Denitrification in a clearcut Loblolly pine (*Pinus taeda* L.) plantation in the southeastern US*

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Summary We examined denitrification and nitrous oxide (N_2O) production in intact soil cores removed from a clearcut southern pine site subjected to different harvest, site preparation, and herbicide treatments. Rates of N_2O production in structurally intact soil cores incubated with acetylene showed that clearcutting stimulated denitrification but that rates varied by sample date and post-harvest site treatment. The site was harvested in December 1980. In September 1982 denitrification was greater in sheared, piled and disked (SPD) plots than in chopped or reference (uncut) plots; the following May, rates were higher in seven of the eight treatment plots than in the reference plot, and were highest in three of the four herbicide-treated plots. On both sample dates denitrification rates were correlated with nitrification potentials and nitrate pool sizes in the plots, and nitrate added to cores from all treatments significantly stimulated denitrification. Nitrate supply thus appeared to regulate denitrification at this site. Relative to harvest or site preparation losses of nitrogen, denitrification is not a major vector of N loss at this coniferous site; under post-harvest conditions, however, denitrification may be of the same magnitude as leaching losses.

Introduction

Several recent studies and reviews have reported losses of nitrogen associated with harvesting and site preparation in southern pines[17, 18, 22, 24, 27]. All demonstrated that nitrogen losses vary depending upon the intensity of harvest and site preparation; windrowing in particular led to nitrogen losses which were substantially greater than estimated nitrogen inputs over a 25–30 year rotation[8].

These findings raise concerns that long-term productivity of southern pines could be reduced by continued intensive management. Moreover, existing estimates of nitrogen losses are incomplete. Not all include estimates for nitrogen losses in erosion and leaching, and none include estimates for gaseous losses such as denitrification, the biological reduction of soil nitrate to N_2O and N_2. Because nitrate production generally increased in clearcut sites[6,23], the potential for denitrification could be increased as well. While the methodology for direct measurements of denitrification is still developing and thus results must be interpreted cautiously, recent studies in other regions suggest that clearcutting can substantially enhance denitrification[7,12].

We report here estimates for denitrification and nitrous oxide production in a recently cleared loblolly pine (*Pinus taeda* L.) experimental site in the North Carolina Piedmont. Plots subjected to combinations of harvest, site preparation, and herbicide practices were sampled to 1) determine whether forest cutting causes increased denitrification at this southern pine site; 2) determine whether differences in management practices lead to differences in rates of denitrification; and 3) indicate the factors likely regulating rates of denitrification in these soils.

Materials and methods

Study site

One 5 ha block of an experimental installation which included combinations of different harvest, site preparation, and herbicide practices was used for measurements of denitrification. The site was located on Champion International land on the outer Piedmont near Henderson, North Carolina; it was managed by the Site Productivity Study of the Southern Forest Research Center, North Carolina State University.

Soils of the site are clayey, kaolinitic, thermic Typic Hapludults of the Cecil series, a widespread Piedmont soil. Soil characteristics before and after harvesting and site preparation were described by Gent and others[3]; selected soil characteristics are summarized in Table 1. The vegetation of the site was a 22-year old loblolly pine plantation at the time of harvest. It was cut by a commercial logger during November–December 1980, except for a 1 ha forested plot which was retained as a reference stand. Half of the treatment block was harvested using conventional stem-only techniques with a diameter limit of 10 cm, while the other half received a simulated whole-tree harvest that included the removal of all pines and hardwood samplings down to 7 cm diameter together with attached branches and leaves. Half of each harvest treatment was then prepared for planting by drum chopping in June 1981 and attempting a largely unsuccessful burn in November 1981 that covered about 10% of the surface; the other half of each harvest treatment was prepared by shearing and piling the remaining vegetation with a KG blade and double disking the interwindrow area in July 1981. The shear-pile operation removed most of the residual forest floor and 178 T ha^{-1} of mineral soil[11]. One year old loblolly pine seedlings were then hand planted over the entire block in March 1982. Nutrient removals and intrasite displacement during harvest and site preparation on this site are summarized in Tew and others[20].

Following site preparation and planting, eight 27 × 42 m plots were established in the cleared area, two per harvest-site preparation combination. One plot in each pair was then randomly selected for herbicide treatment (Velpar™ [hexazinone] grid balls in April 1982, Round-up™ [glyphosphate] in late September 1982), while the other plot received no further treatment.

Table 1. Selected soil properties (0–15 cm depth) of Henderson treatment plots

Harvest intensity	Site preparation	Herbicide	Forest floor (g/m²)	pH[a]	Bulk density[b] (g/cm³)	Organic matter[c] (%C)	Organic N[d] (%)	C:N
Whole-tree	SPD	− Herbicide	380	6.0	0.93	2.03(0.25)	0.18	11.2
		+ Herbicide	150	5.7	1.14	1.38(0.17)	0.09	15.3
	Chopped	− Herbicide	1290	5.3	1.07	3.54(0.37)	0.12	29.5
		+ Herbicide	1900	5.5	1.14	2.98(0.38)	0.09	33.1
Stem-only	SPD	− Herbicide	175	5.6	1.07	1.96(0.44)	0.14	14.0
		+ Herbicide	220	5.6	1.05	1.55(0.07)	0.10	15.5
	Chopped	− Herbicide	2400	5.0	1.25	2.72(0.53)	0.07	38.9
		+ Herbicide	2010	4.8	1.16	1.91(0.17)	0.07	27.3
Reference (uncut)			2190	na	0.85	2.50(0.30)	na	na

na = not available, SPD = sheared, piled, disked.
a) Fall 1981. b) September 1983. c) September 1982; Walkley-Black method; standard errors are in parentheses (n = 5 cores). d) September 1982.

Denitrification assays

In both September 1982 and May 1983 we collected 20 structurally intact soil cores from the surface 15 cm of each of the eight treatment plots and the control plot. No attempt was made to exclude surface organic material other than stumps and other large woody debris. Cores were collected in 2.2 cm diameter × 20 cm long acrylic tubes with a slide-hammer punch auger, stoppered, and removed to the laboratory for incubation within 8–10 h of sampling.

All cores were subjected to two incubation periods. The first spanned a 24 h period at 20–22°C during which N-gas production was assumed equivalent to *in situ* rates. Rates of denitrification measured in short term laboratory incubations of agricultural soils do not differ much from estimates of field rates based on ^{15}N experiments in the same soils[10], and rates of N_2O production in a random subset of 6 of our cores sampled at 4 h intervals were linear over the 24 h period. The second incubation period was used to examine the effects of various experimental treatments applied to the cores immediately after the first incubation period. We did not check for response linearity over this 44 h (September 1982) or 70 h (May 1983) second period.

Initial core atmosphere samples were collected in evacuated 3 ml rubber stoppered vials (Venoject™, Terumo Scientific, N.J.) after first flushing the cores with 50 ml of air to reduce concentrations of N_2O accumulated during transport. Five milliliters of CaC_2-generated acetylene was then injected into half of the cores from each plot to soil atmosphere concentrations of 15–20% in order to block N_2O reductase and thereby allow estimates of N-gas fluxes from denitrifiers[21]. To estimate N_2O fluxes alone from denitrifiers as well as other potential sources such as nitrifying bacteria[1] and other bacteria and fungi[2], the remaining cores did not receive acetylene.

All cores collected in May were further amended with 4 ml of distilled water to simulate a 1 cm rainfall and thereby further accentuate differences in N_2O production among treatments. After the initial sampling, gas samples were removed after first mixing the atmosphere inside each core by alternately pulling and releasing a *ca.* 300 kPa vacuum with an evacuated syringe.

To evaluate N limitation as a factor regulating denitrification in these sites, all cores were incubated for the period following amendment with either 4 ml of distilled water or 4 ml of 1.5 mM $NaNO_3$. Solutions were injected slowly onto the tops of upright cores.

After incubations were completed, the internal pore + headspace volume of each core was measured with a pressure transducer[9], and percent moisture determined gravimetrically after drying soils at 105°C. N_2O and CO_2 were analyzed by autoinjection gas chromatography[13] in which aliquots (0.4 ml) of stored samples were injected into the sample port of a Varian 3700 gas chromatograph fitted with Porapak-Q columns terminating in ^{63}Ni electron capture detectors.

In addition to denitrification measurements, we analyzed for CO_2 in order to estimate respiration potentials and indirectly evaluate carbon availability. Nitrate pool sizes and nitrification rates in the plots were taken from a companion study[25].

Statistical analysis

One-way analysis of variance was performed on both September 1982 and May 1983 results to delineate the significance of differences among the nine treatments. The capacity of our analytical system limited sampling to only one of the Site Productivity Study's three factorial blocks at the Henderson site, so higher level analysis was not possible and we have assumed that sample variance within the block examined was less than or equal to sample variance in the other blocks. Variance estimates for other nitrogen transformations that have been examined across all blocks[26] supports this assumption. To satisfy homogeneity of variance assumptions all data were log_n transformed before analysis. Treatment means were contrasted for significant differences using least significant difference calculations[16] and estimates of back-transformed means and variance follow Krige[5, 10].

Results

In September 1982 denitrification rates in cores from the sheared, piled, and disked (SPD) plots were 5–8 times greater than rates in cores from the reference stand (84–139 ng N cm^{-2} d^{-1} *vs* 17 ng N cm^{-2} d^{-1};

Table 2. Denitrification and absolute N_2O production during 24 h incubations of soil cores collected from experimental plots in September 1982. Denitrification was estimated by incubating cores in the presence of acetylene (C_2H_2). Values are means ($\pm$ SE) of 10 cores per plot. Asterisks within columns denote significant differences ($p < 0.05$) between a given treatment and the reference plot based on Least Significant Difference measures

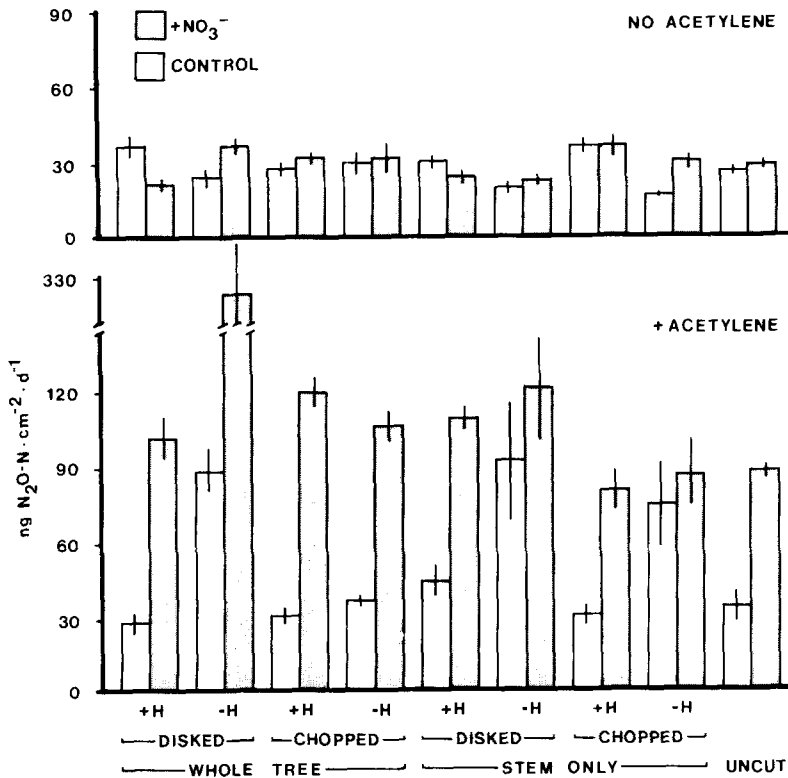| Site treatment			N_2O Production ($ng\,N\,cm^{-2}\,d^{-1}$)	
Harvest intensity	Site preparation	Herbicide	$-C_2H_2$	$+C_2H_2$
Whole-tree	SPD	– Herbicide	17.1(2.5)	83.7(31.4)*
		+ Herbicide	24.1(3.2)	139.0(77.4)*
	Chopped	– Herbicide	39.1(17.5)	17.5(2.2)
		+ Herbicide	11.1(1.9)*	22.1(2.7)
Stem-only	SPD	– Herbicide	33.8(12.0)	120.0(88.7)*
		+ Herbicide	22.0(1.1)	139.0(75.3)*
	Chopped	– Herbicide	23.3(2.3)	18.1(2.6)
		+ Herbicide	16.9(1.6)	19.7(1.6)
Reference (uncut)			20.6(2.2)	17.3(1.6)

SPD = shear, piled, disked

Fig. 1. Denitrification and absolute N_2O production in September 1982 cores in response to added nitrate in 4 ml of water (*right bar* of each pair) or to added water alone (*left bar*). *Vertical lines* bisecting the bars represent standard errors (n = 5 cores per plot). H = Herbicide.

Table 3. Nitrate pool sizes and nitrification potentials (nitrate produced in 30 d buried bag incubations) in treatment plots in September 1982 and May 1983 (Vitousek and Matson 1985). Values are means ($\pm$ SE) of 3 transects per treatment plot

Site treatment			September 1982		May 1983	
Harvest intensity	Site preparation	Herbicide	NO_3^- pool (μg N/g soil)	NO_3^- production (μgN $\cdot$ g^{-1} $\cdot$ 30d^{-1})	NO_3^- pool (μg N/g soil)	NO_3^- production (μgN $\cdot$ g^{-1} $\cdot$ 30d^{-1})
Whole-tree	SPD	− Herbicide	1.0(0.01)	3.4(1.0)	0.3(0.2)	11.7(2.6)
		+ Herbicide	9.6(1.9)	5.3(0.4)	1.6(1.0)	15.1(2.1)
	Chopped	− Herbicide	0.1(0.1)	0(0.1)	0(0)	3.4(0.4)
		+ Herbicide	0(0)	0(0)	0.6(0.1)	11.0(2.7)
Stem-only	SPD	− Herbicide	0.9(0.4)	2.5(0.9)	0.4(0.01)	10.5(2.1)
		+ Herbicide	14.9(2.4)	6.5(1.7)	2.3(0.8)	16.9(6.9)
	Chopped	− Herbicide	0(0)	0(0)	0(0)	4.3(0.7)
		+ Herbicide	3.4(1.7)	0.4(1.3)	1.7(0.7)	11.6(0.8)
Reference (uncut)			0(0)	0(0)	0(0)	0(0)

SPD = sheared, piled, and disked.

Table 2). No other differences among treatments appeared significant; the plots that were chopped rather than sheared, piled and disked denitrified at rates no different from rates in the reference pot. N_2O production in cores without acetylene did not differ much among the nine treatments and no treatment resulted in greater N_2O production than occurred in the reference plot.

Nitrate added to September 1982 cores stimulated denitrification in cores from all site treatments including the reference plot (Fig. 1), but caused little increase in N_2O from cores not treated with acetylene. Also, increased denitrification in SPD plots was positively correlated with enhanced rates of nitrate production ($r = 0.94, p < 0.001, n = 9$) and initial (pre-incubation) nitrate pool sizes ($r = 0.74, p < 0.05, n = 9$) in these plots (Table 3).

In the May 1983 sampling, denitrification rates appeared higher in all but one treatment plot than in the reference plot (Table 4), but were significantly higher only in three of the herbicide-treated plots at this time (Table 3). Added nitrate significantly stimulated both dentrification and absolute N_2O production in cores from all sites (Table 5).

Respiration in soil cores from the uncut reference plot appeared to be greater than twice the rates that we found in six of the eight treatment plots (Table 4) though significantly so in only two cases. Rates were close to those in the reference plot in the two plot that had been chopped and spared the herbicide treatment.

Table 4. Denitrification, absolute N_2O production, and respiration in soil cores collected in May 1983. Cores were pretreated with 1 cm of distilled water to accentuate differences among treatments. See Table 2 legend for further explanation

Site treatment			N_2O ($ng N cm^{-2} d^{-1}$)		CO_2 ($\mu g CO_2 cm^{-2} d^{-1}$)
Harvest intensity	Site preparation	Herbicide	$-C_2H_2$	$+C_2H_2$	$-C_2H_2$
Whole-tree	SPD	− Herbicide	26.9(8.4)	79.3(28.3)	136.0(41.0)*
		+ Herbicide	401.0(247.0)	118.0(63.0)*	199.0(48.0)
	Chopped	− Herbicide	132.0(119.0)	30.6(13.3)	321.0(104.0)
		+ Herbicide	984.0(531.0)*	279.0(165.0)*	187.0(52.0)
Stem-only	SPD	− Herbicide	5.3(4.9)	95.0(37.7)	86.0(30.0)*
		+ Herbicide	10.2(5.4)	41.9(25.9)	201.0(69.0)
	Chopped	− Herbicide	0(0)	5.7(3.7)	305.0(51.0)
		+ Herbicide	169.0(84.0)	415.0(131.0)*	203.0(76.0)
Reference (uncut)			6.0(3.9)	12.3(6.3)	392.0(44.0)

SPD = sheared, piled and disked.

Table 5. Response of cores tabulated in Table 4 to added NO_3^-. Values are means ($\pm$ SE) across all site treatments (n = 36 [distilled water control] or 27 [N treatment]). Asterisks denote significant NO_3^- effects within columns

Amendment	N_2O $(ng\,N\,cm^{-2}\,d^{-1})$		CO_2 $(\mu g\,CO_2\,cm^{-2}\,d^{-1})$	
	$-C_2H_2$	$+C_2H_2$	$-C_2H_2$	$+C_2H_2$
Control	457(235)	439(183)	329(51)	195(32)
$+NO_3^-$	1135(295)*	2912(810)*	194(30)	186(39)

Discussion

Clearcutting stimulated denitrification in this southern pine site, although the magnitude of this repsonse varied both by post-harvest site treatment and time of sampling. In September 1982, for example, denitrification was nearly six times higher in plots that had been sheared, piled and disked (SPD) following forest cutting than in either chopped plots or the uncut control. During the following spring, denitrification in all treatment plots but one was higher than in the reference, and rates were highest in three out of four herbicide treated plots.

We attribute higher denitrification rates to elevated levels of nitrate availability in those plots where denitrification was high. On both sample dates added nitrate substantially enhanced denitrification in cores from all treatment plots and the uncut reference plot. Additionally, both nitrate pool sizes and field nitrification potentials were higher in disked than in non-disked plots in September 1982, and in May 1983 they were generally higher in herbicide-treated plots than in plots that had received no herbicide (Table 3).

Higher nitrate availability in the disked plots in September 1982 was likely due to a greater potential for mineralization and to a lowered capacity for immobilization in these plots[26]. Soil mixing can stimulate both nitrification and labile organic matter oxidation in forest soils[14, 19], and removal of most woody debris from the SPD plots before disking removed substrates which could immobilize N. Both soil C:N ratios and soil organic C pools tended to be lower in the SPD plots than in the chopped plots (Table 1), and ^{15}N experiments[26] showed a lower capacity for immobilization in the SPD plots. In the chopped plots forest floor material was a major sink for mineral ^{15}N, but shear-pile operation had eliminated this pool from the SPD plots. In the May 1983 sampling, enhanced nitrate availability in the herbicide-treated plots was probably related to reduced plant uptake of ammonium and nitrate associated with a lowered plant biomass in these plots.

N_2O produced in the presence of C_2H_2 is the sum of $N_2O + N_2$ produced by denitrifiers. In the absence of acetylene, however, N_2O may be from denitrifiers that are not reducing N_2O to N_2, or from nitrifiers,

fungi, or other processes known to produce N_2O under laboratory conditions. Under our experimental conditions it is not possible to separate denitrification from other sources of N_2O, but two lines of evidence suggest that nondenitrifier sources may be important in these sites. First, N_2O production in individual cores without added acetylene approached and sometimes exceeded rates of denitrification $(N_2O + N_2)$ in cores from the same sites. Only if denitrifiers were producing no N_2 could all of the N_2O produced in the absence of acetylene be from denitrifiers. Second, nitrate might be expected to stimulate denitrifiers in soil but have less or no effect on N_2O produced by sources such as nitrifiers or fungi. In September 1982 added nitrate had little effect on N_2O produced in the absence of acetylene, but substantially enhanced denitrification (Fig. 1); in May 1983 added nitrate stimulated N_2O production in the absence of acetylene, but the increase was disproportionately small relative to the denitrification response. Taken together, these results suggest a source of N_2O such as nitrification than can be inhibited by an acetylene-rich atmosphere and that is little-affected by added nitrate.

Extrapolating our denitrification results of *in situ* rates of N_2 and N_2O losses from these sites is difficult because of assumptions associated with sample times and incubation conditions. Nevertheless, results from the 24 h incubations suggest that denitrification may account for as much as $0.5–1.0\,kg\,N\,ha^{-1}\,month^{-1}$ lost from those plots where measured denitrification was high (*ca.* $150\,ng\,N\,cm^{-2}\,d^{-1}$ in 24 h incubations without added H_2O), and *ca.* $0.06–0.12\,kg\,N\,ha^{-1}\,month^{-1}$ from plots where denitrification appeared low. Precipitation events may boost these estimates somewhat[12] by reducing porespace oxygen and redistributing soluble organic carbon[15], so long as nitrate is neither quickly depleted in nor leached from the sites of active denitrification.

If denitrification is active to an equivalent degree over six months of the year, then annual losses from similar loblolly pine sites might be approximately $3–6\,kg\,N\,ha^{-1}\,yr^{-1}$ where stimulated by disturbance, and $0.4–0.7\,kg\,N\,ha^{-1}\,yr^{-1}$ under undisturbed conditions. These rates are low relative to precipitation inputs $(6–10\,kg\,N\,ha^{-1}\,yr^{-1})$ and to harvest and site preparation losses $(200–600\,kg\,N\,ha^{-1}\,rotation^{-1}$ in our site[20]), but nevertheless may be significant relative to leaching losses in clearcut or intact conifer sites[23,27]. Gosz[4] suggested that aggrading coniferous systems lose $0.5–1.5\,kg\,N\,ha^{-1}\,yr^{-1}$ by leaching; leaching losses in the harvested site we studied could have ranged from $2–20\,kg\,N\,ha\,yr^{-1}$ depending on treatment[26].

Low rates of denitrification may be typical for many coniferous forests: Robertson and Tiedje[12] found very little denitrification in three northern Michigan pine stands at different successional stages, and

Strauss and Firestone (personal communication) documented exceptionally low rates in both an intact mixed conifer forest and an adjacent clearcut in northern California. In both of these studies the authors attributed low rates of denitrification to low *in situ* nitrate availability during times when conditions were otherwise favorable for denitrifiers.

That denitrification was stimulated by forest cutting in some of our site treatments and that rates were relatively high in two recent hardwood clearcuts for which data are availble[7,12] suggest that denitrification may be a substantial post-harvest N-flux in some sites. Melillo and others[7] found high denitrification rates (*ca.* $2\,kg\,N\,ha^{-1}\,month^{-1}$ for a June sample date) in aerobically-incubated but mixed soils from a 2 yr old northern hardwood clearcut. Robertson and Tiedje[12] reported denitrification rates in aerobic intact cores from a clearcut mid-Michigan hardwood site that extrapolate to ca. $3\,kg\,N\,ha^{-1}\,month^{-1}$ during mid summer. These rates are still relatively low compared to harvest losses, but they exceed nitrogen losses by leaching in most clearcut sites[23].

References

1   Blacker A M, Bremner J M and Schmidt E L 1980 Production of nitrous oxide by ammonia-oxidizing chemautotrophic microorganisms in soil. Appl. Environ. Microbiol. 40, 1060–1066.
2   Bleakley B H and Tiedje J M 1982 Nitrous oxide production by organisms other than nitrifiers or denitrifiers. Appl. Environ. Microbiol. 44, 1342–1348.
3   Gent J A, Ballard R, Hassan A E and Cassel D K 1984 Impact of harvesting and site preparation on physical properties in a Piedmont soil. Soil Sci. Soc. Am. J. 48, 173–177.
4   Gosz J R 1981 Nitrogen cycling in coniferous ecosystems. *In* Terrestrial Nitrogen Cycles. Eds. F E Clark and T Rosswall. 33, 405–426. Ecol. Bull. (Stockholm).
5   Krige D G 1981 Lognormal-de Wijsian geostatistics. South African Institute of Mining and Metallurgy Monograph Series, Geostatistics 1, 1–51.
6   Matson P A and Vitousek P M 1981 Nitrogen mineralization and nitrification potentials following clearcutting in the Hoosier National Forest, Indiana. Forest Sci. 27, 781–791.
7   Melillo J M, Aber J D, Steudler P A and Schimel J P 1983 Denitrification potentials in a successional sequence of northern hardwood forest stands. *In* Environmental Biogeochemistry. Ed. R Hallberg. Ecol. Bull. (Stockholm). 35, 217–228.
8   Morris L A, Pritchett W L and Swindel B F 1983 Displacement of nutrients into windrows during site preparation of a flatwood forest. Soil Sci. Soc. Am. J. 47, 591–594.
9   Parkin T B, Kaspar H F, Sexstone A J and Tiedje J M 1984 A gas-flow soil core method to measure field denitrification rates. Soil Biol. Biochem. 16, 323–330.
10   Parkin T B, Sexstone A J and Tiedje J M 1985 Comparison of field denitrification rates determined by acetylene-based soil core and 15-N methods. Soil Sci. Soc. Am. J. 49, 94–98.
11   Pye J M and Vitousek P M 1985 Soil and nutrient removals by erosion and windrowing at a Southeastern U.S. Piedmont site. Forest Ecol. and Mgmt. (*In press*).
12   Robertson G P and Tiedje J M 1984 Denitrification and nitrous oxide production in successional and old growth Michigan forests. Soil Sci. Soc. Am. J. 48, 383–389.

13 Robertson G P and Tiedje J M 1985 An automated technique for sampling the headspace of stoppered gas collection vials. Plant and Soil 83, 453–457.

14 Rommell L G 1935 Ecological problems of the humus layer in the forest. Cornell Univ. Agric. Exp. Sta. Memo No. 170, 28 pp.

15 Sexstone A J, Parkin T B and Tiedje J M 1985 Temporal response of soil denitrification rates to rainfall and irrigation. Soil Sci. Soc. Am. J. 49, 99–103.

16 Snedecor G W and Cochran W G 1967 Statistical Methods, 6th ed. Iowa State Univ. Press, Ames, Iowa.

17 Swindel B F, Marion W R, Harris L D, Morris L A, Pritchett W L, Conde L F, Riekerk H and Sullivan E T 1983 Multi-resource effects of harvest, site preparation, and planting in pine flatwoods. Southern J. Appl. Forestry 7, 6–15.

18 Switzer G L, Moehring D M and Terry T A 1978 Clearcutting vs. alternative timber harvesting-stand regeneration systems: Effects on soils and environments of the South. *In* Forest Soils and Land Use. Ed. C T Youngberg. pp 477–515. Colo. State Univ. Press, Ft. Collins.

19 Tamm C O and Pettersson A 1969 Studies on nitrogen mobilisation in forest soils. Studia for. suec. 75, 3–39.

20 Tew T, Morris L, Allen L and Wells C G 1984 Estimates of nutrient removal and displacement resulting from harvest and site preparation in a *Pinus taeda* plantation in the Piedmont of North Carolina. Site Productivity Study Report #2. North Carolina State University — Southern Forest Research Center. Raleigh, NC.

21 Tiedje J M 1981 Denitrification. *In* Methods of Soil Analysis. Part 2 — Chemical and Microbiological properties, 2nd edition. Eds. A L Page, R H Miller and D R Keeney. pp 1011–1026. American Society of Agronomy, Madison, Wisconsin.

22 Van Hook R I, Johnson D W, West D C and Mann I K 1982 Environmental effects of harvesting forests for energy. Forest Ecol. and Mgmt. 4, 79–94.

23 Vitousek P M and Melillo J M 1979 Nitrate losses from disturbed forests: patterns and mechanisms. Forest Sci. 25, 605–619.

24 Vitousek P M, Allen H L and Matson P A 1983 Impacts of management practices on soil nitrogen status. *In* Maintaining Forest Site Productivity, Proc. Soc. Am. For. Appalachian Chapter, Myrtle Beach, S.C., 25–29.

25 Vitousek P M and Matson P A 1984 Mechanisms of nitrogen retention in forest ecosystems: a field experiment. Science 225, 51–52.

26 Vitousek P M and Matson P A 1985 Disturbance, nitrogen availability, and nitrogen losses: an experimental study in an intensively managed loblolly pine plantation. Ecology 66, 1360–1376.

27 Wells C G and Morris L 1983 Maintenance and improvement of soil productivity. *In* Symposium on the Loblolly Pine Ecosystem, Raleigh, N.C., pp 306–318.