Biogeochemistry 2: 197–210 (1986)

Nitrification potentials in early successional black locust and in mixed hardwood forest stands in the southern Appalachians, USA

FLORENCIA MONTAGNINI,[1] BRUCE HAINES,[1] LINDSAY BORING[2] and
WAYNE SWANK[3]

[1] Department of Botany and Institute of Ecology, University of Georgia, Athens,
GA 30602, USA
[2] School of Forest Resources, University of Georgia, Athens, GA 30602, USA
[3] US Forest Service, Coweeta Hydrologic Laboratory, Southeastern Forest Experiment
Station, Otto, NC 28763, USA

Key words: nitrification, nitrate leaching, successional, N fixation, *Robinia pseudo-acacia*

Abstract. Soil nitrogen mineralisation and nitrification potentials, and soil solution chemistry were measured in black locust (*Robinia pseudo-acacia* L.), in pine-mixed hardwood stands on an early successional watershed (WS6), and in an older growth oak-hickory forest located on an adjacent, mixed hardwood watershed (WS14) at Coweeta Hydrologic laboratory, in the southern Appalachian mountains, U.S.A. Nitrification potentials were higher in black locust and pine-mixed hardwood early successional stands than in the oak-hickory forest of the older growth watershed. Ammonification rates were the main factor controlling nitrification in the early successional stands. There was no evidence of inhibition of nitrification in soils from the older growth oak-hickory forest site.

Within the early successional watershed, black locust sites had net mineralisation and nitrification rates at least twice as high as those in the pine mixed-hardwood stands. Concentrations of exchangeable nitrate in the soil of black locust stands were higher than in pine-mixed hardwoods at 0–15 cm in March and they were also higher at 0–15, 16–30 and 31–45 cm depth in the black locust dominated sites in July. Soil solution nitrate concentrations were higher under black locust than under pine-mixed hardwoods. Areas dominated by the nitrogen fixing black locust had greater nitrogen mineralisation and nitrification rates, resulting in higher potential for leaching losses of nitrate from the soil column in the early successional watershed.

Introduction

Nitrification, the oxidation of ammonium to nitrate, often increases following disturbance in terrestrial ecosystems (Vitousek and Melillo 1979). Thus, increased nitrate loss via stream water is an indicator of certain types of ecosystem stress. Increased stream export of nitrate during periods of intense defoliation in two mixed hardwood watersheds (WS27 and WS36) in the Coweeta Basin (Swank et al. 1981) suggested accelerated rates of nutrient turnover in litter and soil horizons in the defoliated forests. During the mid-1970s, the mean annual nitrate concentration in the stream water draining watershed 6 (WS 6), an early successional ecosystem dominated by the nitrogen fixing black locust (*Robinia pseudo-acacia* L.), was at least three times higher than concentrations in streams draining other disturbed forested ecosystems at the Coweeta Hydrologic Laboratory, North Carolina, in the southern Appalachians, U.S.A. (Swank and Douglass 1977). Nitrate concentrations in the stream draining watershed 6 showed an abrupt increase in 1979 concurrent with infestations of the stem boring beetle (*Megacyllene robiniae* Forster) and defoliating beetles (Chrysomelideae) in the *R. pseudoacacia* stands (Swank personal data).

In an attempt to explain how insect-induced stress led to increased nitrate loss from the early successional WS6, we studied processes involved in this ecosystem-level response. In this paper we report on controls of nitrification in the ecosystem dominated by black locust. The objective was to assess the relationship between black locust, nitrification potentials and nitrate concentrations in the soil and soil solution in this early successional watershed. The following hypotheses were tested: 1) nitrification potentials are controlled by ammonification rates in the early successional watershed, 2) black locust dominated areas have high rates of net nitrogen mineralisation and nitrification, 3) nitrate concentrations in the soil and soil solution are greater in black locust than in pine-mixed hardwood stands of the early successional watershed, and 4) nitrification potential rates are lower in an oak-hickory forest stand located on an adjacent watershed exhibiting lower stream nitrate concentrations than in either black locust or pine-mixed hardwood stands of the early successional watershed.

The oak-hickory forest was chosen for comparison, because it was expected to have low levels of nitrifying activity, and therefore, by contrast, could aid in understanding factors regulating nitrification rates and nitrate concentrations in the early successional forested ecosystem.

Study site

The early successional watershed (WS6) dominated by black locust and the older growth, mixed hardwood watershed (WS14) are part of the 2185 ha Coweeta Hydrologic Laboratory in western North Carolina (35 °N lat, 83 °W long). The basin is located in the Blue Ridge Province of the Southern Appalachian Mountains. The mean annual temperature is 13 °C, the mean annual precipitation is 181 cm, and the mean elevation is 1000 m (Swank and Douglas 1977).

Watershed 6 is an 8.86 ha, north-facing catchment that was clearcut, logged, converted to fescue grass, limed and fertilised in 1958. Two more fertiliser and lime applications were made in 1960 and 1965 (Johnson and Swank 1973). Starting in May 1966 and for two years thereafter, the grass cover was killed by herbicide application (Douglass et al. 1969) and the watershed was left for natural revegetation. In 1969 the watershed was dominated by a dense cover of a variety of herbaceous species; in 1970, woody shrubs became established; and in 1980 the watershed was dominated by black locust, blackberries (*Rubus spp.*), and numerous vines (*Vitis spp.*, *Clematis spp.*, and *Smilax spp.*). Presently, dense black locust stands occupy 44% of the watershed on the northwest-facing area and 29% of the watershed on the northeast aspect. A remaining 12 and 15% are occupied by northwest-facing pine-mixed hardwood and northeast-facing mesic mixed hardwood stands, respectively, which have low densities of black locust. In 1982, 21% of the black locust trees were standing dead, and 18% had greater than 50% crown dieback, primarily resulting from damage by the locust stem borer (*Megacyllene robiniae* Forster).

The dominant soil series at low elevations and in coves is the Brevard-Saunookee, a member of the fine-loamy, mixed mesic family of Humic Hapludults (Swank personal data). On the slopes and ridges soils belong to the Evard-Cowee series, a member of the loamy, mixed, mesic, shallow family of Typic Hapludults. Textural analysis showed similar sandy loam A_1 horizons on both northeast and northwest facing sites at four elevations from stream banks to ridges. The depth of surface horizons increased from the ridges to the stream.

The mixed hardwood watershed 14 is a 61.1 ha catchment supporting an uneven-aged forest dominated by *Quercus spp.* and *Carya spp.* The most important understory species are mountain laurel (*Kalmia latifolia* L.) and rose-bay rhododendron (*Rhododendron maximum* L.)(Day and Monk 1974). American chestnut (*Castanea dentata* (Marsh.) Borkh.) was originally a major constituent of the forest but was reduced to a minor component by the chestnut blight in the middle 1930's (Johnson and Swank 1973). Logging in the area ceased in 1923 and the forest has had no human disturbance at least since 1924 (Swank and Douglass 1977). The same soil series as those on the early successional watershed are dominant: Evard-Cowee stony loams on the slopes and Brevard-Saunookee stony loams on the lower elevations (Swank personal data).

Methods

In order to assess the impact of black locust on nitrification, WS6 was categorised by vegetation and aspect for soil sampling. Colour infrared imagery and quadrat analysis were used to locate three stands: a northeast and a northwest aspect stand dominated by black locust, and a northwest aspect pine-mixed hardwood stand. Three parallel transects, each from low to high elevation on the slopes were established in each stand so as to divide it into three sections of approximately equal size. The distance between transects ranged from 15 to 20 meters being closer together at the bottoms and farther apart at the tops of the slopes. Three 5 m x 5 m plots were located along each transect, at three elevations from stream banks to ridge tops on the slopes. Thus, there were a total of nine plots per stand, with three plots per elevation. Nine plots were also located in an oak-hickory forest stand located on the adjacent watershed (WS14) at comparable physiographic locations. Sampling was performed in March and July 1982.

Soils were sampled at 0–15, 16–30 and 31–45 cm depths using of a 2.5 cm diameter soil corer. Five cores were combined for a plot sample and were refrigerated at 4 °C for 24 to 72 hours until the time of analysis. Field moist soils were passed through a 4-mm sieve. Four-gram subsamples were extracted with 20 mls of 2 N KCl and shaken mechanically for one hour. NO_3-N and NH_4-N were measured on the filtrates with a Technicon Auto-Analyzer (Technicon 1970). Other subsamples were oven dried at 70 °C for gravimetric determination of moisture content.

Soil solution was sampled at 30 and 60 cm depth with porous cup lysimeters (Hansen and Harris 1975). Solution samples were collected biweekly and analysed for NO_3-N and NH_4-N with a Technicon Auto-Analyzer (Technicon 1970).

Nitrogen mineralisation and nitrification potentials were measured by thirty-day aerobic incubations in the laboratory (Keeney 1982). Temperature and moisture conditions were kept uniform through the incubation period; thus, differences in ammonium and nitrate production between samples were due to activity of bacteria and quality and amount of substrate initially present in the soil. From each of the nine composite soil samples collected from each stand, field moist soil sub-samples of 0–15 and 16–30 cm depth were incubated at 22 °C in an environmental chamber for one month. At the end of the incubation period the samples were extracted and analysed for NH_4-N and NO_3-N. Final minus initial nitrate concentrations provided a measure of net nitrate production over the incubation period. Final minus initial concentrations of total mineral N (nitrate + ammonium) gave an estimate of laboratory net N mineralisation rates. There were no differences in moisture content of the soils between stands, therefore no adjustment for uniform water content was needed for the incubations.

To test for the presence of substances inhibitory to nitrification in the soils of the older growth mixed hardwood forest, incubations were run on mixtures of soil from black locust and oak-hickory stands. Three grams of field moist soil collected from each of the nine plots in the older growth mixed hardwood forest stand were mixed with three grams of soil collected from nine plots under black locust. Nine 6 gram incubations of oak-hickory and black locust soil were also run for comparison. All samples were incubated for two weeks and were processed as described above. Soils for this experiment were collected in May 1983.

For determination of general soil characteristics, air dried subsamples were processed for total Kjeldahl nitrogen (TKN) by acid digestion on a heater block, and by colorimetric determination of NH_4-N (Technicon 1977). Percent organic carbon was measured by the Walkley-Black wet oxidation technique (Allison 1975). Double acid extraction (0.025 N H_2SO_4 and 0.05 N HCl) was performed on the soils (Nelson et al. 1953), and extracts were analysed for cations and P with a Jarrell-Ash plasma emission spectrograph (Jones 1977). Exchangeable hydrogen was determined following the procedure of Adams and Evans (1962), in which soil pH is measured in a buffered solution of p-nitrophenol, borate, potassium chloride and potassium hydroxide. Cation exchange capacity was calculated as the sum of Na, Ca, Mg, K and exchangeable H^+ concentrations in milli-equivalents per 100 grams of soil. The pH was measured on air dry samples using a 1:1 (weight to weight) soil:deionised water mixture and a glass electrode. Statistical analysis was performed using SAS (Helwig and Council 1979). Analysis of variance was performed with the use of the GLM procedure of SAS.

Results

Nitrate concentrations and nitrification potentials were slightly higher in all the lower elevation plots than in the remaining plots in the early successional WS6, but differences between elevations as determined by analysis of variance ($P < 0.05$), were not statistically significant. Therefore results were averaged over the three elevations, making a total of nine plots for each stand. Also, there were no differences in results from the black locust plots located on different slope aspects; therefore data were averaged together making a total of eighteen plots for black locust. In the oak-hickory forest stand, results were also averaged over the three elevations.

Soil and soil solution nitrate and ammonium concentrations

Nitrate concentrations in soils from the black locust sites at the three depths were significantly higher than under pine-mixed hardwoods in July (Table 1). In March, a time of lower temperatures and less biological activity, concentrations were significantly higher only at 0–15 cm. These results identify black locust stands as sites with highest nitrate concentrations throughout the soil profile and indicate that these sites are the primary areas of WS6 where nitrate leaching losses may take place.

Soil nitrate concentrations in the oak-hickory forest stand in WS14 were several times lower than in either pine-mixed hardwoods or black locust stands (Table 1).

Soil ammonium concentrations were lower in the oak-hickory forest than in either pine-mixed hardwoods or black locust stands. There were no significant differences in soil ammonium concentrations between black locust and pine-mixed hardwoods at any depth, for either March or July (Table 1).

Soil solution NO_3-N concentrations were higher in both black locust and pine-mixed hardwoods than in the older oak-hickory stand (Table 2). At both 30 and 60 cm depth, soil solution nitrate concentrations were higher in black locust than in pine-mixed hardwood stands of the successional watershed. Soil solution NH_4-N concentrations were undetectable in the three stands (Table 2).

Table 1. Soil NO_3-N and NH_4-N concentrations, laboratory-determined set N mineralisation and nitrification rates for black locust ($n = 18$) pine-mixed hardwood ($n = 9$) and oak-hickory forest stands ($n = 9$)(means and standard errors). Common superscript letters in a line for a given date indicate no significant differences between sites ($P < 0.05$) as determined by analysis of variance and Duncan's Multiple Range Test

	Black locust		Pine-mixed hardwoods		Oak hickory	
	March	July	March	July	March	July
NO_3-N (mg/kg)						
0–15 cm	4.45 (0.26)^{a}	3.25 (0.42)^{a}	1.98 (0.62)^{b}	0.50 (0.22)^{b}	0.26 (0.02)^{c}	0.02 (0.02)^{b}
16–30 cm	1.56 (0.15)^{a}	0.86 (0.16)^{a}	1.02 (0.36)^{a}	0.02 (0.02)^{b}	0.38 (0.04)^{b}	0.0 (0.0)^{b}
31–45 cm)	1.40 (0.11)^{a}	0.50 (0.08)^{a}	0.97 (0.23)^{a}	0.11 (0.03)^{b}	0.34 (0.04)^{b}	0.14 (0.04)^{b}
NH_4-N (mg/kg)						
0–15 cm	3.92 (0.46)^{a}	2.62 (0.20)^{a}	4.26 (0.56)^{a}	3.16 (0.82)^{a}	1.34 (0.19)^{c}	0.25 (0.08)^{c}
16–30 cm	3.31 (.0.20)^{a}	2.18 (0.15)^{a}	3.46 (0.40)^{a}	2.36 (0.38)^{a}	2.16 (0.16)^{c}	0.95 (0.32)^{c}
31–45 cm	2.78 (0.31)^{a}	2.03 (0.17)^{a}	2.90 (0.42)^{a}	1.61 (0.29)^{a}	2.30 (0.14)^{c}	0.93 (0.02)^{c}
Net N mineralisation rate (mg kg^{-1} 30 $days^{-1}$)						
0–15 cm	34.94 (4.29)^{a}	30.94 (1.37)^{a}	12.02 (3.53)^{b}	12.00 (3.32)^{b}	4.41 (1.36)^{c}	2.14 (0.45)^{c}
16–30 cm	12.21 (2.90)^{a}	7.39 (0.73)^{a}	3.58 (1.56)^{b}	3.44 (1.07)^{b}	2.87 (0.63)^{b}	0.27 (0.28)^{c}
Net nitrification rate (mg kg^{-1} 30 $days^{-1}$)						
0–15 cm	34.53 (4.34)^{a}	34.26 (1.36)^{a}	9.45 (3.59)^{b}	15.74 (4.11)^{b}	0.32 (0.06)^{c}	0.79 (0.47)^{c}
16–30 cm	12.02 (2.81)^{a}	10.24 (0.90)^{a}	2.89 (1.14)^{b}	4.58 (1.25)^{b}	0.11 (0.05)^{c}	0.29 (0.12)^{c}

Table 2. Soil solution NO_3-N concentrations (mg/l) at 30 and 60 cm depth (means and standard errors) in black locust, pine-mixed hardwoods and oak-hickory forest stands. Results averaged through six collections from October 1983 to January 1984. There were nine collectors at each depth in black locust and pine-mixed hardwood stands, and three collectors at 30 cm depth in the oak-hickory forest stand

Depth (cm)	Black locust	Pine-mixed hardwoods	Oak-hickory forest
30	3.23 (0.34)	0.07 (0.02)	0.02 (0.01)
60	5.35 (0.57)	0.11 (0.076)	–

Nitrogen mineralisation and nitrification rates

Net N mineralisation rates were more than twice as high under black locust than under pine-mixed hardwoods in both March and July (Table 1). This fact points to black locust stands as sites of rapid N turnover.

Nitrification potential rates at 0–15 cm depth under black locust were at least twice as high as those under pine-mixed hardwoods in both March and July. Most of the nitrifier activity in both stands was in the top 15 cm of the soil, the rates being about three times higher in the 0 to 15 cm layer than in the 16 to 30 cm soil layer. Net nitrification potential rates were only slightly higher during the summer.

In both pine-mixed hardwood and black locust stands of the early successional watershed, net N mineralisation rates were close to nitrification rates. Nitrification rates were less than mineralisation rates only in March in pine-mixed hardwoods. As most of the ammonium was consumed during the incubation time, the availability of ammonium appears to be the main factor controlling nitrification in both pine-mixed hardwood and black locust stands.

In the older growth oak-hickory forest, net nitrification rates were only 7% and 37% of net N mineralisation rates in March and July, respectively (Table 1). Apparently, low nitrification rates were not a result of the presence of inhibitory substances: results from the black locust/oak-hickory soil mixture incubations showed no evidence of an inhibitory effect from the oak-hickory forest soils. Nitrification rates in black locust averaged 19.98 ± 2.53 mg NO_3-N kg^{-1} 14 $days^{-1}$ ($\bar{x} \pm$ S.E.), in the older growth forest it was undetectable, and in a mixture of the two soils it averaged an intermediate value of 7.80 ± 1.21. If no inhibition occurred, the expected nitrification rate for the mixture would have been half the value of the black locust soils, i.e. 9.9. The nitrification rate of the mixture was only slightly lower than expected.

General soil characteristics

Within the early successional watershed, no significant differences were found in soil total N, organic C or C:N ratios between black locust and pine-mixed hardwood stands (Table 3). Total N concentrations were higher in the oak-hickory forest stand than in black locust or pine-mixed hardwood stands in March (Table 3).

Table 3. Soil chemical characteristics for black locust ($n = 18$) pine-mixed hardwood ($n = 9$) and oak-hickory ($n = 9$) forest stands (means and standard errors). Common superscript letters in a row for a given date indicate no significant differences between sites ($P < 0.05$) as determined by analysis of variance and Duncan's multiple range test

	Black locust		Pine-mixed hardwoods		Oak-hickory	
	March	July	March	July	March	July
Total N (%)						
0–15 cm	0.122(0.005)^{b}	0.142(0.005)^{a}	0.144(0.013)^{b}	0.118(0.007)^{a}	0.179(0.006)^{a}	0.158(0.007)^{a}
16–30 cm	0.058(0.004)^{b}	0.062(0.005)^{a}	0.084(0.013)^{b}	0.056(0.005)^{a}	0.098(0.009)^{a}	0.088(0.007)^{a}
31–45 cm	0.040(0.004)^{b}	0.038(0.004)^{a}	0.054(0.010)^{b}	0.029(0.005)^{a}	0.061(0.004)^{a}	0.042(0.006)^{a}
Organic C (%)						
0–15 cm	2.38(0.10)^{b}	2.63(0.15)^{b}	2.82(0.18)^{a}	2.38(0.11)^{b}	3.54(0.31)^{a}	3.74(0.22)^{a}
16–30 cm	1.15(0.07)^{b}	1.26(0.08)^{b}	1.48(0.29)^{a}	0.96(0.09)^{b}	1.90(0.20)^{a}	1.94(0.23)^{a}
C/N						
0–15 cm	19.72(0.70)^{a}	18.34(0.58)^{a}	20.08(1.09)^{a}	20.55(1.20)^{a}	19.94(1.58)^{a}	22.23(0.79)^{a}
16–30 cm	20.28(0.77)^{a}	21.18(1.18)^{a}	20.07(4.69)^{a}	17.11(0.40)^{a}	19.24(0.59)^{a}	21.52(1.43)^{a}
Ca (mg/100 g)						
0–15 cm	73.51(6.90)^{a}	77.26(5.89)^{a}	60.78(4.94)^{a}	47.39(2.87)^{b}	20.68(9.45)^{b}	17.88(4.42)^{c}
16–30 cm	30.69(3.66)^{a}	32.20(4.08)^{a}	27.81(4.49)^{a}	20.62(2.39)^{a}	11.32(4.75)^{b}	7.72(3.10)^{b}
K (mg/100 g)						
0–15 cm	11.39(0.96)^{a}	9.44(0.87)^{a}	9.94(1.45)^{a}	7.74(0.95)^{a}	6.09(0.26)^{b}	6.09(0.25)^{a}
16–30 cm	6.85(0.79)^{a}	6.27(0.75)^{a}	5.78(1.02)^{a}	4.84(0.76)^{a}	4.08(0.36)^{b}	4.59(0.40)^{a}
Mg (mg/100 g)						
0–15 cm	14.90(1.38)^{a}	15.09(1.25)^{a}	11.83(0.84)^{a}	11.57(0.89)^{b}	5.35(1.16)^{b}	5.37(0.80)^{c}
16–30 cm	8.62(0.71)^{a}	8.17(0.80)^{a}	7.10(0.60)^{a}	7.05(0.80)^{a}	3.90(0.79)^{b}	4.10(0.65)^{b}
P (mg/100 g)						
0–15 cm	1.07(0.13)^{a}	0.980(0.102)^{a}	0.709(0.058)^{a}	0.607(0.045)^{a}	0.659(0.025)^{b}	0.723(0.030)^{b}
16–30 cm	0.57(0.12)^{a}	0.391(0.029)^{a}	0.426(0.057)^{a}	0.317(0.020)^{a}	0.393(0.029)^{b}	0.525(0.035)^{a}

Table 3 (*continued*)

	Black locust		Pine mixed hardwoods		Oak-hickory	
	March	July	March	July	March	July
Exchangeable H (mg/100 g)						
0–15 cm	5.50(0.13)^{b}	6.29(0.10)^{b}	5.94(0.27)^{b}	6.43(0.25)^{b}	9.16(0.004)^{a}	8.20(0.30)^{a}
16–30 cm	5.24(0.19)^{b}	6.26(0.16)^{b}	5.98(0.35)^{b}	6.37(0.29)^{b}	7.75(0.36)^{b}	7.56(0.28)^{a}
pH						
0–15 cm	–	5.83^{a}	–	5.71^{a}	–	4.73^{b}
Cation exchange capacity (milliequivalents/100 g)						
0–15 cm	10.72(0.43)^{a}	11.67(0.37)^{a}	10.24(0.46)^{a}	9.98(0.26)^{b}	10.81(0.53)^{a}	9.71(0.25)^{b}
16–30 cm	7.67(0.35)^{a}	8.73(0.30)^{a}	8.12(0.57)^{a}	8.13(0.37)^{a}	8.76(0.41)^{a}	8.43(0.34)^{a}
Base saturation (%)						
0–15 cm	47.35(2.31)^{a}	45.18(1.90)^{a}	41.73(1.89)^{a}	35.29(1.94)^{b}	14.05(3.72)^{b}	15.42(2.70)^{b}
16–30 cm	20.79(1.88)^{a}	27.40(2.09)^{a}	26.01(1.59)^{a}	21.58(1.89)^{a}	11.07(2.77)^{b}	10.01(1.83)^{b}

Soil concentrations of calcium and magnesium were higher in both stands of the early successional watershed than in the oak-hickory forest stand in March and July. Potassium and phosphorus were significantly higher in the early successional watershed in March (Table 3). The percent base saturation was higher in the soils of the early successional watershed (Table 3).

Cation exchange capacity, percent base saturation, calcium, magnesium and phosphorus were higher for the 0–15 cm depth in black locust than in pine-mixed hardwood stands in July (Table 3). The pH of the soils at 0–15 cm depth was 5.8 in black locust, 5.7 in pine-mixed hardwoods, and 4.7 in the oak-hickory forest stand (Table 3).

Discussion

Factors controlling nitrification in the black locust, pine-mixed hardwoods and oak-hickory forests

Many investigators have examined the controls of nitrification in temperate terrestrial ecosystems (Rice and Pancholy 1973, Jones and Richards 1977, Lodhi 1977, 1982, Matson and Vitousek 1981, Montes and Christensen 1979, Robertson and Vitousek 1981, Robertson 1982, Vitousek et al. 1982). Robertson and Vitousek (1981) found that rates of nitrification appeared to be controlled by rates of mineralisation in primary and secondary successional seres. Nitrification seemed to be controlled by availability of ammonium in the majority of the primary successional sites and in all sites in the secondary successional sere (Robertson 1982). Montes and Christensen (1979) did not find conclusive evidence of higher nitrification in early successional stages, and additions of ammonium and lime to soil incubations stimulated nitrification in most cases. These authors suggested that their results could have been influenced by differences between soils such as texture and chemical composition from the different vegetation types. Rice and Pancholy (1973), and Lodhi (1977, 1982), showed evidence of the existence of inhibitory substances to nitrification in later successional sites, supporting the hypothesis of progressive inhibition of nitrification through the course of ecological succession. Vitousek et al. (1982) investigated the controls of potential N mineralisation, nitrate production and nitrate mobilisation in a wide range of forest ecosystems. They found a direct relationship between the amount of N in annual litterfall and the proportion of forest floor N mineralised in laboratory incubations. No direct relationship was found between nitrification and soil characteristics such as pH and base saturation. They found a positive correlation between the mean concentration of soil mineral N (mostly ammonium) and the rate of nitrate production upon incubation in the laboratory.

In the early successional WS6 ecosystem, the rate of ammonification appeared to be the main factor controlling nitrification in both black locust and in non-black locust areas. The primary reason for high nitrification rates in the entire watershed may be related to its treatment history. The soils of this watershed, with higher nutrient content and higher pH, possibly as a result of liming and fertilising history, may be more favourable for the growth of nitrifiers than the soils of the older growth mixed hardwood forest stand.

Within the early successional watershed, net nitrification rates were higher in black locust than in pine-mixed hardwood stands. Lower pH, cation and P content of the pine-mixed hardwood soils could result in lower nitrification in this forest. However when soil laboratory incubations were amended with $CaCO_3$ to increase Ca content and pH (Montagnini 1985) nitrification increased only 10% in both pine-mixed hardwoods and black locust soils. In another experiment (Montagnini 1985), all the added NH_4-N was nitrified in both black locust and pine-mixed hardwood amended soil incubations, suggesting that NH_4-N availability rather than any other soil chemical characteristic is controlling nitrification in these two forests.

In black locust stands, higher N inputs, as a result of N fixation, may be the main factor resulting in high N mineralisation and nitrification rates. Substantial quantities of N fixation were documented for black locust in a regenerating clearcut (WS7) at Coweeta (Table 4) (Boring and Swank 1984a), and inputs to the soil may be high as a result of N fixation. Black locust, with high N tissue content, (Boring and Swank 1984b) may contribute more N in litterfall (Bartuska and Lang 1981, Hirschfeld et al. 1984), throughfall and root and nodule turnover than do trees in the pine-mixed hardwood stands. Moreover, we suggest that insect-induced stress associated with high stand mortality may accelerate these processes and increase ammonium availability for nitrification.

Table 4. Nitrification potentials for sites with and without black locust on a regenerating clearcut (WS7) for 2–6 years old successional vegetation and in an older growth oak-hickory forest of an adjacent control watershed (WS2) in the Coweeta basin. Values were averaged from November 1979 through June 1983 (means and standard errors)

	Regenerating clearcut		Older growth forest
	With black locust ($n = 44$)	Without black locust ($n = 54$)	($n = 34$)
Net nitrification potentials (mg nitrate kg soil^{-1} 33 days^{-1})	26.99 (4.42)	6.30 (2.09)	4.56 (1.42)
Ca (mg/100 g)	67.97 (10.16)	47.47 (15.52)	3.77 (0.55)
P (mg/100 g)	1.054 (0.082)	0.847 (0.067)	0.617 (0.030)
pH	5.61	4.96	5.32

Soil total N concentrations were not significantly different between pine-mixed hardwood and black locust stands in the early successional watershed. Ike and Stone (1958) found N accumulation in the 0–45 cm soil layer beneath 16–20-year-old black locust stands in Tompkins County, New York, with statistically significant increases occurring only in the 0–15 cm soil depth. Jencks et al. (1982) reported that N concentrations at 0–5, 5–10 and 10–15 cm depth were higher in mine soils seeded with black locust than in adjacent native soils in West Virginia; the rate of increase was slower in the lower depths. In the present study, differences in N accretion in the soil may not have been detected at 0–15 or 16–31 cm depth, due to: 1) fast soil N turnover, 2) leaching of organic N from the soil column, or 3) slow accretion taking place only at shallower depths of soil, with potential differences not detectable at 0–15 cm.

Nitrification rates were very low in the older growth oak-hickory forest of WS14. In the experiment to test for the presence of inhibitory substances to nitrification in the soils of this forest, rates were found to be intermediate between those expected from a 100% black locust soil and those expected for an oak-hickory forest soil. If inhibitory substances were present, lower nitrification rates would have been expected. Allelochemic inhibition does not appear to influence low nitrification rates in the soils of this forest.

From the results of this study it is not clear if pH influences low nitrification in the mixed hardwood forest soils of WS14. When $CaCO_3$ was added to laboratory incubations of the oak-hickory forest soils of WS14 on two different occasions (Montagnini 1985) there was no increase in nitrification in comparison with control, unamended soils. Additionally, no significant increase in nitrification was detected following $CaCO_3$ amendment of oak-hickory forest soils which had been mixed with soils of high nitrifying activity, suggesting that the interaction of low Ca, low pH and low populations of nitrifiers was not the cause of low nitrification in the soils of this forest (Montagnini 1985).

Nitrate losses from the black locust dominated watershed

On WS6 black locust dominated areas have high rates of net N mineralisation and nitrification, increasing the potential for leaching losses of nitrate from the soil column. Nitrate concentrations in soil solution sampled with porous-cup lysimeters at 30 and 60 cm depths were also higher under black locust than in pine-mixed hardwoods (Table 2). Boring and Swank (1984b) also reported that the soil under 4, 17 and 38 year old black locust stands at Coweeta had elevated nitrate concentrations.

These results support the hypothesis of Vitousek et al. (1981, 1982) that the amount of N circulated (mineralised from soil and taken up by plants) annually prior to perturbation is probably the main factor controlling leaching losses of nitrate from terrestrial ecosystems. In black locust forest stands, with high N inputs and fast soil N turnover, soil mineral N may be available much in excess of plant uptake and bacterial immobilisation. In the absence of sufficient plant utilisation or high denitrification, significant amounts of nitrate could be leached from the soil column and into the stream water. In the black locust dominated ecosystem a disturbance such as tree death may be of sufficient magnitude to disrupt even more the balance between N mineralisation and plant uptake. This imbalance would result in even higher availability of nitrate to be leached from the system.

Acknowledgements

This research was supported by contract 12-11-008-876 from US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina and by grant BSR 8216081 from the US National Science Foundation to the University of Georgia. We thank W. Hagen and R. Bomar for their assistance in the field and laboratory, respectively, and C. Jordan, H. Neufeld, K. Mattson and P. Groffman for reviewing the manuscript. Thanks are extended to G.P. Robertson for his encouragement. C. Ingram, L. Gibbs and L. Allen typed the manuscript.

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