



Effects of afforestation of a páramo grassland on soil nutrient status

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Received 24 September 2003; received in revised form 27 October 2003; accepted 30 December 2003

Abstract

Plantations of radiata pine (*Pinus radiata*) cover more than 4,000,000 ha worldwide [P.B. Lavery, D.J. Mead, *Pinus radiata*: a narrow endemic from North America takes on the world, in: D.M. Richardson (Ed.), *Ecology and Biogeography of Pinus*, Cambridge University Press, Cambridge, 1998, pp. 432–449]. In many areas, including the Ecuadorian Andes, these plantations have been established on former grasslands. Although this land use has grown over the past four decades in Ecuador, little is known about the effect of the change in vegetation cover on nutrient cycling in the high-altitude grassland systems where the plantations are frequently established. We examined changes in soil nitrogen, phosphorus, and acidity with stand age, using a chronosequence of stands ranging from 0 to 25 years of age. The effects of planting the grasslands with pine were most notable near the soil surface (0–10 cm), although in some cases changes deeper in the A horizon were also large. Total nitrogen concentrations became increasingly depleted along the chronosequence at intermediate depth ($P = 0.04$), while N was gained in the litter ($P = 0.02$) and upper-A horizon ($P = 0.001$) until the plantations reached 20 years, at which point it again declined. In the top 10 cm, concentrations of NO_3^- increased dramatically under pine ($P < 0.001$), while NH_4^+ was lower than in grasslands ($P = 0.04$). Unlike nitrogen, neither total nor available phosphorus was significantly altered by the change in vegetation. Soil pH was higher in the grassland soils (5.5) than under pine stands of any age ($P < 0.01$), all of which had a mean pH of 5.2. Acidification under pine occurred only in the top 10 cm, with no differences in pH at other depths, indicating that it is being driven by soil processes that predominate in the near-surface environment. These results demonstrate that the change of vegetation can affect soil properties on a decadal time scale, with implications for long-term site productivity.

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Keywords: Nitrogen; Phosphorus; Soil acidity; Nutrient cycling; Afforestation; *Pinus*; Páramo grassland

1. Introduction

In recent decades, plantations of fast-growing exotic tree species have become an increasingly important land use in the tropical Andes, where native alpine grasslands (páramos) have been converted to plantations of exotic conifers. Monterey pine (*Pinus radiata*) is one of the most commonly used species in these

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plantations and, worldwide, it has become the most widely planted species for plantation forestry due to the fact that it is fast-growing and is in demand on the world market (Lavery and Mead, 1998). Monterey pine began to be planted in the Ecuadorian páramo in the 1920s, with wide-scale planting beginning in the 1960s; as of the late 1990s, approximately 36% of the total area of forest plantations in Ecuador was planted with this species (Cerdeña, 1999), most of which are located in the páramo. These plantations have been established for purposes including erosion control in degraded areas and timber production. It has been suggested that an increase in the area under plantation forestry could reduce pressure on native forests in Ecuador (Ponce, 2000), which are rapidly being depleted (INEFAN, 1995), and help meet the increasing demand for timber both domestically and internationally. In addition, some pine plantations in Ecuador have been established under pilot projects associated with the Kyoto Protocol's Clean Development Mechanism, with the objective of sequestering carbon. Finally, the harvesting and sale of mushrooms (*Suillus luteus*, a mycorrhizal fungus) that grow in association with pines (Kenny-Jordan et al., 1999) has become the primary reason for establishing and maintaining pine plantations in some parts of Ecuador.

Although this land use has grown over the past four decades, little is known about the effect of the change in vegetation cover on nutrient cycling in these systems. In general, the role of vegetation in the process of soil formation is well documented (Jenny, 1941, 1980; Kelly et al., 1998). As noted by Richter et al. (1994), it is frequently assumed that forests will have a beneficial effect on soils, and it has been suggested that trees have a nutrient enrichment effect on soils in some temperate regions that have been converted from grasslands to pine plantations (Davis and Lang, 1991). Studies of exotic conifer plantations in temperate regions indicate alterations in a number of soil chemical properties (Hamilton, 1965; Fisher and Eastburn, 1974; Turner and Lambert, 1988; Richter et al., 1994; Scholes and Nowicki, 1998), including lower pH and increased nutrient availability (Davis and Lang, 1991). However, while some research exists on the influence of native woody species on páramo soils (Pérez, 1992), the character of changes effected by exotic species on these systems is largely unknown, as little quantitative data is available on nutrient

dynamics in high-altitude tropical plantations. Such data have implications for long-term nutrient availability and the maintenance of site productivity (Turner and Lambert, 1988).

Our objective was to examine changes in soil acidity and nitrogen and phosphorus dynamics with stand age after the conversion of páramo grasslands to pine plantations. The importance of stand age is illustrated by the findings of Turner and Kelly (1985) who indicated that the most significant changes in the nutrient status of the soil are likely to occur in plantations that are 10–20 years old. For this reason, comparisons of stands of various ages to adjacent grasslands are useful for understanding how nutrient status changes as the plantation matures (Davis and Lang, 1991).

2. Methods

2.1. Study area

The study was conducted in a pine plantation owned by Aglomerados Cotopaxi, S.A., covering approximately 7700 ha in Cotopaxi province in north-central Ecuador (0°40'S, 78°30'W). The plantation is located to the northwest of Cotopaxi volcano, a stratovolcano covered by glaciers and snow (Hall and Mothes, 1994) that was extremely active in the 18th and 19th centuries, but has not erupted from 1904 to the present (Barberi et al., 1995). Soils in the study area are derived from volcanic ash and pumice from Cotopaxi, are very young in age, and are at an early stage of soil development. Andisols are the dominant soil order in páramos, most of which are in areas of active volcanism, while at the altitude where the study was conducted Cryands and Udands are common (Lips, 1998). The plantation was established on páramo grasslands, which occur in a vegetation belt between approximately 3200 and 4700 m a.s.l. and are dominated by tussock grasses. In Cotopaxi, *P. radiata* has been planted in the grasslands, between 3000 and 3800 m a.s.l., without clearing or burning of the existing vegetation before the first planting. The plantation included stands ranging from 0 to 25 years of age, allowing for a chronosequence of stands to be established. The stands were divided into four age classes: grassland (representing age 0), young pine (5–10 years

old), intermediate-aged pine (15–20 years old), and old pine (20–25 years old). Three stands were located in each vegetation age class except the 5–10-year-old pine, for which only one stand could be located.

The chronosequence approach implies a space-for-time substitution, which requires careful site selection. While the biota varied among age classes, other factors of soil formation, including topography, climate, parent material, and time (Jenny, 1941), were held constant. All sites were located between 3400 and 3500 m a.s.l., while variations in slope were minimized ($<8^\circ$). All stands were located on soils derived from recent volcanic ash and pumice from Cotopaxi and were in close proximity (<2500 ha area), with consistent soil morphology among all stands. In addition, although páramo grasslands are used for agriculture in some locations, in the higher altitude areas of the plantation where the study sites were located agriculture was not practiced and the native páramo vegetation was intact at the time of plantation. No site preparation, such as tillage or clearing of the existing vegetation, was conducted at any of the sites and no fertilizers were applied at any point in the rotation. All pine stands included were located in parts of the plantation where neither thinning nor pruning had been done.

Mean annual precipitation at Cotopaxi station (at 3590 m) is 1130 mm, with a dry period between June and August, and the mean annual temperature is 8.1°C (INAMHI, 2001).

2.2. Sampling

We established $20\text{ m} \times 10\text{ m}$ plots within each selected stand for sampling. In each plot, we took 10 randomly located soil samples from the 0–10 cm depth, which we refer to as the “upper tier” of the A horizon. Because these grasslands have an overthickened A horizon, we divided it into two tiers, with more intensive sampling in the upper tier, which we expected to be more sensitive to the change in vegetation. Two soil pits were dug to a depth of 1 m in a subset of stands and samples were taken from each genetic horizon (including the lower tier of the A horizon; the AC and C horizons) for chemical analysis. Roots and rocks were removed by hand after returning from the field and half of each sample was air-dried for total chemical analysis while the

other half was kept refrigerated for analysis of inorganic nutrients. Litter samples were taken in triplicate from the top of the litter layer in one stand per age class and were air-dried.

2.3. Laboratory analyses

Samples were transported to Colorado State University, where analysis was done in the Soil Testing Laboratory and the Natural Resources Ecology Laboratory. The air-dried soil samples were sieved (aggregates were broken to pass through a 2 mm sieve); these and the litter samples were ground and analyzed for total nitrogen using a Leco 1000 CHN analyzer (Leco Corp., St. Joseph, MI). These soil samples were also used for analysis of total phosphorus on three surface horizon samples per stand and one soil pit (all horizons) per stand. Total phosphorus was analyzed with a nitric and perchloric acid digestion and read for P by inductively coupled plasma (ICP) spectrometry. Extractable nitrogen and phosphorus were determined for three upper-A horizon samples per stand and all horizons of one soil pit per stand, using field-moist samples. NH_4^+ and NO_3^- were determined in 2 M KCl extracts and the solutions were analyzed on a Lachat Instruments AE Flow Injection Autoanalyzer (Lachat Instruments, Milwaukee, WI). Available phosphorus was determined using the Bray method. A reagent was made by adding NH_4F and HCl to deionized water and adjusting the pH of the solution to 2.6 with diluted HCl. Twenty milliliters of solution was added to 2 g of soil, then shaken for 5 min and filtered. One milliliter of extract was added to 12 ml deionized water and 2 ml of phosphorus color developing reagent; after 10 min, the absorbance was read on a spectrophotometer. Percent dry matter was used to convert these values to a dry weight basis. The pH of three upper-A horizon samples per site was determined for 25 g of soil using a 1:1 field-moist soil:deionized water solution. The pH of a saturated paste was determined for all soil pit samples.

2.4. Statistical analyses

Statistical analysis was done with SPSS (SPSS Inc., 1995), using analysis of variance (ANOVA). Before performing ANOVA, the data were checked for normality and Levene's test was used to test for equality

of variances. One-way ANOVAs were used where these assumptions were met, with vegetation age class as the factor and the probability of Type I error set at 0.05. Where differences among age classes were significant, REGWF (Ryan–Einot–Gabriel–Welsch F) post hoc tests were used to compare means. Non-parametric Kruskal–Wallis tests were used for variables that did not meet the assumptions and could not be corrected by transformations. Where differences among age classes were significant, tests were done of all pairwise comparisons among the four age classes (i.e. six tests). The experimentwise error rate was adjusted using the formula provided by Zar (1999); the comparisonwise alpha was determined to be 0.013 for each of the six tests. Due to the small sample size, Kruskal–Wallis tests were also used for the samples from the soil pits to test for differences among age classes within a single horizon (e.g. differences among age classes within the AC horizons).

3. Results

Planting páramo grasslands in Cotopaxi with pine had large effects on soil nitrogen and pH and relatively minor effects on soil phosphorus. The effects on nutrient status were most notable near the soil surface (0–10 cm), although in some cases differences in the lower tier of the A horizon were also large. There were no significant differences for any of the variables considered for the AC and C horizons, which have undergone minimal weathering and have very low total nutrient concentrations.

3.1. Soil nitrogen

Total nitrogen concentrations in the litter and upper-A horizon were both significantly different among age classes ($P = 0.02$ and 0.001 , respectively) and followed similar patterns (Fig. 1). N concentrations in the litter declined from grasslands to young pine, were

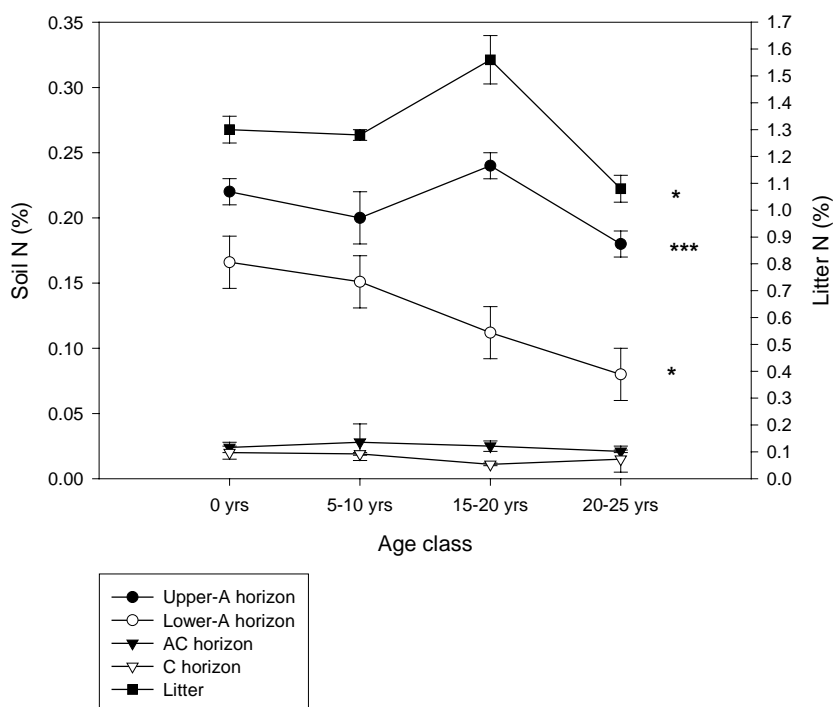


Fig. 1. Total nitrogen concentrations (mean \pm S.E.) with depth for each of the four vegetation age classes. Asterisks indicate significant differences among age classes (** $P < 0.001$; * $P < 0.05$). The A horizon was divided into two tiers; upper-A horizon samples were taken from the 0–10 cm layer. Significance was determined using one-way ANOVAs followed by REGWF for the upper-A horizon ($n = 30$ per age class, except $n = 10$ for 5–10 years pine), and Kruskal–Wallis tests for all other horizons (for each horizon $n = 6$ per age class, except $n = 2$ for 5–10 years pine) and litter ($n = 3$ per age class).

Table 1
Mean nitrogen concentrations (\pm S.E.) by vegetation age class

	Vegetation age class			
	0 year	5–10 years	15–20 years	20–25 years
Litter				
Total N (%)	1.30 (0.05) ab	1.28 (0.02) b	1.56 (0.09) a	1.08 (0.05) b
Soil				
Upper-A horizon				
Total N (%)	0.22 (0.01) a	0.20 (0.02) ab	0.24 (0.01) a	0.18 (0.01) b
NH ₄ ⁺ (mg/kg)	6.8 (2.1)*	1.2 (0.6)*	1.5 (0.4)*	1.7 (0.5)*
NO ₃ ⁻ (mg/kg)	0.3 (0.3) a	30.9 (6.3) b	34.4 (4.6) b	39.7 (6.7) b
Lower-A horizon				
Total N (%)	0.17 (0.02) a	0.15 (0.02) ab	0.11 (0.02) ab	0.08 (0.02) b
NH ₄ ⁺ (mg/kg)	2.1 (na) a	2.2 (na) a	4.5 (1.7) a	2.6 (1.5) a
NO ₃ ⁻ (mg/kg)	1.7 (na) a	6.4 (na) a	11.0 (1.6) a	5.5 (0.8) a

The A horizon was divided into two tiers; upper-A horizon samples were taken from the 0–10 cm layer. Within each row, means followed by different letters are significantly different from each other at $P \leq 0.05$. Significance was determined using one-way ANOVAs followed by REGWF for litter and upper-A horizon total N; all other variables were analyzed with Kruskal–Wallis tests. For litter, $n = 3$ per age class; for upper-A horizon soils, $n = 30$ per age class (except $n = 10$ for 5–10 years pine) for total N, $n = 9$ per age class (except $n = 3$ for 5–10 years pine) for other variables; for lower-A horizon soils, $n = 6$ per age class (except $n = 2$ for 5–10 years pine) for total N, $n = 3$ per age class (except for 0 year and 5–10 years pine, where $n = 1$ and no statistical analysis was done) for other variables.

* Although the Kruskal–Wallis test indicated significant differences among age classes ($P = 0.04$), none of the pairs were significantly different using the adjusted, comparisonwise alpha of 0.013.

highest in the intermediate-age pine stands, and declined again after 20 years under pine (Table 1). In the upper-A horizon, the highest nitrogen concentrations were in the grasslands (0.22%) and 15–20 years pine stands (0.24%), while N concentrations were significantly lower in the oldest pine stands (0.18%) (Table 1). There were also significant differences in total nitrogen in the lower tier of the A horizon ($P = 0.04$), with a linear decline in nitrogen concentration with stand age (Table 1, Fig. 1). At this depth, total N was 0.17% in the grasslands, and declined dramatically in both the 15–20 and 20–25 years pine stands, so that the total soil nitrogen concentration in the oldest pine stands was less than half that in the grasslands at this depth.

Significant differences in extractable nitrogen ($P = 0.04$ for NH₄⁺ and $P < 0.001$ for NO₃⁻) were found in the upper-A horizon between the grasslands and the other three age classes, with opposite patterns for NH₄⁺ versus NO₃⁻ (Table 1). In the case of ammonium, the highest concentrations were in the grasslands. In contrast, almost no nitrate was present in the grassland soils, but concentrations increased dramatically in the other three age classes. In contrast to the upper-A horizon,

there were no significant differences in NH₄⁺ ($P = 0.70$) or NO₃⁻ ($P = 0.12$) among age classes in the lower tier of the A horizon (Table 1). However, nitrate was still low at this depth in the grasslands and higher in the other three vegetation age classes.

3.2. Soil phosphorus

There were no significant differences in total phosphorus among age classes for the upper or lower tier of the A horizon ($P = 0.13$ and 0.19, respectively) (Table 2). In the lower-A horizon, mean values for total phosphorus were generally low, and there was considerable variation within age classes. There were no significant differences in extractable phosphorus in either tier of the A horizon ($P = 0.37$ and 0.12, respectively), although, in the upper tier, it tended to be higher in the two oldest age classes than in the two younger age classes (Table 2).

3.3. Soil pH

Soil pH was higher in the grassland soils (5.5) than the other three age classes, all of which had a mean pH

Table 2
Mean soil phosphorus concentrations (\pm S.E.) by age class

	Vegetation age class			
	0 year	5–10 years	15–20 years	20–25 years
Upper-A horizon				
Total P (%)	0.030 (0.003) a	0.033 (0.001) a	0.034 (0.002) a	0.026 (0.002) a
Bray P (mg/kg)	34.4 (4.9) a	33.7 (3.1) a	43.9 (2.9) a	42.2 (5.5) a
Lower-A horizon				
Total P (%)	0.023 (na) a	0.009 (na) a	0.014 (0.006) a	0.004 (0.003) a
Bray P (mg/kg)	17.2 (na) a	27.1 (na) a	25.3 (0.4) a	13.6 (3.4) a

The A horizon was divided into two tiers; upper-A horizon samples were taken from the 0–10 cm layer. Within each row, means followed by different letters are significantly different from each other at $P \leq 0.05$. Significance was determined using one-way ANOVAs followed by REGWF for upper-A horizon samples ($n = 9$ per age class, except $n = 3$ for 5–10 years pine) and Kruskal–Wallis tests for lower-A horizon samples ($n = 3$ per age class, except for first two age classes where $n = 1$ and no statistical analysis was done).

of 5.2 ($P < 0.01$; Fig. 2). This indicates that a decline in pH occurred between the time of plantation and 10 years of age, but no further decline occurred at later stages of stand development. However, this change

only affected the upper tier of the A horizon (0–10 cm depth), while in the lower-A horizon there was no significant difference in pH among age classes ($P = 0.65$).

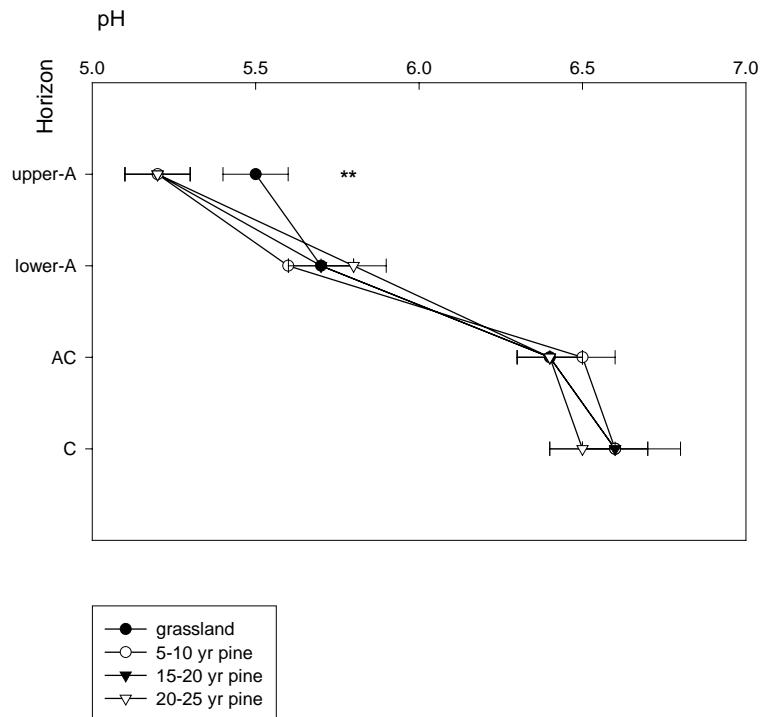


Fig. 2. Mean pH (mean \pm S.E.) with depth for each of the four vegetation age classes. Asterisks indicate significant differences among age classes ($^{***}P < 0.01$). The A horizon was divided into two tiers; upper-A horizon samples were taken from the 0–10 cm layer. Significance was determined using one-way ANOVAs followed by REGWF for the upper-A horizon ($n = 9$ per age class, except $n = 3$ for 5–10 years pine) and Kruskal–Wallis tests for all other horizons (for each horizon $n = 6$ per age class, except $n = 2$ for 5–10 years pine).

4. Discussion

4.1. Nitrogen dynamics with stand age

Jobbágy and Jackson (2004) have described the vertical redistribution and change in bioavailability of nutrients that can occur with vegetation change. The “nutrient pumping” effect they observed after conversion of grasslands to eucalyptus plantations resulted in the redistribution of nutrients, reducing concentrations of highly cycled nutrients at intermediate depths and increasing them at the soil surface. Although they focus on micronutrients that are derived from the lithosphere, in general, there should be a shallower distribution for nutrients with a higher “cycling intensity”. In other systems that have undergone vegetation change, similar patterns have been seen for other nutrients. For example, in several studies of pine plantations, it has been suggested that, because pine roots tend to reach greater depths than those of grasses, they are able to absorb nutrients from lower soil horizons, which are redistributed to the soil surface through litterfall and throughfall (Turner and Kelly, 1985; Davis and Lang, 1991; Parfitt et al., 1997).

This type of nutrient redistribution appears to have occurred with nitrogen after the conversion of grasslands to pine at Cotopaxi. Nitrogen became increasingly depleted along the chronosequence at intermediate depth, while it was gained in the litter and surface mineral soil until the plantations reached 20 years; however, after 20 years, it again declined (Fig. 1). This pattern may be explained by changing nutrient use and accumulation with stand development. The accumulation of nitrogen in tree biomass is expected to be greatest within the first 15 years of plantation (Gholz et al., 1985; Turner and Kelly, 1985), and much of this accumulated nitrogen is allocated to foliage (Switzer and Nelson, 1972). As the N concentrations in the trees increase, some of this nitrogen will be returned to the surface soil through litterfall. At Cotopaxi, the N concentration in litter was highest in the 15–20 years pine stands, reflecting the maximum accumulation of N in the biomass, then declined in the 20–25 years pine stands. N concentrations in the soils from the upper tier of the A horizon mirrored this pattern, with a peak in N between 15 and 20 years. At the same time total N continuously

declined at intermediate depth (lower-A horizon). Because the AC and C horizons are minimally weathered and have very low nutrient concentrations, the change in vegetation did not have an effect at those depths (Fig. 1).

In addition to altering the vertical distribution of nutrients, vegetation change can affect their bioavailability (Jobbágy and Jackson, 2004). Although no significant change occurred below 10 cm depth, in the upper-A horizon soils at Cotopaxi, NO_3^- concentrations increased dramatically under pine, while NH_4^+ was lower than in grasslands (Table 1). It should be noted that the measurements of inorganic nitrogen represent a single point in time, but the magnitude of the differences between grasslands and pine suggest that there is a change associated with vegetation type. There are likely a number of factors influencing this change in nitrogen availability. First, the lower pH under plantations may play a role. Andisols have a decreasing ability to retain exchangeable bases with decreasing pH, so that NH_4^+ is less likely to be retained under leaching conditions (Wada, 1985). In addition, as pH decreases, anion retention capacity increases, resulting in the large capacity of Andisols to retain anions, including nitrate (Wada, 1985). These factors may help to explain why, as pH declined under pine at Cotopaxi, the soils had lower NH_4^+ concentrations and higher NO_3^- concentrations. Another possible factor, suggested in other plantation studies, is that increased nitrogen mineralization early in stand development may exceed plant needs (Parfitt et al., 1997). If plant growth in the páramo is phosphorus-limited rather than nitrogen-limited (Hofstede, 1995), nitrogen mineralization may be in excess of plant needs beyond the early stages of stand development. Higher rates of nitrification could occur if ammonification exceeds plant demand, and this could explain why the large soil nitrate pools persist in the older pine stands.

Other factors that may contribute to these differences include varying abilities of plants to take up different forms of inorganic nitrogen. For example, in a study of pine (*P. caribaea*) and other trees planted in the Brazilian Amazon, Smith et al. (1998) found increased nitrate pools under pine and suggest that the smaller fine root biomass under pine may result in a failure to compete with nitrifiers for available NH_4^+ . Fine root production under pine is likely lower than in

páramo grasslands and this may contribute to higher rates of nitrate production relative to grasslands. In addition, there may also be a difference in uptake of NO_3^- between the two vegetation types (Smith et al., 1998), with pine taking up less NO_3^- than the grasses.

4.2. Soil phosphorus

Although the increase in available phosphorus with stand age was not significant, the tendency toward higher extractable P in the upper-A horizon soils under pine was consistent with a number of other studies (Ohta, 1990; Davis and Lang, 1991; Belton et al., 1995; Cavelier and Tobler, 1998). Nonetheless, given suggestions that phosphorus availability could increase by two to four times under pine in New Zealand (Belton et al., 1995), where pine is planted in areas of montane grassland, the changes in extractable phosphorus at Cotopaxi were quite small. Available P can increase as organic P is mineralized or as sorbed P becomes available. The evidence from New Zealand suggests that much of the increase in available phosphorus is attributable to increased mineralization under pine (Belton et al., 1995). The pool of inorganic P that is not available to plants may also be altered by the introduction of pine, particularly in Andisols. Much of the inorganic phosphorus in volcanic soils tends to be bound to Al or Fe hydrous oxides or allophane and is unavailable for plant uptake (Crews et al., 1995). P fixation is strongly influenced by soil pH, and becomes increasingly fixed to Al and Fe at pH lower than 6 (Frossard et al., 1995). However, the change in pH under pine at Cotopaxi was probably not large enough in magnitude to have had an effect on P fixation, particularly given the fact that soil pH was already below 6 in the grasslands.

4.3. Soil acidification

Changes in pH can be expected on time scales of a few decades following changes in land use such as afforestation (Binkley et al., 1989). In Cotopaxi, the change in pH appears to have occurred relatively rapidly—in less than one decade—with no further changes in the following decade. The magnitude of the change—0.3 pH units—was less than that in some other studies (e.g. Rhoades and Binkley, 1996; Jobbágy and Jackson, 2003), but similar to results for *P. radiata* in New Zealand (Parfitt et al., 1997). Jobbágy

and Jackson (2003) describe several mechanisms of acidification following the conversion of grasslands to plantations and suggest that the vertical pattern of acidification in the soil profile can provide an indication as to which of these processes is dominant.

The accumulation of cations in tree biomass is a frequently cited mechanism of acidification in afforestation studies. Cation accumulation appears to be particularly important in pines (Brand et al., 1986; Binkley et al., 1989; Richter et al., 1994), specifically for *P. radiata*, which tends to accumulate large concentrations of cations in its biomass, contributing to acidification in the rooting zone (Parfitt et al., 1997). This should produce a pattern of maximum acidification below 10 cm (Jobbágy and Jackson, 2003). However, at Cotopaxi, acidification under pine occurred only in the top 10 cm, with no differences in pH at other depths (Fig. 2), where roots are also present. These data suggest that cation accumulation in the biomass is not the primary driver of acidification in these soils, and that other biologically mediated processes that predominate near the soil surface, such as carbon dioxide, organic acid, and chelate production, are the primary regulators of soil acidification.

A decrease in pH has often been found to result from afforestation with conifers, as well as some broadleaf plantations, due to the greater acidity of the litter relative to the native vegetation (Hamilton, 1965; Davis and Lang, 1991; Essex and Williams, 1993; Rhoades and Binkley, 1996, under *Eucalyptus* and *Albizia*; Lips and Hofstede, 1998). This should be reflected in maximum acidification at the soil surface (Jobbágy and Jackson, 2003), a pattern consistent with the results from Cotopaxi. Another source of acidification may come from nitrification (Parfitt et al., 1997), which could also produce a pattern in which acidification occurs primarily at the soil surface. There were large pools of NO_3^- in the soils from the top 10 cm under pine in Cotopaxi, while the differences in NO_3^- between grassland and pine were much smaller in the lower-A horizon. This pattern would be consistent with the idea that nitrification plays an important role in altering pH.

An increase in the production of carbonic acid in association with increased decomposition may also result in additional inputs of acids. In Cotopaxi, increased decomposition is likely responsible, at least in part, for lower soil organic carbon under pine

(Farley et al., 2004), and may contribute to acidification in those soils. However, this process should produce a vertical pattern in which acidification is dominant at depth (Jobbágy and Jackson, 2003), so that it does not appear to explain the pattern at Cotopaxi.

5. Implications for site productivity

The results from Cotopaxi demonstrate that the change of vegetation can affect important soil properties on a decadal time scale, with implications for long-term site productivity. The pattern of nitrogen cycling at Cotopaxi indicates that N is being redistributed under pine from intermediate depths to the surface. Jobbágy and Jackson (2004) suggest that one of the possible consequences of this type of nutrient uplift is that greater amounts of nutrients could be lost after being transferred closer to the soil surface. The fact that the accumulation of N at the surface did not persist in the oldest stands at Cotopaxi suggests that such losses may be occurring and that nitrogen depletion may become a problem in subsequent rotations of pine. Soil acidity has important implications for site productivity as well (Jobbágy and Jackson, 2003); however, the lack of change in soil pH after 10 years under pine suggests that most of the effect of soil acidity on nutrient availability has already been observed in the older stands. Neither soil acidity nor soil phosphorus appears likely to constrain future rotations, but measurements of these and other soil characteristics following harvesting will help to elucidate the full effect of this land use system on biogeochemistry in these high-altitude equatorial sites.

Acknowledgements

We thank Juan Pablo Fontecilla and Aglomerados Cotopaxi, S.A., for access to the plantation and assistance in carrying out the study. Thanks to Galo Medina for support in Ecuador and to Rebecca McCulley for helpful comments on an earlier version of this manuscript. This material is based upon work supported by the National Science Foundation under Grant no. 0002352; the Graduate School of the University of

Colorado-Boulder; the University of Colorado-Boulder Developing Areas Research and Training Program, and the Colorado State University Agricultural Experimental Station.

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