High altitude tropical secondary forests: a competitive carbon sink?

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Abstract

High altitude tropical regions have been heavily deforested and offer large areas for carbon offsets by secondary forest regeneration. However, a general assumption exists that productivity, and thus, carbon sequestration of high altitude forests is low, but the scarcity of data from high altitude tropical forests does not allow for a sound confirmation of this assumption. To determine the carbon sequestration potential of natural forest regeneration and reforestation efforts at high altitudes, aboveground biomass was quantified of several successional stages of two monospecific secondary forests in the high Ecuadorian Andes. The studied forests were, at 3200 m, an *Alnus acuminata* forest with 8-, 20-, 30- and 45-year-old stands and, at 3600 m, a *Polylepis incana* forest with 6-, 15- and 30-year-old stands and old growth forest without known age. Both trees are pioneer species. Additionally, a soil survey was conducted and leaf N/P ratios and N and P retranslocation rates were determined. Total aboveground biomass (TAGB) estimates of the oldest stages of the two forests were 241 Mg ha^{-1} for the *Alnus* and 366 Mg ha^{-1} for the *Polylepis* forest. Productivity, expressed as annual aboveground biomass accumulation (ABA) was in both forests highest in the establishment phase (14.2 and 15.0 Mg ha^{-1} per year at 8 and 6 years, respectively) due to high sapling numbers, and then slowed down significantly (5.9 and 6.9 Mg ha^{-1} per year, respectively at age 30). TAGB and ABA figures of the investigated forests are comparable to those of lowland tropical forests and do not indicate a significant decrease of these parameters at higher altitudes in the tropics. Analysis of site conditions, ecological requirements and ecophysiological properties of the tree species indicated that in both cases an optimal combination of these factors strongly favoured forest growth. It is not possible to verify whether our forests are representative for other high altitude tropical forests or if they should be treated as exceptional cases. The results do show, however, that high carbon offsets at high altitudes are possible. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Aboveground biomass; Carbon sequestration; Tropical secondary forests; High Andean forest; Ecuador; *Alnus*; *Polylepis*

1. Introduction

The role of tropical secondary forests as a carbon sink, either by natural or man-induced regeneration, is receiving increasing attention in the debate on the global carbon cycle. Indeed, over 40% of the C stored

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in terrestrial biomass is stored in tropical forests (Brown and Lugo, 1982; Dixon et al., 1994; Phillips et al., 1998), of which 40% are secondary and in some stage of regeneration (Brown and Lugo, 1990). The potential for CO_2 sequestration by regenerating forests and reforestation is considerable (Dixon et al., 1994; Houghton, 1996). Brown et al. (1996) give an overview of global estimates for the potential quantity of C that might be sequestered and conserved by forest management between 1995 and 2050. These estimates imply that roughly one third of the global potential would be accounted for by secondary forest regeneration in the tropics. Being a natural process, forest regeneration also has the benefit of being relatively cheap and of conserving biodiversity, water and soil resources.

Studies on the C sink role of tropical forest regeneration have concentrated mainly on tropical lowland forests (Brown and Lugo, 1982, 1990; Nabuurs and Mohren, 1995; Dabas and Bhatia, 1996; Deans et al., 1996; Scatena et al., 1996; Hughes et al., 1999, among others). This is not surprising since 85% of the world's tropical forests are located in the lowland biomes as opposed to 15% in montane areas (FAO, 1993). Only little research on carbon dynamics has been carried out in montane forest systems and the number of available studies decreases with altitude. Most authors observe or assume a decrease of forest biomass per hectare and/or of productivity with altitude (Edwards and Grubb, 1977; Weaver and Murphy, 1990; Delaney et al., 1997; Raich et al., 1997; Bruijnzeel and Veneklaas, 1998; Waide et al., 1998; Aiba and Kitayama, 1999), though studies exist that do not confirm this assumption (Brown and Lugo, 1982).

Many montane forests are under high human pressure (Hamilton et al., 1995) and its deforestation rates are estimated at about 1.1% annually over the past years (Doumenge et al., 1995). In Ecuador, for example, remnants of the forests in the densely populated ''inter-Andean valley'' (2000–4000 m), between the two Andean mountain chains, nowadays cover no more than 3% of the original area (Brandbyge and Holm-Nielsen, 1992) and of all Andean forests in Ecuador only 25% are left (Harcourt and Sayer, 1996). If we only consider economically marginal agricultural lands in the Ecuadorian Andes, there is already an area of hundreds of thousands of hectares that could be used for carbon sequestration

through forest regeneration. Those marginal lands are usually found near the timberline at high altitudes. Investments from developed countries into carbon sequestration in the Ecuadorian Andes are already being made. An example is a recent reforestation program, financed by the Dutch FACE foundation, which uses high altitude marginal lands (up to 3800 m) for large-scale forest plantations. Mixtures of native tree species are planted which in time are intended to develop into natural forests (FACE Foundation: http:\\www.facefoundation.nl).

We investigated the carbon sequestration potential of high altitude regenerating forests by assessing the aboveground biomass of several successional stages of two monospecific secondary forests in the Andes of Ecuador. The tree species that formed the canopy of these forests were *Alnus acuminata* H.B.K. (Betulaceae), a native Alder species, and *Polylepis incana* H.B.K. (Rosaceae). Both are relatively wide spread tree species in the Northern Andes and well known for their suitability for small to middle scale agroforestry and reforestation programs (Brandbyge, 1992; Añazco Romero, 1996). Additionally, in order to understand local plant-soil relations and their relevance for forest growth we surveyed the soils in the forests studied and studied N and P cycling in the tree species.

2. Methods

2.1. Study sites and species

2.1.1. Oyacachi Alnus forest

The Oyacachi *Alnus* forest is situated at 2500–3200 m in a valley on the Amazonian slopes of the Andes, within the Cayambe-Coca Ecological Reserve, Napo Province, Ecuador (00°13′S 78°03′W), about 45 km east of the capital Quito. DIVA (1997) give an extensive description of the physical, cultural and biological characteristics of the Oyacachi area. Precipitation in the valley (2000–2500 mm) is two to three times larger than potential evapotranspiration. Soils are classified as Andosols and formed in volcanic ashes, the youngest deposits originating from the Cayambe volcano eruption of about 600 years ago (Marocco et al., 1994). The volcanic rocks overly low metamorphic schists, which locally crop out.

The valley itself, about 1 km wide, is U-shaped as a result of glacial activity and is prone to frequent landslides due to the humid conditions. Such landslides can cover quite extensive areas on the valley bottom. Many of these landslides are covered with monospecific forests of *A. acuminata* of various age. This species, native to the Andes, is known to be a relatively fast-growing pioneer, to have a symbiotic relationship with a nitrogen fixing actinomycete, and to produce wind-dispersed seeds that germinate rapidly. These traits enable *A. acuminata* to swiftly colonise free spaces, such as landslides (DIVA, 1997; Murcia, 1997) and it is therefore considered as a suitable catalyst species for forest regeneration, and thus, for carbon sequestration. *Alnus* trees are of regular, straight and tall stature (20–25 m) with a relatively narrow, open crown. They prefer moist site conditions and well-drained soils (Carlson and Dawson, 1985; Añazco Romero, 1996).

The Oyacachi valley is inhabited by an indigenous community, which uses the *Alnus* forests on a small scale as a wood resource for handicraft products and construction (DIVA, 1997). The main logging areas are situated at several km distance from our study sites and therefore the forests we investigated had not been significantly disturbed, although some trees had been felled, especially in the older stands. Several local people confirmed the ages of the forests by remembering the landslide events. Following their indications, we were able to select forests with ages of 8, 20, 30 and 45 years for our study. The sites are situated at altitudes between 3100 and 3200 m, where mean annual temperatures are 10–11 °C (DIVA, 1997). Mature monospecific *Alnus* forest does not exist, since this pioneer species will be gradually replaced by other tree species as soon as mortality of mature *Alnus* trees occurs. Changes in site conditions as a result of forest succession, of which light limitation for the photosensitive seeds and saplings probably plays the most important role (Ruiz Peña and Orozco de, 1986), inhibit the establishment of new *Alnus* trees.

2.1.2. Pifo Polylepis forest

The Pifo forest with *P. incana* is situated on the western slope of the eastern Andean mountain chain, which drains into the inter-Andean valley. The location (00°14′S 78°15′W) is about 25 km east of Quito and 20 km southwest of Oyacachi, in the Parroquia of Pifo, Pichincha province. The forest grows on the ±150 m wide bottom of a glacial valley, at an elevation of 3600 m. Climatic data are available from the Papallacta climatic station, at a distance of 10 km from the forest and at the same altitude. However, this station lies on the eastern (Amazonian) slopes of the Andes and can therefore not be representative for the study site. Nevertheless, its climatic data can serve as an indication. Mean annual precipitation at Papallacta is 1500 mm, evapotranspiration 554 mm per year and mean relative air humidity is 93.3%. There is no season with moisture deficit. Annual mean temperature is 6.6 °C (Martinez, 1995). DIVA (1997) use a lapse rate for the Oyacachi area, which, if applied to the Pifo site, results in a mean annual temperature of 8 °C. Soils are formed in young volcanic ashes that are high in biotite and were deposited 330 years ago by the last major eruption of the Cotopaxi volcano, which did not reach the Oyacachi area (Hall and Mothes, 1984). Although, the valley is also U-shaped, landslides are not as frequent as in the Oyacachi valley, probably because of the absence of an impermeable subsoil close to the surface.

Large parts of the valley bottom are covered with monospecific *P. incana* forests of varying age. This species is native to the Andes of Ecuador and Peru and has an altitudinal range from 3500 to 4300 m. The trees are of gnarled and twisted stature and are up to 12 m tall. They do not seem to have a clear preference for a specific soil type or moisture regime (Brandbyge and Holm-Nielsen, 1992; Kessler, 1995). *Polylepis* as a genus has VA-mycorrhiza, which possibly explains its ability to colonise raw soils and to dominate the forest communities where it occurs (Kessler, 1995). Mixed stands, although less common, can also be observed. The occurrence of *Polylepis* forests is believed to have been strongly reduced by human influences (Simpson, 1986; Kessler, 1995).

The major part of the *Polylepis* forests at Pifo is privately owned and guarded. Parts of the forests are used for extensive grazing by cattle and for fuel wood collection. By means of interviews with an old guardian and an elder local herdsman, we were able to select homogeneous forest patches of 6-, 15- and 30-year-old and old growth forest. The 6-year-forest, about 5 m wide, established on the fringe of a dirt road of that age. The 15-year-forest re-colonised a cleared forest area that was used as a pasture for 2

years. The 30-year-forest established on a landslide. Of the history of the old growth forest we have no details other than that our informants could neither remember a time when this forest did not exist, nor whether the forest had ever been of smaller stature.

2.2. Biomass subsampling

Data were collected in the field in October and November 1998. We applied a non-destructive bio-mass estimation method, as opposed to the direct method of clear-cutting and weighing the actual stand-ing vegetation on a known surface. Normally, a non-destructive or indirect method estimates forest woody mass by means of the consecutive measuring, felling and weighing of a limited number of trees and then extrapolating these data to larger scale tree inventories using regression equations. We were not, however, in a position to fell any trees in the two forests. Neither could we use regression equations from other studies, because they do not exist for the given species, nor for any other forests at these altitudes. We, therefore developed a new method, based on partial harvesting of tree crowns, on bole volume and mass calculations and on extrapolation to tree inventory data.

The tree inventory was carried out in three plots per secondary forest stage. Plot size depended on the size and the age of the forest patch and varied from 50 to 1000 m^2, with 1000 m^2 as the standard in the older forests. If possible all three plots were taken from the same patch. Selection criteria for the patches and plots were low to absent human disturbance, regular surface and similar slope. Within the plot, all living trees with dbh > 3 cm (diameter at breast height: 1.30 m) were measured for dbh, bole height and total tree height.

Sample trees were selected for bole volume mea-surements and crown mass sampling: three to five trees per plot in the *Polylepis* forest and a total of seven trees in the *Alnus* forest. Bole volume was measured by subdividing the bole into straight compartments and measuring the top and bottom diameters and length of these compartments. The volume of each compartment was then calculated assuming a cylinder with the average of the top and bottom diameters. More and smaller compartments were necessary for volume calculation of the gnarled *Polylepis* boles than for the straight *Alnus* boles. The ratio between the cumulative volume of the bole compartments (the

actual measured volume) and the volume of the bole if it were a cylinder is called the form factor (Ff). Ff, therefore expresses the conicity of the tree. The bole mass of all trees measured in the tree inventory, was thus, calculated using the formula:

$$Mb = WD(\tfrac{1}{4}\pi(dbh)^2 \times Hb \times Ff_a) \tag{1}$$

in which the second term is bole volume (m^3) and Mb: bole mass (Mg), WD: average wood density (Mg m^{-3}), obtained from crown samples, dbh: dia-meter at breast height (m), Hb: bole height (m), Ff$_a$: average form factor of all sampled trees of a species.

In the older *Alnus* forests, some trees had been logged: 5% of the individuals in the 20-year-forest, 10% in the 30-year-forest and 11% in the 45-year-forest. The diameter of the stumps was measured and corrected to dbh. Extrapolation from the various dia-meters measured on the sample tree boles showed that for *Alnus* the base diameter is on average 8% larger than dbh. A regression equation using dbh and bole volume was calculated with all living *Alnus* trees in a plot and this equation was then used to estimate the bole volume of the logged trees.

Crown mass of the sample trees was estimated by harvesting an eye-estimated portion of the crown, which was usually between 20 and 40%. We consider errors in the eye-estimation not to be higher than 0.15. The harvest was subdivided into a branches compart-ment and a branchlets/leaves compartment, which were each weighed in the field. Three subsamples of each compartment were weighed in the field and then oven dried in the lab at 90 °C until constant weight was reached. Crown mass was calculated using dry weight/ fresh weight ratios and extrapolation to full crown size. One of the subsamples from the branches compartment was always taken from the base of the branch, closest to the bole. The volume of this subsample was measured prior to drying, and was used to calculate wood density (WD).

For the *Polylepis* sample trees within each forest age a regression equation was calculated with bole volume as the independent and crown mass as the dependent variable. This equation was then used to calculate crown mass for all *Polylepis* trees in the plots of the specific forest age. Insufficient *Alnus* trees were sampled for regression analysis per age class, so for this species the average bole volume/crown mass ratio

was applied to all classes. This method was justified by the relatively small variability within the determined ratios of the sampled *Alnus* trees (average = 0.25; S.D. = 0.05; $n = 7$). Bole and crown mass combined for all trees within the plots were finally extrapolated to tree mass per hectare.

In the 6 years *Polylepis* forest, trees were hardly bigger than large shrubs and branching started from the base. Here, four trees representative for the observed range of tree sizes were harvested and weighed completely, which was justified by high tree densities. Extended tree counting was conducted over a larger area of the forest patch. All counted trees were then given the average weight (average = 22.87 kg/tree, S.D. = 8.45) of the sampled trees and the result was extrapolated to tree mass per hectare.

Tree mass of other species present, often as small trees in the understorey of the 20-, 30- and 45-year-*Alnus* forests, was estimated using the same general method as described above. One representative tree per species was sampled and its form factor, bole volume/crown mass ratio and wood density applied to the other trees present in the plots. Standing and fallen dead tree mass, provided the trees had not yet seriously decayed, was calculated as above, but not counting the crown and using a specific wood density derived from field samples. In the 8-year-*Alnus* forest, an additional class of dying trees was identified, also with its specific wood density.

Understorey and ground litter biomass were determined in three $4 \, \text{m}^2$ subplots per plot. All living vegetation of dbh < 3 cm and all dead, but not fermented vegetation within these subplots was collected and weighed in the field. Dry weight/fresh weight ratios of three representative subsamples were determined using the method described above, then used to extrapolate to hectare level. Understorey biomass may have been negatively influenced by extensive grazing in the 6-, 15-year- and old growth *Polylepis* forests.

2.3. N and P recycling

Fully developed and undamaged fresh leaves were collected from different 8-, 15- and 20-year-old *Alnus* trees and from 15-year-old and old growth *Polylepis* trees in February 2000. From the same trees leaves were collected that had recently fallen or that were about to fall, loosened from the tree by gentle shaking.

For N and P concentration and N/P ratio determination, the leaves were ground and then oven dried in the laboratory at 70 °C. Subsamples of 100 mg were destroyed with H_2SO_4 and H_2O_2 at 340 °C. N and P were measured spectrophotometrically on a continuous flow analyser.

2.4. Soil sampling and analysis

Superficial soil samples (0–5 cm in mineral soil) were taken from each plot, either in one mixed sample of 10 subsamples or in two mixed samples of five subsamples each. This was repeated twice: one sample with known volume (taken with a soil probe) for moisture content and bulk density determination (drying at 105 °C for 24 h), the other without known volume for chemical analysis. The samples were analysed for P (Bray II), organic matter (Walkley Black), K (colorimetrically) and pH-H_2O (1:2) at the soil laboratory of Servicio Ecuatoriano de Sanidad Agropecuario (SESA-MAG) in Tumbaco. Statistical methods included regression analyses for inter-parameter and soil/forest age relationships within each forest and a one-way ANOVA to compare parameter values between the *Alnus* and *Polylepis* forests.

3. Results

3.1. Aboveground biomass accumulation during succession

Total aboveground biomass (TAGB) was 241.4 Mg ha^{-1} in the *Alnus* forest after 45 years and 365.6 Mg ha^{-1} in the *Polylepis* old growth forest. Both forest types reached their highest productivity (expressed as annual biomass accumulation (ABA), which is calculated as TAGB at a certain age divided by that age) in the first 7 to 8 years of growth (14.2 and 15 Mg ha^{-1} per year for the *Alnus* and *Polylepis* forest, respectively; Table 1). In the *Alnus* forest, almost half (113.8 Mg ha^{-1}) of TAGB of the 45-year-forest had already developed after 8 years. In the *Polylepis* forest, one-fourth (90 T ha^{-1}) of TAGB of the old growth forest was standing after 7 years. The primary cause of this high growth rate was the establishment of very high densities of saplings (19,000 individuals per hectare in the *Alnus* forest,

Table 1
Average total aboveground biomass (TAGB in Mg ha^{-1}) and biomass of the contributing compartments, annual biomass accumulation (ABA, Mg ha^{-1} per year) and tree density (individuals per hectare) of the high montane Ecuadorian *Alnus* and *Polylepis* forest plots

Oyacachi *Alnus*	8 years	1 S.E.[a]	20 years	1 S.E.	30 years	1 S.E.	45 years	1 S.E.
TAGB	113.8	13.78	118.1	31.62	176.9	15.37	241.4	12.80
Total living tree	86.6	7.02	113.7	30.65	151.1	7.65	219.5	5.71
Bole	70.4	4.78	86.1	28.21	106.9	5.24	168.2	1.01
Crown	16.2	2.24	27.6	2.45	44.2	2.42	51.3	4.71
Dying tree	6.3	1.12	0	0	0	0	0	0
Dead tree	2.6	0.33	0.2	0.01	0.7	0.03	3.4	0.03
Understorey	7.4	2.55	1.6	0.36	4.8	1.73	6.8	3.48
Litter	11.0	2.76	3.1	0.59	18.3	5.95	11.8	3.53
ABA	14.2	–	5.9	–	5.9	–	5.4	–
Tree density	19000	–	2747	–	1037	–	1533	–
Pifo *Polylepis*	6 years	1 S.E.	15 years	1 S.E.	30 years	1 S.E.	Old forest	1 S.E.
TAGB	90.0	17.62	93.0	15.96	205.9	40.62	365.6	58.63
Total living tree	77.3	16.48	77.2	11.20	165.9	38.09	326.0	45.85
Bole	–	–	51.9	4.45	97.8	11.23	217.3	24.84
Crown	–	–	25.3	6.75	68.1	26.86	108.7	10.90
Dying tree	0	0	0	0	0	0	0	0
Dead tree	0	0	0	0	0	0	0	0
Understorey	0	0	2.5	0.81	0	1.02	5.5	1.71
Litter	12.7	1.14	13.2	3.95	40.0	1.51	34.0	11.07
ABA	15.0	–	6.2	–	6.9	–	–	–
Tree density	4370	–	3283	–	4333	–	1333	–

[a] 1 S.E.: 1 standard error.

4400 individuals hectare with three to five stems each in the *Polylepis* forest), which clearly demonstrates the colonising capacities of both species. After establishment, individual tree growth initiated competition for resources, resulting in lower tree densities (2747 in 20-year-*Alnus*, 3283 in 15-year-*Polylepis*). In the *Alnus* forest, this process had already been initiated at 8 years, as evidenced by the relatively high contribution to TAGB of dying trees (6.3 Mg ha^{-1}). TAGB increase slowed down by this self-thinning process and tree biomass was about the same in the 15- (77.2 Mg ha^{-1}) and 6-year (77.3 Mg ha^{-1}) *Polylepis* forests. At some point after this, individual tree growth surpassed the, by now lesser, inhibiting effects of tree mortality and caused a new increase in forest ABA in the *Polylepis* forest (6.5 and 6.9 Mg ha^{-1} per year in the 15- and 30-year-forest, respectively). In the *Alnus* forest, growth remained constant at 5.9 Mg ha^{-1} per year until a slow decrease had been initialised at 45 years to 5.4 Mg ha^{-1} per year. Growth is expected to continue until maximum TAGB is reached at maturity.

Woody biomass was calculated making use of the wood densities that were obtained from the wood samples taken to the laboratory. In the *Alnus* forests, wood density varied between 0.39 Mg m^{-3} in the 8-year-forest and 0.43 Mg m^{-3} in the 45-year-forest. For *Polylepis* no relationship with forest age was found and the average density of all samples was 0.44 Mg m^{-3} (S.D. = 0.06, $n = 24$).

Understorey biomass did not depend on forest age. In the 6- and 30-year-*Polylepis* forests no understorey vegetation at all was found, due to dense canopy coverage. The 15-year and old growth *Polylepis* forests were more open, which did allow some understorey vegetation to develop (2.5 and 5.5 Mg ha^{-1}, respectively). Litter accumulation showed a trend of increase with forest age in the *Polylepis* forest (up to 40 Mg ha^{-1} in the 30-year-forest), but not in the *Alnus* forest. Dead and dying tree mass were absent in the *Polylepis* forest. This may be explained by fuel wood collection by local inhabitants of the valley.

Contributions to TAGB by other species than *Alnus* in the Oyacachi forest were first noticeable in the 30-year-forest and increased in the 45-year-forest (average 7 and 15%, respectively; Table 2). Contributions to the number of tree individuals by these species were much higher (37 and 43%, respectively), showing that these individuals were still of small stature. In the *Polylepis* forest, very few individuals of other species were found.

3.2. N and P recycling

N concentrations in living *Alnus* leaves were twice as high as in living *Polylepis* leaves (35.4 and 17.5 mg g^{-1}, respectively; Table 3), P concentrations were 1.5 times higher (2.4 and 1.7 mg g^{-1}, respectively). Retranslocation of N out of dying leaves was high (56.5%) in *Polylepis* and low in *Alnus* (17.5%), while instead retranslocation of P was higher in *Alnus* (48.3%) and lower in *Polylepis* (32.6%). N:P ratios in living leaves had values around 14 in *Alnus* and around 10 in *Polylepis*.

3.3. Soils

In the soils, under the *Alnus* forests, organic matter percentage and pH showed a significant correlation ($R^2 = 0.57$, $^{**}P < 0.01$; Table 4, Fig. 1). Both parameters were very variable (pH range: 3.6–6.4, organic matter range: 3–58%). No other parameters showed significant correlations, but the coincidence of the lowest pH, highest organic matter percentage and highest P concentration (8.8 ppm) has to be mentioned. None of the parameters showed any correlation with forest age. P and K concentrations (ppm) were relatively low (P: average = 2.7, S.D. = 3.23; K: average = 78.5, S.D. = 40.40).

In the soils, under the *Polylepis* forests, no correlation between pH and organic matter was observed (Table 4, Fig. 1), nor any other significant correlation between the parameters. None of the parameters showed any correlation with forest age. Variability was small in pH values (average = 6.2, S.D. = 0.43), but relatively high in the other parameters. pH, P and K values were significantly higher under the *Polylepis* forests than under the *Alnus* forests (ANOVA; pH: $F = 58.07$, $^{**}P < 0.01$; P:$F = 15.57$, $^{**}P < 0.01$; K:$F = 35.62$, $^{**}P < 0.01$).

4. Discussion

4.1. Validity check of the applied method

The validity of the biomass estimation method used in this study was tested by comparison with other non-destructive estimation methods which, given the lack of high altitude studies were limited to lowland forests. We compiled regression equations from different studies and applied them to our data on the 45-year-*Alnus* forest (Table 5). Since *Alnus* trees are straight and tall and therefore relatively well comparable with lowland rain forest trees, we consider the application of regression equations from lowland forests as a good test for the trustworthiness of our results. We did not apply the equations to the *Polylepis* forest, because of the gnarled and multi-stemmed growth form of this tree species. Nevertheless, since the same method was applied for both forests, we assume that the results of the validity test of the method in one forest hold for both.

Our biomass estimation method provides the lowest values as compared to the other regression equations (Table 5). This might be due to *Alnus*' lower wood density relative to most lowland forest tree species, since the four equations that include wood density as a parameter (Eqs. (2), (4), (5) and (6)) give results that are relatively close to ours. Another parameter that seems important is tree height, since most of the equations that resulted in estimates close to ours, included this factor. This indicates that the average height of lowland forests trees is higher than that of our *Alnus* trees. We conclude from the comparison that our method yields results that are comparable to those of other non-destructive methods, although they may be relatively low. Another observation is that biomass regression equations seem to be site specific and that it would be erroneous to apply them onto other sites or even other life zones than they were developed for.

4.2. Forest growth patterns

The explosive growth that we found during the first years of establishment in both *Alnus* and *Polylepis* forests was also found in other forest regeneration studies (Brown and Lugo, 1982, 1990; Uhl and Jordan, 1984; Scatena et al., 1996). These studies all describe initial regeneration of a disturbed forest by pioneer

Table 2
Contribution (%) of each tree species present in the 12 high montane Ecuadorian *Alnus* forest plots to the number of individuals and to tree biomass (between brackets) in the plot

Age	8 years			20 years			30 years			45 years		
Plot no.	1	2	3	1	2	3	1	2	3	1	2	3
Species												
Alnus acuminata	100 (100)	100 (100)	100 (100)	97 (99)	99 (100)	95 (99)	73 (98)	65 (86)	50 (94)	54 (92)	63 (92)	53 (72)
Meriania sp.				3 (0.6)	0.6 (0.01)							
Gynoxys sp.					(0.05)							
Weinmannia sp.						1 (0.4)	4 (0.3)	4 (0.3)	4 (0.1)			
Miconia sp.1						3 (0.2)	6 (0.5)	2 (0.1)	13 (2)	3 (0.6)	2 (2)	3 (0.06)
Solanum sp.						2 (0.4)		1 (0.03)	6 (2)	10 (2)	17 (5)	19 (4)
Miconia sp.2							4 (0.2)	9 (0.6)	4 (0.4)	5 (5)	2 (0.6)	1 (0.01)
Piper bogotense							12 (0.3)	9 (0.1)	21 (0.5)	25 (0.9)	14 (0.8)	7 (0.1)
Asteraceae							2 (0.5)	10 (13)	3 (0.3)			9 (0.9)
Guarea sp.										3 (0.6)	0.8 (0.04)	3 (0.1)
Oreopanax sp.										0.8 (0.09)		
Buddleja bullata											5 (23)	
No. of species	1	1	2	3	4	6	7	7	6	7	8	

Table 3
Concentrations, retranslocation rates (average between brackets) and ratios of the elements N and P in living and dead leaves of high montane Ecuadorian *Alnus* and *Polylepis* forests of varying age

Age (years)	*N* (mg/g)	Retranslocation (%)	*P* (mg/g)	Retranslocation (%)	*N:P*
Alnus					
Living					
8	35.1		2.6		13.5
15	35.4		2.6		13.6
20	31.8		2.1		15.1
Dead					
8	25.2	28.2	0.8	69.2	
15	31.5	11.0	1.5	42.3	
20	27.6	13.2 (17.5)	1.4	33.3 (48.3)	
Polylepis					
Living					
15	17.6		1.8		9.8
Old	17.4		1.6		10.9
Dead					
15	6.5	63.1	1.3	27.8	
Old	8.7	50.0 (56.5)	1	37.5 (32.6)	

tree species that tend to colonise free spaces in great densities. However, in the absence of free spaces, for example in a dense grass cover, forest succession would be inhibited (Aide et al., 1996; Sarmiento, 1997). This is what probably occurred in the 15-year-*Polylepis* forest, which established itself on a site that had for two years been used as a pasture. Its tree biomass is lower than that of the 6-year-forest. Such influence of initial site conditions and land use history on forest growth was also found by Brown and Lugo (1990) and Hughes et al. (1999) who state that the TAGB of secondary forests on severely disturbed sites was consistently lower than that of secondary forests on slightly disturbed sites. As the explosive initial growth in both the *Alnus* and *Polylepis* forests was caused by very high sapling densities it is likely that forest plantations, where trees are usually planted at regular distances, will not show such a growth pattern.

Assessing forest growth patterns by means of a comparative study on forest patches with different ages has the flaw that these patches will never be entirely comparable. In our case, the initial site conditions and also the intensity of human influences, such as the fuel wood collection at Pifo, are differences that have to be taken into account when interpreting the results. However, the results from plots of a certain age are well comparable and the growth patterns (trends between ages) easily explainable. The impact of human influence in the forests is low, but may have resulted in a slight underestimation of actual TAGB and ABA.

For both investigated forests prediction of biomass at maturity is impossible. For the *Alnus* forest we expect that in its mature state the *Alnus* trees will have been replaced by other species, a process that is already active in the 30- and 45-year-forests. Of the old growth *Polylepis* forest, we do not know the age, nor if it has reached maturity yet. We cannot predict whether its TAGB will increase, decrease or remain constant in the future. Nevertheless, although we do not know what the biomass of our studied forests will be at maturity, we know that at least for the first generation of trees it is unexpectedly high. Apart from natural regeneration, we can assume that systems based on reforestation with these two species might, in the first 50 years or so, also attain considerable biomass, and thus, sequester high amounts of carbon, at least if planted under the same conditions as in the present study.

4.3. Comparison with forests at lower altitudes

The compilation of data in Table 6 shows that no clear trends can be detected in aboveground biomass

Table 4
Results of chemical and physical analysis of soil samples taken under high montane Ecuadorian *Alnus* and *Polylepis* forests of varying age[a]

Site (forest type)	Age	Plot no.	pH (H_2O)	Organic matter (%)	P (ppm)	K (ppm)	Moisture content (%)	Bulk density (kg m^{-3})
Oyacachi (*Alnus*)	8	1	3.7	45	8.8	40	75.2	694
		2	5.2	4	0.2	80	98.1	597
		3	5	3	1.2	40	106.8	576
	20	1	3.6	58	8.8	90	102.5	540
		2	4	34	2	150	131.2	452
		2	6.4	3	tr	170	129.5	456
		3	5.3	24	3.5	90	92.5	570
	30	1	4.5	36	1	80	78.8	587
		2	5.1	26	5.8	60	148.2	369
		3	4.9	13	0.2	40	37.6	842
	45	1	4.3	20	tr	60	41.9	848
		2	4.3	13	tr	60	79.6	581
		3	4.1	28	3.5	60	80.7	656
Pifo (*Polylepis*)	6	1	6.4	19	8.8	210	34.7	554
		2	6.5	21	18	290	40.2	600
		3	6.1	28	8.8	210	36.3	466
		3	6.6	8	0.2	210	–	–
	15	1	6.5	14	9.8	250	97.7	523
		1	6.5	22	5.2	80	86.0	563
		2	5	27	16.5	250	73.1	553
		2	6.5	26	7.5	280	79.8	472
		3	6.4	37	17	260	56.2	500
	30	1	5.5	17	5.2	150	32.6	700
		2	6.1	29	3.2	260	32.2	797
		3	6.4	37	3.2	80	43.1	761
	Old	1	6.5	11	11	340	94.9	547
		1	6.8	15	14.5	340	81.9	620
		2	6.5	34	8.5	260	67.9	648
		2	6.5	31	8	260	79.0	554
		3	6.2	16	tr	80	70.0	620
		3	6.3	10	8.8	210	65.0	607

[a] tr: trace.

figures of mature forests in relation to altitude, although it is noticeable that the highest values (TAGB > 400 Mg ha^{-1}) are all from lower altitude forests. The results for our forests which, to our knowledge, are at the highest altitudes so far investigated in the tropics, fall in the middle of the data-range. These results do not support the general assumption of decreasing TAGB with increasing altitude. Also, adding our data of successional biomass productivity to those of other tropical secondary forests (Table 7), we again did not observe a consistent decrease of productivity with altitude. Our values for both the *Alnus* and *Polylepis* forests are in all age classes intermediate within the range of Annual Biomass Accumulations, except for the 45-year-*Alnus* forest, which

has almost the highest ABA in its class. Even the 15-year-*Polylepis* forest does not have a conspicuously low ABA, despite its initial development having been inhibited by pasture.

In contrast to the findings of Brown and Lugo (1982) and Delaney et al. (1997), the data in Table 6 seem to be more variable within life zones (lowlands, lower montane, upper montane) than between these zones, suggesting that aboveground biomass is in general more determined by local site conditions (soils, geomorphology, climate, tree species, etc.) than by altitude. Apparently there is a large overlap in productivities of montane and lowland forests and only the highest values are outside the montane forests range. This is reflected in Table 6 which shows that
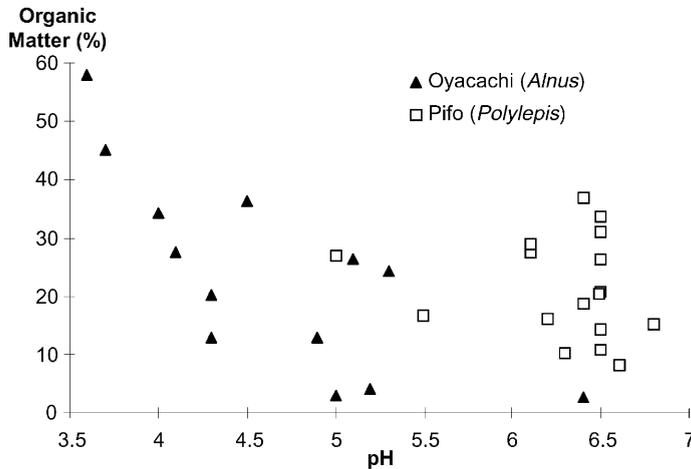
Fig. 1. Relationships between organic matter content and pH in soils at Oyacachi and Pifo sites in the high Ecuadorian Andes.

highest values for TAGB and tree biomass occur at lower altitudes.

4.4. Why are biomass and productivity surprisingly high?

The pioneer nature of both *A. acuminata* and *P. incana* can well explain the high productivity levels in the early successional stages of our two forests. However, the question remains what causes the high productivity levels of the older successional stages and the surprisingly high total biomass values. Since our forests are more or less monospecific, the autoecology of the two tree species may in part provide answers.

4.4.1. Autoecology of Alnus

Rapid growth of *Alnus* is mainly a result of the species' morphological and ecophysiological properties, in combination with (partly) favourable site conditions. Its very efficient association with nitrogen-fixing micro organisms and its relatively soft wood (37% density) apparently not only favour high productivity in the establishment phase, but also at greater ages.

Table 5
Compilation of regression equations found in literature for aboveground biomass estimations of wet and moist tropical lowland forests and results of application of these equations to the forest inventory data of the three *Alnus* 45-year-plots[a]

	Equation	Life zone	Source	Plot 1	Plot 2	Plot 3
(1)	Our method	High Andes	This study	122	133	160
(2)	$Y = \exp\{-2.904 + 0.993 \ln (D^2HS)\}$	Wet tropical	Overman et al., 1994	138	166	174
(3)	$Y = \exp\{-3.3012 + 0.9439 \ln (D^2H)\}$	Wet tropical	Brown et al., 1989	155	187	176
(4)	$Y = \exp\{-0.906 + 1.177 \ln (D^2S)\}$	Wet tropical	Overman et al., 1994	160	189	192
(5)	$Y = \exp\{-2.4090 + 0.9522 \ln (D^2HS)\}$	Moist tropical	Brown et al., 1989	160	193	194
(6)	$Y = (\exp\{-2.409 + 0.9522 \times \ln(D^2HS)\})1.03/10^3$	Wet tropical	Hughes et al., 1999	164	197	187
(7)	$Y = \exp\{-1.020 + 1.185 \ln (D^2) + 1.071 \ln (S)\}$	Wet tropical	Overman et al., 1994	167	197	200
(8)	$Y = 13.2579 - 4.8945 (D) + 0.6713\, D^2$	Wet tropical	Brown et al., 1989	195	230	209
(9)	$Y = \exp\{-3.1141 + 0.9719 \ln (D^2H)\}$	Moist tropical	Brown et al., 1989	244	294	283
(10)	$Y = 38.4908 - 11.7883 (D) + 1.1926\, D^2$	Moist tropical	Brown et al., 1989	308	361	339
(11)	$Y = \exp\{-0.435 + 2.12 \ln (D)\}$	Wet tropical	Rai and Proctor, 1986	377	452	395
(12)	$Y = \exp\{1.54934 + 2.39376 \ln (D)\}$	Moist temperate	Wharton and Griffith, 1993	727	857	811

[a] The table is ordered by ascending results. Y: tree dry weight biomass (Mg); D: dbh (m); H: tree height (m); S: wood density (Mg m^{-3}).

Table 6
Aboveground tree biomass and total aboveground biomass (TAGB), both in Mg ha^{-1} dry weight, of several mature tropical moist and humid forests. Locations are arranged by altitude (m)

Location	Altitude	Soils	Tree biomass	TABG	Reference
Lowlands					
Lowland moist forest, Pará, Brazil	Low	Poor	242	295	Cochrane and Schulze, 1999
Lowland moist forest, Pará, Brazil	Low	–	185	–	Higuchi et al., 1994
Lowland moist forest, Roraima, Brazil	Low	–	228	–	Higuchi et al., 1994
Lowland pluvial forest, Chocó, Colombia	90	Poor	191	272	Rodríguez Jiménez, 1988
Lowland humid forest; Darién, Panamá	100	?	259	363	Golley et al., 1971
Lowland wet forest, Malaysia	100	–	475	528	Kira, 1977[a]
Lowland rainforest, Amazonian Venezuela	120	Poor	261	338	Uhl and Jordan, 1984
Lowland moist forest, Ghana	150	–	213	307	Greenland and Kowal, 1960[a]
Lowland rainforest, México	200	Rich	371	403	Hughes et al., 1999
Humid rainforest, India	200	Poor	454	–	Rai and Proctor, 1986
Lowland wet forest, Amazonian Colombia	200	Poor	351	–	Overman et al., 1994
Lowland moist forest, Venezuela	240	–	358	396	Delaney et al., 1997
Lowland humid forest, Puerto Rico	320	–	–	226	Scatena et al., 1993
Lowland wet forest, Puerto Rico	500	–	148	–	Briscoe and Wadsworth, 1970[a]
Lower montane forest, Puerto Rico	500	Rich	365	–	Ovington and Olson, 1970
Lower montane					
Metrosideros stands on old lava, Hawaii	700	Rich	108	123	Raich et al., 1997
Humid rainforest, India	800	Poor	649	–	Rai and Proctor, 1986
Lower montane cloud forest, Puerto Rico	900	Poor	92	–	Olander et al., 1998
Metrosideros stands on old lava, Hawaii	1660	Rich	68	81	Raich et al., 1997
Upper montane					
Montane moist forest, Andes, Venezuela	2250	Poor	348	409	Grimm and Fassbender, 1981
Montane wet forest, Pacific slope, Ecuador	2300	Rich	242	255	Hofstede and Aguirre, 1999
Montane moist forest, Venezuela	2400	–	346	394	Delaney et al., 1997
Montane wet forest, New Guinea	2500	Rich	295	310	Edwards and Grubb, 1977
Upper montane wet forest, South-Ecuador	2800	Poor	114	149	Hofstede and Aguirre, 1999
Upper montane wet forest, Venezuela	2820	–	314	354	Delaney et al., 1997
Oyacachi, *Alnus* forest, Ecuador (45 years)	3200	Rich	220	241	This study
Pifo *Polylepis* forest, Ecuador	3600	Rich	326	366	This study

[a] Cited in Edwards and Grubb (1977).

Precipitation at Oyacachi is optimal for *Alnus* and the soils of the landslides are well drained. The altitude of the site is, however, close to the upper distributional limit of the species (Carlson and Dawson, 1985; Añazco Romero, 1996). Also potentially restricting to growth seem to be the soils at Oyacachi, which are Andosols known for their poor availability of P as a result of P fixation. The landslides on which the *Alnus* forests established are a mixture of weathered, acidic topsoil material with a high organic matter content and the deeper, unweathered, less acidic ashes and schists. Soils under *Alnus* are known for their acidification connected with the production of acids upon decomposition of *Alnus* litter and concurrent nitrification. This is reflected in the clear relation between pH and organic matter content (see Fig. 1). These aspects bear no relation to stand age, hence the spread in the values can probably be attributed to differences in acid buffering capacity resulting from within site soil variability. At low pH the abundant active Al in the soil fixes phosphate. However, the highest P values were found in the *Alnus* plots with the lowest pH, which will be due to the high organic matter content and concurrently reduced activity of Al.

Our results indicate that *Alnus* is relatively efficient in P-retranslocation before leaf abscision (48%), which could be part of the trees solution for P limitation in the acidic soils and suggests that mycorrhiza are of subordinate importance for the P-cycle. This

Table 7

Productivity of several secondary tropical moist and humid forests. Productivity is expressed as aboveground biomass accumulation (ABA = standing crop TAGB age^{-1})[a]

Forest location and age	Altitude	Soils	ABA (Mg ha^{-1} per year dry weight)				Reference
			0–10 years	11–20 years	21–40 years	>40 years	
Lowland rainforest, Guatemala; 6 years	Low	–	7.5				Snedaker, 1970[b]
Lowland rainforest, Colombia; 4 years	Low	–	12.1				Gamble et al., 1969[b]
Lowland rainforest, Panamá; 6 years	Low	–	7.2				Ewel, 1971
Lowland rainforest, Congo; 5, 18 years	Low	–	15.3[b]	6.7[c]			Bartholomew et al., 1953
Lowland rainforest, Magdalena, Colombia; 16 years	Low	–		12.6			Fölster and de las Salas, 1976[c]
Puerto Rico rainforest; 20, 21, 50 years	?	Poor		4.9	5.2	1.6	Lugo, unpublished data[c]
Lowland rainforest, Venezuela; 35, 60, 80 years	Low	Poor			3.1	2.6, 2.0	Saldarriaga et al., 1986[c]
Lowland humid forest, India; 50 years	Low	–				3.6	Singh and Ramakrishnan, 1982[c]
Lowland rainforest, Puerto Rico, 44 years	Low	–				3.8	Jordan and Farnworth, 1982
Lowland rainforest, Venezuela; 5 years	120	Poor	8				Uhl and Jordan, 1984
Lowland wet rainforest, México; 7 years	150	Poor	7.5				Williams-Linera, 1983
Lowland rainforest, México; 4, 20, 30, 50 years	200	Rich	15.1	13.5	8.5	5.7	Hughes et al., 1999
Luquillo Mountains, Puerto Rico; 5 years	320	–	16.3				Scatena et al., 1996
Moist hill forest, north-eastern India; 15 years	Hills	Poor		8.1			Ramakrishnan and Toky, 1981[c]
Montane moist forest, Venezuela, 24 years	2820	–			4.6		Veillon, 1985[d]
Oyacachi, Alnus forest, Ecuador; 8, 20, 30, 45 years	3200	Rich	14.2	5.9	5.9	5.4	This study
Pifo, Polylepis forest, Ecuador; 6, 15, 30 years	3600	Rich	15.0	6.2	6.9		This study

[a] Locations are arranged by altitude (m).
[b] Cited in Uhl and Jordan, 1984.
[c] Source: Brown and Lugo, 1990, Fig. 3, Table 3. These data are approximate.
[d] Cited in Brown and Lugo, 1990.

retranslocation is comparable with those known from other tropical montane cloud forests (Bruijnzeel and Proctor, 1995).

4.4.2. Autoecology of Polylepis

The surprisingly high productivity of the Pifo *Polylepis* forest must, as in the *Alnus* forest, be seen as the result of optimal site conditions given the eco-physiological properties of this species. Environmental conditions at the Pifo site are relatively favourable for forest growth. Water is abundant and cons-tant and temperatures are relatively high. Although, Andosols are known for their P fixation, this occurs especially at lower pH and in weathered volcanic ashes (Wada, 1985; Van Reeuwijk, 1991). The non-acidic soils at Pifo are very young volcanic ashes with a high acid buffering capacity, as evidenced by the results of soil analysis, and consequently a lesser P fixation. We have no data on soil nitrogen content, but we can identify N limitation from the N/P ratios (<14; Koerselman and Meuleman, 1996) obtained for the fresh *Polylepis* leaves.

Polylepis has what seems to be a perfect set of physiological adaptations for the conditions at Pifo. Firstly, the implied N limitation of the soil is overcome by relatively effective N retranslocation (57%) before leaf abscision, which is higher than the values given for a number of tropical montane cloud forests by Bruijnzeel and Proctor (1995). Vélez et al. (1998) have found N retranslocation rates of 80% for *P. quadrijuga* in Colombia. This could indicate that the retransloca-tion efficiency may increase with stronger N limita-tion. An additional solution for N limitation of the soil are the N inputs that can be expected from the VA-mycorrhiza which are associated to *Polylepis* as a genus (Kessler, 1995). Secondly, the Pifo site at 3600 m altitude roughly has an average daily tem-perature of 8 °C, which is the optimum for daily carbon gain (photosynthesis minus respiration) of *P. sericea* in Venezuela (Goldstein et al., 1994). Fina-lly, the same Venezuelan study showed very high photosynthetic capacity and high dark respiration levels. They explain these as adaptations to cold climates and high irradiation conditions, for which they need extra chemical energy for damage control, which is provided by the high photosynthesis and respiration levels. Because of the relatively low altitude for the species at the Pifo site, its metabolism

might be favoured because frost incidence is low. We do not know if P. incana behaves the same way as *P. sericea*, but similarities are likely.

5. Conclusions

We have found surprisingly high TAGB and ABA in two forests at high altitudes, given the assumption of decreasing tropical forest biomass with increasing altitude. One way of interpreting these results is to argue that if two different forest systems with different tree species, different soils and parent materials and probably different climatic conditions can show such high biomass levels, we can assume that other high altitude forest systems in the northern Andes or even in the tropics in general might also contain considerable biomass. On the contrary, one can argue that the situation of both forests is not representative for other high altitude forests. The high biomass found could be the result of a combination of favourable site conditions and tree species that possess a number of favourable characteristics (fast growth, efficient physiological adaptations to N and P limitations and to high altitude climatic conditions in the case of *Polylepis*). Can we contradict the assumption of decreasing biomass with increasing altitude or have we found two exceptions to the rule? We conclude that additional research is needed in other high altitude forest systems before we can answer this question. The results do show, however, that high carbon offsets in secondary forests at high altitudes are possible and that reforestation efforts for carbon sequestration can therefore be worthwhile, especially when similar species are used under environmental conditions similar to the ones in this study.

of their drying ovens. We express our gratitude to the people of Oyacachi and Pifo for assistance and accommodation during the fieldwork.

References

Aiba, S., Kitayama, K., 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. Plant Ecol. 140, 139–157.

Aide, T.M., Zimmerman, J.K., Rosario, M., Marcano, H., 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica 28 (4a), 537–548.

Añazco Romero, M.J., 1996. El aliso. Proyecto de desarrollo forestal campesino en los Andes del Ecuador (DFC), Quito, 166 pp.

Bartholomew, M.V., Meyer, J., Laudelot, H., 1953. Mineral nutrient immobilisation under forest and grass fallow in the Yangambi (Belgian Congo) region. Publications de L'Institut National pour L'Étude Agronomique du Congo Belge, Série Scientifique, Vol. 57, 27pp.

Brandbyge, J., 1992. The planting of local woody species in the páramo. In: Balslev, H., Luteyn, J.L. (Eds.), Páramo: An Andean Ecosystem Under Human Influence. Academic press, London, pp. 265–274.

Brandbyge, J., Holm-Nielsen, L.B., 1992. Reforestación de los Andes Ecuatorianos con especies nativas. Central Ecuatoriana de Servicios Agrícolas (CESA), Quito, 90 pp.

Briscoe, C.B., Wadsworth, F.H., 1970. Stand structure and yield in the Tabonuco forest of Puerto Rico. In: Odum, H.T., Pigeon, R.F. (Eds.), A Tropical Rain Forest. U.S.A.E.C., Oak Ridge, TN, USA, pp. B-79–89.

Brown, S., Gillespie, A.J.R., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. For. Sci. 35 (4), 881–902.

Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14 (3), 161–187.

Brown, S., Lugo, A.E., 1990. Tropical secondary forests. J. Trop. Ecol. 6, 1–25.

Brown, S., Sathaye, J., Cannell, M.G.R., Kauppi, P.E., 1996. Mitigation of carbon emissions to the atmosphere by forest management. Common For. Rev. 75 (1), 80–91.

Bruijnzeel, L.A., Proctor, J., 1995. Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? In: Hamilton, L.S., Juvik, J.O., Scatena, F.N. (Eds.), Tropical Montane Cloud Forests. Proceedings of an International Symposium on Ecological Studies. 110, Springer-Verlag, New York, pp. 39–63.

Bruijnzeel, L.A., Veneklaas, E.J., 1998. Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. Ecology 79 (1) 3–9.

Carlson, P.J., Dawson, J.O., 1985. Soil nitrogen changes, early growth, and response to soil internal drainage of a plantation of Alnus jorullensis in the Colombian highlands. Turrialba 35, 141–150.

Cochrane, M.A., Schulze, M.D., 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. Biotropica 31 (1), 2–16.

Dabas, M., Bhatia, S., 1996. Carbon sequestration through afforestation: role of tropical industrial plantations. Ambio 25 (5), 327–330.

Deans, J.D., Moran, J., Grace, J., 1996. Biomass relationships for tree species in regenerating semi-deciduous tropical moist forest in Cameroon. For. Ecol. Manage. 88, 215–225.

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Bello Quintero, N., 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. J. Trop. Ecol. 13, 697–708.

DIVA, 1997. Oyacachi—people and biodiversity. Center for Research on Cultural and Biological Diversity of Andean Rainforests (DIVA), Ronde, Denmark. Technical reports: 2, 120 pp.

Dixon, R.K., Brown, S., Houghton, A.M., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon Pools and flux of global forest ecosystems. Science 263, 185–190.

Doumenge, C., Gilmour, D., Ruíz, P.M., Blockhus, J., 1995. Tropical montane cloud forests: conservation status and management issues. In: Hamilton, L.S., Juvik, J.O., Scatena, F.N. (Eds.), Tropical Montane Cloud Forests. Proceedings of an International Symposium on Ecological Studies, Vol. 110. Springer-Verlag, New York, pp. 24–37.

Edwards, P.J., Grubb, P.J., 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. J. Ecol. 65, 943–969.

Ewel, J., 1971. Biomass changes in early tropical succession. Turrialba 21, 110–112.

FAO, 1993. Forest resource assessment 1990: tropical countries. FAO Forestry Paper 112. FAO, Rome.

Fölster, H., de las Salas, G., 1976. Litter fall and mineralisation in three tropical evergreen stands, Columbia. Acta Centífica Venezolana 27, 196–202.

Gamble, J.F.S., Snedaker, S.C., associates, 1969. Bioenvironmental and radiological-safety feasibility studies: Atlantic–Pacific Interoceanic canal. Batelle Memorial Institute, Columbus, OH, USA.

Goldstein, G., Meinzer, F.C., Rada, F., 1994. Environmental biology of a tropical tree line species, *Polylepis* sericea. In: Rundel, P.W., Smith, A.P., Meinzer, F.C. (Eds.), Tropical Alpine Environments: Plant Form and Function. Cambridge Univerity Press, Cambridge, pp. 129–151.

Golley, F.B., McGinnis, J.T., Clements, R.G., 1971. La biomasa y la estructura mineral de algunos bosques de Darién en Panamá. Turrialba 21 (2), 189–196.

Greenland, D.J., Kowal, J.M.L., 1960. Nutrient content of the moist tropical forest of Ghana. Plant and Soil 12 (2), 154–174.

Grimm, U., Fassbender, H.W., 1981. Ciclos bioquímicos en un ecosistema forestal de los Andes Occidentales de Venezuela I. Inventario de las reservas orgánicas y minerales (N, P, K, Ca, Mg, Mn, Fe, Al, Na). Turrialba 31 (1), 27–37.

Hall, M.L., Mothes, P.A., 1984. Tefroestratigrafia holocenica de los volcanoes principales del valle interandino, Ecuador. In: Marocco, R. (Ed.), El contexto geológico del espacio físico ecuatoriano. Estudios de Geografía 6. Corporación Editora Nacional, Quito, pp. 47–68.

Hamilton, L.S., Juvik, J.O., Scatena, F.N., 1995. The Puerto Rico tropical cloud forest symposium: introduction and workshop synthesis. In: Hamilton, L.S., Juvik, J.O., Scatena, F.N. (Eds.), Tropical Montane Cloud Forests. Proceedings of an International Symposium on Ecological Studies, Vol. 110. Springer-Verlag, New York, pp. 1–23.

Harcourt, C.S., Sayer, J.A.. (Eds.), 1996. The conservation atlas of tropical forests: the Americas. Simon & Schuster, New York, 340 pp.

Higuchi, N., dos Santos, J.M., Imagana, M., Yoshida, S., 1994. Aboveground biomass estimate for Amazonian dense tropical moist forest. Mem. Fac. Agric. Kagoshima Univ. 30, 43–54.

Hofstede, R., Aguirre, N., 1999. Biomasa y dinámica del carbono en relación con las actividades forestales en la Sierra del Ecuador. In: Medina, G., Mena, P. (Eds.), El páramo como espacio de mitigación de carbono atmosferico. Serie Páramo 1. Ediciones Abya Yala, Quito, pp. 29–51.

Houghton, R.A., 1996. Converting terrestrial ecosystems from sources to sinks of carbon. Ambio 25 (4), 267–272.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of México. Ecology 80 (6), 1892–1907.

Jordan, C.F., Farnworth, E.G., 1982. Natural versus plantation forests: a case study of land reclamation strategies for the humid tropics. Environ. Manage. 6 (6), 485–492.

Kessler, M., 1995. Present and potential distribution of *Polylepis* (Rosaceae) forests in Bolivia. In: Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L. (Eds.), Biodiverstiy and Conservation of Neotropical Montane Forests. New York Botanical Garden, New York, pp. 281–294.

Kira, T., 1977. Community architecture and organic matter dynamics in tropical lowland rain forests of southeast Asia, with special reference to Pasoh forest, West Malaysia. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), Tropical Trees as Living Systems. IVth Cabot Symposium, Harvard. Cambridge University Press, London.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation *N:P* ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450.

Martinez, M.A.G., 1995. Descripción del bosque de yagual (*Polylepis* sp.) en el área de Pifo y estudio de los problemas de su regeneración. Thesis, Universidad Nacional de Loja, Loja.

Murcia, C., 1997. Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. For. Ecol. Manage. 99, 163–170.

Nabuurs, G.J., Mohren, G.M.J., 1995. Modeling analysis of potential carbon sequestration in selected forest types. Can. J. For. Res. 25 (7), 1157–1172.

Olander, L.P., Scatena, F.N., Silver, W.L., 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manage. 109, 33–49.

Overman, J.P.M., Witte, H.J.L., Saldarriaga, J.G., 1994. Evaluation of regression models for aboveground biomass determination in Amazon rainforest. J. Trop. Ecol. 10, 207–218.

Ovington, J.D., Olson, J.S., 1970. Biomass and chemical content of El Verde Lower Montane Rain forest plants. In: Odum H.T., Pigeon, R.F. (Eds.), A Tropical Rain Forest. U.S.A.E.C., Oak Ridge, TN, pp. H-53–77.

Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Núñez, P.V., Vásquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., Grace, J., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282, 439–442.

Rai, S.N., Proctor, J., 1986. Ecological studies on four rainforests in Karnataka, India. I. Environment, structure, floristics and biomass. J. Ecol. 74, 439–454.

Raich, J.M., Russell, A.E., Vitousek, P.M., 1997. Primary productivity and ecosystem development along an elevational gradient on Manua Loa, Hawai'i. Ecology 78 (3), 707–721.

Ramakrishnan, P.S., Toky, O.P., 1981. Soil nutrient status of hill agro-ecosystems and recovery pattern after slash and burn agriculture (jhum) in north-eastern India. Plant and Soil 60 (1), 41–64.

Rodríguez Jiménez, L.V.A., 1988. Consideraciones sobre la biomasa, composición química y dinámica del bosque pluvial tropical de colinas bajas, Bajo Calima, Buenaventura, Colombia. Serie Documentación 16. Convenio CONIF-Holanda, Bogotá, 36 pp.

Ruiz Peña, M.C., Orozco de, A.M., 1986. Efectos de la luz y los reguladores del crecimiento sobre el porcentaje de germinación de *Alnus acuminata H.B.K.* (Betulaceae). Perez-Arbelaezia 1 (2), 211–224.

Saldarriaga, J.G., West, D.C., Thorp, M.L., 1986. Forest succession in the Upper Rio Negro of Colombia and Venezuela. Environmental Sciences Division Publication No. 2694 (ORNL/TM9712), Oak Ridge, TN, USA.

Sarmiento, F.O., 1997. Arrested succession in pastures hinders regeneration of Tropandean forests and shreds mountain landscapes. Environ. Conserv. 24 (1), 14–23.

Scatena, F.N., Silver, W., Siccama, T., Johnson, A., Sánchez, M.J., 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after hurricane, Hugo, 1989. Biotropica 25 (1), 15–27.

Scatena, F.N., Moya, S., Estrada, C., Chinea, J.D., 1996. The first five years in the reorganisation of aboveground biomass and nutrient use following hurricane hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28 (4a), 424–440.

Simpson, B.B., 1986. Speciation and specialisation of *Polylepis* in the Andes. In: Vuilleumier, G., Monasterio, M. (Eds.), High Altitude Tropical Biogeography. Oxford University Press and the American Museum of Natural History, New York, pp. 304–316.

Singh, J., Ramakrishnan, P.S., 1982. Structure and function of a sub-tropical humid forest of Meghalaya. I. Vegetation, biomass and its nutrients. In: Proceedings Indian National Science Academy (Plant Science) 91 (3), 241–253.

Snedaker, S.C., 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala, Thesis. University of Florida. Gainesville, FL, 131 pp.

Uhl, C., Jordan, C.F., 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology 65 (5), 1476–1490.

Van Reeuwijk, L.P., 1991. Andosols. In: Driessen, P.M., Dudal, R. (Eds.). The Major Soils of the World. Agricultural University Wageningen, Leuven Catholic University, Zutphen, The Netherlands, pp. 57–64.

Veillon, J.P., 1985. El crecimiento de algunos bosques naturales de Venezuela en relación con los parámetros del medio ambiente, Revista Forestal Venezolana 29, 5–122.

Vélez, V., Cavelier, J., Devia, B., 1998. Ecological traits of the tropical tree line species *Polylepis* quadrijuga (Rosaceae) in the Andes of Colombia. J. Trop. Ecol. 15, 771–787.

Wada, K., 1985. The distinctive properties of Andosols. Adv. Soil Sci. 2, 174–223.

Waide, R.B., Zimmerman, J.K., Scatena, F.N., 1998. Controls of primary productivity: lessons from the Luquillo Mountains in Puerto Rico. Ecology 79 (1), 31–37.

Weaver, P.L., Murphy, P.G., 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. Biotropica 22 (1), 69–82.

Wharton, E.H., Griffith, D.M., 1993. Methods to estimate total forest biomass for extensive forest inventories: applications in the north-eastern US north-eastern forest experiment station research papers: NE-681. United States Department of Agriculture, Forest Service, Radnor, Pennsylvania.

Williams-Linera, G., 1983. Biomass and nutrient content in two successional stages of tropical wet forest in Uxpanapa, Mexico. Biotropica 15 (4), 275–284.