# PROGRESSIVE N LIMITATION IN FORESTS: REVIEW AND IMPLICATIONS FOR LONG-TERM RESPONSES TO ELEVATED $CO_2$

DALE W. JOHNSON[1]

*Natural Resources and Environmental Science, University of Nevada, Reno, Nevada 89557 USA*

*Abstract.* Field studies have shown that elevated $CO_2$ can cause increased forest growth over the short term (<6 years) even in the face of N limitation. This is facilitated to some degree by greater biomass production per unit N uptake (lower tissue N concentrations), but more often than not, N uptake is increased with elevated $CO_2$ as well. Some studies also show that N sequestration in the forest floor is increased with elevated $CO_2$. These findings raise the questions of where the "extra" N comes from and how long such growth increases can continue without being truncated by progressive N limitation (PNL). This paper reviews some of the early nutrient cycling literature that describes PNL during forest stand development and attempts to use this information, along with recent developments in soil N research, to put the issue of PNL with elevated $CO_2$ into perspective. Some of the early studies indicated that trees can effectively "mine" N from soils over the long term, and more recent developments in soil N cycling research suggest mechanisms by which this might have occurred. However, both the early nutrient cycling literature and more recent simulation modeling suggest that PNL will at some point truncate the observed increases in growth and nutrient uptake with elevated $CO_2$, unless external inputs of N are increased by either N fixation or atmospheric deposition.

*Key words: carbon dioxide; deficiency; elevated $CO_2$; forests; litter; nitrogen; nutrient uptake; progressive N limitation; soil N cycling; stand development.*

## INTRODUCTION

Nitrogen is unique among nutrients in that it has no soil mineral source, is ultimately derived completely from atmospheric inputs, and rarely accumulates to any significant amount in ionic forms on soil exchange complexes. In contrast to other nutrients, whose soil ionic pools may well exceed vegetation content, soil mineral N pools are nearly always much smaller than the annual uptake of plants; therefore soil mineral N pools must turn over many times per year to meet plant needs. For all of these reasons, N is almost completely tied to ecosystem C pools (Vitousek et al. 1979, Paul and Clark 1989, Johnson 1992, Shaver et al.1992). Thus, it is not surprising that N is frequently the most growth-limiting nutrient or that ecosystem responses to elevated $CO_2$ are intimately tied to N responses (e.g., Shaver et al. 1992).

The major N cycling processes have been known for decades; however, quantification of these processes, especially the gaseous phases, has proven to be very difficult, leaving large uncertainties in forecasting long-term N budgets (e.g., Binkley et al. 2000). The N cycle is especially relevant to experiments with elevated $CO_2$, including those at the stand level using free-air $CO_2$ (FACE) technology. Many of these studies have shown that growth responses and increased aboveground N

sequestration can occur and persist over the short term even in the face of N limitation (Johnson et al. 1997, 2003a, 2004, Curtis et al. 2000, Finzi et al. 2002, 2004, Hamilton et al. 2002). The obvious question is how long such growth increases can continue before being truncated by N limitation.

Thus, the prospect of progressive N limitation (PNL) with elevated $CO_2$ has been raised (Luo et al. 2004) and is highlighted in this Special Feature in *Ecology*. The concept of PNL during forest stand development was introduced decades ago and is well-established in the literature on forest nutrient cycling (Rennie 1955, Ovington and Madgwick 1959, Ovington 1962, Heilman 1966, Cole 1981, Turner 1981, Gholz et al. 1985). A review of these older concepts and the results supporting or negating them is warranted in the present context of elevated $CO_2$ response. The purpose of this paper is to review the older literature describing PNL in forest ecosystems; to describe more recent and relevant results on N cycling in soils, including some that challenge some of the older paradigms; and to attempt to relate these results to the question of PNL development in ecosystems subjected to elevated $CO_2$.

## REVIEW OF PROGRESSIVE NUTRIENT LIMITATION DURING FOREST STAND DEVELOPMENT

### Chronosequence studies and calculations

Among the first to suggest the possibility of increasing nutrient limitation with stand development was Rennie (1955), who noted that the nutrient demands of

plantation forests growing on *Calluna* soils in England could not be supported without soil nutrient degradation unless supplemented by fertilizer. Ovington (1959) noted the same basic patterns in a chronosequence study of Scots pine (*Pinus sylvestris* L.) in England. Along with the increase in tree biomass, he also found a steady buildup of forest floor mass and nutrient content over 55 years, and a much reduced role of understory vegetation in nutrient uptake after crown closure. Ovington (1959) also calculated that conventional timber harvesting (bole only) would remove minimal nutrients from the ecosystem. Cole et al. (1968) and Gessel et al. (1973) calculated that soil N reserves apparently would have to be tapped in order to support observed N accumulations in tree biomass and forest floor in Douglas-fir (*Pseudotsuga menziesii*) forests in Washington State, USA.

In their classic study of forest stand development, Switzer and Nelson (1972) put these findings into a new perspective and identified three major phases of stand development in a loblolly pine (*Pinus taeda* L.) plantation in Mississippi: a phase of nutrient accumulation, prior to canopy closure (when trees are accumulating nutrient-rich foliar biomass, understory is often dominant, net annual nutrient increment in biomass is very high, forest floor is often accumulating, and recycling via the litterfall–decomposition pathway is minimal); a phase of nutrient cycling after canopy closure (during which litterfall matches new foliage growth, understory declines, foliar biomass stabilizes, net annual increment decreases sharply, and the annual uptake of nutrients necessary to supply growing tissues is met largely by recycling); and a stage of decline (where senescence ensues and both uptake and increment decline). A schematic representation of this sequence is shown in Fig. 1A. Their calculations suggested that by year 20 in the loblolly pine plantation studied, the annual uptake of nutrients by trees was satisfied almost completely by recycling, both between the plant–soil system and within the plant, requiring little uptake from the soil. Noting the contribution of internal cycling within the plant (hereafter referred to as translocation) to the annual nutrient requirements for new growth (up to 50% for P and 39% for N), they proposed an expansion of the conceptual model of nutrient cycling in forests held at the time. Earlier conceptual models of nutrient cycling in forests (Remezov 1959, Curlin 1970) recognized two components of biogeochemical cycling: (1) a geochemical component that was external to plant–soil system and included atmospheric inputs and leaching, and (2) a biological component, internal to the plant soil system. Switzer and Nelson (1972) proposed a three-component model: geochemical cycling, as in (1); biogeochemical cycling, as in (2); and biochemical cycling, which consisted of nutrient transfers within the plant.

Later chronosequence studies by Miller et al. (1979), Turner (1981), and Gholz et al. (1985) in plantation
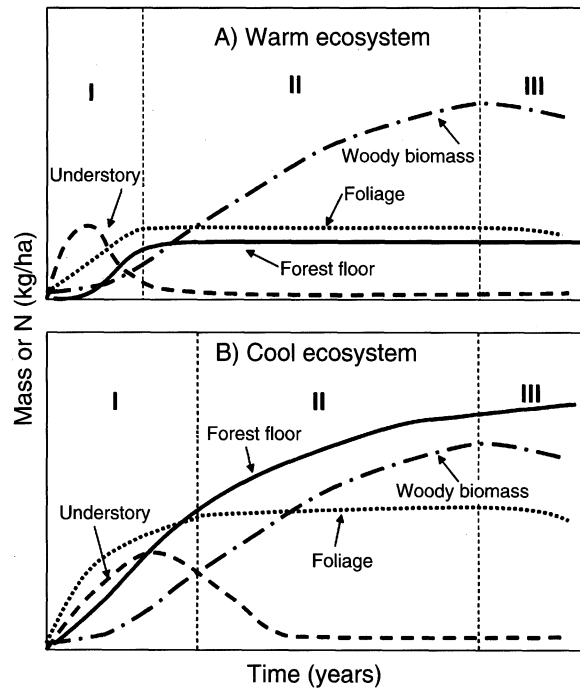


FIG. 1. Schematic representation of changes in nutrient pools during stand development in (A) a warm system where the forest floor reaches steady state, and (B) in a cold system where the forest floor continues to accumulate. During phase I, prior to canopy closure, nutrients accumulate in foliar biomass, understory is often dominant, net annual nutrient increment in biomass is very high, forest floor is often accumulating, and recycling via the litterfall–decomposition pathway is minimal. During phase II, after canopy closure, litterfall matches new foliage growth, understory declines, foliar biomass stabilizes, net annual increment decreases sharply, and the annual uptake of nutrients necessary to supply growing tissues is met largely by recycling. The forest floor may reach steady state during phase II in warm ecosystems. During phase III, senescence ensues, and both uptake and increment decline. Forest floor accumulation may escalate because of increased woody litterfall associated with tree mortality.

forests revealed patterns similar to those noted by Switzer and Nelson (1972). The latter authors also found that the rates of accumulation of nutrients in tree biomass and forest floor well exceeded rates of atmospheric deposition and concluded that either N fixation or soil sources were needed to balance the books. Miller et al. (1979) described the nutrient cycles of Corsican pine (*Pinus nigra* var. *maritima*), with and without fertilization, growing on coastal sands in Scotland where the pines were becoming increasingly nutrient deficient with age. Miller et al. (1979) expanded and refined the biochemical concept posed by Switzer and Nelson (1972) by defining three kinds of nutrient pools within the tree: a nonmobile, or structurally bound pool; a mobile pool, consisting of recent root and foliar uptake and includes temporary seasonal storage; and a potentially mobile pool that can be used to make up for an inadequate supply from the mobile pool. Miller et al.

(1979) described how nutrient transfers between these pools could account for the ability of coniferous trees to survive on very nutrient-poor soils and their prolonged responses to fertilization.

In a chronosequence study of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco.) stands in Washington State, USA, Turner (1981) found many of the same patterns found by Ovington (1959) and Switzer and Nelson (1972). Like Switzer and Nelson (1972), Turner noted reduced understory biomass and nutrient content after crown closure. Unlike Switzer and Nelson (1972), however, he found a steady increase in forest floor mass and nutrient content over 95 years, with no sign of reaching a steady-state condition. This scenario is depicted in Fig. 1B. Turner (1981) calculated that an average of nearly 10 kg N·ha$^{-1}$·yr$^{-1}$ over and above atmospheric inputs was needed from either fixation or soil mineralization to account for the observed increases in tree and forest floor N content. Turner (1981) had no measures of dry N deposition. At a later time when pollutant inputs were probably greater than when Turner did his study, very detailed estimates provided values averaging 2.1 kg N·ha$^{-1}$·yr$^{-1}$ at the same site (Johnson and Lindberg 1992), which were insufficient to account for the apparent N deficit. Turner (1981) presumed that the trees in the older stands had to rely on N uptake from the forest floor to a greater extent than trees in the younger stands, a speculation supported by other studies in the region that showed increased rooting in forest floor during later stages of forest stand development (Kimmins and Hawkes 1978, Grier et al. 1981, Vogt et al. 1983). Turner (1981) found that forest floor accumulation was apparently exacerbated by the inhibitory effects of cooler temperatures (a full 8°C lower in the older than in the youngest stand, presumably because of more insulation by thicker litter) and higher C:N ratio litterfall in the older stands. The higher C:N ratio of litter in the older stands was attributed to increased C:N ratio of needle litterfall as well as a greater proportion of woody tissues in litterfall. The higher C:N ratio in needle litterfall was due to increased internal translocation with age, a response that he hypothesized was due to the increasing N limitation with age (progressive N limitation). In a chronosequence of slash pine (*Pinus elliottii* Eng.) stands in Florida, USA, Gholz et al. (1985) found patterns of biomass and nutrient accumulations, decomposition, and internal translocation that were very similar to those found by Turner (1981), and they also found an apparent decline in soil total N and extractable P with stand age.

The N imbalance/PNL issue is not limited to plantation forests. Heilman (1966) found increasing N deficiency with advancing succession in black spruce (*Picea mariana* P. (Mill.)) in interior Alaska, USA. He found that as the moss layers thickened in these stands, the soils became increasingly cold, causing the permafrost layer to migrate upward, retarding decomposition and exacerbating the N deficiency. When Bor-
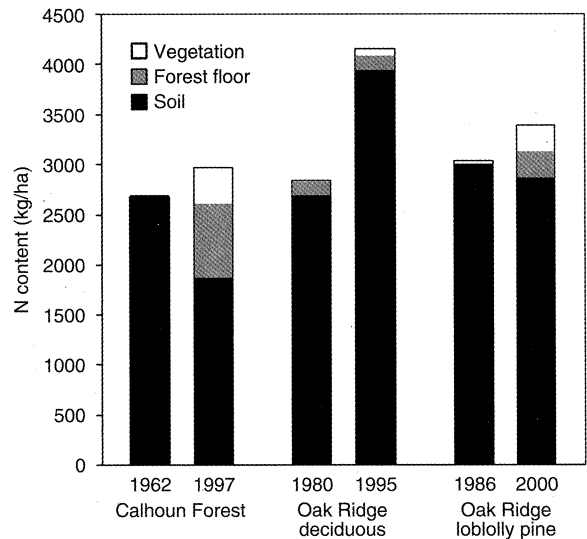


FIG. 2. Changes in nitrogen content over time in a loblolly pine forest at Calhoun, South Carolina (left), a deciduous forest at Oak Ridge, Tennessee (middle), and a loblolly pine forest at Oak Ridge, Tennessee. Data are from Richter and Markewitz (2001), Johnson and Todd (1998), and Johnson et al. (2003).

mann et al. (1977) calculated how much N in excess of atmospheric deposition would be needed to account for the increments in biomass and forest floor, they estimated an imbalance of ~14 kg N·ha$^{-1}$·yr$^{-1}$ for an aggrading hardwood forest in New Hampshire, USA. They assumed that this imbalance was met by N fixation, but it also could have been due to nitrogen removal from the mineral soil. Chestnut et al. (1999) calculated an N imbalance of ~8–20 kg N·ha$^{-1}$·yr$^{-1}$ for a late-successional forest in Puerto Rico, which they assumed could be accounted for by uptake from soils or N fixation.

### Resampling studies

Wells and Jorgensen (1975) reviewed the results of some plantation studies involving loblolly pine in North and South Carolina, USA. They noted high rates of biomass and N accumulation in both vegetation and forest floor components over the first 16 years (39 kg N·ha$^{-1}$·yr$^{-1}$), and found that soil N reserves were depleted by an amount very close to this (38 kg N·ha$^{-1}$·yr$^{-1}$). They speculated that this apparent "mining" of soil N was made possible by rhizosphere microbial activity in the pines. Richter et al. (2000) and Richter and Markewitz (2001) summarized the later results from Calhoun Forest (one of the sites studied by Wells and Jorgensen [1975]) over a 40-year period, putting it into historical perspective with respect to previous land use in cotton farming. They noted that the combined N increment in biomass (366 kg/ha) and forest floor (740 kg/ha), a total of 1106 kg/ha, was largely compensated by declines in soil N (−823 kg/ha) over 40 years of stand development (Fig. 2, left).

They further noted that most of the soil depletion occurred over the first 25 years of stand development when demands from the vegetation were highest. After age 30, there were no further increments in tree biomass or N content because mortality equaled increment. Forest floor mass and N increment continued to increase through age 40, however, perhaps partly due to fire suppression.

Several long-term resampling studies near Oak Ridge, Tennessee, USA, have taken place over the last three decades, and all have produced different results. All took place within a relatively small geographic area (2–4 km apart) with similar climate and soils (Ultisols derived from dolomite). Studies in mature deciduous forests on Walker Branch Watershed over a 21-year period (1972–1993) showed either stable or declining soil C and N in various plots (Trettin et al. 1999). In contrast, soils in a nearby naturally regenerating deciduous forest showed inexplicably large increases in soil C and N over a 15-year period (1980–1995) following harvesting (Johnson and Todd 1998) (Fig. 2, middle). In the latter study, ecosystem N contents seemed to increase at a rate approaching 100 kg N·ha$^{-1}$·yr$^{-1}$, most of which accumulated in the soil. This occurred in the absence of any significant N-fixing vegetation and with an atmospheric deposition rate on the order of 10 kg N·ha$^{-1}$·yr$^{-1}$ (Johnson and Todd 1998). Although we remained skeptical about the magnitude of these soil N increases (see Binkley et al. [2000] for a discussion of soil N changes in this study and many others), extensive quality assurance checks failed to reveal any problems that could account for them, and thus they were duly reported. In yet another contrast, Johnson et al. (2003b) found a slight, nonsignificant decline in soil C and N over the first 18 years of growth in a nearby loblolly pine plantation (Fig. 2, right). They estimated an average annual N accumulation in trees and forest floor of ~20 kg N·ha$^{-1}$·yr$^{-1}$, whereas N deposition at a nearby site was on the order of 10 kg N·ha$^{-1}$·yr$^{-1}$. They calculated that the soil N depletion of 10 kg N·ha$^{-1}$·yr$^{-1}$ needed to balance the budget could have occurred and gone undetected in this ecosystem. This collection of studies showed that patterns of ecosystem N development can vary enormously within a very small geographic region, depending upon vegetation and site history; overgeneralizations are hazardous.

Foster et al. (1995) demonstrated the value of long-term resampling studies by comparing chronosequence-based estimates with resampling over time for N budgets in jack pine (*Pinus banksiana*) forests in Ontario, Canada. They found that the chronosequence-based estimates of N accumulation in biomass and forest floor were much lower than real-time measurements over 21- to 23-year intervals. In contrast to the chronosequence studies by Turner (1981), Foster et al. (1995) found that the mineral soil supplied over half of the total N uptake at age 50. They found no effect of stand age on decomposition rate, no pattern of increased reliance of the forest floor for N sources of uptake over time, and no evidence of a slowdown in N uptake and cycling over time in this study.

On a whole-ecosystem level, the studies cited in the previous sections leave little doubt that the accumulations of N in living and dead biomass often exceed known inputs of N, and in many cases this has led to severe nutrient deficiencies with stand age in young, rapidly growing forests with low nutrient inputs. This does not mean that PNL will proceed indefinitely, however: in overmature stands, one could well expect greatly reduced uptake and possible increases in nutrient availability and leaching, especially if atmospheric deposition were high (e.g., Vitousek and Reiners 1975, Johnson et al. 1991). Also, measures of nutrient availability in soils may not necessarily reflect the same patterns as total nutrient contents in soil, litter, and vegetation. Ryan et al. (1997) concluded that there were no general patterns of nutrient availability with stand age, based upon a review of the literature on changes in leaching, resin bag nutrient retention, mineralizeable N by incubation, and $^{15}$N pool dilution with stand age. Griffiths and Swanson (2001) found the typical increases in forest floor mass (and presumably N content) over time, but they found no pattern in available N (soil mineral N or mineralizable N) in a Douglas-fir forest.

### Process-level studies of nutrient cycling in forests

Despite the obvious logistical problems and scaling, some process-level studies of nutrient cycling in forests are relevant to the issue of PNL and therefore merit review here. Specifically, studies on translocation and decomposition have been conducted in situ within a forest stand. Studies of uptake processes have been conducted in a greenhouse setting only, and will not be reviewed here.

*Translocation.*—In a classic experiment on translocation and its response to nutrient availability, Turner (1977) described an experiment in which he stressed Douglas-fir trees for N on the one hand by adding sugar, sawdust, and non-nitrogen nutrients to stimulate microbial competition; on the other hand he provided improved and even luxuriant N supplies by adding fertilizer. The N-stressed trees showed increased translocation and litterfall during the first year after this treatment as new growth requirements required the tapping of N stores in older foliage, causing them to prematurely senesce. In the fertilized plots, translocation and litterfall were reduced as the trees stored the added N in old foliage and relied more on external sources of N for the new growth requirements (Fig. 3).

Nambiar and Fife (1991) directly challenged Turner's (1977) conclusions, criticizing his assumptions (i.e., that older foliage concentrations were equal to new foliage concentrations when new) and citing many examples, both from their own work and that of others,
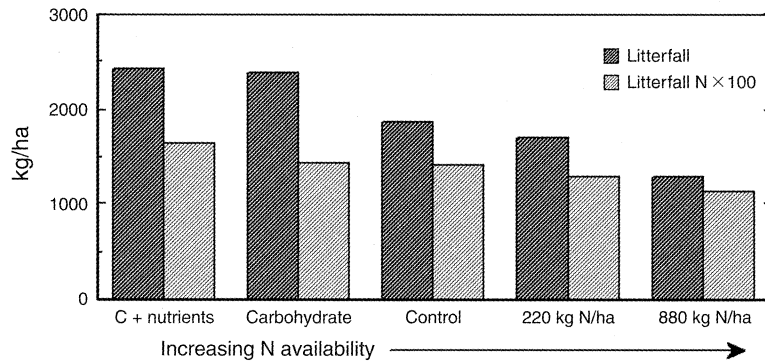
FIG. 3. Litterfall biomass and N flux in Douglas-fir forest plots treated with (from left to right): carbohydrates + nutrients (C + nutrients), carbohydrates alone, no treatment, and urea-N at either 220 kg/ha or 880 kg/ha. The figure is adapted from Turner (1977).

in which translocation is greater in trees with better N status. However, Nambiar and Fife (1991) as well as others (e.g., Chapin and Kedrowki 1983, Birk and Vitousek 1986, Knops et al. 1997) typically estimated translocation on a per needle basis rather than on a stand level, and they did not report the effects of N treatments on litterfall N return. It is quite conceivable that percentage translocation on a per needle basis was greater in the high-N treatments in Turner's (1977) experiment. A major finding of the experiment, however, was that fertilization caused decreases in litterfall mass and N content and therefore more translocation on a stand level, whereas the carbohydrate treatments caused increases in litterfall mass and N content and therefore less translocation on a stand level. As noted by Turner (1977), these effects are only a temporary buffer, and it can be expected that both litterfall mass and N content will increase in the fertilized treatments to levels above those in the control once a new steady-state foliage biomass is achieved, a pattern consistent with that observed by Birk and Vitousek (1986) in a series of fertilized loblolly pine stands.

*Decomposition and N mineralization.*—One feature of PNL is that of slowed decomposition because of low C:N ratios in litterfall resulting from reduced foliar N concentrations. As will be discussed later, the extent to which elevated $CO_2$ might cause such an effect is not clear; however, a review of some recent studies of the effects of N on decomposition is in order.

The classic concept of microbial competition for N and the negative effects of C:N ratio on decomposition are being challenged and modified in some interesting ways. In the past, it was commonly assumed that competition between plant roots, heterotrophs, and nitrifiers for $NH_4^+$ dictates the fate of N in ecosystems and that microbes are better competitors for N than roots (e.g., Johnson and Edwards 1979, Vitousek et al. 1979, Riha et al. 1987). Schimel and Bennett (2004) challenged this view and posed a new paradigm for plant–microbial competition that may be highly relevant to the PNL question. They assert that trees can effectively compete

with soil microbes in two basic ways: (1) by taking up organic N released by the depolymerization of N-containing polymers by microbial extracellular enzymes (including those released by mycorrhizae); and (2) by invading N-rich microsites that exist, at least temporarily, even in relatively N-limited conditions. McClain et al. (2003) discuss the presence of hot spots and hot moments as a result of natural heterogeneity in biogeochemical systems. Roots, with their elongated structure and exploratory habit, presumably can tap into these hot spots and hot moments, and thereby might effectively mine the soil for N over time.

The fact that most N in soils is associated with organic matter has led many forest soil scientists and ecologists to assume that N retention in forest ecosystems is controlled almost exclusively by biological processes. Relatively little attention has been given to nonbiological N retention in soils, even though such reactions have been known for more than 50 years (Mattson and Koulter-Anderson 1942a, b). Aside from $NH_4^+$ fixation in 2:1 clays, abiotic reactions between $NH_4^+$, $NO_3^-$, and organic matter can cause significant amounts of N accumulation over the long term. Physical condensation reactions of phenols (originating from partially degraded lignin and some fungal pigments) with either amino acids or $NH_3$ can result in the formation of "brown, nitrogenous humates" (Mortland and Wolcott 1965, Nömmik 1965, 1970, Nömmik and Vahtras 1982, Paul and Clark 1989). These reactions are known to be of major importance following N fertilization (accounting for >50% of applied N in some cases; Foster et al. [1985]). Schimel and Firestone (1989) found that abiotic reactions between mineral N and organic matter accounted for as much as 20% of N incorporation in an unfertilized soil in the Sierra Nevada Mountains of California, USA. In a laboratory study, Johnson et al. (2000c) found that abiotic $NH_4^+$ retention accounted for as little as 7% of total immobilization in N-poor Sierran soils, and up to 87% of the retention in N-saturated soils from the Smoky Mountains of North Carolina, USA. Microbial uptake
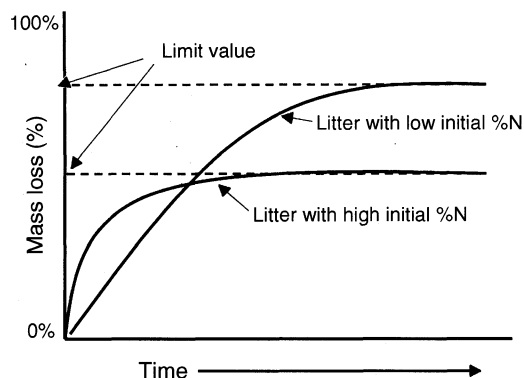
FIG. 4.  Schematic representation of the theoretical changes in loss of litter mass over time with high and low initial N concentrations. The figure is adapted from Berg and McClaugherty (2003).

may account for most (80–95%) of the short-term incorporation of soil N (e.g., Schimel and Firestone 1989, Davidson et al. 1990), but the microbial N pool is transient in nature and may not be as important for long-term N accumulation as the smaller, but cumulatively more important, nonbiological fluxes into humus.

In their comprehensive review of decomposition processes, Berg and McClaugherty (2003) noted that the long-known suppressive effect of lignin on litter decomposition is probably more closely related to the associated increased concentrations of N during decomposition that suppress the formation of ligninase and, therefore, lignin decomposition. Berg and McClaugherty (2003) describe decomposition as a three-stage process, in which the first stage is controlled largely by nutrient concentrations and readily available solutes, the second stage is controlled largely by lignin decomposition rate, and the third stage is one in which decomposition slows considerably as organic matter enters the near humus condition. During this final stage, litter mass approaches an asymptote that is referred to as a limit value, which remains constant for an indefinite period of time. Fig. 4 depicts these patterns. During the first stage of decomposition, N concentration has a positive effect on decomposition rate (as per the traditional effects of the C:N ratio). However, in the latter stages of decomposition, the reactions previously described have an inhibitory effect as N combines with lignin to form extremely recalcitrant compounds and, in fact, largely controls the limit value. This relatively new model of decomposition has interesting implications for the issue of PNL with elevated $CO_2$, which will be discussed.

### ELEVATED $CO_2$ AND N CYCLING PROCESSES

The effects of elevated $CO_2$ on N cycling have been reviewed before (Johnson et al. 1998, Norby and Cotrufo 1998, Hungate 1999, Hungate et al. 1999, Norby et al. 1999, 2000, 2001, Zak et al. 2003); the reader is referred to these sources for a more comprehensive

treatment of the subject. The focus of this paper is the potential for PNL, and the following discussion will be limited to those results that pertain to this issue.

### Plant uptake and N budgets

Although tissue N concentrations are often reduced with elevated $CO_2$, this is often more than offset by the increases in biomass, necessitating increased N uptake in plants (Johnson et al. 1997, 2003a, 2004, Finzi et al. 2002, 2004). In some cases, elevated $CO_2$ also causes an increase in mass and N content of the forest floor (e.g., Johnson et al. 2003a, Finzi et al. 2004). Thus, elevated $CO_2$ seems to facilitate greater N accumulation in aboveground organic components of the ecosystem, even with N limitation. This raises two obvious questions: (1) where does this "extra" N come from and (2) how long can this increased N uptake continue?

Potential sources of the "extra" N include fixation (symbiotic or free-living), atmospheric deposition, increased N mineralization, and increased root growth and soil exploration. Elevated $CO_2$ has been found to stimulate symbiotic N fixation in several studies (Norby 1987, Arnone and Gordon 1990, Thomas et al. 1991, Hungate et al. 1999), but not in every case (e.g., Arnone 1999). Recently, Hungate et al. (2004) found that symbiotic N fixation in a leguminous vine (Galcatica elliottii Nutt.) declined over time during an open-top chamber study in a Florida scrub oak ecosystem. They speculated that this decline was due to the progressive deficiency of molybdenum. The potential role of nonsymbiotic N fixation is much smaller than that of symbiotic fixation, and the only study to date on the effects of elevated $CO_2$ on nonsymbiotic N fixation showed no $CO_2$ effect (Verburg et al. 2004).

A second possibility for finding the "extra" N for uptake with elevated $CO_2$ is from increased N mineralization. The effects of elevated $CO_2$ on soil N mineralization are mixed, with some studies finding increases (e.g., Körner and Arnone 1992, Zak et al. 1993, Carnol et al. 2002), some finding decreases (Diaz et al. 1993, Berntson and Bazzaz 1996, Johnson et al. 1996, Cotrufo et al. 1998), and some finding no effect (O'Neill 1994, Randlett et al. 1996, Gloser et al. 2000, Zak et al. 2000b, 2003, Finzi et al. 2002, Holmes et al. 2003, Barnard et al. 2004). Some of these results are perplexing, in that $CO_2$ often stimulates additional N uptake and even soil N depletion without any measurable change in soil N mineralization or soil N availability (Johnson et al. 1997, 2000a, b, 2003a, Allen et al. 2000, Zak et al. 2000a, 2003, Finzi et al. 2002). One possible reason for these seemingly contradictory results is that our measures of soil N mineralization and soil N availability are not sensitive enough to detect the changes in N mineralization rates that took place.

A third possibility is increased N uptake because of increased root growth and soil exploration (Norby et al. 1987, Rogers et al. 1992, Day et al. 1996, Tingey

et al. 1996, Pregitzer et al. 2000). The conceptual model of plant–microbial competition posed by Schimel and Bennett (2004) is of obvious relevance here. Increased root and mycorrhizal growth with elevated $CO_2$ can be expected to enhance root invasion of N-rich hot spots at hot moments (McClain et al. 2003), and may well be the explanation of where the "extra" N for uptake with elevated $CO_2$ comes from in the absence of additional N inputs. This could potentially result in lower total N with elevated $CO_2$ over time, as was in fact found by Johnson et al. (2000a).

### Decomposition and N cycling

A possible cause of PNL with elevated $CO_2$ noted early on by Strain (1985) is that of reduced litter quality and decomposition rates because of lower tissue N concentration, a scenario very similar to that of progressive nutrient deficiency described in the earlier nutrient cycling literature (e.g., Turner 1977, 1981). This early speculation led to many studies on the effects of elevated $CO_2$ on decomposition, the results of which have been mixed and generally inconclusive (O'Neill 1994, Randlett et al. 1996, Hirschel et al. 1997, Scherzer et al. 1998). In a comprehensive review of the literature, Norby et al. (2000) found that elevated $CO_2$ had little or no effect on N resorption in field-grown trees, implying that reduced N concentrations in live foliage would also cause lower N concentrations in litterfall, perhaps leading to reduced decomposition with elevated $CO_2$. However, the consensus of a workshop on the effects of elevated $CO_2$ on litter quality was that the effects were generally very small and that the reduced decomposition–slowed N cycling hypothesis "has been laid to rest" (Norby and Cotrufo 1998). However, some of the lack of response in litter decomposition may be a result of the low sensitivity of the techniques used (such as litterbag studies). As will be noted later in this paper, simulation studies indicate that even slight changes in litter quality continue to have long-term effects on growth response to elevated $CO_2$.

Over the short term, a reduction in litterfall N concentration could indeed slow decomposition rate, as speculated by Strain (1985) some time ago. However, the studies by Berg and McClaugherty (2003) clearly indicate that the long-term prospects for sequestration of both N and C in litter are greater with higher initial litterfall N concentrations. Thus, reduced litter N concentration may actually cause less N sequestration in the forest floor over the long term. The changing patterns of decomposition and C and N sequestration in decomposing litter over the long term could substantially alter the predictions of the development of PNL and the long-term ecosystem responses to elevated $CO_2$. To my knowledge, these mechanisms have not yet been included in models of ecosystem response to elevated $CO_2$.

### Potential for progressive N deficiency with elevated $CO_2$

Because of the paucity of stand-level experiments with elevated $CO_2$ and the relatively short time spans over which such studies have been conducted, the actual evidence for PNL with elevated $CO_2$ is still sparse and incomplete. Studies now in progress in closed-canopy forests, especially those using FACE technology (e.g., Allen et al. 2000, Oren et al. 2001, Finzi et al. 2002, 2004, Finzi and Schlesinger 2003, Johnson et al. 2003a, 2004), will help to address this issue if they proceed for a sufficient length of time. Updates of those studies will be presented in this volume, and therefore they will not be reviewed here.

Many simulation modeling efforts have addressed the prospects for PNL with elevated $CO_2$ and merit a short review here. McMurtrie and colleagues have extensively explored the possibility of PNL with elevated $CO_2$ using the G'DAY (Generic Decomposition and Yield) model (Comins and McMurtrie 1993, McMurtrie and Comins 1996, Medlyn et al. 2000). Their simulations point strongly to the importance of soil N availability in controlling the long-term ecosystem response to elevated $CO_2$. For example, Medlyn et al. (2000) simulated the effects of elevated $CO_2$ and temperature on forests on a decadal time scale using the G'DAY model. They found that elevated $CO_2$ caused a transient, positive growth response that was truncated by N limitations. In contrast, increased temperature caused prolonged growth increases because it stimulated soil N mineralization.

Rastetter and colleagues used MEL (Multiple Element Model) to explore the N constraints on responses to elevated $CO_2$ over various time scales, and found responses similar to those obtained by G'DAY (Rastetter et al. 1991, 1997, Rastetter and Shaver 1992). For example, Rastetter et al. (1997) found that the responses of an eastern deciduous forest to an instantaneous increase in $CO_2$ varied according the time scale of analysis. Over a short (<1 year) time scale, vegetation C:N ratio and primary production increased, but N uptake did not. Over a time scale of a few years, plant N uptake increased because of increased allocation of energy to fine roots. Because of this, there was a net movement of N from soil to biomass over a scale of decades. On a time scale of centuries, however, continued ecosystem responses to elevated $CO_2$ were constrained by the possibility of increases in ecosystem N content. The simulations thus suggest that short-term responses are markedly different from long-term responses.

Johnson (1999) explored the interactions between elevated $CO_2$ and N cycling using simulations generated by the Nutrient Cycling Model (NuCM) for the *Pinus taeda* site at Duke, North Carolina and a mixed-deciduous site at Walker Branch, Tennessee near the ORNL FACE site. The simulations tested whether N
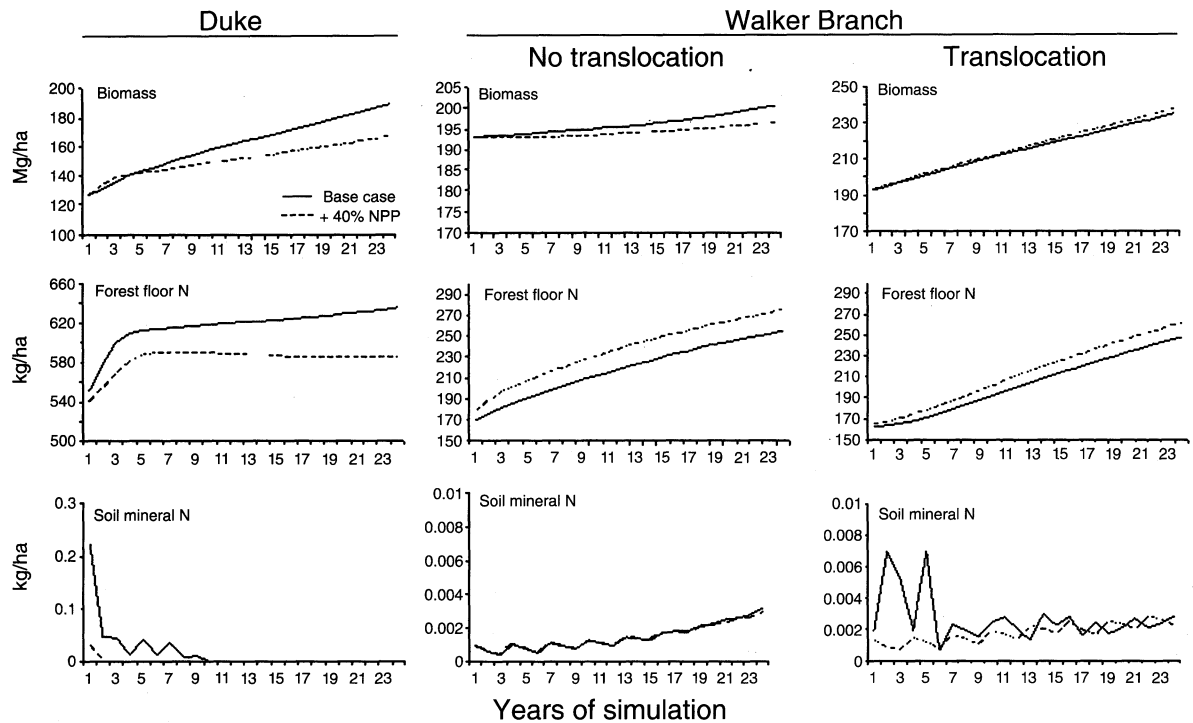
FIG. 5. Simulated biomass, forest floor N content, and soil mineral N ($NH_4^+$ + $NO_3^-$) for Duke, North Carolina, and Walker Branch, Tennessee, USA, using the Nutrient Cycling Model (NuCM). The scenarios include control (base case, no change) and increased target net primary production by 40%. For Walker Branch, scenarios with and without translocation are shown. Data are from Johnson (1999).

limitation would prevent growth increase in response to elevated $CO_2$ on a decadal time scale, and whether growth response to $CO_2$ in N-limited systems could be facilitated by increased biomass/N (reduced concentration) and/or increased litter N mineralization. The scenarios included (1) reduced foliar N concentrations; (2) reduced wood N concentrations, (3) increased target net primary production (NPP), and (4) no change. The increased NPP scenario is the most interesting and relevant to the actual results from nearby field studies of elevated $CO_2$ at these sites, which showed increased NPP and increased N uptake (Johnson et al. 2003a, 2004, Finzi et al. 2004). At the Duke site, increased target NPP caused greater growth for the first four years, but after that, sequestration of N in the forest floor and the resultant decline in soil mineral N reversed this pattern so that, by the end of the 24-year simulation, biomass was actually lower in the increased NPP scenario (Fig. 5). At the Walker Branch site, increasing target NPP caused a slight (7%) increase in growth and this was maintained throughout the 24-year simulation when translocation was allowed. As at Duke, there was an increase in forest floor N sequestration, but this was not large and apparently did not cause reductions in simulated mineral N sufficient to cause a reversal in the biomass pattern. When translocation was not allowed, however, increasing NPP

caused a slight decrease in growth along with an increase in forest floor N sequestration (Fig. 5).

These simulations posed the counterintuitive hypothesis that increased biogeochemical cycling of N (via increased litterfall N) can cause reduced growth in an N-limited system such as the Duke site because of increased accumulation of N in the forest floor and soil. Translocation (removal of N from senescing leaves prior to litterfall) could mitigate this response by allowing the trees to maintain a greater proportion of N taken up rather than recycle it back to the forest floor and soil where it can be immobilized. Eliminating translocation at Walker Branch changed the sign as well as the magnitude of the responses in three of the four scenarios simulated. NuCM currently does not allow translocation in coniferous species, and thus the effects of translocation on N cycling in the Duke simulations are not known.

Whether elevated $CO_2$ facilitates N uptake or not over the short term, it would seem that the long-term prospects for continued growth responses are poor unless additional N is supplied by either N fixation or increased atmospheric deposition. This is evident not only from the formal simulation modeling exercises just described, but also from simple logic: although soil N stores are usually very large in relation to plant uptake (Cole and Rapp 1981), they are not infinite. It

would seem that diminishing returns must ultimately set in as soil labile pools are depleted, unless additional N is supplied. Atmospheric N deposition is apparently increasing in many parts of the world (Galloway et al. 1995) and may facilitate continued growth responses to elevated $CO_2$ as well as produce growth increases in its own right.

## SUMMARY AND CONCLUSIONS

Progressive nitrogen limitation as a result of rapid growth has been well-documented in the older nutrient cycling literature from plantation forests. Progressive nitrogen limitation has been attributed largely to accumulation of N in both biomass and forest floor components in excess of any known inputs, and is not completely offset by the well-documented "mining" of soil N in some instances. New insights into nutrient cycling processes have shown how soil N mining can occur (Schimel and Bennett 2004) and describe counterintuitive mechanisms by which forest floor N sequestration can be enhanced rather than reduced by greater N concentrations in litterfall (Berg and McClaugherty 2003). However, these new findings do not change the basic reasoning or conclusions drawn from previous nutrient budget studies as to the basic causes of PNL, namely, sequestration of N in vegetation and forest floor components.

Field studies have shown that elevated $CO_2$ can cause increased growth even in the face of N limitation over the short term (<6 years). This is facilitated, to some degree, by greater biomass production per unit N uptake (lower tissue N concentrations), but, more often than not, N uptake is increased with elevated $CO_2$ as well. Most studies to date have indicated little or no effect of elevated $CO_2$ on soil N mineralization rate, and thus the most likely mechanism for the observed increase in N uptake is the commonly observed increase in root growth, facilitating greater soil exploration. Experience from the early nutrient cycling literature, as well as simulation modeling, suggests that PNL will at some point truncate the observed increases in growth and nutrient uptake with elevated $CO_2$, despite efficient N cycling and soil mining, unless external inputs of nutrients are increased.

## LITERATURE CITED

Allen, A. A., J. A. Andrews, A. C. Finzi, R. Matamala, D. D. Richter, and W. H. Schlesinger. 2000. Effects of free-air $CO_2$ enrichment (FACE) on belowground processes in a *Pinus taeda* forest. Ecological Applications 10:437–448.

Arnone, J. A. 1999. Symbiotic $N_2$ fixation in high alpine grassland: effects of four growing seasons of elevated $CO_2$. Functional Ecology 13:383–387.

Arnone, J. A., and J. C. Gordon. 1990. Effect of nodulation, nitrogen fixation, and $CO_2$ enrichment on the physiology,

growth, and dry mass allocation of seedlings of *Alnus rubra* Bong. New Phytologist 116:55–66.

Barnard, R., L. Barthes, X. Le Rous, H. Harmens, A. Raschi, J.-F. Soussana, B. Winlker, and P. W. Leadly. 2004. Atmospheric $CO_2$ elevation has little effect on nitrifying and denitrifying enzyme activity in four European grasslands. Global Change Biology 10:488–497.

Berg, B., and C. McClaugherty. 2003. Plant litter. Decomposition, humus formation, carbon sequestration. Springer-Verlag, Heidelberg, Germany.

Berntson, G. M., and F. A. Bazzaz. 1996. Belowground positive and negative feedbacks on $CO_2$ growth enhancement. Plant and Soil 187:119–134.

Binkley, D., Y. Son, and D. Valentine. 2000. Do forests receive occult inputs of nitrogen? Ecosystems 3:321–331.

Birk, E. M., and P. M. Vitousek. 1986. Nitrogen availability and nitrogen-use efficiency in loblolly pine stands. Ecology 67:69–79.

Bormann, F. H., G. E. Likens, and J. M. Melillo. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. Science 196:981–983.

Carnol, M., L. Hogenboom, M. Ewa Jach, J. Remacle, and R. Ceulemans. 2002. Elevated $CO_2$ in open top chambers increases net nitrification and potential denitrification. Global Change Biology 8:590–598.

Chapin, F. S., III, and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64:376–391.

Chestnut, T. J., D. J. Zarin, W. H. McDowell, and M. Keller. 1999. A nitrogen budget for late-succesional hillslope tabunoco forest, Puerto Rico. Biogeochemistry 46:85–108.

Cole, D. W. 1981. Nitrogen uptake and translocation by forest ecosystems. Ecological Bulletins (Stockholm) 33:219–232.

Cole, D. W., S. P. Gessel, and S. F. Dice. 1968. Distribution and cycling of nitrogen, phosphorus, potassium, and calcium in a second-growth Douglas-fir forest. Pages 197–213 in H. E. Young, editor. Primary production and mineral cycling in natural ecosystems. University of Maine Press, Orono, Maine, USA.

Cole, D. W., and M. Rapp. 1981. Elemental cycling in forest ecosystems. Pages 341–409 in D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, London, UK.

Comins, H. N., and R. E. McMurtrie. 1993. Long-term response of nutrient-limited forests to $CO_2$ enrichment; equilibrium behavior of plant–soil models. Ecological Applications 3:666–681.

Cotrufo, M. F., P. Ineson, and A. Scott. 1998. Elevated $CO_2$ reduces the nitrogen concentration of plant tissues. Global Change Biology 4:43–54.

Curlin, J. W. 1970. Nutrient cycling as a factor in site productivity and forest fertilization. Pages 313–326 in C. T. Youngberg and C. R. Davey, editors. Tree growth and forest soils. Oregon State University Press, Corvallis, Oregon, USA.

Curtis, P. S., C. S. Vogel, X. Wang, K. S. Pregitzer, D. R. Zak, J. Lussenhop, M. Kubiske, and J. A. Teeri. 2000. Gas exchange, leaf nitrogen, and growth efficiency of *Populus tremloides* in a $CO_2$-enriched atmosphere. Ecological Applications 10:3–17.

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.

Day, F. P., E. P. Weber, C. R. Hinkle, and B. G. Drake. 1996. Effects of elevated atmospheric $CO_2$ on fine root length and distribution in an oak–palmetto scrub ecosystem in central Florida. Global Change Biology 2:143–148.

Diaz, S., J. P. Grime, J. Harris, and E. McPherson. 1993. Evidence of feedback mechanism limiting plant response to elevated carbon dioxide. Nature 364:616–617.

Finzi, A. C., E. H. DeLucia, J. G. Hamilton, D. D. Richter, and W. H. Schlesinger. 2002. The nitrogen budget of a pine forest under free air $CO_2$ enrichment. Oecologia 132:567–578.

Finzi, A. C., E. H. DeLucia, and W. H. Schlesinger. 2004. Canopy N and P dynamics of a southeastern US pine forest under elevated $CO_2$. Biogeochemistry 69:363–378.

Finzi, A. C., and W. H. Schlesinger. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. Ecosystems 6:444–456.

Foster, N. W., E. G. Beauchamp, and C. T. Corke. 1985. Reactions of $^{15}$N-labelled urea with Jack pine forest floor materials. Soil Biology and Biochemistry 17:699–703.

Foster, N. W., I. K. Morrison, P. W. Hazlett, G. D. Hogan, and M. I. Salerno. 1995. Carbon and nitrogen cycling within mid- and late-rotation jack pine. Pages 355–375 in W. W. McFee and J. M. Kelly, editors. Carbon forms and functions in forest soils. American Society of Agronomy, Madison, Wisconsin, USA.

Galloway, J. N., W. H. Schlesinger, H. Levy,II, A. Michaels, and J. L. Schnoor. 1995. Nitrogen fixation: anthropogenic enhancement—environmental response. Global Biogeochemical Cycles 9:235–252.

Gessel, S. P., D. W. Cole, and E. C. Steinbrenner. 1973. Nitrogen balances in forest ecosystems of the Pacific Northwest. Soil Biology and Biochemistry 5:19–34.

Gholz, H. L., R. F. Fisher, and W. L. Pritchett. 1985. Nutrient dynamics in slash pine plantation ecosystems. Ecology 66:647–659.

Gloser, V., M. Ježikova, A. Lüscher, M. Frehner, H. Blum, J. Nösberger, and U. A. Hartwig. 2000. Soil mineral nitrogen availability was unaffected by elevated atmospheric $pCO_2$ in a four year old field experiment (Swiss FACE). Plant Soil 227:291–299.

Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Canadian Journal of Forest Research 11:155–167.

Griffiths, R. P., and A. K. Swanson. 2001. Forest soil characteristics in a chronosequence of harvested Douglas-fir forests. Canadian Journal of Forest Research 31:1871–1879.

Hamilton, J. G., E. H. DeLucia, K. George, S. L. Naidu, A. C. Finzi, and W. H. Schlesinger. 2002. Forest carbon balance under elevated $CO_2$. Oecologia 131:250–260.

Heilman, P. E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes of interior Alaska. Ecology 47:825–834.

Hirschel, G., C. Körner, and J. A. Arnone. 1997. Will rising atmospheric $CO_2$ affect litter quality and in situ decomposition rates in native plant communities? Oecologia 110:387–392.

Holmes, W. E., D. R. Zak, K. S. Pregitzer, and J. S. King. 2003. Soil nitrogen transformations under *Populus tremloides*, *Betula papyrifera*, and *Acer saccharum* following 3 years exposure to elevated $CO_2$ and $O_3$. Global Change Biology 9:1743–1750.

Hungate, B. A. 1999. Ecosystem responses to rising atmospheric $CO_2$: feedbacks through the nitrogen cycle. Pages 265–285 in Y. Luo and H. A. Mooney, editors. Carbon dioxide and environmental stress. Academic Press, San Diego, California, USA.

Hungate, B. A., P. Dijkstra, D. W. Johnson, C. R. Hinkle, and B. G. Drake. 1999. Elevated $CO_2$ increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. Global Change Biology 5:1–9.

Hungate, B. A., P. D. Stiling, P. Dijkstra, D. W. Johnson, M. E. Ketterer, G. J. Hymus, C. R. Hinkle, and B. G. Drake.

2004. $CO_2$ elicits long-term decline in nitrogen fixation. Science 304:1291.

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

Johnson, D. W. 1999. Simulated effects of elevated $CO_2$ on nitrogen cycling using the NuCM model. Tree Physiology 19:321–327.

Johnson, D. W., J. T. Ball, and R. F. Walker. 1997. Effects of $CO_2$ and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. Plant and Soil 190:20–40.

Johnson, D. W., W. Cheng, and J. T. Ball. 2000a. Effects of [$CO_2$] and nitrogen fertilization on soils planted with ponderosa pine. Plant and Soil 224:99–113.

Johnson, D. W., W. Cheng, and J. T. Ball. 2000b. Effects of $CO_2$ and N fertilization on decomposition and N immobilization in ponderosa pine litter. Plant and Soil 224:115–122.

Johnson, D. W., W. Cheng, and I. C. Burke. 2000c. Biotic and abiotic nitrogen retention in a variety of forest soils. Soil Science Society of America Journal 64:1503–1514.

Johnson, D. W., W. Cheng, J. D. Joslin, R. J. Norby, N. T. Edwards, and D. E. Todd,Jr. 2004. Effects of elevated $CO_2$ on nutrient cycling in a sweetgum plantation. Biogeochemistry 69:379–403.

Johnson, D. W., and N. T. Edwards. 1979. Effects of stem girdling on biogeochemical cycles in a mixed deciduous forest in eastern Tennessee. II. Soil nitrogen mineralization and nitrification rates. Oecologia 40:259–271.

Johnson, D. W., P. H. Henderson, J. T. Ball, and R. F. Walker. 1996. Effects of $CO_2$ and N on growth and N dynamics in ponderosa pine: results from the first two growing seasons. Pages 23–40 in G. W. Koch and H. A. Mooney, editors. Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, California, USA.

Johnson, D. W., B. A. Hungate, P. A. Dijkstra, G. Hymus, D. R. Hinkle, P. Stiling, and B. G. Drake. 2003a. The effects of elevated $CO_2$ on nutrient distribution in a fire-adapted scrub oak forest. Ecological Applications 13:1388–1399.

Johnson, D. W., and S. E. Lindberg. 1992. Atmospheric deposition and forest nutrient cycling: a synthesis of the integrated forest study. Springer-Verlag, New York, New York, USA.

Johnson, D. W., R. B. Thomas, K. R. Griffin, D. T. Tissue, J. T. Ball, B. A. Strain, and R. F. Walker. 1998. Effects of $CO_2$ and N on growth and N uptake in ponderosa and loblolly pine. Journal of Environmental Quality 27:414–425.

Johnson, D. W., and D. E. Todd. 1998. The effects of harvesting on long-term changes in nutrient pools in a mixed oak forest. Soil Science Society of America Journal 62:1725–1735.

Johnson, D. W., D. E. Todd, Jr., and V. R. Tolbert. 2003b. Changes in ecosystem carbon and nitrogen in a loblolly pine plantation over the first 18 years. Soil Science Society of America Journal 67:1594–1601.

Johnson, D. W., H. Van Miegroet, S. E. Lindberg, R. B. Harrison, and D. E. Todd. 1991. Nutrient cycling in red spruce forests of the Great Smoky Mountains. Canadian Journal of Forest Research 21:769–787.

Kimmins, J. P., and B. C. Hawkes. 1978. Distribution and chemistry of fine roots in a white spruce–subalpine fir stand in British Columbia: implications for management. Canadian Journal of Forest Research 8:265–279.

Knops, J. M. H., W. D. Koenig, and T. H. Nash III. 1997. On the relationship between nutrient use efficiency and fertility in forest ecosystems. Oecologia 110:550–556.

Körner, C., and J. A. Arnone. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. Science 257:1672–1675.

Luo, Y., et al. 2004. Progressive nitrogen limitation of eco-system responses to rising atmospheric $CO_2$. BioScience 54:731–739.

Mattson, S., and E. Koulter-Anderson. 1942a. The acid–base condition in vegetation, litter, and humus. V. Products of partial oxidation and ammonia fixation. Lantbrukshögskolans Annaler 10:284–332.

Mattson, S., and E. Koulter-Anderson. 1942b. The acid–base condition in vegetation, litter, and humus. VI. Ammonia fixation and humus nitrogen. Lantbrukshögskolans Annaler 11:107–134.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, E. Mayorga, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.

McGuire, A. D., J. M. Melillo, and L. A. Joyce. 1995. The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon dioxide. Annual Review of Ecology and Systematics 26:473–503.

McMurtrie, R. E., and H. N. Comins. 1996. The temporal response of forest ecosystems to doubled atmospheric $CO_2$ concentration. Global Change Biology 2:49–57.

Medlyn, M. E., R. E. McMurtrie, R. C. Dewar, and M. P. Jeffreys. 2000. Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric $CO_2$ concentration. Canadian Journal of Forest Research 30:873–888.

Miller, H. G., J. M. Cooper, J. D. Miller, and O. J. L. Pauline. 1979. Nutrient cycles in pine and their adaptation to poor soils. Canadian Journal of Forest Research 9:19–26.

Mortland, M. M., and A. R. Wolcott. 1965. Sorption of inorganic nitrogen compounds by soil materials. Agronomy 10:150–197.

Nambiar, E. K. S., and D. N. Fife. 1991. Nutrient translocation in temperate conifers. Tree Physiology 9:185–207.

Nömmik, H. 1965. Ammonium fixation and other reactions involving a nonenzymatic immobilization of mineral nitrogen in soil. Agronomy 10:198–257.

Nömmik, H. 1970. Non-exchangeable binding of ammonium and amino nitrogen by Norway spruce raw humus. Plant and Soil 33:581–595.

Nömmik, H., and K. Vahtras. 1982. Retention and fixation of ammonium and ammonia in soils. Agronomy 22:123–172.

Norby, R. J. 1987. Nodulation and nitrogenase activity in nitrogen-fixing woody plants stimulated by $CO_2$ enrichment of the atmosphere. Physiologia Plantarum 71:77–82.

Norby, R. J., and M. F. Cotrufo. 1998. A question of litter quality. Nature 396:17–18.

Norby, R. J., M. F. Cotrufo, P. Ineson, E. G. O'Neill, and J. P. Canadell. 2001. Elevated $CO_2$, litter chemistry, and decomposition: a synthesis. Oecologia 127:153–165.

Norby, R. J., T. M. Long, J. S. Hartz-Rubin, and E. G. O'Neill. 2000. Nitrogen resorption in senescing tree leaves in a warmer, $CO_2$-enriched atmosphere. Plant and Soil 224:15–29.

Norby, R. J., E. G. O'Neil, W. G. Hood, and R. J. Luxmoore. 1987. Carbon allocation, root exudation, and mycorrhizal colonization of Pinus echinata seedlings grown under $CO_2$ enrichment. Tree Physiology 3:203–210.

Norby, R. J., S. D. Wullschleger, C. A. Gunderson, D. W. Johnson, and R. Cuelemans. 1999. Tree response to rising $CO_2$ in field experiments: implications for the future forest. Plant, Cell, and Environment 22:683–714.

O'Neill, E. G. 1994. Responses of soil biota to elevated atmospheric carbon dioxide. Plant and Soil 165:55–65.

Oren, R., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maier, K. V. R. Schäfer, H. McCarthy, G. E. Hendry, S. G. McNulty, and C. G. Katu. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a $CO_2$-rich atmosphere. Nature 411:469–472.

Ovington, J. D. 1959. The circulation of minerals in plantations of Pinus sylvestris L. Annals of Botany 23:229–239.

Ovington, J. D. 1962. Quantitative ecology and the woodland ecosystem concept. Advances in Ecological Research 1:103–192.

Ovington, J. D., and H. A. I. Madgwick. 1959. Distribution of organic matter and plant nutrients in a plantation of Scots pine. Forest Science 5:344–355.

Paul, E. A., and F. E. Clark. 1989. Soil microbiology and biochemistry. Academic Press, New York, New York, USA.

Pregitzer, K. S., D. R. Zak, J. Maziasaz, J. D. Forest, P. S. Curtis, and J. Lussenhop. 2000. Interactive effects of atmospheric $CO_2$ and soil-N availability on fine roots of Populus tremloides. Ecological Applications 10:18–33.

Randlett, D. L., D. R. Zak, K. S. Pregitzer, and P. S. Curtis. 1996. Elevated atmospheric carbon dioxide and leaf litter chemistry: influences on microbial respiration and net nitrogen mineralization. Soil Science Society of America Journal 60:1571–1577.

Rastetter, E. B., G. Ågren, and G. R. Shaver. 1997. Responses of N-limited ecosystems to increased $CO_2$: a balanced-nutrition, coupled-element-cycles model. Ecological Applications 7:444–460.

Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie, and J. D. Aber. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in $CO_2$, climate and N deposition. Tree Physiology 9:101–126.

Rastetter, E. B., and G. R. Shaver. 1992. A model of multiple element limitation for acclimating vegetation. Ecology 73:1157–1174.

Remezov, N. P. 1959. Methods of studying the biological cycles of elements in forests. Pochvovedenie 1:71–79.

Rennie, P. J. 1955. Uptake of nutrients by mature forest growth. Plant and Soil 7:49–95.

Richter, D. D., and D. Markewitz. 2001. Understanding soil change: soil sustainability over millennia, centuries and decades. Cambridge University Press, Cambridge, UK.

Richter, D. D., D. D. Markewitz, P. R. Heine, V. Jin, J. Raikes, K. Tian, and C. G. Wells. 2000. Legacies of agricultural and forest regrowth in the nitrogen of old-field soils. Forest Ecology and Management 138:233–248.

Riha, S. J., G. S. Campbell, and J. Wolfe. 1987. A model of competition for ammonium among heterotrophs, nitrifiers, and roots. Soil Science Society of America Journal 50:1463–1466.

Rogers, H. H., C. M. Peterson, J. N. McCrimmon, and J. D. Cure. 1992. Response of plant roots to elevated atmospheric carbon dioxide. Plant, Cell and Environment 15:749–752.

Ryan, M. G., D. Binkley, and J. H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. Advances in Ecological Research 27:214–262.

Scherzer, A. J., J. Rebbeck, and R. E. J. Boerner. 1998. Foliar nitrogen dynamics and decomposition of yellow-poplar and eastern white pine during four seasons of exposure to elevated ozone and carbon dioxide. Forest Ecology and Management 109:355–366.

Schimel, J. P., and J. Bennett. 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology 85:591–602.

Schimel, J. P., and M. K. Firestone. 1989. Inorganic N incorporation by coniferous forest floor material. Soil Biology and Biochemistry 21:41–46.

Shaver, G. R., W. D. Billings, F. S. Chapin, III, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel, and E. B. Rastetter. 1992.

SPECIAL FEATURE

Global change and the carbon balance of arctic ecosystems. BioScience **42**:433–441.

Strain, B. R. 1985. Physiological and ecological controls on carbon sequestering in terrestrial ecosystems. Biogeochemistry **1**:219–232.

Switzer, G. L., and L. E. Nelson. 1972. Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. Soil Science Society of America Proceedings **36**:143–147.

Thomas, R. B., D. D. Richter, H. Ye, P. R. Heine, and B. R. Strain. 1991. Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium* (Jacq.) Walp.) exposed to elevated to atmospheric carbon dioxide. Oecologia **88**:415–421.

Tingey, D. T., M. G. Johnson, D. L. Phillips, D. W. Johnson, and J. T. Ball. 1996. Effects of elevated $CO_2$ and nitrogen on the synchrony of shoot and root growth in ponderosa pine. Tree Physiology **16**:905–914.

Trettin, C. A., D. W. Johnson, and D. E. Todd, Jr. 1999. Forest nutrient and carbon pools: a 21-year assessment. Soil Science Society of America Journal **63**:1436–1448.

Turner, J. 1977. Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. Forest Science **23**:307–316.

Turner, J. 1981. Nutrient cycling in an age sequence of western Washington Douglas-fir stands. Annals of Botany **48**:159–169.

Verburg, P. S. J., W. X. Cheng, D. W. Johnson, and D. E. Schorran. 2004. Nonsymbiotic nitrogen fixation in three-year-old Jeffrey pines and the role of elevated [$CO_2$]. Canadian Journal of Forest Research **34**:1979–1984.

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.

Vogt, K. A., E. E. Moore, D. J. Vogt, M. J. Redlin, and R. L. Edmonds. 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Canadian Journal of Forest Research **13**:429–437.

Wells, C. G., and J. R. Jorgensen. 1975. Nutrient cycling in loblolly pine plantations. Pages 137–158 *in* B. Bernier and C. H. Winget, editors. Forest soils and land management. Proceedings of the Fourth North American Forest Soils Conference. Les Presses de l'Universite Laval, Quebec, Canada.

Zak, D. R., W. E. Holmes, A. C. Finzi, R. J. Norby, and W. H. Schlesinger. 2003. Soil nitrogen cycling under elevated $CO_2$: a synthesis of forest FACE experiments. Ecological Applications **13**:1508–1514.

Zak, D. R., K. S. Pregitzer, P. S. Curtis, J. A. Teeri, R. Fogel, and D. L. Randlett. 1993. Elevated atmospheric $CO_2$ and feedback between carbon and nitrogen cycles. Plant and Soil **151**:105–117.

Zak, D. R., K. S. Pregitzer, P. S. Curtis, C. S. Vogel, W. E. Holmes, and J. Lussenhop. 2000a. Atmospheric $CO_2$, soil-N availability, and allocation of biomass and nitrogen by *Populus tremloides*. Ecological Applications **10**:34–46.

Zak, D. R., K. S. Pregitzer, J. S. King, and W. E. Holmes. 2000b. Elevated atmospheric $CO_2$, fine roots, and the response of soil microorganisms: a review and hypothesis. New Phytologist **147**:201–222.

SPECIAL FEATURE