

Soil Organic Carbon and Water Retention after Conversion of Grasslands to Pine Plantations in the Ecuadorian Andes

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ABSTRACT

Tree plantations in the high elevations of the tropics constitute a growing land use, but their effect on ecosystem processes and services is not well known. We examined changes in soil organic carbon (C) and water retention in a chronosequence of *Pinus radiata* stands planted in páramo grasslands in Cotopaxi province, Ecuador. Water retention at 10, 33, and 1,500 kPa declined with stand age, with soils in the oldest pine stands retaining 39%, 55%, and 63% less water than grassland soils at the three pressures tested. Soil organic C in the 0–10-cm depth also declined with stand age, from 5.0 kg m⁻² in grasslands to 3.5 kg m⁻² in 20–25-year-old pine stands ($P < 0.001$); at greater depth in the A horizon, C contents decreased from 2.8 to 1.2 kg m⁻² ($P = 0.047$). There were no significant differences among age classes in the AC and C horizons ($P = 0.15$ and $P = 0.34$, respectively), where little or no weathering of the primary material has occurred. Inputs of C may be affected by the significantly higher carbon–nitrogen (C:N) ratio of the litter under older pine stands ($P = 0.005$), whereas outputs are influenced by

substrate quality as well as soil environmental factors. Soil ratios at the 0–10 cm depth were significantly higher in grasslands and young pine stands ($P < 0.001$), whereas carbon–phosphorous (C:P) ratios at 0–10-cm depth followed a similar but not significant trend. However, there was no significant difference in short-term decomposition rates ($P = 0.60$) when the soils were incubated under uniform temperature and moisture conditions. In páramo ecosystems, where high soil moisture plays an important role in retarding decomposition and driving high C storage, the loss of water retention after afforestation may be the dominant factor in C loss. These results suggest that soil C buildup and water retention respond rapidly to changes in biota and need to be assessed with regard to implications for C sequestration and watershed management.

Key words: soil organic carbon; soil water retention; land-use change; afforestation; pine plantation; *Pinus*; páramo; Andes; ecosystem services.

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INTRODUCTION

Tree plantations established in areas where carbon (C) stocks were previously relatively low have the potential to act as C sinks (Cuevas and others

1991), and it has been suggested that tropical plantations in particular could play an important role in efforts to reduce atmospheric carbon dioxide (CO₂) concentrations (Brown and others 1986; Bashkin and Binkley 1998). A better understanding of the role of tree plantations in C sequestration has become increasingly important since the creation of the Clean Development Mechanism (CDM) under the Kyoto Protocol to the United Nations Framework Convention on Climate Change. The CDM enables developed countries to meet part of their emission reduction requirements by carrying out reforestation and afforestation projects in developing countries (Smith and Scherr 2002). Such C sequestration projects are among several factors that have led to the establishment of exotic pine plantations in Ecuador (Smith and Scherr 2002), where the trees have been planted mostly in equatorial alpine grasslands known as páramos. CDMs have played an important role in plantations established over the past decade, while most older plantations were established to provide timber or fuelwood, or with the objective of erosion control in degraded areas. Although many of the original plantations in highland Ecuador were established under the assumption that they would provide services such as erosion control and water regulation, in fact very little is known in this region regarding their effect on any ecosystem processes, including soil C storage and water retention.

In addition to sequestering C in the biomass, afforestation is expected to increase soil C (Brown and others 1986; Johnson 1992), in particular where tree plantations are established on previously cultivated or otherwise degraded soils (Bashkin and Binkley 1998). However, the establishment of woody vegetation on grasslands does not necessarily lead to an increase in soil C (Kaye and others 2000), and in some cases losses of soil C may be large enough to offset gains in biomass C (Jackson and others 2002). Whether soil C increases or decreases with afforestation may be determined by a number of factors, including previous land use (Paul and others 2002), site preparation (Zinn and others 2002), type of species planted (Paul and others 2002; Resh and others 2002), climate (Paul and others 2002; Guo and Gifford 2002), and soil type (Jackson and others 2002), including chemical and physical properties of soils that influence the level of resistance of soil organic C (SOC) to degradation (Swift 2001).

Páramo soils, most of which occur in areas with active volcanism, are dominated by Andisols,

which derive from volcanic ash and tend to stabilize organic matter through the formation of organic-mineral complexes that physically protect humus against decomposition (Dahlgren and others 1993; Wada 1985). As such, the mean residence time of organic carbon (OC) is much higher in Andisols (Dahlgren and others 1993), resulting in as much as two times greater OC storage than other mineral soils (Torn and others 1997). In páramo soils, these mineralogical properties combine with large amounts of belowground organic matter inputs from the grasses characteristic of these ecosystems and cool, consistently humid conditions, which contribute to the slow rate of decomposition (Luteyn 1992; Hofstede 1995). In these soils, afforestation may cause a loss of soil carbon (Hofstede and others 2002), at least in part offsetting gains in C sequestered in the biomass of planted trees.

In addition to stabilizing large amounts of soil C, páramos play an important role in local and regional hydrology. They serve as the primary water catchments for much of the northern Andes and are key to the provision of water to highland cities and towns (Luteyn 1992; Podwojewski 1999). Andisols tend to have large soil organic matter (SOM) contents as well as a broad pore size distribution and a large volume of mesopores and micropores within the soil aggregates, contributing to their exceptionally large water retention capacity (Nanzyo and others 1993; Wada 1989). However, some kinds of disturbance can lead to irreversible drying in Andisols, causing the loss of water retention and in some cases water repellency, leading to lower water storage (Podwojewski and Poulenard 2000; Poulenard and others 2001). The degree to which afforestation in páramo grasslands may affect water storage is unclear, because there is very little information on the effect of pine plantations on this ecosystem service.

Although many studies of the effects of conifer plantations on soil properties have been carried out in temperate regions (for example, Hamilton 1965; Turner and Lambert 1988; Richter and others 1994), less information is available on the changes induced by plantations in the tropics (Joshi and others 1997; Paul and others 2002; Zinn and others 2002), and in particular in the highland tropics (exceptions include Lundgren 1978; Cortés and others 1990; Hofstede and others 2002). Information specific to these regions is necessary to help orient local policy makers, who will make decisions regarding the implementation of tree plantations, in general, and CDM projects in particular, as well as those who will certify CDM and sustainable

forest management projects that take into account both economic and environmental considerations.

The objective of this study was to address this issue by examining a multi-age *Pinus radiata* plantation in highland Ecuador that allowed for the examination of changes with stand age. The questions addressed were (a) Is there a difference in soil C and/or soil water retention between páramo grasslands and *P. radiata* stands? and (b) Is there a trend in these soil characteristics with stand age?

METHODS

Study Area

The study was conducted in a pine plantation belonging to Aglomerados Cotopaxi, S.A., covering approximately 7,700 ha in Cotopaxi province, in north-central Ecuador (0°40' S, 78°30' W). Mean annual precipitation at Cotopaxi station (3,590 m a.s.l.) is 1,130 mm; mean annual temperature is 8.1°C (INAMHI 2001). The plantation is located to the northwest of Cotopaxi volcano, which is active and erupted on numerous occasions in the 18th and 19th centuries, with the last eruption occurring in 1904 (Barberi and others 1995). Soils in the study area are derived from volcanic ash and pumice from Cotopaxi and are very young in age; because they are at a very early stage of soil development, organic matter accumulation has not reached the levels of older páramo soils. The native vegetation in páramos, which generally range from 3,200 to 4,700 m a.s.l., is dominated by tussock grasses. In Cotopaxi, *Pinus radiata* (Monterey or Radiata pine) has been planted in the grasslands, between 3,000 and 3,800 m a.s.l., without clearing or burning of the existing vegetation before the first planting.

The characteristics of the study site enabled an assessment of soil properties as a function of vegetation type (grasses versus pines) and as a function of time of occupation by the exotic vegetation. The plantation included stands ranging from 0 to 25 years of age, which 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); those classes constituted the vegetation chronosequence. Three plots 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 with careful site selection allows for temporal effects to be inferred by the analysis of stands of different ages over a relatively short-term study period.

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 3,400 and 3,500 m a.s.l. and variations in slope were minimized (less than 8°). All stands were located on soils derived from recent volcanic ash and pumice, and the soil morphology was consistent among all plots studied. In addition, although agriculture is commonly practiced in páramo grasslands, in this case 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 are 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.

Sampling

Soil sampling involved locating 20 × 10 m plots within each selected stand and taking 10 randomly located soil samples from the 0–10-cm depth, where most of the effects of a change in vegetation on soils are expected to be seen (Alban 1982; Turner and Kelly 1985). Additional sampling consisted of digging two soil pits to a depth of 1 m in a subset of stands and sampling by genetic horizon. Roots and rocks were removed by hand after returning from the field, and half of each sample was air-dried while the other half was kept refrigerated. Undisturbed volumetric samples (100 cm³ volume) were taken from the A horizon of all pits, as well as from all horizons to 1 m in one pit per age class, and were kept refrigerated. Soil temperature was taken once in each pit at 50-cm depth to eliminate variations due to readings being taken at different times of day or under different weather conditions. Litter samples were taken in triplicate from one stand per age class and air-dried.

Laboratory Analyses

All samples were transported to Colorado State University, where the analyses were conducted. 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 C and nitrogen (N) using a Leco 1000 CHN analyzer (Leco., St. Joseph, MI, USA). Soil samples were tested for total phosphorus (P) with a nitric and perchloric acid digestion and read for P by inductively coupled plasma (ICP) spectrometry.

Three additional soil samples from the 0–10-cm depth were taken from three stands per age class (except, one stand for 5–10-year-old pine) and composited to obtain a single sample per stand. The composite samples were incubated for 13 weeks at mean annual temperature (8°C) and field capacity moisture to assess short-term decomposition rates. The respiration rate was measured at weeks 1, 5, 9, and 13 by circulating CO₂-free air through a sealed jar for 15 min and measuring CO₂ concentration after 15–24 h. Flux was calculated as CO₂ increase (μmol CO₂ per mol air in jar) divided by the time the jar was sealed, and expressed as the rate per mol of soil C in the sample. Soil C was determined with a Leco CHN analyzer.

Analysis of water retention capacity of the soils at saturation, 10 kPa, 33 kPa (field capacity), and 1,500 kPa (wilting point) was done using pressure plates on the undisturbed volumetric samples from the A horizon. The samples were placed in 100-cm³ cylinders, saturated, weighed to determine water retention at saturation, and then tested for water retention at successively higher pressures. Bulk density was determined after oven-drying undisturbed samples for 24 h at 105°C; these samples were weighed before and after drying to determine field moisture content.

Statistical Analyses

Statistical analysis was done using analysis of variance (ANOVA) to test for the effect of stand age. Before performing ANOVA, the data were checked for normality and 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, REG-WF (Ryan-Einot-Gabriel-Welsch F) post hoc tests were used to compare means. Nonparametric Kruskal-Wallis tests were used for variables that did not meet the assumptions and could not be corrected by transformations. Because of 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 (for example, differences among age classes within the A horizons). Where differences among age classes were significant, Kruskal-Wallis tests were done on all pairwise comparisons among the four age classes, using an adjusted comparison-wise α of 0.013 (Zar 1999). The soil respiration data were analyzed with a repeated-measures ANOVA, and a one-way ANOVA for the cumulative decomposition rates.

RESULTS

Soil Carbon

Total C concentrations in the surface horizon (0–10-cm depth) were significantly different among age classes ($P < 0.001$). There were no significant differences in bulk density ($P = 0.16$), so that, whether considering C concentrations or stocks, the highest values were found in the páramo grasslands (4.2%, or 5.0 kg m⁻²) and the lowest in the oldest pine stands (2.8%, or 3.5 kg m⁻²) (Table 1). There was also significantly lower soil C with stand age in the A horizon of the soil pits ($P = 0.047$), where samples were taken from the middle of the horizon (mean depth = 13 cm). At this depth, the mean soil C concentration decreased with stand age, from 2.8% in the grasslands to 1.2% in the 20–25-year-old pine (Table 1). There were no significant differences among age classes for the subsurface horizons (AC and C horizons) ($P = 0.15$ and $P = 0.34$, respectively), where little or no weathering of the primary material has occurred, and soil C was minimal for all age classes (Figure 1).

The laboratory incubation demonstrated that there was no significant difference among age classes in rate of decomposition over the 13-week period ($P = 0.65$) or in cumulative decomposition rates ($P = 0.60$) under uniform conditions of temperature and moisture (Table 2). The C:N ratio in the surface horizon was significantly higher ($P < 0.001$) in the grasslands and youngest pine stands (19.3 and 17.7, respectively) than in pine stands more than 15 years old (15.2–15.9) (Table 3). Differences in C:P ratios at this depth were not significant ($P = 0.35$), although, like C:N, they were highest in the grasslands and declined in the other three age classes. C:N ratios in the A horizon soil were not significantly different among age classes ($P = 0.053$), but were highest in the grasslands. The C:N ratio of the litter was significantly higher in the oldest pine stands (47.6) than in the other age classes ($P = 0.005$) (Table 3).

Soil Water Retention and Temperature

Determination of soil hydrological properties yielded significant differences among age classes for water content at 10 kPa ($P = 0.02$), 33 kPa ($P < 0.001$), and 1,500 kPa ($P < 0.01$). In contrast, saturation water content was not significantly different among vegetation age classes ($P = 0.36$) (Table 4). The pattern in water contents was similar for all of the pressures tested, with the highest water contents in the grasslands and declining

Table 1. Bulk Density and Mean Soil Carbon Concentrations (\pm SE) by Vegetation Age Class and Horizon.

Age class	Surface Horizon (0–10 cm)			A Horizon			AC Horizon			C Horizon		
	Bulk Density (g cm ⁻³)	C (%)	C (kg m ⁻²)	Bulk Density (g cm ⁻³)	C (%)	Bulk Density (g cm ⁻³)	Bulk Density (g cm ⁻³)	C (%)	Bulk Density (g cm ⁻³)	Bulk Density (g cm ⁻³)	C (%)	C (%)
	Grassland	1.17 (0.03) ^a	4.2 (0.2) ^a	5.0 (0.3) ^a	1.00 (0.00) ^a	2.8 (0.6) ^a	0.70 (0.00) ^a	0.60 (0.00) ^a	0.2 (0.0) ^a	0.70 (0.00) ^a	0.60 (0.00) ^a	0.1 (0.0) ^a
5–10-y pine	1.12 (0.03) ^a	3.3 (0.3) ^{bc}	3.7 (0.3) ^{bc}	1.05 (0.05) ^a	2.2 (0.5) ^{ab}	0.75 (0.05) ^a	0.65 (0.05) ^a	0.2 (0.0) ^a	0.75 (0.05) ^a	0.65 (0.05) ^a	0.1 (0.0) ^a	0.1 (0.0) ^a
15–20-y pine	1.20 (0.03) ^a	3.5 (0.1) ^b	4.3 (0.2) ^b	1.00 (0.00) ^a	1.4 (0.2) ^b	0.70 (0.00) ^a	0.70 (0.00) ^b	0.2 (0.0) ^a	0.70 (0.00) ^a	0.70 (0.00) ^b	0.1 (0.0) ^a	0.1 (0.0) ^a
20–25-y pine	1.25 (0.02) ^a	2.7 (0.2) ^c	3.5 (0.2) ^c	1.00 (0.00) ^a	1.2 (0.3) ^b	0.70 (0.00) ^a	0.70 (0.00) ^b	0.1 (0.0) ^a	0.70 (0.00) ^a	0.70 (0.00) ^b	0.1 (0.0) ^a	0.1 (0.0) ^a

C, carbon. Within each column, 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 the surface horizon, and Kruskal-Wallis tests for all other horizons.

Surface horizon: $n = 30$ per age class (except, $n = 10$ for 5–10 year-old pine) for C; $n = 2$ –6 per age class for bulk density. For each of the other three horizons: $n = 2$ –6 per age class for C and bulk density.

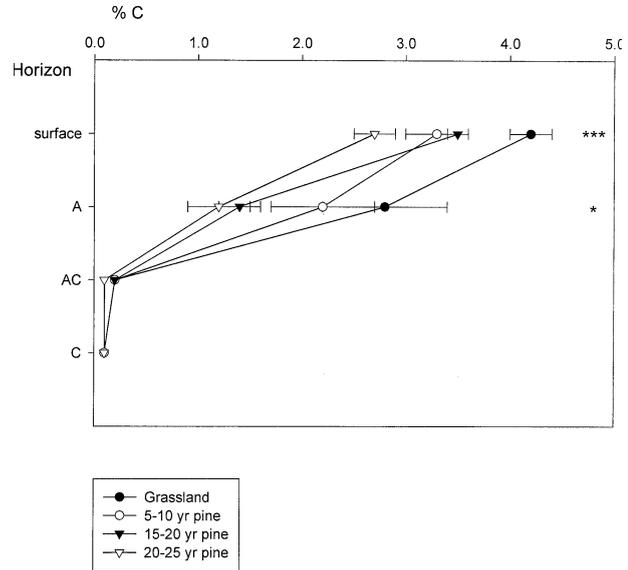


Figure 1. Soil carbon (C) concentrations (mean + SE) with depth for each of the four vegetation age classes. Asterisks indicate significant differences among age classes) *** $P < 0.001$; * $P < 0.05$). Surface horizon refers to samples taken from the 0–10 cm layer; samples from all other depths were taken from the center of the horizon. $n = 30$ per age class (except, $n = 10$ for 5–10 year-old pine) for surface horizon samples; $n = 2$ –6 per age class for each of the other horizons.

amounts in successively older pine stands; this pattern mirrors the decline in soil C in the A horizon. Although the grasslands had the highest water contents and the oldest pine stands had the lowest water contents at all pressures, the divergence among age classes was largest at 33 kPa and 1,500 kPa (Figure 2). Field moisture contents were also significantly different among age classes ($P < 0.001$). Contents ranged from 15% to 38% (volume), with the highest values in the grasslands (Table 4). The trend from grasslands to the oldest age class indicated a linear decline in soil moisture with stand age.

Significant differences were found for soil temperature ($P < 0.01$), which was lowest in the grasslands and 15–20-year-old pine stands (9.6°C) and highest in the 5–10- and 20–25-year-old pine sites (11.8 and 11.4°C, respectively) (Table 4).

DISCUSSION

Soil Carbon

Both the loss of original soil C and the incorporation of new soil C have been found to play a role in changing C contents in other systems that have been converted from grassland to woody vegeta-

Table 2. Means of Decomposition Rate (\pm SE) for Soil Carbon ($\text{nmol mol C}^{-1} \text{s}^{-1}$) and Cumulative Loss Rate (mmol C mol C^{-1}), for each Vegetation Age Class

Age Class	Week 1 ($\text{nmol C}/$ mol C/s)	Week 5 ($\text{nmol C}/$ mol C/s)	Week 9 ($\text{nmol C}/$ mol C/s)	Week 13 ($\text{nmol C}/$ mol C/s)	Cumulative ($\text{mmol C}/$ mol C)
0 y	1.39 (.02)	1.16 (.06)	0.86 (.03)	0.85 (.11)	9.05 (.46)
5–10 y	1.67 (na)	1.21 (na)	0.92 (na)	0.96 (na)	10.00 (na)
15–20 y	1.55 (.11)	1.22 (.09)	0.97 (.11)	0.85 (.06)	9.69 (.66)
20–25 y	1.49 (.28)	1.31 (.16)	1.03 (.09)	0.99 (.10)	10.30 (1.21)
P value				0.65	0.60

n = 3 composite samples per age class (except, *n* = 1 for 5–10-year-old pine; this age class was excluded from statistical analysis, but the values are given for reference). na = not applicable

The P value reported below week 13 refers to the result of a repeated-measures ANOVA using data from the 4 individual weeks when decomposition was measured. The P value for cumulative decomposition is the result of a one-way ANOVA.

Table 3. Mean Carbon–Nitrogen (C:N) and Carbon–Phosphorus (C:P) Ratios (\pm SE) by Vegetation Age Class

Age Class	Surface horizon (0–10 cm)		A Horizon	Litter
	C:N	C:P	C:N	C:N
Grassland	19.3 (0.3) ^a	145.3 (22.8) ^a	16.0 (1.6) ^a	34.3 (1.7) ^a
5–10 y pine	17.7 (0.5) ^a	106.7 (11.2) ^a	14.2 (1.8) ^a	37.3 (1.8) ^a
15–20 y pine	15.2 (0.2) ^b	103.1 (3.1) ^a	12.2 (0.2) ^a	32.6 (1.8) ^a
20–25 y pine	15.9 (0.3) ^b	107.3 (17.2) ^a	14.6 (1.2) ^a	47.6 (2.1) ^b

Total N and total P were used for C:N and C:P ratios.

Within each column, 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, except for C:P and A horizon C:N, which were analyzed with S. Kruskal-Wallis tests. *n* = 30 per age class (except, *n* = 10 for 5–10-year-old pine) for surface horizon C:N; *n* = 3–9 per age class for C:P; *n* = 2–6 per age class for A horizon C:N; *n* = 3 per age class for litter C:N.

tion (Jackson and others 2002). Similarly, the decline in soil C under pine at Cotopaxi is likely the result of changes in both inputs and outputs of C. Establishment of pine plantations, including site preparation and other factors as well as tree growth, affect inputs by altering the quantity and location (above versus belowground) of organic matter additions to the soil. In particular, afforestation is expected to alter the depth and distribution of plant roots (Jackson and others 2000), as well as root production and turnover (Guo and Gifford 2002). Carbon losses from the soil, determined primarily by losses through decomposition, may be affected by changes in substrate quality, by changes in soil moisture or temperature that affect soil microbial activity (Ohta 1990; Lips and Hofstede 1998; Jug and others 1999), and by changes in the microbial communities themselves (Chapela and others 2001).

The replacement of grasslands with plantations may result in a reallocation of C from belowground—where in volcanic soils it tends to be stabilized by noncrystalline minerals (Torn and others 1997)—to aboveground. In plantations, a shift in vegetation cover occurs as the stands age (Hofstede

and others 2002), with grasses becoming shaded out by the trees (Turner and Lambert 1988). Grasses generally form extensive fine-root systems, and the input of root biomass is thought to be the major contributor to SOM in grasslands (Kelly and others 1996; Guo and Gifford 2002), whereas root production and turnover by pine or other conifers tends to be lower than that of grasses (Scott and others 1999; Guo and Gifford 2002). In Cotopaxi, the shift in vegetation cover, with a decline in herbaceous cover in particular in the 15–20-year-old stands, may account for part of the decline in soil C with stand age.

In contrast to grasslands, most detritus under pine is in the form of litter added to the surface (Scott and others 1999). This, however, may not translate into soil C storage (Pauker and Seastedt 1996; Guo and Gifford 2002). At Cotopaxi, the C:N ratio of the litter was higher in the oldest pine stands than in the other three vegetation age classes. This suggests that litter from older pine stands should decompose more slowly and may cause a delay in the incorporation of litter into the mineral soil. Quideau and others (2001) described this type of pattern under planted

Table 4. Mean Soil Temperature (at 50-cm depth) and Mean Water Content (\pm SE) in the A Horizon by Vegetation Age Class.

Age Class	Temp. at 50 cm ($^{\circ}$ C)	Field Moist Water Content (%)	Saturation Water Content (%)	10 kPa Water Content (%)	33 kPa Water Content (%)	1,500 kPa Water Content (%)
0 Y	9.6 (0.3) ^a	38 (3) ^a	49 (5) ^a	36 (4) [*]	31 (3) ^a	24 (3) ^a
5–10 Y	11.8 (0.4) ^b	20 (1) ^{abc}	50 (na) ^a	26 (1) [*]	18 (9) ^b	14 (3) ^{ab}
15–20 Y	9.6 (0.3) ^a	21 (1) ^b	46 (3) ^a	24 (1) [*]	17 (1) ^b	14 (2) ^b
20–25 Y	11.4 (0.0) ^b	15 (1) ^c	42 (2) ^a	22 (1) [*]	14 (1) ^b	9 (1) ^b
P value	0.006	0.000	0.36	0.02	0.000	0.008

All values are volumetric water contents (weight of soil at given pressure–dry weight)/volume of soil.

$n = 1–2$ per age class for temperature and saturation water content; $n = 2–6$ per age class for 10 kPa water content; $n = 3–9$ per age class for 33 and 1,500 kPa water content and field moisture. na = not applicable.

Within each column, 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 the variables 33 and 1,500 kPa water content.

Kruskal-Wallis tests were used for the other variables.

*Although the Kruskal-Wallis test indicated significant differences among age classes ($P = 0.02$), none of the pairs were significantly different using the adjusted, comparisonwise α of 0.013. However, the largest differences were between grassland and 15–20-year-old pine ($P = 0.04$) and grassland and 20–25-year-old pine ($P = 0.02$).

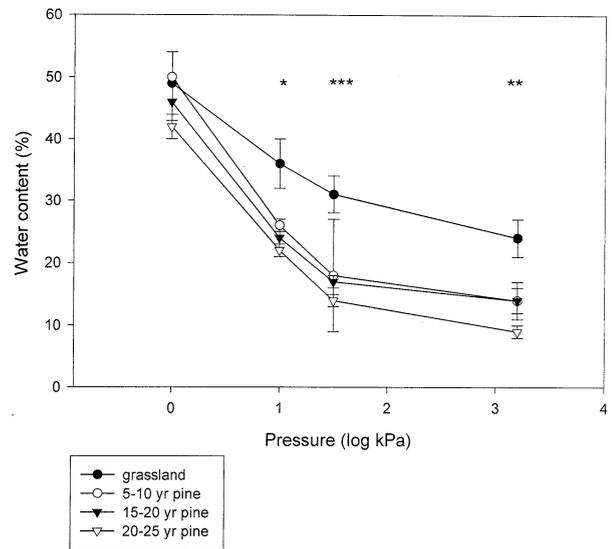


Figure 2. Volumetric water content (mean \pm SE) of A horizon soils by vegetation age class. Asterisks indicate significant differences among age classes (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$). Water contents were tested at saturation, 10 kPa, 33 kPa, and 1,500 kPa. $n = 1–2$ per age class for saturation; $n = 2–6$ per age class for 10 kPa; $n = 3–9$ per age class for 33 and 1,500 kPa.

Coulter pine (*Pinus coulteri*) and suggest that a large part of the litterfall is decomposed to CO_2 at the surface rather than being incorporated into the mineral soil. A similar phenomenon may occur at Cotopaxi (where the average thickness of the litter layer increased from 4 cm in the two youngest age classes to 7 cm in the two oldest age classes), contributing to the large decline in C in the mineral soil over the chronosequence.

A number of factors influencing losses of soil C may also be altered under pine. First, large differences in soil moisture were found among age classes. In Cotopaxi, field moisture in the A horizon of the oldest pine stands was less than half that in the grasslands, and the lower water content of the pine stands likely plays an important role in producing the lower C contents. This suggestion is consistent with the literature on woody invasion as well as that on the dynamics of highland tropical humid ecosystems. Jackson and others (2002) demonstrated the importance of soil moisture in controlling SOC concentrations after woody invasion. Those authors found that, when drier grassland sites were invaded with woody vegetation, SOC increased; however, on wetter sites one-fifth to one-half of soil C was lost after woody invasion. In the wet páramo sites, therefore, a decline in soil C after conversion of grass-

land to pine should be expected. It has been found that the mechanism by which moisture controls soil C storage in other tropical humid upland systems is through lowering redox potential and decreasing decomposition (Schuur and others 2001). This mechanism appears to be important in páramo ecosystems as well, where high soil moisture is considered to be among the most important factors in retarding decomposition and driving high C storage. Drying of the soil causes an increase in decomposition and a loss of soil C (Hofstede and others 2002; Hofstede 1995) and may be the dominant factor in soil C loss after afforestation. This could cause a positive feedback whereby, as SOM declines, soils are less able to retain water and, as a result, decomposition may accelerate, causing further declines in SOM. It should be noted that low soil temperature is also considered to be an important factor in slowing decomposition in páramos (Lips 1998), and the establishment of a plantation may increase soil temperature, accelerating decomposition of soil C. However, the trend in soil temperature was not consistent with the trend in SOC loss at Cotopaxi, in particular in the 15–20-year-old stands, which had the same mean soil temperature as the grasslands but significantly lower soil C.

The quality of the substrate also may influence the rate at which decomposition of organic material occurs. Soil C:N ratios in the 0–10-cm depth varied significantly among age classes, with the highest ratio in the grasslands and the lowest in the intermediate-aged pine, followed by the oldest pine (Table 3). Although C:P ratios were not significantly different among ages, the pattern was similar to that of C:N ratios; the ratio in the grasslands was 145.3 compared to 103.1–106.7 for the pine stands (Table 3). The lower C:N and C:P ratios of the soil in the older pine stands should favor more rapid degradation of SOM there. However, C:N ratios were not significantly different among age classes in the mid-A horizon (Table 3), yet SOC declines there were greater than in the surface horizon. Furthermore, there was no significant difference in decomposition rates when the soils from the 0–10-cm depth were incubated in the laboratory under uniform temperature and moisture conditions. Although the incubation only assesses short-term decomposition rates, together these factors suggest that changes in soil environment may play a more important role than substrate quality in controlling decomposition at Cotopaxi, and that the decrease in soil moisture under pine may be the dominant factor in loss of soil C.

In addition to these factors, there may be other variables that contribute to the loss of soil C following afforestation. It has been suggested that the ectomycorrhizal fungi that are introduced with Monterey pine in plantations in páramo grasslands are able to access nonhost C, such that soil C fixed in the grasslands prior to the introduction of pine is oxidized (Chapela and others 2001). Others have suggested a role for pine roots in stimulating decomposition, by breaking soil structure, which reduces physical protection of soil C (Guo and Gifford 2002).

Soil Water Retention

A shift from herbaceous to woody vegetation can cause rapid changes in the ecosystem water balance (Jackson and others 2000; Duncan 1995; Fahey and Watson 1991). A decline in soil moisture after afforestation is often attributed to greater canopy interception and evapotranspiration by trees than grasslands (Dye 1996; Le Maitre and others 1996). However, in Cotopaxi, the introduction of pine also had a marked influence on the water retention capacity of the soils, reflecting the alteration of soil properties in addition to altered water use.

The change in soil water retention capacity with stand age is likely associated with the decline in SOM that also occurred along the chronosequence. Soil organic matter is one of the factors that contributes to the high water retention capacity of Andisols, because it promotes the formation of stable soil aggregates, creating a large volume of mesopores and micropores, which hold capillary and hygroscopic water, respectively (Nanzoyo and others 1993). The results from Cotopaxi demonstrate that there was little difference between grassland and pine soils when the soils were saturated, although the difference was much greater at higher tension, reflecting water held in meso- and micropores. This suggests a change in pore size distribution and perhaps a reduction in fine pores under pine. The loss of SOM under pine could contribute to this change, although pine roots may also play a role. It has been hypothesized that pine roots may break soil structure (Guo and Gifford 2002), and the volume of meso- and micropores would be reduced in the absence of strong aggregate formation (Nanzoyo and others 1993), contributing to the loss of water retention capacity. Again, a positive feedback may occur, whereby a loss of water retention capacity contributes to a loss of SOM, further reducing the ability of the soil to retain water.

IMPLICATIONS OF REGIONAL AFFORESTATION

The shift in the location of total ecosystem C from below- to aboveground and the decline in SOC have implications for long-term C storage. Soil C in the grassland sites at Cotopaxi is low relative to other páramo sites due to the young age of the soils and the fact that they are at a very early stage of C accumulation. However, the rate of C accumulation appears to be quite rapid in these soils. Barberi and others (1995) dated the uppermost paleosol in nearby soils at 290 ± 80 y bp, which was overlain with two layers of lapilli. As such, it is unlikely that the A horizons at Cotopaxi have developed over a period longer than approximately 300 years. Schlesinger (1997) cites soil C accumulation rates of $1\text{--}12$ g C m⁻² y⁻¹, with the highest rates under cool, humid conditions and the most rapid rate for a young volcanic ash soil. Assuming this rate for Cotopaxi, an accumulation of 3.6 kg C m⁻² would be expected over 300 years, yet the average C content in the top 10 cm in the Cotopaxi grasslands was 5.0 kg C m⁻² and that of the entire A horizon (mean depth = 32.5 cm) was 6.3 kg C m⁻².

Planting these sites with pine contributes to aboveground C accumulation while the trees are growing. However, at the same time, it has the effect of halting the process of soil C accumulation. In the absence of pine, C accumulation would continue in these soils and, although the rate would decline as the soils age, accumulation likely would not level off for several thousand years (Chadwick and others 1994). In older páramo soils, where A horizons can be 2 m in depth, soil C has been found to reach levels as high as 170 kg C m⁻² (Hofstede 1999). Although this study does not provide evidence of a net gain or loss of total ecosystem C (including aboveground living biomass and litter as well as SOM), it does clearly show that afforestation in Cotopaxi results in a tradeoff of belowground for aboveground C. This suggests that the C stock is being transferred from a pool that is more stable over a longer time period to one where C is much more susceptible to loss by fire and to disappearance of the litter layer runoff with. At the time of harvesting (25 years), slash and litter are typically burned prior to planting the second rotation, so that some of this aboveground C pool is returned to the atmosphere.

The effect of plantations on water retention, given the irreversible drying that can occur in Andisols, is of particular relevance for issues of watershed management. Although unsaturated Andisols have high hydraulic conductivity relative

to other mineral soils, their hydraulic conductivity decreases rapidly as soil water content declines (Nanzyo and others 1993). It has been demonstrated here that, although water contents in grasslands remain relatively high at high negative potentials, the soils under pine drop rapidly in water content. A decrease in water yield from catchments as tree cover increases has been found in a number of other studies of afforestation (Jackson and others 2000; Bosch and Hewlett 1982) and a similar effect can be expected in Cotopaxi. The effect of pine on soil water contents therefore has implications for water storage and provision to lower elevations.

Ecosystem management must include long-term sustainability, including the sustainability of ecosystem processes such as hydrologic flux and storage and biogeochemical cycling and storage (Christensen and others 1996). This study suggests that, although plantation forestry in páramo grasslands may provide some economic benefits, it constitutes a tradeoff in which key ecosystem services—specifically soil C storage and water retention—appear to be severely diminished. This study brings into question the soundness of promoting afforestation in páramo ecosystems with the objective of C sequestration and highlights the importance of considering both aboveground and belowground changes in C when calculating C credits. It also suggests that plantation forestry in páramos may not be sustainable in the long term with respect to the maintenance of the hydrologic function of páramo grasslands. Although the information provided here is site-specific, it confirms many of the findings from pine plantations in other parts of the world and the few studies that exist in the Andes. It helps to clarify some of the ecosystem level effects that can be expected under pine plantations in highland Ecuador and can be useful for policy makers and landowners who will make decisions about this land use and its appropriateness.

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