabolism and susceptibility to herbivory are likely to increase with N-cycling rates. As with foliage, this could lead to more rapid turnover of fine-root tissue.

The conclusion that root turnover and relative production are related to N availability as indicated in Fig. 1d, and its underlying assumptions, require more extensive testing at local and regional to global scales. The combined use of minirhizotron-based root observations and fine-root-biomass sampling (Hendrick & Pregitzer, 1992, 1993) are providing additional insights into root dynamics. Also, useful information on root dynamics is forthcoming from measurements of natural ^{14}C contents of fine roots, forest-floor components and respired CO_2 (Gaudinski *et al.*, 2000), from studies using ^{15}N tracers (Hendricks *et al.*, 1997) and root ingrowth cores (Raich *et al.*, 1994). Another promising approach is that of Jenkinson *et al.* (1999) who integrated information on soil $\delta^{14}\text{C}$, $\delta^{13}\text{C}$, total C and microbial C and on biomass removal in burning,

grazing and harvesting to calculate the level of plant C needed to enter soils annually to maintain soil C in savanna sites. Their approach allows estimation of belowground production by difference and could provide more definitive estimates of root production than presently exist.

FINE ROOTS AND N DEPOSITION

Hendricks *et al.* (1993) compared the hypothesis that fine-root turnover increases with N availability with alternative hypotheses that turnover either does not change or decreases as N availability increases. They suggested that mechanisms contributing to increases in root-turnover rates with N cycling were similar to those contributing to increases in foliage turnover. Recent results (Fig. 2) further suggest that similar eco-physiological processes drive increases in root turnover as follows. Higher N availability and lower fine-root biomass on relatively N-rich soils lead to greater N uptake per unit fine-root mass. Higher fine-root N concentrations are required for enzyme synthesis that is necessary for active nutrient uptake. Higher metabolic rates on more N-rich sites increase the sink strength of fine roots, thereby increasing the absolute allocation of C below ground (Fig. 3). Because above- plus belowground production also increases with N availability, proportionally less C might be allocated to fine-root than to aboveground production. Fine-root turnover increases (or life span decreases) as more C is consumed in growth, maintenance and uptake respiration and as proportionally less C is allocated to structural and defensive compounds. This is consistent with Hendricks *et al.* (2000) who also reported higher concentrations of soluble C in fine-root tissues from forests which were richer in N. Higher N concentrations and lower C allocation to defensive compounds is likely to increase susceptibility to mortality and consumption by soil fauna and to more rapid decomposition. As with leaf litter on richer sites, more rapid decomposition of fine roots on sites with low C:N ratios feeds back to maintain high N-

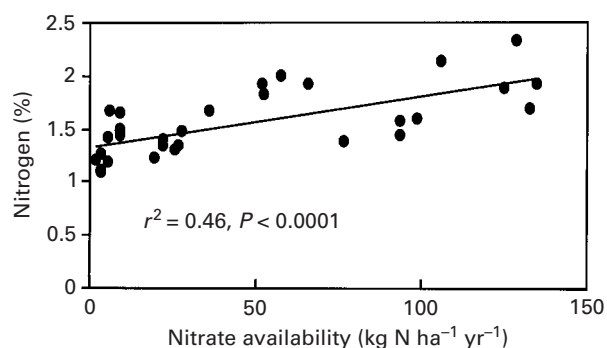


Fig. 2. Nitrogen content in fine roots sampled from forests along a nitrate-availability gradient in Wisconsin and New England forests. From Hendricks *et al.* (2000).

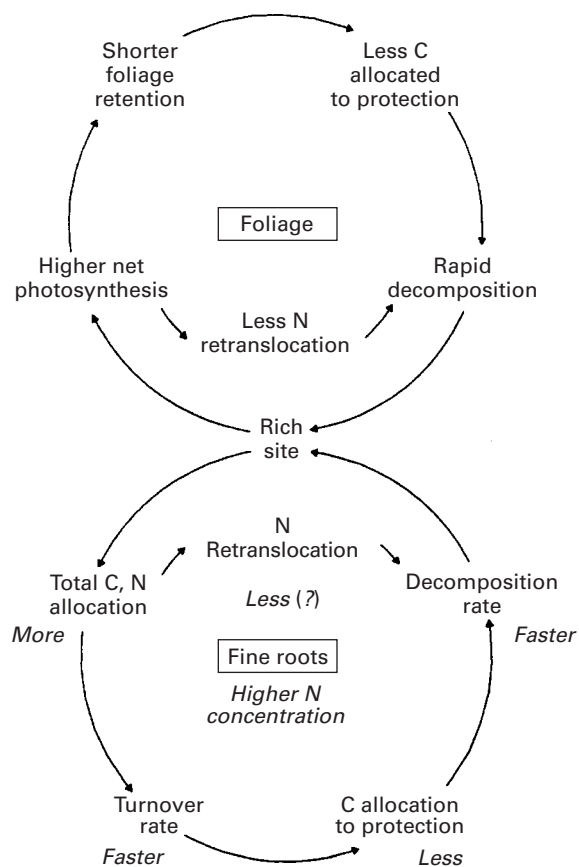


Fig. 3. Above- and below-ground feedbacks that could feedback to increase foliar and fine-root turnover when soil N availability is high. Modified from Hendricks *et al.* (1993).

cycling rates. It is unclear, however, whether fine roots retranslocate significant amounts of N before death and whether retranslocation from senescent fine roots varies with N availability.

If turnover, production and decomposition of root and foliar tissues are similarly influenced by N availability, fine-root responses to N deposition could be similar to those of leaves as hypothesized by Aber *et al.* (1989, 1998). Hypotheses regarding changes in root dynamics with N deposition are shown in graphical representations (Fig. 4) in a figure modified from Aber *et al.* (1989, 1998). If chronically elevated N deposition increases net N-mineralization rates in soil (either directly or indirectly via feedbacks such as greater N mineralization from N-enriched litter) or nitrate availability to plant roots, then more N becomes available for root uptake and enzyme synthesis in fine-root tissues. Greater N uptake leads to higher N concentrations and metabolism in fine roots. Increased photosynthesis (resulting from increased foliar N) provides more photosynthate to meet the metabolic demands of greater root growth and nutrient uptake. However, other factors such as less allocation to defensive compounds and faster metabolism feed back to shorten fine-root life spans (or to

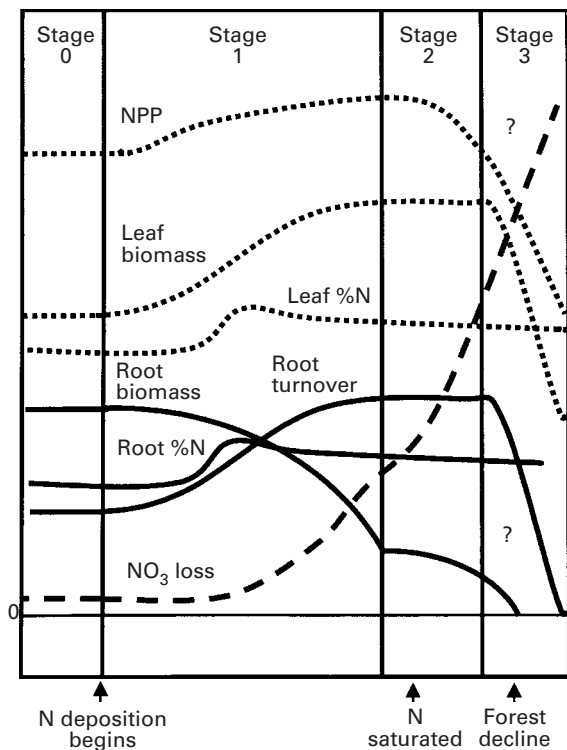


Fig. 4. Hypothesized fine-root responses (solid lines) to chronic N deposition. Stages, as described in Aber *et al.* (1989) represent ecosystem responses to N loading. Stage 0 represents pre-N deposition conditions. Stage 1 follows the onset of elevated N deposition. Where N limits growth, increases in foliar and fine root N could lead to increased N concentrations in resource acquiring organs (leaves and fine roots), greater turnover and increases in net primary production (NPP). These increases, however, might be difficult to detect, particularly at low rates of N input. Nitrate losses above background levels can occur, but they are not large. If forests advance to Stage 2, nitrate losses increase and biomass responses are more easily detected. If forest decline (Stage 3) occurs, tree mortality is high, NPP decreases, and nitrate losses are large.

increase turnover) (Fig. 3). Increased turnover offsets increased growth and fine-root biomass gradually declines as both above- and belowground production increase. The combination of increased nitrification (Gundersen *et al.*, 1998) and lower fine-root biomass would be likely to exacerbate nitrate-leaching losses. If, after prolonged and highly elevated N deposition, forests advance to later stages of N saturation and forest-stand decline, nutrient imbalances and other stresses could eventually serve to disrupt fine-root functions. For example, calcium (Ca) concentrations increased with recovery of mycorrhizal associations and fine-root 'vitality' when large N inputs were removed by collecting and filtering forest throughfall on roof-covered Scots pine (*Pinus sylvestris*) plots subject to high rates of N deposition (Boxman *et al.*, 1995). A multiple-site study of fine-root responses across experimental and geographical N-deposition gradients in Europe (the NITREX and EXMAN studies; Wright & Rasmussen, 1998) showed that mycorrhizal

associations were diminished and fine-root biomass declined under high rates of N deposition (Boxman *et al.*, 1998). Lower incidences of mycorrhizal associations, lowered Ca:N ratios, or dramatically diminished fine-root biomass as observed at the NITREX sites, could serve to diminish uptake efficiencies of fine roots for N and possibly other nutrients. Such impacts on fine roots would feed back to exacerbate forest decline.

It is important to realize that advanced stages of N saturation represent end points that are difficult to predict. Many, if not the vast majority of forests receiving excess N deposition might approach states of N saturation or stand decline (Fig. 4, stages 2, 3) very slowly if at all. Forests receiving comparatively low rates of N deposition could remain at early stages for prolonged periods. Still, it might be expected that N deposition would result in increased root growth and turnover and decreases in fine-root biomass to the extent that soil N and nitrate availability increase.

CONCLUSIONS

Predicting forest fine-root responses to chronically elevated N deposition is compromised by limited knowledge of the way in which fine-root production might vary in relation to soil N availability to tree roots. Insufficient multiple-site comparisons of fine-root dynamics along N-availability and N-deposition gradients exist to allow for strong conclusions. Moreover, conclusions are highly dependent on methods used to estimate fine-root production. Critical review of methods for estimating root production suggests that many studies using biomass sampling to estimate root production, though providing more data than other methods combined, are highly suspect. As such, generalizations about relationships between fine-root production and either aboveground production or soil N availability based on multi-site comparisons of biomass-based fine-root production estimates are probably misleading. Independent analyses of forest C and N budgets to estimate root turnover and production provide better-constrained and possibly more robust estimates of root processes. Element budgets, together with chemical compositions of fine roots sampled along N-availability gradients suggest several working hypotheses.

- Fine root and foliar dynamics are similarly influenced by and feed back to maintain soil N availability.
- Although fine-root biomass typically decreases as N availability increases, fine-root turnover and production increase, with increases in aboveground production and litterfall, across N-availability gradients.
- If N deposition increases N availability to plants, net N mineralization or nitrification in forests,

then fine-root biomass will be likely to decrease. However, fine-root turnover and production will probably increase.

- Although the absolute rates of root production probably increase along N-availability gradients, the proportion of total above- plus belowground production accounted for by fine roots probably decreases with N availability.
- Decreased root biomass in forests at late stages of N saturation will contribute to dissolved-nitrate losses.

These hypotheses require further testing by more extensive and rigorous applications of ecosystem element budgets and by new methods that hold potential for providing insights into patterns and controls of root dynamics.

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