16. Changes in Soil Nitrogen Pools and Transformations Following Forest Clearcutting

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Factors that regulate the cycling of nitrogen are important determinants of the metabolism and organization of forest ecosystems (Gosz 1981; Melillo 1981). The nitrogen cycle includes a number of important gaseous components and is strongly regulated by biological processes, particularly those mediated via microbial populations. The cycle of this element is closely coupled to the cycles of other essential elements (e.g., C, S). Thus, the dynamics of nitrogen may largely regulate the productivity of forests and their response to intensive management and other exogenous disturbance (Kimmins 1977; Swank and Waide 1980; Vitousek 1981; Johnson 1984). Because nitrogen transformations are so tightly coupled to other biogeochemical processes, it is especially difficult to predict a priori impacts of human disturbance on forest metabolism and nitrogen cycling.

The storage and turnover of nitrogen in soil pools are essential components of the forest nitrogen cycle. In most temperate forests, 80 to 90% of the total nitrogen capital may be localized in labile and recalcitrant forms of soil organic matter (Rodin and Bazilevich 1967; Cole and Rapp 1980; Swank and Waide 1980; Melillo 1981). Factors which regulate rates at which nitrogen is stored and subsequently mineralized from these soil pools determine both the availability of nitrogen for uptake by plants and microorganisms (Keeney 1980) and the losses of nitrogen from the forest ecosystem to the atmosphere and to drainage waters (Vitousek and Melillo 1979). Thus, information on these factors is prerequisite to understanding and managing forests. Yet it is those processes which regulate soil nitrogen storage and turnover which are the most poorly understood portions of the forest nitrogen cycle, and about which improved knowledge is urgently needed.

Since the initiation of Coweeta research on forest productivity and nutrient cycling in the late 1960s (Douglass and Hoover, Chapter 2), major emphasis has been placed on the nitrogen cycle. Early work focused on the solution flux of nitrogen through forested watersheds (Swank and Waide, Chapter 4), the cycling of nitrogen through vegetation pools (Monk and Day, Chapter 11), nitrogen inputs to and release from forest litter layers (Cromack and Monk 1975), and biological transformations of nitrogen in forest litter layers and soils, particularly microbial gaseous transformations (Cornaby and Waide 1973; Todd et al. 1975b, 1978). This work was synthesized in the form of a compartment model by Mitchell et al. (1975). This model included estimates of nitrogen standing crops in and transfer rates among 15 storage pools, and rates of nitrogen exchange with the surrounding environment.

This model of nitrogen cycling in an aggrading mixed hardwood forest was implemented to predict and assess likely consequences of intensive management on long-term forest productivity and nitrogen cycling (Waide and Swank 1976, 1977). Swank and Waide (1980) subsequently provided comparative analyses of nitrogen cycling at Coweeta and three other well-studied forest ecosystems, and identified components of the forest nitrogen cycle which appeared to be most susceptible to management impacts. These components were the mineralization of nitrogen from decaying litter and stable soil organic matter, nitrogen inputs via biological dinitrogen fixation, and losses via denitrification. Nitrogen losses due to removal of forest products and leaching to drainage waters were quantitatively less important than these processes in relation to long-term changes in site productivity.

At the time this earlier research was completed, data on changes in nitrogen dynamics immediately following forest disturbance were not available for any forested watershed at Coweeta. Such data were important to verify model predictions and to document both the extent of disruption of forest nitrogen cycling immediately following disturbance and the patterns, rates, and mechanisms of forest recovery. To satisfy this need, a forest clearcutting experiment was implemented. Detailed studies of the treated watershed began 2 years prior to cutting and are still in progress. In this chapter we summarize select results of this ecosystem experiment. Specifically, we focus on changes in soil nitrogen storages and transformations following forest clearcutting. We emphasize major changes at the watershed scale of resolution. Detailed analyses of spatial and temporal variability in nitrogen standing crops and transformations, and of causal relations among measured variables, will appear in subsequent papers. Related data on this experiment are discussed in the chapters by Boring et al. (Chapter 12) and Swank (Chapter 25). Other studies on nitrogen cycling in disturbed watersheds at Coweeta have recently been completed by Montagnini (1985) and White (1986).

Methods

Site Description and Treatment History

Research described here was conducted on Watershed 2 (WS 2) and WS 7. WS 2 served as the control and is located adjacent to WS 7. Vegetation on this 12.1 ha south-facing watershed consists of a mixed hardwood forest (cove hardwoods at low elevations and along ravines, oak-hickory on side slopes) which has been undisturbed since 1924 except for the chestnut blight. Soils are predominantly Fannin fine sandy

loams (fine-loamy, micaceous, mesic Typic Hapludults), with Chandler gravelly loams (coarse-loamy, micaceous, mesic Typic Dystrochrepts) predominating on upper slopes and ridges.

WS 7 is a south-facing, 58.7 ha catchment. Prior to logging, vegetation consisted of three major forest types (see Figure 12.1 of Boring et al., Chapter 12): (1) cove hardwoods at lower elevations and along ravines at intermediate elevations; (2) mesic (southeast-facing) and xeric (southwest-facing) oak-hickory forests on intermediate-elevation side slopes; and (3) pine-hardwood forests at upper elevations and on ridges. Soils are similar to those on WS 2.

Treatment of WS 7 can be separated into three components: road construction and stabilization, logging, and site preparation. Three roads were constructed during mid-April through mid-June 1976, covering about 5% of total watershed area. Road cuts and fills were stabilized by seeding grass and applying fertilizer and lime both following construction and again in July 1977 and June 1978. Logging began in January 1977 and continued through June 1977. Approximately 28% of the watershed was not logged due to the poor quality of timber, 56% was logged with a mobile cable system, and 16% (slopes $<20\%$) was logged with tractor skidding. Site preparation was completed in October 1977, and consisted of clearfelling all remaining stems ≥ 2.5 cm dbh.

Sample Collection

Prior to logging, vegetation was inventoried on 142 0.08 ha plots systematically located over WS 7. Sixteen of these were selected randomly (stratified by vegetation zone) as intensive study plots for prelogging sampling. After logging, 12 of 142 plots were selected in a stratified random fashion. Sampling was conducted on WS 2 only following treatment of WS 7, on four randomly located plots. Sampling commenced in March 1975 on a biweekly schedule through February 1979, when the frequency changed to a monthly basis. No samples were collected during the period of August 1976 to July 1977. Results are summarized here through the October 1980 sampling period.

On each sampling date, bulk soil samples were collected from 0 to 10 cm and 10 to 30 cm soil depths. These two depths generally correspond to the A and AB-Blt (Hapludults) or A and AB-Bw (Dystrochrepts) soil horizons, respectively. On each watershed, one-half of the total number of plots were sampled on alternate dates. Samples were placed on ice and returned to the laboratory within 1 day of collection. Samples were then refrigerated (4°C) until analysis, which occurred within 1 week of collection. Chemical analyses (except NO_3-NH_4) were performed on air-dried samples; biological (and NO_3-NH_4) analyses, on field-moist samples.

Resulting data were subjected to analysis-of-variance procedures to detect significant differences between sampling depths and following forest removal. A significance level of $a = 0.05$ was employed in these analyses.

Changes in Soil Microenvironments

Many of the changes in nitrogen cycling processes to be discussed are largely due to altered soil microenvironments resulting from removal and successional recovery of the forest canopy. To evaluate impacts of these changes, direct measures were made of

soil moisture and temperature on each sampling date (Table 16.1). Moisture was determined gravimetrically in the laboratory. Temperature was measured directly in the field (0-10 cm depth only) at the time of sampling.

Removal of the forest canopy resulted in large increases in radiation reaching the forest floor. As a consequence, soil temperatures were elevated during the first postcut year. During the first summer of postcut sampling, temperature readings in the range of 40 to 60°C were common. Rapid recovery of the canopy (leaf area index was 68% of control values by the third year (Chapter 12)) provided shade and moderated soil temperatures.

Removal of the canopy during clearcutting also reduced evapotranspiration, and resulted in elevated soil moisture levels during the first year. However, increased solar radiation inputs and soil temperatures also accelerated the drying of surface soil horizons following precipitation events. Canopy recovery provided shade as well as partial recovery of evapotranspiration. Thus, soil moisture had returned to precutting levels by the third year of sampling.

These postcutting changes in soil microenvironments had adverse impacts on overall microbial biomass and metabolism, as revealed by measures of soil ATP concentrations and CO_2 evolution. For example, average soil ATP pools declined about 60% (from about 71 $\mu g\ m^{-2}$ to about 29 $\mu g\ m^{-2}$) in the first year following forest removal. Similarly, total soil CO_2 evolution declined about 32% in the first post-treatment year, from 8.3 $g\ m^{-2}\ d^{-1}$ to 5.7 $g\ m^{-2}\ d^{-1}$. The harsh soil microenvironments in the first year following treatment also negatively impacted soil microarthropod populations and surface litter decomposition processes (Abbott et al. 1980; Seastedt and Crossley 1981; Abbott and Crossley 1982). Even in this first postcut year, however, short bursts of high microbial activity were observed in fall and spring during brief periods of warm, moist soil conditions. Measures of CO_2 evolution and ATP concentrations suggested that general microbial growth processes had recovered to near pretreatment levels after three years, coincident with canopy recovery and the moderation of soil microenvironments.

Changes in Soil Organic Matter and Nitrogen Pools

Organic Matter

Soil organic matter (SOM) was determined using Walkley-Black titrations (Nelson and Sommers 1982). For both watersheds, SOM concentrations were significantly higher in the upper sampling depth (Table 16.2). Following clearcutting of WS 7, SOM values increased substantially (74%) in the 0 to 10 cm depth and to a lesser extent (17%) in the 10 to 30 cm depth. Thus, postcutting differences between the two depths were greater than precutting differences. Both the differences between depths and following clearcutting were statistically significant. SOM concentrations increased immediately following treatment, reaching peak values after about 1 year. Thereafter, concentrations declined slightly. However, even after 3 years, SOM values were still significantly greater than prior to cutting at both depths.

The exact source of these post-treatment SOM increases is not known, particularly the large increases in the upper sampling depth. These increases presumably include

Table 16.1. Changes in Soil Microenvironments Following Forest Clearcutting at Coweeta

Variable	Units	Depth (cm)	WS 2	WS 7 Precut	WS 7 Postcut, Yr 1[a]	WS 7 Postcut, Yrs 1–3[a]
Soil moisture	g g^{-1}	0-10	0.35 (0.05)[b]	0.35 (0.02)	0.56 (0.04)	0.34 (0.04)
		10-30	0.29 (0.04)	0.30 (0.01)	0.36 (0.01)	0.26 (0.02)
Soil temperature	°C	0-10	13.3 (0.6)	13.6 (0.8)	16.9 (0.7)	12.8 (1.1)
		10-30	ND[c]	ND	ND	ND

[a] To indicate temporal trends in the variables of interest, resulting from successional recovery of vegetation, postcutting data for WS 7 are summarized separately for Year 1 (August 1977–July 1978) and Years 1-3 (August 1977–October 1980). Note that the first year of soil sampling began near the end of the first summer of vegetation regrowth.
[b] Data displayed as $\bar{x}$ (SE) over the period of interest.
[c] Not determined.

organic matter inputs from mortality and turnover of fine roots, and from the decay and leaching of surface litter layers following forest removal. Fine root turnover has been shown to contribute large amounts of organic matter to soil pools in temperate deciduous forests (Harris et al. 1980; McClaugherty et al. 1982; Aber et al. 1985). Dominski (1971) and Covington (1981) documented reductions in surface litter mass following forest removal at Hubbard Brook and other sites in the White Mountains of New Hampshire. Rapid decomposition of logging residues in the first 7 years following watershed treatment, particularly in the smaller size fractions (≤ 5 cm diameter), contributed to SOM increases (Mattson 1986), though not immediately following site preparation. The more modest SOM increase at the lower depth indicated that some C was transported downward, probably in water-soluble form, but also that most of the C inputs were metabolized and immobilized or respired in the upper 10 cm of soil.

Increases were not observed in SOM values following the whole-tree harvesting of another Coweeta watershed, WS 48 (Waide et al. 1985), suggesting that the decay of logging slash (removed from WS 48) played some role in the large SOM increases on WS 7. However, Boring and Swank (1984a) documented SOM increases in surface soil horizons of successional forests on several other disturbed watersheds at Coweeta.

Table 16.2. Changes in Soil Organic Matter and Nitrogen Pools Following Forest Clearcutting at Coweeta[a]

Variable	Units	Depth (cm)	WS 2	WS 7 Precut	WS 7 Postcut, Yr 1	WS 7 Postcut, Yrs 1-3
Organic matter	%	0-10	7.4 (0.3)	6.5 (0.2)	11.3 (0.6)	11.1 (0.5)
		10-30	4.8 (0.4)	4.6 (0.1)	5.4 (0.3)	5.5 (0.2)
Total Kjeldahl N	%	0-10	0.19 (0.01)	0.17 (0.01)	0.28 (0.02)	0.25 (0.06)
		10-30	0.14 (0.01)	0.13 (0.01)	0.16 (0.01)	0.16 (0.01)
NO_3^-	μg g^{-1}	0-10	1.6 (0.4)	1.2 (0.2)	4.3 (0.8)	3.2 (0.6)
		10-30	2.1 (0.7)	1.0 (0.1)	3.0 (0.7)	1.9 (0.3)
NH_4^+	μg g^{-1}	0-10	3.1 (0.3)	4.6 (1.1)	9.2 (1.6)	8.9 (1.2)
		10-30	3.0 (0.4)	3.6 (0.7)	4.2 (0.5)	3.8 (0.3)

[a] Refer to footnotes to Table 16.1.

Edwards and Ross-Todd (1983) observed no changes in SOM levels following forest harvesting in Tennessee. Precut SOM values at that site were 2 to 7 times lower than values measured on WS 7. Also, in contrast to WS 7 results, these authors reported increased soil respiration rates (1.5 to 2 X) following cutting which may have precluded SOM increases.

Total Nitrogen

The above discussions of SOM changes following cutting are important in terms of their influence on soil organic N pools. Total N (TKN) was determined as NH_4^+, using the cyanurate–salicylate reaction with autoanalysis following micro-Kjeldahl digestion (Bremner and Mulvaney 1982; Reynolds et al. 1986). Patterns in TKN values paralleled those for SOM (Table 16.2), i.e., statistically higher concentrations in the 0 to 10 cm depth and statistically significant increases following logging, particularly in the upper sampling depths. TKN values peaked shortly after completion of site preparation and have declined slowly since. After 3 years, TKN values were still significantly elevated above precutting measurements.

Much of the postcutting increase in TKN in the upper 10 cm of soil is due to comparable increases in SOM. TKN increases in this upper sampling depth (65%) were slightly less than SOM increases, possibly due to the wide C:N ratios of logging slash left on site. Also, some of this increase must have resulted from microbial immobilization of nitrogen mineralized following cutting. Microbial uptake of N was shown to be an important mechanism retaining N in disturbed forests, particularly in response to large standing crops of C in decaying logging residues (Vitousek and Matson 1984). Increases in TKN values in the lower sampling depth (23%) were slightly greater than SOM increases. These TKN increases at the 10 to 30 cm depth thus resulted partly from the leaching of water-soluble SOM and low-molecular-weight organic N compounds from the upper 10 cm of soil, and also from the immobilization of mineral N percolating downward through the soil profile. For example, NO_3-concentrations in porous cup lysimeter collections were much higher on WS 7 than on WS 2 at both 30 cm (0.50 vs 0.04 mg L^{-1}) and 100 cm (0.25 vs 0.01 mg L^{-1}) depths (Waide et al. 1985).

Mineral Nitrogen

Soil concentrations of NH_4^+ and NO_3^- were determined using the Berthelot and diazotization reactions, respectively, with autoanalysis following extraction of field-moist samples with 2 *M* KCl (Technicon 1971a, 1971b; Keeney and Nelson 1982; Reynolds et al. 1986). Soil NH_4^+ concentrations were highly variable among sampling dates and sites (Table 16.2). In spite of this high variability, statistically significant increases (100%) in NH_4^+ were observed in the 0 to 10 cm depth following cutting. Although NH_4^+ concentrations did not differ between the two sampling depths prior to forest removal, post-harvest concentrations were significantly higher in the upper 10 cm than in the 10 to 30 cm depth. These patterns in NH_4^+ are expected in relation to the large increases in SOM and TKN in the 0 to 10 cm depth and to the higher mineralization rates measured there (see next section). Soil NH_4^+ concentrations in this upper depth peaked midway through the first post-treatment year and then declined slightly. However, concentrations were still significantly elevated after 3 years. Increases in NH_4^+ in the 10 to 30 cm depth were not significant.

Much less variability was observed in soil NO_3^- concentrations (Table 16.2). Differences between the two sampling depths were not statistically significant before or after logging. However, postcutting concentrations were statistically higher at both 0 to 10 cm (25%) and 10 to 30 cm (200%) depths. At both depths, soil NO_3^- concentrations peaked midway through the first post-harvest year and then declined, but were still significantly above precut values after 3 years. Declines in NO_3^- were slightly greater in the lower sampling depth. These patterns are explained by the higher NH_4^+ concentrations and mineralization-nitrification rates in the upper 10 cm of soil (see next section), and by the high mobility of NO_3^- in the moist forest soils on WS 7 following forest removal.

Changes in Soil Nitrogen Transformations

Nitrogen Mineralization

To assess the regulation of observed mineral N dynamics by microbial processes, mineralization and nitrification potentials were measured in the laboratory. Mineralization and nitrification rates were quantified as the changes in total mineral N and NO_3^-, respectively, over a 33-day aerobic incubation at standard temperature (25 °C) and moisture (33% of dry weight) conditions (Keeney 1982; Reynolds et al. 1986). For these two processes only, samples were collected on a monthly basis from the intensive study sites previously described beginning in November 1979. Sampling frequency decreased to a quarterly basis in November 1980; data are summarized here through May 1982. Thus, sampling for these two processes began 2 years after completion of site preparation on WS 7, and continued during the time period when soil organic matter and nitrogen concentrations were declining. Because of the mobility of mineral N, data are summarized here for the O2 litter layer as well as 0 to 10 and 10 to 30 cm soil depths.

For both watersheds, mineralization potentials declined consistently and significantly from the O2 litter layer through the 10 to 30 cm soil depth (Table 16.3). Rates in the O2 layer were slightly higher on WS 2, whereas rates at both soil depths were slightly greater on WS 7. None of these watershed differences were statistically significant, however.

Because of the time lag involved in these data, it is difficult to relate mineralization results to the previous data on mineral N concentrations. Measurements of mineralization potentials made at the same time on WS 48 immediately following whole-tree harvesting provide some basis for interpreting the data from WS 7. On this watershed, mineralization potentials in the O2 litter layer declined significantly (75%) in the first year following harvest, and then increased slightly (30%) over the next 2 years. At the 0 to 10 cm depth, rates remained unchanged in the first post-harvest year and then increased (45%), whereas at the 10 to 30 cm depth rates increased (100%) in the first year after cutting and then remained constant. Because of different post-harvest SOM dynamics in the two watersheds, these trends can be extrapolated to WS 7 only with caution. Also, overall soil mineralization potentials were higher on WS 48, perhaps due to the removal of logging residues. Nonetheless, results from WS 7 appear to be consistent with the temporal trends observed on WS 48.

Table 16.3. Changes in Potential Rates of Nitrogen Mineralization and Nitrification Following Forest Clearcutting at Coweeta[a]

Process	Units	Depth	WS 2	WS 7 Postcut
Potential nitrogen mineralization rate	$\mu g\ g^{-1}\ 33d^{-1}$	O2[b]	415 (53)[c]	359 (32)
		0-10 cm	17.8 (3.2)	21.7 (3.1)
		10-30 cm	7.6 (1.8)	10.1 (1.5)
Potential nitrification rate	$\mu g\ g^{-1}\ 33d^{-1}$	02	5.8 (2.2) (1.4%)[d]	88.4 (18.1) (25%)
		0-10 cm	4.5 (1.7) (25%)	15.4 (3.1) (71%)
		10-30 cm	2.9 (1.2) (38%)	8.2 (1.7) (81%)

[a] Mineralization and nitrification potentials measured from November 1979–May 1982.
[b] Refers to O2 litter layer.
[c] Data displayed as x (SE).
[d] Values represent the percentage of mineralized N which is subsequently nitrified.

Thus, when mineralization potentials are converted to total fluxes (e.g., $g\ m^{-2}\ yr^{-1}$), integrated over the profile, and corrected for actual field temperature and moisture conditions, data in Table 16.3 suggest modest increases in total nitrogen mineralization on WS 7 on the order of 1 to 3 g N $m^{-2}\ yr^{-1}$ in the first 1 to 3 years following forest removal. These increased rates contributed to the increased concentrations of mineral N discussed above, particularly considering overall reductions in soil heterotrophic activity (reduced ATP levels and CO_2 efflux), and reduced net uptake of N into plant biomass (Boring et al., Chapter 12) in the first few years of successional recovery.

Nitrification

Nitrification potentials tended to decline consistently from the O2 litter layer through the 10 to 30 cm soil depth on both watersheds (Table 16.3). Because of high variability, these differences among sampling depths were not statistically significant except for the O2 layer on WS 7. However, nitrification potentials did increase significantly (3 to 15 X) following clearcutting at all sampling depths. Expressed as a percentage of mineralized N, nitrification potentials increased with depth and following logging of WS 7 (Table 16.3). When integrated over the profile and corrected for actual field temperature and moisture conditions, these nitrification potentials suggest increases in nitrogen fluxes on the order of 3 to 5 g N $m^{-2}\ yr^{-1}$. These results are consistent with observed increases in soil NO_3^- concentrations and total NO_3^- export from WS 7 (Chapter 25). Comparable increases in nitrification potentials have been measured on other disturbed watersheds, at Coweeta (Montagnini 1985) and elsewhere (Vitousek et al. 1982).

These nitrification potential assays were also consistent with MPN assays of nitrifying bacteria using the microtiter procedure of Rowe et al. (1976). Numbers of both NH_4^+- and NO_2^--oxidizing bacteria were highly variable and did not differ statistically between the two soil depths (Table 16.4). However, numbers of both groups of nitrifiers increased substantially following clearcutting, although the increases in NO_2^--

Table 16.4. Changes in Numbers of Nitrifying Bacteria in Soils Following Forest Clearcutting at Coweeta[a]

Component	Units	Depth (cm)	WS 2	WS 7 Precut	WS 7 Postcut, Yr 1	WS 7 Postcut, Yrs 1-3
NH_4^+ oxidizing bacteria	Bacteria g^{-1}	0-10	46 (14)	25 (6)	270 (100)	470 (130)
		10-30	65 (33)	18 (4)	170 (50)	320 (110)
NO_2^- oxidizing bacteria	Bacteria g^{-1}	0-10	49 (16)	ND	220 (80)	310 (110)
		10-30	53 (16)	ND	83 (23)	130 (30)

[a] Refer to footnotes to Table 16.1.

oxidizers were not significant at the 10 to 30 cm depth. Numbers of nitrifying bacteria continued to increase into the second year following forest removal. This pattern is consistent with nitrification potential measurements on WS 48 following whole-tree harvesting. The magnitudes of increases in nitrifying bacterial populations are similar to values reported by Likens et al. (1968) following forest clearcutting at Hubbard Brook, and by Todd et al. (1975a) and Montagnini (1985) for other disturbed watersheds at Coweeta.

A third measure of nitrification rates on WS 2 and WS 7 employed the chlorate-inhibition procedure (Belser and Mays 1980) during the time period July 1980 through December 1981. These data also showed increases (50 to 100%) in rates following logging of WS 7 at both soil depths. However, large variances and small sample sizes precluded detection of statistical differences between depths or associated with forest removal.

Denitrification

Denitrification potentials were measured on WS 2 and WS 7 as the rate of N_2O production in acetylene-inhibited soil slurries (Swank and Caskey 1982) during Phase I of denitrification (Smith and Tiedje 1979). This assay measures the maximum activity of denitrifying enzymes present in the soil at the time of sampling. As with several other assays, sampling for this process began 2 years after completion of site preparation, and spanned the period October 1979 through February 1982.

Measured rates were lowest in the upper sampling depth on WS 2, and higher and nearly equal for the other watershed-depth combinations (Table 16.5). Because of the extremely large variability in measured rates, no statistical differences were detected between sampling depths or watersheds (i.e., associated with clearcutting).

In order to place these rates into some perspective, estimates of total denitrification fluxes on the two watersheds were calculated by correcting Phase I rates for field temperatures and NO_3^- concentrations, and then relating corrected rates to the occurrence of discrete precipitation events. Temperature corrections were based on the equation of Rickman et al. (1975), as described by Caskey and Schepers (1985). Correction for measured NO_3^- values assumed Michaelis–Menton kinetics (Bowman and Focht 1974; Caskey and Schepers 1985), with an experimentally determined Michaelis constant of

Table 16.5. Changes in Rates of Denitrification and Nitrogen Fixation in Soils Following Forest Clearcutting at Coweeta[a]

Process	Units	Depth (cm)	WS 2	WS 7 Precut	WS 7 Postcut
Denitrification[b]	nl N_2O g^{-1} hr^{-1}	0-10	10.0 (3.5)	ND	61.0 (27.7)
		10-30	54.1 (34.0)	ND	55.9 (31.7)
Nitrogen fixation[c] (acetylene reduction)	nl C_2H_2 g- d^{-1}	0-10	2.44 (0.42)	12.8 (3.0)	97.3 (73.7)
		10-30	0.92 (0.17)	7.9 (2.1)	30.8 (22.5)

[a] Refer to footnotes to Table 16.1.
[b] Denitrification rates measured from October 1979–February 1982.
[c] Nitrogen fixation rates measured over the same time period as shown in Table 16.1; postcut refers to years 1-3 following treatment, August 1977–October 1980.

10.74 mM. Estimated fluxes were about 5 and 11 kg N ha^{-1} yr^{-1} for WS 2 and WS 7, respectively. These estimates are similar in magnitude to values reported by Robertson and Tiedje (1984) for successional oak-hickory forests in Michigan. Earlier, Swank and Waide (1980) simulated denitrification fluxes for uncut and clearcut hardwood forests at Coweeta as about 11 and 16 kg N ha^{-1} yr^{-1}, respectively. Estimated fluxes cited above are slightly lower than these simulation predictions, but the increase attributable to cutting is comparable.

More recent studies of denitrification on other Coweeta watersheds call into question the magnitude of the above flux estimates. But these studies also confirm the expectation of some increase in denitrification losses following disturbance, largely due to increased NO_3^- transport into the riparian zone of disturbed watersheds. Davidson (1986) conducted intensive field studies of denitrification rates on a control (WS 18) and a disturbed watershed (WS 6), as well as factorial laboratory experiments on major regulatory variables (O_2 tension, NO_3^- concentrations, available C). Results of these studies suggest that soil denitrification fluxes from undisturbed forests are no more than 1 kg N ha^{-1} yr^{-1}, and are perhaps much less. Increased N losses are expected following forest disturbance, but annual flux estimates at a watershed scale are not possible based on available information. Interpretation of these results in regard to clearcutting responses will require synthesis of field measurements of soil moisture, temperature, and NO_3^- concentrations; climatological data on the occurrence of precipitation events; and laboratory studies on controlling variables with process-oriented simulation models of hydrologic and nutrient transport in forest soils.

Nitrogen Fixation

Nitrogen inputs to temperate deciduous forests via biological dinitrogen fixation occur predominantly through the activity of symbiotic associations *(Frankia, Rhizobium)* in the roots of early-successional tree species, free-living bacteria in litter and soil layers, and epiphytic lichens living on the external surfaces of trees and decaying wood (Melillo 1981; Waughman et al. 1981; Boring et al. 1986). Nitrogen fixation potentials have previously been measured on other Coweeta watersheds for all the above components except tree symbioses (Cornaby and Waide 1973; Todd et al. 1975b, 1978). Based on these results, significant nitrogen inputs via epiphytic lichens or associated with

decaying logging residues would not be expected during the initial phase of recovery (e.g., 0 to 5 years) following forest removal. Thus, WS 7 research initially focused on N inputs via tree symbioses and free-living bacteria.

A species which predominates in early successional forests in the Southern Appalachians following major disturbance such as clearcutting is black locust (*Robinia pseudoacacia*), a woody legume nodulated with *Rhizobium* species. The role of *Robinia* in forest succession and the amount of N fixed by this symbiosis have been extensively studied, both on WS 7 and on older clearcuts within the Coweeta Basin (Boring and Swank 1984a, 1984b; Chapter 12). Locust regeneration occurs predominantly via sprouting; early sprout growth is rapid. These sprouts represent potentially significant inputs to forest N cycles. Biomass and nitrogen accretion of locust stands, as well as biomass and C_2H_2-reducing activity of root nodules, have been measured. Total stand N increased 48, 75, and 33 kg N ha^{-1} yr^{-1}, and nodule biomass was 8, 106, and 4 kg ha^{-1}, in 4-, 17-, and 38-year old stands, respectively. Peak rates of N fixation thus appear to occur in early to intermediate stages of forest succession, declining thereafter. In the youngest stand studied (on WS 7), N-fixing activity was estimated as 30 kg N ha^{-1} yr^{-1} based on extensive measurements of nodule biomass and activity of freshly excised nodules. Assuming that N-fixing activity is proportional to the density of *Robinia* stems, a weighted average of 10 kg N ha^{-1} yr^{-1} for all of WS 7 was calculated. Although dense locust stands at Coweeta may experience extensive mortality after 15 to 25 yrs, the nitrogen fixed by this symbiosis could impact forest N dynamics for 50 years or longer.

Nitrogen fixation potentials of free-living bacteria in litter and soil layers of WS 7 were measured in the laboratory (22°C) on field-moist samples with the C_2H_2-reduction assay (Hardy et al. 1973; Todd et al. 1978; Knowles 1982; Reynolds et al. 1986). Rates of free-living N fixation in the soil were highly variable, particularly after forest removal (Table 16.5). Differences among sites varied over 1 to 2 orders of magnitude. Highest rates tended to occur in mesic, fertile sites within the mid-elevation chestnut oak vegetation type. These were also the sites of highest symbiotic activity. When the logarithmic distribution of these data was taken into account, N-fixing potentials were shown to be significantly higher in the 0 to 10 cm soil depth, and on WS 7 prior to logging than on WS 2. Rates also increased substantially (3 to 8x) following clearcutting on WS 7. Highest rates tended to occur into the second postcutting year, declining slightly thereafter.

This extensive data base on free-living N fixation provides the basis for estimating N inputs to the forest ecosystem via this process. To facilitate this goal, recent studies have evaluated the temperature dependence of measured C_2H_2-reduction rates (Reynolds et al. 1986). When these results are combined with field-measured soil temperatures, the following estimates of free-living inputs to soil N pools are obtained: for WS 2, 0.3 kg N ha^{-1} yr^{-1}; WS 7 precut, 1.7 kg N ha^{-1} yr^{-1}; WS 7 postcut (years 1 to 3), 9.7 kg N ha^{-1} yr^{-1}. These values revise downward earlier estimates of potential N fixation inputs to Coweeta forests in relation to actual field conditions. Increases in free-living N inputs following cutting are thus estimated at about 8 kg N ha^{-1} yr^{-1}. The major unknown in these estimates of free-living inputs, as with estimates of symbiotic inputs, involves ^{15}N verification of C_2H_2:N_2 ratios. Nonetheless, although symbiotic N inputs are substantially higher within dense locust stands, free-living N inputs are of comparable magnitude averaged over WS 7. The duration of elevated free-living N-fixing

activity in soils on WS 7 is unknown, but may be on the order of 6 to 12 yrs, the major determinant probably being successional declines in soil C levels.

As the successional recovery of the forest ecosystem on WS 7 proceeds, decaying logging residue may become an important site of N fixation. Because of the large amounts of decaying wood remaining on WS 7 after treatment (ca. 12 kg m^{-2} in the >5 cm diameter fraction), even modest rates of N fixation could result in substantial N inputs to the forest ecosystem. Thus, complete estimates of N inputs will require detailed future research on this component.

Summary and Conclusions

Together with data on N export in drainage waters (Chapter 25) and N cycling through vegetation pools (Chapter 12), results reported here provide an integrated picture of changes in forest N cycling processes on WS 7 following clearcutting. Soil organic matter and nitrogen pools increased (20 to 70%) immediately following forest removal. Proportionately larger increases (20 to 250%) in mineral N pools were also observed. These increases in available mineral N may be attributed to slight increases in soil N mineralization (ca. 25%, or 1 to 3 g N m^{-2} yr^{-1}), substantial increases in nitrification (ca. 200%, or 3 to 5 g N m^{-2} yr^{-1}), and reductions in general soil heterotrophic activity and plant N uptake in the first few years after logging. Increases in both symbiotic (ca. 1 to 3 g N m^{-2} yr^{-1}) and free-living (ca. 1 g m^{-2} yr^{-1}) fixation also added additional N to soil pools.

Only small fractions of these increases in available soil N were exported from WS 7 in drainage waters (ca. 0.1 g N m^{-2} yr^{-1}). Small increases of unknown magnitude in N losses via denitrification also occurred. But, the majority of these increased soil mineral N supplies were retained on site and recycled through rapidly regrowing early successional vegetation pools. Larger fractions of this vegetation uptake of N cycled through labile leaf tissues (rather than being stored in wood) than was the case in control forests (Chapter 12; see also White 1986 for comparable results on disturbed WS 6). Subsequent increases in soil heterotroph activity, associated with the recovery of the forest canopy and the moderation of harsh soil microenvironments, probably provided a secondary sink of N immobilization, stimulated by large C pools in decaying logging residues.

In subsequent papers resulting from this ecosystem experiment, detailed analyses of spatial and temporal variability in soil N pools and transformations, as well as of causal relationships among measured variables and processes, will provide additional insights into the mechanisms responsible for patterns reported here. Moreover, detailed studies on WS 7 will continue to document patterns, rates, and mechanisms of recovery in forest N cycling processes. Nonetheless, several dominant themes emerge from this analysis of early successional changes in forest N cycling processes: substantial acceleration of rates of N turnover in soil pools and of N recycling through labile vegetation components; rapid recovery of vegetation and microbial processes which foster conservation of N supplies on site; and coupled soil processes which make mineral N available for rapid uptake by early successional plant species, thus contributing to the resilience of the forest ecosystem following logging disturbance.