Determinants for successful reforestation of abandoned pastures in the Andes: Soil conditions and vegetation cover

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ABSTRACT

The Andes of Ecuador are known for their outstanding biodiversity but also as the region with the highest deforestation rate in South America. This process is accompanied by accelerating degradation and loss of environmental services. Despite an extraordinary richness in native tree diversity, more than 90% of all forest plantations established in Ecuador consist of exotic species, primarily *Eucalyptus* spp. and *Pinus* spp. This is mainly due to the lack of information about the autecological and synecological requirements of the native species.

The present study aims at providing basic knowledge on the early height development of native species in comparison to exotics. 12,000 seedlings of exotic and native species were planted in experimental trials at three sites of different successional stages: recently abandoned pastures (*Setaria sphacelata*), bracken (*Pteridium arachnoideum*) and shrubs. The results presented in this study refer to the status of the seedlings 3 years after planting. Soil data were revealed from soil core analysis from a total of 1008 soil samples distributed systematically over all plots. Soil chemical data were derived from a subsample of 125 randomly selected soil core sites. Soil properties in the study area emerged to be extremely heterogeneous. More than 60% of all plots presented two or more soil clusters. Soils in general were very poor in plant available N. Soil heterogeneity affected extractable Mn and Mg, dominating vegetation cover in turn affected Mn and P. Differences in soil properties had a strong effect for *Eucalyptus saligna* and *Alnus acuminata*. Manual above ground weeding showed species-specific effects: *Tabebuia chrysantha* and *Heliocarpus americanus* showed improved height growth, while that of *Cedrela montana* was reduced. There is evidence that *A. acuminata* can compete in growth with exotic species. Early successional species and exotics performed best on pasture dominated sites. Height growth of the mid-successional species *C. montana* was facilitated by bracken fern under certain soil conditions, and shrubs facilitated growth of *T. chrysantha*. The results indicate that reforestation with native species in Ecuador is possible but requires intensive consideration of interactions with soil properties and accompanying vegetation. Macroscopic soil core analysis can be a suitable instrument for detecting small-scale variation of soil properties. Nevertheless, a characterisation of both small-scale variation as well as variation on higher spatial scales, for instance by aerial photographs, is essential for effective planning of reforestation measures in the Andes.

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1. Introduction

Tropical mountain forests in general and the Ecuadorian Andes in particular are known for their outstanding biodiversity (Brummit and Lughada, 2003). Besides their richness in vascular plants, the montane forests of Southern Ecuador even hold some world records of diversity, for instance for bryophytes (Parolly et al., 2004) and geometrid moths (Brehm et al., 2005). However, this exceptional diversity is threatened by habitat loss as a result of the highest deforestation rate within South America (FAO, 2006; Mosandl et al., 2008). Thus, two aspects in this context deserve major attention: resolving the causes for deforestation and fostering reforestation activities.

The deforestation cycle in the South Ecuadorian Andes is usually initiated by extraction of high value timber species, resulting in an economical degradation of the forest value for the

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land users. Similar to other areas in the tropics (Otsamo et al., 1995; Hooper et al., 2002), these forests are burned and converted into pastures for cattle raising (Mosandl et al., 2008). Frequent burning of the pastures reduces germination, growth and survival of tree seedlings (Hooper et al., 2002) and frequently leads to degraded landscapes, dominated by bracken fern *Pteridium arachnoideum*. The introduced pasture grass *Setaria sphacelata* is frequently used in our study area due to its high productivity (Rhoades et al., 2000; Makeschin et al., 2008). Both grasslands and bracken are described to be major barriers for the establishment of tree seedlings (Holl, 2002; Hartig and Beck, 2003; Griscom et al., 2008).

Tropical ecosystems are not only important refuges for biodiversity (Barthlott et al., 2005) but also play an existential role for livelihood as indicated by the heavy deforestation (Stoian, 2005; Quang and Nato, 2008). Thus, the need for subsistence is a major driver for deforestation (Davidar et al., 2007; Wunder, 2000; Lopez, 2003). The success of reforestation efforts strongly depends on species that can fulfil the demands of the people and cope with the given site conditions and predominant competing vegetation.

Today, about 90% of all forest plantations in Ecuador consist of introduced species (FAO, 2006), mainly *Eucalyptus* spp. and *Pinus* spp. (*i.e. E. saligna, E. globulus, P. patula, P. radiata*). This can be explained by the good availability of planting material, existence of clear silvicultural management concepts, proven good productivity, but also the lack of knowledge regarding the silvics of the native species (Stimm et al., 2008). It is known that plantations with exotic species can facilitate secondary succession of native species (Brockerhoff et al., 2008; Feyera et al., 2002). However, large-scale exotic plantations lead to landscape homogenization (Lamb et al., 2005), and can even raise ecological problems, for instance with soil properties (Islam et al., 1999), fire susceptibility, stability, diseases and low diversity (Manchester and Bullock, 2000; D'Antonio and Meyerson, 2002; Lamb et al., 2005).

Unfortunately scientific studies on reforestation in Ecuador particularly with native species are very sparse (Brandbyge and Holm-Nielsen, 1986; Knoke et al., in press). Therefore, comparative studies with exotics and native species are of major importance. A special focus has to be given to the synecological and autecological site requirements of the native species as how a species accommodates itself to the environmental conditions at a given site is keystone to ensuring low mortality and good growth performance. However, autecological requirements depend strongly on soil properties, while synecological requirements depend on the surrounding vegetation. Consequently, for best planting success both aspects must be considered (Evans and Turnbull, 2004; Lamb et al., 2005).

Surrounding vegetation can either facilitate (e.g. nutrient input of litter, shading effects) or hamper growth of planted trees (e.g. light or root competition). Competition can be regulated by several measures (e.g. weeding, plowing, herbicides, fertilization) to optimize the growth of naturally regenerated or planted seedlings (Evans and Turnbull, 2004). Another option is to take advantage of the facilitating effects of the surrounding vegetation by choosing tree species whose synecology corresponds to the situation at the given site. For instance, the fast growth of most exotic tree species can be attributed to their early successional (pioneer) status (Sawyer, 1993). It is well established that mid and late successional species have completely different physiological behaviour than early successional species (Bazzaz and Picket, 1980) and thus should respond to different vegetation stages of planting sites (Dobson et al., 1997; Parrotta and Knowles, 1999; Ashton et al., 2001; Feyera et al., 2002; Piotto et al., 2004; Kelty, 2006).

While the successional stage of a site can easily be revealed from field surveys or satellite imagery, it is much harder to

consider the tremendous variation in the micro-site conditions as they prevail in the Ecuadorian Andes. In Mid-Europe macroscopic soil core analysis is a proven valuable instrument for determination of suitable planting sites (Arbeitskreis Standortskartierung, 2003). However, there is limited knowledge regarding if these techniques can be transferred to the complex neotropical montane ecosystems.

For detection of synecological requirements, we established experimental reforestation trials on abandoned pastures comparing exotic species with native species of different successional status. These were planted on three sites along a successional gradient in the montane forest ecosystem of Southern Ecuador. In the following text the term "successional status" will be used for the planted trees, the term "successional stage" in turn will be used for the surrounding vegetation. The autecological requirements and their interactions with synecological requirements were detected by soil core analysis.

The specific objectives of the study were to detect (1) effects of above ground weeding on the height development of planted tree species, (2) species-specific reactions to successional sites, (3) if macroscopic soil core analysis is a suitable method for predicting differences in height development, (4) if macroscopic soil core analysis can reveal differences in soil chemical properties, and (5) possible interactions between dominating vegetation cover and soil properties.

2. Materials and methods

2.1. Study area

The field experiment was conducted from 2003 to 2006 at the research station "Estación Científica San Francisco" at km 34 along the road from Loja to Zamora in South Ecuador. The station is geographically located at 3°58′17.21″ south, 79°04′44.08″ west at an elevation of 1840 m a.s.l. The study area is characterised by perhumid climatic conditions with 2200 mm annual rainfall and a slightly drier season around November. Average temperature is 15.3 °C with a very low annual fluctuation (1.2 °C) compared to the mean daily fluctuation (11.1 °C) (Bendix et al., 2006). Two dominant groups of rocks were identified for the study area: meta-siltstones/-sandstones/quartzites and slates/phyllites (Makeschin et al., 2008). The key elements for distinguishing the rock types are Al, K, Mg, Fe, Na, and Ca dependent from the mineral content. Makeschin et al. (2008) state that forest, pasture and sites with secondary vegetation of the study area are comparable in a priori soil mineralogy. Dominant soil types in the forest are Cambisols and Histosols (Wilcke et al., 2008), those under pastures and secondary vegetation Cambisols, Podzols, Gleysols, whereby podzolisation dominates gleyic processes under pastures (Bahr, 2007). The soils display a high degree of small-scale heterogeneity (Wilcke et al., 2002). Natural disturbances like land slides further increase the soil heterogeneity in the study area (Wilcke et al., 2003). Anthropogenic replacement ecosystems recovering from slash-and-burn can be stratified into three major vegetation types (Martinez et al., 2008), which constitute a successional gradient from pasture, bracken to the shrub stage (Hartig and Beck, 2003), according to hypotheses (2) and (4). In each of these successional stages, four hectares were delineated for the establishment of experimental reforestation plots (Aguirre, 2007):

(a) "pasture": 1800–2100 m a.s.l. (UTM coordinates 713475, 9560931), average inclination of 53% (6–90), aspect South, dominated by the grasses *S. sphacelata*, *Melinis minutiflora*, *Axonopus compressus*;

(b) "bracken": 1850–2100 m a.s.l. (UTM coordinates 714299, 9561044), average inclination of 69% (10–90), aspect South,

dominated by *P. arachnoideum*, *Ageratina dendroides*, *Baccharis latifolia*;

(c) advanced successional stage "shrub": 2000–2200 m a.s.l. (UTM coordinates 712269, 9560293), average inclination of 44% (5–55), aspect South, dominated by *Ageratina dendroides*, *Myrsine andina*, *Brachyotum* sp.

2.2. Study species

We selected tree species from three different ecological groups (hypothesis H2). The nomenclature follows Jørgensen and León Yanéz (1999). *Heliocarpus americanus* and *Alnus acuminata* are fast growing species of early successional status in their natural habitat. The mid-successional species *Tabebuia chrsyantha*, *Juglans neotropica* and *Cedrela montana* are characterised by a very high timber value. *Pinus patula* and *Eucalyptus saligna* as exotic species are widely used for reforestation in Ecuador.

2.3. Experimental settings

The experimental setting follows a randomized block design with different successional stages as blocks. Species and treatments are completely randomized. The three blocks have same altitude, same aspect, identical soil clusters (Fig. 3) and are located in the same valley at distances of less than 3 km between each other, so that climatic differences can be neglected. Thus, possible differences of tree development between blocks can mainly be attributed to effects of the dominating vegetation.

Seeds of the exotic species were purchased from the local seed market; those of the native species were collected in the adjacent primary forest from at least 10 dominant healthy individuals with well developed crowns and straight stem forms and raised under semi-controlled conditions in our experimental nursery in Loja (Stimm et al., 2008). The mean temperature of 15 °C corresponds closely to the environmental conditions of the reforestation areas. After germination, the seedlings were transplanted into 560 cm^3 polyethylene containers with a substrate that consisted of a 2:1:1 mixture of mine sand, Páramo humus and forest humus. Before planting to the field, all seedlings were subject to a 2-month hardening phase in the nursery.

In total, 336 plots were established, with 112 plots randomly distributed per successional stage. On each plot of 10.8 m × 10.8 m, 25 seedlings were planted between May and September 2003 with a spacing of 1.8 m and with eight repetitions per species and treatment. In the present study we present the growth data of 3 years after planting. Before planting herbs, grasses and ferns were eliminated on all plots by machete, only woody vegetation was not removed. On half of the plots this weeding treatment was repeated every 6 months for 2 years, the remaining half was left as reference without further treatments (according to H1). Consequently, the experimental design for the reforestation is: 7 species × 3 successional sites × 2 weeding treatments × 8 repetitions = 336 plots.

Complementary to the planting trials we conducted a field survey of the respective site factors (hypotheses H3, H4, and H5). Therefore, we extracted three soil samples per reforestation plot using a soil core "Pürckhauer". Every soil sample was extracted between four surrounding tree seedlings at fixed positions within the plot, at distances of 0.9 m between soil sample and plants. For each soil horizon the following parameters were recorded in the field, applying the guidelines of Arbeitskreis Standortskartierung (2003): size (cm), texture, colour by Munsell (Hue, Value and Chroma), stone content, root intensity, bulk density, and pH (H$_2$O). Besides the soil core parameters, we registered also the site factors of inclination and altitude for every soil sample. In total, we analyzed 1008 soil core samples (336 plots × 3 soil core samples).

For further chemical analysis, 125 soil samples were extracted randomly from all mineral soil horizons of the 1008 soil core sites by digging a soil pit for each sample. Soil samples were oven-dried at 40 °C. All samples were homogenized. CEC and pH were analyzed on soil fraction <2 mm. C and N were analyzed on ground soil material (smaller than 63 μm). Effective cation exchange capacity (CEC) was calculated by percolation with 0.5N NH$_4$Cl-solution at pH 4.3 as sum of exchangeable Ca, Mg, K, Na, Mn, Al, and Fe (see Lüer and Böhmer, 2000). Base saturation was calculated as the proportion of charge equivalent of extractable Ca + K + Na + Mg of the effective CEC. Plant available P was extracted by citric acid after VDLUFA (1991). The concentrations of organic C and N were determined with a CHNS analyzer. In order to detect whether different site clusters, based on macroscopic soil core analysis, can reveal differences in chemical parameters (hypothesis H4), an additional two-factorial, univariate ANOVA was conducted separately for horizon A, B and subsoil. For analysis of individual chemical soil parameters as dependent values we defined site cluster (clusters 1–3) and vegetation units (pasture, bracken, shrub) as the two major independent factors and analyzed the other chemical parameters as covariates.

2.4. Data processing

According to the top height approach, which is frequently used for characterisation of site potentials (Sharma et al., 2002), we analyzed the growth of the highest plant out of the four seedlings surrounding each of the soil core samples. This corresponds to the top height of the 25% highest plants. Additional parameters like root collar diameter, leaf area, etc. were measured, too, but as the aim of the present study is to characterise the site potential for tree growth we chose the top height approach.

A factor analysis was used as a starting point (SPSS 16.0) in order to reduce the number of variables by building background factors which are correlated to the initial variables. The model with the best adaptation (Kaiser–Mayer–Olkin value = 0.688, Bartlett test $p < 0.001$) and concomitantly lowest number of components ($n = 5$) could explain 63% of the variation. All variables were standardized before analysis. For the extraction of the factors we used the principal component analysis. We only included factors with Eigenvalues >0 into the model (Table 1). The corresponding factor values were attributed to each soil core sample.

In hypotheses H3 and H4 we wanted to investigate whether differences in macroscopic soil parameters can reveal differences in height growth. Thus by conducting a cluster centre analysis, the

Table 1
Correlation coefficients of site factors and corresponding principal components. Site factors include plot-based parameters (inclination, altitude) and horizon-based parameters (A and B horizon). The five extracted components were used for subsequent cluster analysis. Correlations with $r > 0.5$ in bold show no overlap of soil parameters between components.

Site factor	Component				
	1	2	3	4	5
Inclination	0.223	0.124	0.213	**−0.479**	0.062
Altitude	**−0.669**	−0.386	0.001	0.150	0.159
Roots [cm]	0.311	**0.588**	0.043	0.475	0.193
Core [cm]	−0.387	0.334	0.412	0.108	0.429
A. size	0.414	0.491	0.005	**0.539**	0.261
A. sand	**0.774**	0.151	−0.161	−0.389	0.054
A. clay	**−0.715**	−0.142	0.139	0.452	−0.065
A. stones	0.425	−0.037	−0.148	−0.072	0.465
A. pH	0.360	0.360	**0.596**	−0.016	−0.294
B. size	−0.375	−0.280	**0.568**	−0.334	0.296
B. sand	**0.616**	−0.492	0.145	0.234	−0.171
B. clay	−0.480	**0.569**	−0.171	−0.422	0.159
B. stones	0.352	−0.496	0.145	−0.026	0.479
B. density	0.433	**−0.518**	−0.091	0.170	0.158
B. pH	0.250	−0.019	**0.798**	0.014	−0.137

five factors resulting from factor analysis were clustered into three groups with highest possible similarity of factor combinations within and highest possible differences between the groups.

The growth of the 25% highest plants was used as the dependent variable for two different ANOVA models.

Firstly: independent variables for a three-factorial ANOVA on the species level: site factors as result from cluster analysis (clusters 1–3), vegetation units (pasture, bracken, shrub), above ground competition (with above ground weeding and without).

Secondly: independent variables for a, four-factorial ANOVA: successional status of planted trees (early successional, mid-successional, exotic tree species), site factors as result from cluster analysis (clusters 1–3), vegetation units (pasture, bracken, shrub), above ground competition (with above ground weeding and without).

3. Results

3.1. Management of aboveground competition (H1)

The multifactorial ANOVA (light ecology, vegetation cover, site cluster, weeding and interactions) did not reveal any effect of aboveground weeding neither as independent factor nor as interacting factor. However, on the species level, *C. montana* reacted significantly negatively to weeding as single independent factor ($p = 0.015$); *Heliocarpus* ($p = 0.053$) and *Tabebuia chrysantha* ($p = 0.055$) in contrast reacted positively (see Fig. 1). Aboveground weeding of *C. montana* interacts on a lower significance level with vegetation cover ($p = 0.07$, Fig. 2) and with site cluster plus vegetation cover ($p = 0.084$)). *Pinus*, in contrast, showed significant response only for the interaction vegetation cover × weeding
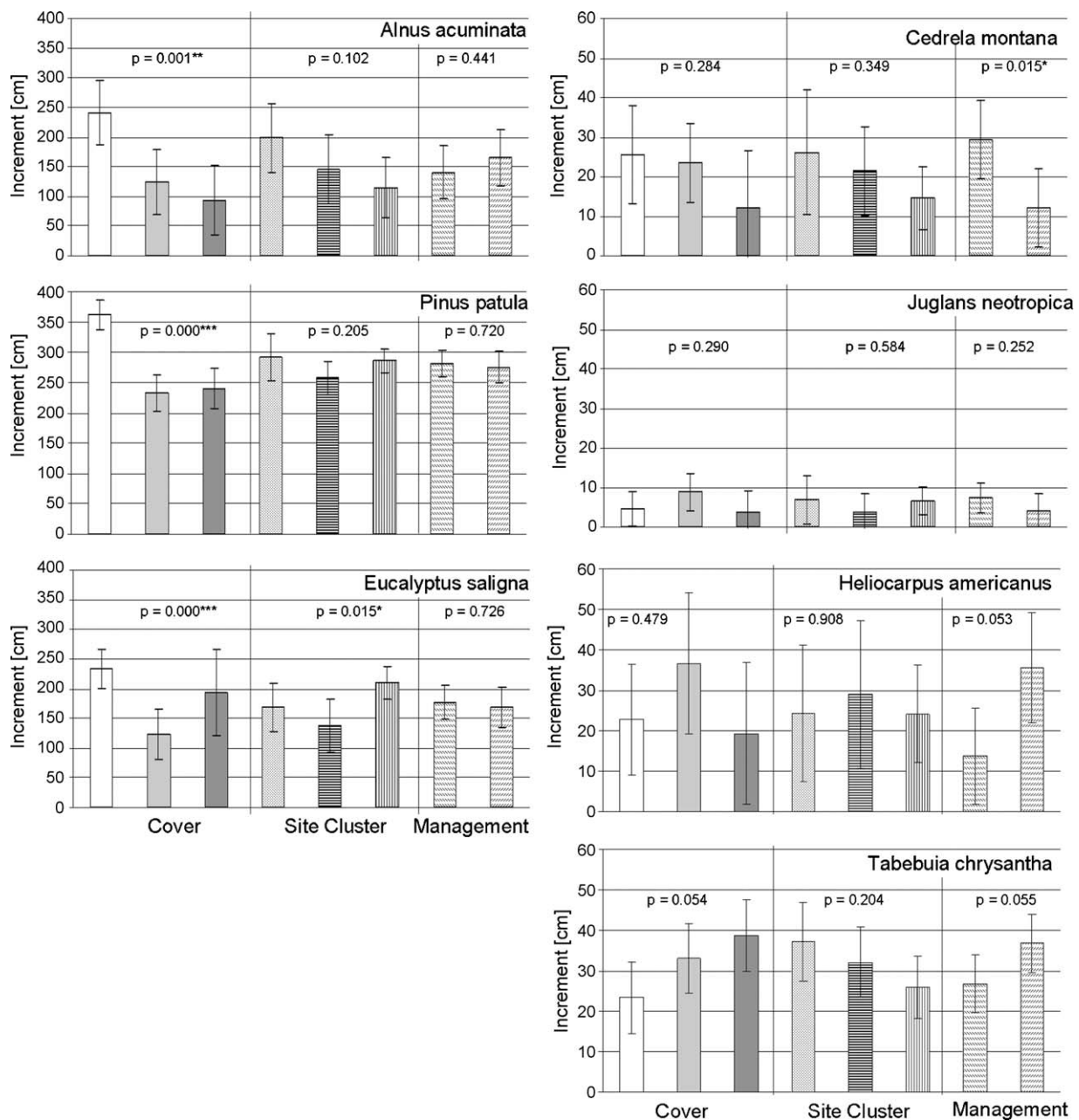

Fig. 1. Influence of competing vegetation cover on the growth performance of 3-year-old seedlings from five native species (*Alnus acuminata*, *Cedrela montana*, *Juglans neotropica*, *Heliocarpus americanus*, *Tabebuia chrysantha*) and two introduced species (*Pinus patula* and *Eucalyptus saligna*). From left to right: pasture (white bars), bracken (bright grey), shrub (dark grey), site clusters 1–3 from left to right and above ground weeding (without and with from left to right). Note that figures on the right have different scales than those on the left. Confidence intervals represent $p = 0.95$.
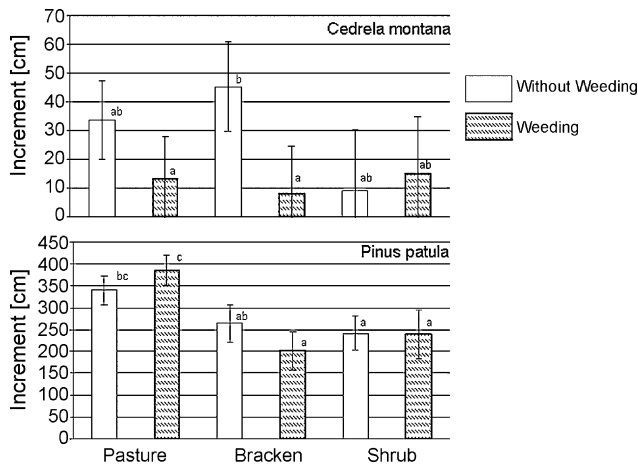
Fig. 2. Effects of interactions weeding × competing vegetation on growth performance for the 3-year-old plants of *P. patula* and *C. montana*. Different letters correspond to significant differences (confidence level *p* = 0.95).

(p = 0.026), but the effect is rather poor (Fig. 2). It is notable that weeding under shrub cover had no effect for any species.

3.2. Species-specific differences between successional sites (H2)

The vegetation cover had significant effects (Fig. 1) for the three species *A. acuminata* (p = 0.001), *P. patula* (p < 0.001) and *E. saligna* (p < 0.001), with *Tabebuia chyrsantha* almost reaching the significance level (p = 0.054). *Alnus* and *Pinus* behave like typical early successional species with the significantly best height growth on the pasture site. *T. chrysantha* showed the opposite behaviour, with best growth on shrub followed by bracken and least on the pasture site. The exotic species *Pinus* and *Eucalyptus* are the only species that reacted poorly on the bracken site, where in contrast *Heliocarpus* and *Juglans* surprisingly showed the best height growth. However, vegetation cover in general had no significant effect for the latter species.

3.3. Soil core parameters as predictor for top height of planted trees (H3)

Based on soil and site parameters obtained directly from the field, we could identify three different site clusters. The frequency of plots with homogeneous site conditions was relatively low; in more than 60% of all plots with dimensions of only 10.75 m × 10.75 m we could identify two or more site clusters. The three site clusters were present in all the three successional stages. However, Cluster 3 prevailed at the shrub and bracken sites, while for the pasture, Cluster 1 had the highest frequency (Fig. 3).
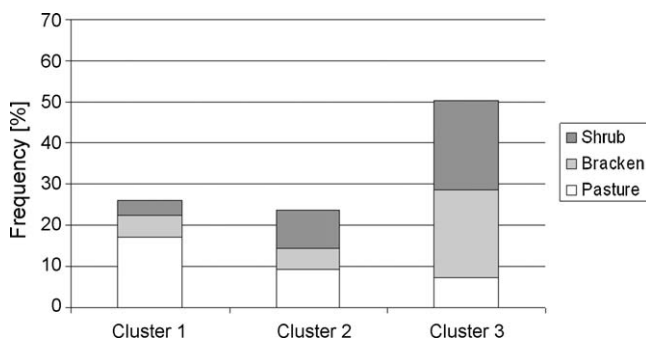

Fig. 3. Frequency of site clusters among sites with the dominant vegetation on experimental block "pasture" (white bars), "bracken" (light grey), "shrub" (dark grey), total = 100%.

Table 2
Differences of site factors between the site clusters 1–3 in the first two horizons (A and B). The values represent means and standard errors.

Site factors	Horizon	Cluster 1	Cluster 2	Cluster 3
Inclination [%]		62.2 ± 1.0	58.7 ± 1.2	60.2 ± 1.0
Size [cm]	A	44.6 ± 1.1	46.1 ± 1.3	55.0 ± 0.9
	B	41.0 ± 0.9	33.6 ± 0.8	31.2 ± 0.5
Sand [%]	A	35.6 ± 1.2	31.6 ± 1.2	29.5 ± 0.7
	B	29.1 ± 0.7	26.4 ± 0.8	23.2 ± 0.5
Silt [%]	A	31.0 ± 0.8	33.1 ± 0.8	33.7 ± 0.5
	B	34.9 ± 0.5	35.8 ± 0.5	37.5 ± 0.3
Clay [%]	A	33.0 ± 0.8	35.3 ± 0.8	36.8 ± 0.5
	B	36.2 ± 0.5	38.2 ± 0.6	39.5 ± 0.4
pH	A	5.2 ± 0.02	5.1 ± 0.02	5.2 ± 0.02
	B	4.8 ± 0.02	4.6 ± 0.02	4.7 ± 0.02

The differences between the soil core parameters were relatively small. The pH under shrub (5.1 ± 0.03, mean and STE) was slightly lower than under pasture (5.2 ± 0.01) and bracken (5.3 ± 0.02). Cluster 3 is characterised by a slightly taller A-horizon and higher silt and clay proportions in the first two horizons. Cluster 1 is slightly steeper and sandier than the others. Cluster 2 is intermediate with all parameters with the exception of a slightly lower pH than the other clusters (Table 2).

Despite these relatively small differences in parameters revealed directly from soil cores in the field, significant differences could be revealed for *Eucalyptus* (p = 0.015) with Cluster 3 showing the best height growth. *Alnus*, *Cedrela*, and *Tabebuia* however, performed best on Cluster 1 (n.s.). *Alnus* and *Eucalyptus* showed the biggest difference (almost by a factor of 2) between the means of their best and worst site clusters, whereas *Pinus*, *Juglans* and *Heliocarpus* showed almost no differences between the site clusters (Fig. 1).

3.4. Macroscopic soil core analysis as predictor for chemical soil properties (H4)

Despite relatively low differences in parameters derived directly from macroscopic soil core analysis, pronounced differences in several chemical parameters could be identified for the site clusters. For instance, cluster analysis revealed significant differences in chemical soil properties for Mn and Mg in the B-horizon and the C–N ratio in the subsoil (Table 3). While site cluster 1 is characterised by higher extractable Mn and lowest *K* values, site cluster 3 shows higher extractable K and plant available P (Table 3). Site cluster 2 exhibits lower available P, and on the pasture site significantly higher C–N ratio in the subsoil in comparison to clusters 2 and 3 (p = 0.035).

The dominating vegetation cover on the successional sites had a significant effect on P and extractable Mn in the B-horizon. Pastures showed high P concentrations in the first two horizons, and high extractable Ca and K. Bracken stages in contrast were richer in extractable Mn, Mg, and N (Table 4) and poor in available P. In general the Al concentrations were very high, accompanied by low base saturation. The base saturation in the A-horizon follows the successional gradient from pasture, bracken to shrub stage. It is notable that the shrub stage in general had very low C and cation values in the A-horizon in comparison to the other successional stages.

3.5. Interactions between successional stage, site cluster and above ground weeding (H5)

It is notable that both, successional status of planted species and stage of surrounding vegetation had a significant effect on the height growth of planted trees as single factors and as well as interactions (p < 0.001). Exotic species performed significantly

Table 3
Differences in chemical soil parameters (mean ± standard deviation) between the three site clusters 1–3 for the first three horizons of the mineral soil. All exchangeable ion values are presented in ion equivalents [IE μmol g^{-1}]. Significant parameters and values are presented in bold, different letters indicate significant differences. Asterisks symbolize levels of significance.

Site cluster	Horizon	C [%]	N [%]	C:N*	P [μg/g]	Al	Fe	Mn***	Ca	K	Mg*	CEC	BS [%]
1	A	5.4 ± 0.54	0.26 ± 0.04	21.3 ± 1.41	38.2 ± 15.7	71.6 ± 25.5	1.12 ± 0.16	0.23 ± 0.27	6.5 ± 5.0	1.45 ± 0.65	1.92 ± 1.35	90.1 ± 20.1	13.0 ± 9.7
	B	0.8 ± 0.16	0.06 ± 0.01	14.2 ± 1.05	12.6 ± 14.8	23.4 ± 11.0	0.31 ± 0.27	**0.14 ± 0.32A**	1.0 ± 0.8	0.68 ± 0.29	**0.27 ± 0.15A**	26.6 ± 11.9	10.2 ± 5.4
	Subsoil	0.4 ± 0.03	0.04 ± 0.00	**10.8 ± 1.72A**	3.5 ± 5.0	20.8 ± 7.7	0.06 ± 0.05	0.02 ± 0.01	0.6 ± 0.2	0.46 ± 0.20	0.13 ± 0.06	22.8 ± 8.0	8.1 ± 2.9
2	A	5.3 ± 0.75	0.25 ± 0.05	22.3 ± 1.65	26.2 ± 4.9	78.1 ± 21.3	3.59 ± 2.00	0.11 ± 0.06	7.4 ± 4.5	1.95 ± 0.69	4.04 ± 1.44	105.0 ± 15.0	14.0 ± 5.6
	B	0.9 ± 0.10	0.08 ± 0.01	12.8 ± 1.15	10.0 ± 9.5	26.7 ± 9.6	0.23 ± 0.18	0.09 ± 0.15	0.9 ± 0.8	0.82 ± 0.31	0.39 ± 0.43	30.0 ± 9.6	9.9 ± 5.6
	Subsoil	0.5 ± 0.29	0.04 ± 0.01	14.2 ± 10.0	4.1 ± 2.3	11.3 ± 0.1	0.01 ± 0.01	0.09 ± 0.08	0.7 ± 0.2	0.71 ± 0.06	0.15 ± 0.09	13.4 ± 0.1	15.4 ± 0.2
3	A	4.9 ± 0.51	0.26 ± 0.03	18.8 ± 0.66	39.5 ± 25.8	78.2 ± 28.9	2.27 ± 1.83	0.15 ± 0.17	5.3 ± 3.1	2.97 ± 3.46	3.45 ± 2.00	99.4 ± 29.7	14.3 ± 10.2
	B	1.1 ± 0.19	0.08 ± 0.01	12.4 ± 0.70	9.7 ± 14.5	32.6 ± 14.1	0.23 ± 0.29	**0.07 ± 0.14B**	1.1 ± 1.4	0.81 ± 0.91	**0.40 ± 0.69B**	36.7 ± 16.1	8.2 ± 4.8
	Subsoil	0.8 ± 0.12	0.06 ± 0.01	**11.7 ± 1.21B**	6.3 ± 8.2	22.4 ± 9.5	0.18 ± 0.25	0.04 ± 0.06	0.8 ± 0.7	0.87 ± 0.60	0.51 ± 0.91	25.6 ± 9.8	11.7 ± 5.5

Table 4
Differences in chemical soil parameters (mean ± standard deviation) between the three successional sites pasture, bracken and shrubs for A- and B-horizon and subsoil. Al exchangeable ion values are presented in ion equivalents [IE μmol g^{-1}]. Significant parameters and values are presented in bold, different letters indicate significant differences between successional sites. Asterisks symbolize levels of significance.

Successional site	Horizon	C [%]	N [%]	C:N	P** [μg/g]	Al	Fe	Mn***	Ca	K	Mg	CEC	BS [%]
Pastures	A	5.2 ± 0.49	0.26 ± 0.03	20.8 ± 0.94	45.9 ± 26.5	65.7 ± 23	1.46 ± 1.2	0.14 ± 0.20	7.8 ± 4.3	2.84 ± 3.8	2.79 ± 1.6	87.9 ± 20.5	17.4 ± 11.1
	B	1.2 ± 0.12	0.07 ± 0.01	15.1 ± 0.79	**14.3 ± 13.4A**	30.1 ± 14	0.24 ± 0.2	**0.03 ± 0.05A**	0.9 ± 0.7	0.73 ± 0.4	0.24 ± 0.1	33.1 ± 14.0	8.3 ± 4.4
	Subsoil	0.7 ± 0.15	0.05 ± 0.01	12.6 ± 1.61	8.0 ± 9.0	20.2 ± 7	0.09 ± 0.2	0.01 ± 0.01	0.9 ± 0.7	0.68 ± 0.5	0.16 ± 0.1	22.8 ± 7.2	10.3 ± 4.9
Bracken	A	5.8 ± 0.73	0.31 ± 0.03	18.3 ± 0.71	22.6 ± 10.0	93.0 ± 28	4.29 ± 2.0	0.23 ± 0.20	3.9 ± 2.4	2.65 ± 0.7	4.63 ± 2.6	113.6 ± 27.5	11.6 ± 6.4
	B	0.9 ± 0.09	0.09 ± 0.01	10.3 ± 0.59	**5.1 ± 6.2B**	25.2 ± 12	0.19 ± 0.17	**0.08 ± 0.08A**	0.5 ± 0.5	0.94 ± 0.4	0.48 ± 0.4	28.2 ± 12.1	9.6 ± 4.7
	Subsoil	0.7 ± 0.15	0.07 ± 0.01	10.2 ± 1.63	2.4 ± 4.0	19.5 ± 10	0.21 ± 0.31	0.08 ± 0.08	0.5 ± 0.3	1.09 ± 0.6	0.87 ± 1.2	22.8 ± 10.8	13.9 ± 4.9
Shrubs	A	3.7 ± 0.53	0.18 ± 0.02	20.5 ± 1.39	30.2 ± 8.7	76.5 ± 28	1.53 ± 0.8	0.14 ± 0.13	3.7 ± 1.5	1.40 ± 0.4	2.38 ± 0.8	97.5 ± 29.1	9.0 ± 3.3
	B	0.8 ± 0.33	0.06 ± 0.02	11.4 ± 0.76	7.7 ± 15.4	32.8 ± 13	0.32 ± 0.4	**0.15 ± 0.29B**	1.5 ± 1.7	0.73 ± 1.2	0.51 ± 0.9	39.1 ± 16.4	8.5 ±± 5.8
	Subsoil	0.7 ± 0.19	0.05 ± 0.01	13.7 ± 2.08	9.3 ± 10.6	25.1 ± 11	0.14 ± 0.1	0.02 ± 0.01	1.5 ± 1.1	0.36 ± 0.1	0.18 ± 0.1	28.0 ± 11.4	10.3 ± 6.8

better than light demanding species. Mid-successional species performed in general worse than light demanding species but significantly only on pastures. For exotic species and the light demanding species the earliest successional stage "pasture" is by far the best environment. However, it is important to note that no species group showed significant differences between the advanced successional stages "bracken" and "shrub". In contrast to exotics and light demanding species, mid-successional species performed worse on pastures than on other successional stages, but this effect was not significant.

Fig. 4 shows that exotic species perform significantly the best on pastures and site cluster 3, which in contrast is the worst site cluster for the light demanding species on the pasture site. This highlights the importance of deliberate matching of site conditions and successional stage for successful reforestation. The differences between site clusters are relatively low for the other successional stages and for the mid-successional species. Including "weeding" in the analysis as an additional factor results in tremendous differences between the treatments. For example, the best environmental setting for *Cedrela* ($p = 0.84$, Fig. 5) is site cluster 1 in the bracken stage without mechanical weeding (74.0 cm). However, in the bracken and pasture stage cluster 2 also results in acceptable growth with 38.3 cm and 57.3 cm, respectively.
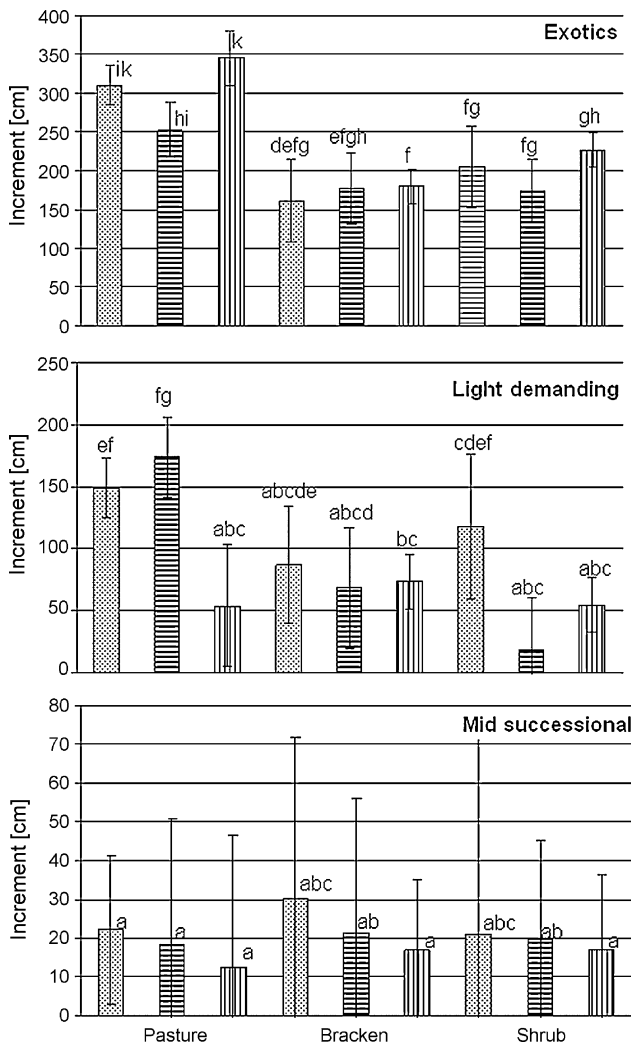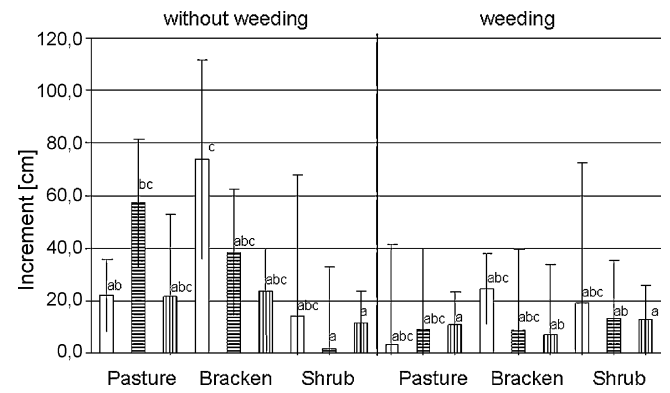

Fig. 5. Interactions for *C. montana* (weeding × dominating vegetation × site cluster, ANOVA, $p = 0.084$) between dominating vegetation on experimental block (*x*-axis), site cluster (1 = white bars, 2 = horizontally hatched, 3 = vertically hatched) and weeding of above ground vegetation (without and with from left to right), confidence intervals $p = 0.95$.

Planting in the shrub stage or weeding lead to very poor growth for all site clusters with this species.

4. Discussion

4.1. Above ground competition and performance of planted tree species (H1)

Suppressing weedy vegetation is recommended as one technique for assisting natural regeneration (Shono et al., 2007). As small-scale farmers in developing countries often cannot afford the investment in chemical site preparation, manual weeding will continue to play an important role, especially for reforestation measures by land users who depend on livelihood. Grasses, bracken fern and many other competing plants survive manual above ground weeding and resprout quickly (Hooper et al., 2002). Thus, the ecological effect of this management technique on abandoned pastures is mainly limited to control of light conditions.

In the present study the enormous investment in the manual control of the competitive vegetation was not compensated for by appropriate height growth of the seedlings, except in the cases of *T. chrysantha* and *H. americanus*. As Eckert (2006) revealed, chemical treatment of the ground vegetation with glyphosate was much more efficient than manual control for *Cedrela* and *Tabebuia*. However, similar to plowing, large-scale application of herbicides on the steep slopes of the Andes may lead to higher erosion and disturbances of the water budget (Evans and Turnbull, 2004) and consequently should be restricted to areas with lower slope angles only.

Growth rates of *Cedrela* apparently suffered under the manual weeding which may be an effect of reduced shading and subsequent drought stress during the dry season, and high root competition (Castro et al., 2002; Eckert, 2006; Weber et al., 2008). In the old-growth forest adjacent to the reforestation site, *Cedrela* already showed drastically reduced growth when canopy openness exceeded 30% (Kuptz et al., unpublished data). These findings are supported by Uhl (1987) who found that especially large seeded and more shade tolerant species have poor performance under the higher irradiances, higher temperatures and decreased humidity characteristic of such patches. Similar to the behaviour of *Cedrela* in our study area, many native species also reacted negatively to mowing in reforestation trials in *Sacharum* grasslands as a result of increased radiation (Hooper et al., 2002). Thus, these environmental factors are the most likely behind the poor development of *Cedrela* and possibly *Juglans* in our mowed plots, too.

Fig. 4. Interaction (successional status × dominating vegetation × site cluster, ANOVA $p = 0.003$) between successional status of planted seedling (from top to bottom), dominating vegetation on experimental block (*x*-axis) and site cluster 1 (squared), 2 (horizontally hatched) and 3 (vertically hatched) with confidence intervals $p = 0.95$. Note that graphs have different scales.

Davidson et al. (1998) found much better growth for *H. americanus* in northern Ecuador than did we. This can mainly be attributed to their initial herbicide treatment with glyphosate prior to planting. Eckert (2006) showed clearly that tree growth in pastures is much better after glyphosate treatment in comparison to mechanical weeding.

4.2. Species-specific differences between succesional sites (H2)

In conventional reforestation activities, trees are usually planted directly in areas that are manually or chemically cleared or burned. These conditions may be more favourable for pioneer and many exotic species but not for mid and late successional species. It is not yet a very well established reforestation measure in the tropics to adapt tree species to the successional stage of the dominating vegetation at the reforestation site (Dobson et al., 1997; Wishnie et al., 2007; Lamb et al., 2005). The widespread intensive site preparation prior to planting and the corresponding limitation to monocultures of early successional and exotic species are some of many obstacles for the establishment of mixed forests with high biodiversity. Some studies have already proven that for the tropics, a combination of early and late successional species can provide ecological and economical benefits (Parrotta and Knowles, 1999; Ashton et al., 2001; Kelty, 2006). Many valuable timber species belonging to the mid-successional group require a slight shelter, in our case *C. montana*, *J. neotropica* and *T. chrysantha*. Thus, one key question for the consideration of these species in reforestation measures is which successional stage and which combination of site factors corresponds best for which species? Besides the obvious advantages for biodiversity, planting one or several valuable tree species into an area of advanced natural succession (enrichment planting) could provide a facilitating effect for the establishment of the plants (Vandermeer, 1989; Carpenter et al., 2004), and a more effective recovery of soil properties (Zheng et al., 2005).

Some authors assume that bracken hinders reforestation (Humphrey and Swaine, 1997). Our data show that this is not valid for our mid-successional species. In general, these species performed similar or even better under bracken or shrubs in comparison to pastures (Figs. 2 and 5). Under Cluster 1 conditions (high Mn) *C. montana* achieved best height growth at the bracken site (high N, Mg, Mn, and low available P, Fig. 5). It is surprising that the mid-successional species could not profit more from the environmental conditions at the shrub site. This can possibly be attributed either to the inferior shading capacity of the shrubs compared to the dense cover of bracken (Humphrey and Swaine, 1997) or to reduced nutrient supply in the soil due to higher plant uptake by the shrubs. External factors like microclimate, which could not be included in the experimental settings as covariables could also cause differences between the experimental blocks, which consist of the three succesional stages (Nepstad et al., 1990; Vieira and Nepstad, 1994; Aide et al., 1996). Thus, the influence of the dominating vegetation cover has to be discussed with caution. The height growth of light demanding and exotic species at the shrub site was also not convincing (Fig. 5) indicating that this site may be characterised by generally poorer environmental conditions.

Pastures can be very competitive and cause high mortality and slow growth of tree species in many cases (Otsamo et al., 1995; Pedraza and Williams-Linera, 2003). Despite higher root competition on pastures, some tree species apparently grow better in grasses than under shrubs. This can be explained by possible allelopathic effects of shrubs, differences in root depths and fine root density (Gerhardt and Frederikksson, 1995; Sun et al., 1995; Holl, 1998). Another reason could be the intensive C-dynamic under *Setaria* leading to high C contents in comparison to other land use types (Rhoades et al., 2000; Makeschin et al., 2008).

It is well established that exotic species generally grow very fast, but some native species are able to compete in survival and growth (González and Fisher, 1994; Islam et al., 1999; Wishnie et al., 2007). Thus, the good height growth of *Alnus* is in line with these findings. From hundreds and thousands of tree species in Ecuador, broader experiences for reforestation exists for only less then 10, mainly due to limited knowledge on seed ecology and plant propagation (Stimm et al., 2008). Thus, success of reforestation efforts with native species in Ecuador depends strongly on future research on these topics. Our data support the general finding that early successional species perform better than mid-successional species in the first years of plantation (Davidson et al., 1998). However, it must be recognized that site conditions and surrounding vegetation are of major importance and adequate management concepts to cope with these items are not yet available. Furthermore, the slower growth of mid-successional species *Tabebuia* and *Cedrela* could be a temporal effect in the initial stage of plantations. For instance, in long term reforestation trials in Puerto Rico, surprisingly many merchantable tree species grew faster in the second 33-year period than in the initial 22 years of observation (Silver et al., 2004). If the interactions between sites factors and the single tree species are properly understood, the micro-environmental conditions at the shrub and bracken stages could be used to facilitate the establishment of newly planted trees, especially from later successional stages (Pedraza and Williams-Linera, 2003; Parrotta et al., 1997).

Slowcroft et al. (2004) could not reveal interactions between vegetation cover (grasslands and plantations with *Metrosideros polymorpha* Gaud.) and topographic position. Their findings do not necessarily contradict the significant interactions found in our study, as such significances depend strongly on the number of repetitions in the experimental design.

4.3. Suitability of macroscopic soil core analysis for planning of reforestation measures (H3, H4)

In temperate zones site classification is a common and valuable tool for forest management planning. Despite their importance for planning of reforestation and selection of appropriate species for given site conditions, these instruments are largely missing for tropical landscapes.

Being representative for many regions in the Andes, our study area is characterised by an extremely rugged topography accompanied by a high frequency of landslides which leads to extreme small-scale heterogeneity and a mosaic of soil conditions (Wilcke et al., 2003; Oesker et al., 2008). Makeschin et al. (2008) confirm a very high standard error for the chemical parameters under pasture and fallow stages. Our results show that on 60% of all 10.8 m × 10.8 m plots were occupied by more than one site cluster, and site clusters showed significant differences in soil chemical properties, especially for Manganese. Thus, soil conditions in the study area apparently vary on a very low spatial scale of less than 10 m.

Site classification is commonly based on identification of soil types (FAO, US classification), which requires the detailed analysis of soil profiles in the field combined with chemical soil analysis in the laboratory. The detection of edaphic differences on very low spatial scales with this approach would be extremely laborious, expensive and ineffective. Alternatively, field description of soil cores are successfully used for site characterisation in some countries of the world, for instance in Germany (Arbeitskreis Standortskartierung, 2003), but little is known about the transferability of this methodology to tropical landscapes.

In our study we could identify some distinct species dependent effects between special site clusters and the growth of young seedlings. For instance *Alnus*, *Cedrela*, *Tabebuia* exhibited better

height growth on site cluster 1, while *Eucalyptus* grew best on site cluster 3 indicating species-specific requirements to environmental conditions. The results indicate that parameters derived from soil core description could be used to estimate tree development on abandoned pastures in neotropical mountain areas. However, this methodology requires intensive statistical processing of the data and is actually effective only for some species, although the results still suggest that this approach is a promising perspective for better consideration of natives in future reforestation endeavours.

Ca, K, Mg and BS values on an average are comparable to those of Makeschin et al. (2008) in the same study area. All these elements and additionally Al and Fe were key elements for distinguishing between the major rock groups of the study area, which have variable magnitudes of the easily weatherable minerals muscovite/illite, chlorite and albite according to these authors. Thus, significant correlations between these minerals in the subsoil and horizon B and differences in Mg between site clusters could be attributed to the respective geological parent material.

Mn mobilization and/or lateral Mn removal is often related to acidification/podzolisation and/or reduction conditions in soils (Zech and Drechsel, 1991). In addition to the high spatial heterogeneity of the soil conditions on land slides (Wilcke et al., 2002, 2003), this could explain the differences in extractable Mn between the site clusters.

Studies of several authors confirm that P availability might be less problematic than N. For instance, in a study by Haridasan (1985) *Eucalyptus grandis* performed well with available P (46 ppm) and extractable cations comparable to our results. As Newberry et al. (2002) reported, P did not limit growth of ectomycorrhizal trees on soils with extremely low phosphorous supply. *Pinus radiata* plantations in Northern Ecuador were growing well on soils with higher N values in the A-horizon (0.17–0.22%) (Farley and Kelly, 2004). Experimental reforestation trials with good performance of several native species on Hydrandept soils were much higher in N (0.24%), only slightly higher in extractable cation concentrations and much lower in Aluminium saturations (Davidson et al., 1998). Thus, in comparison to those studies, low N values and high aluminium toxicity in general could be limiting factor for plant growth for our study region, rather than P or extractable cations. In line with our findings of low base cations at the shrub sites, Slowcroft et al. (2004) show that concentrations of extractable base cations and P can be affected rather by the vegetation type than by the topographical position. These results support the hypothesis that early successional stages are rather N limited, but they become more P-limited in later stages (Vitousek et al., 1993; Herbert and Fownes, 1995; Newberry et al., 2002).

4.4. Vegetation cover and site differences are independent factors for the success of reforestation with native and exotic tree species (H5)

In addition to the difficulties in predicting small-scale variations of autecological conditions and their impact on the growth of tree species, it is essential to assess the impact of the competing vegetation. Numerous authors studied plant–soil interactions during the last decades (Cuevas and Medina, 1988; Vitousek et al., 1993), however very limited attention is given to these aspects for planning plantations.

For the three major vegetation types, pastures, bracken and shrubs, there exist several possible limiting factors for tree species. For instance, C4 plants generally have a better water use efficiency than trees. Thus, *S. sphacelata* apparently has competitive advantages on the sun exposed areas in comparison to forest species, especially the mid-successional species which are adapted to slight shading (Bazzaz and Picket, 1980). *Setaria* can store enormous

amounts of C due to its extended fine root system (Rhoades et al., 2000; Makeschin, 2008). This rather advantageous effect for soil fertility, however, is combined with a negative effect for the planted trees: Eckert (2006) has proven that root competition of this grass species is one of the most important barriers for growth of reforestation species, especially for mid-successional species.

In our study the vegetation cover had significant effects on N and P-values. These typical slash- and burn effects were also confirmed by Makeschin et al. (2008) for our study area: N and P are strongly influenced by burning, accompanied by an increase of pH, resulting from alkaline ashes which in turn reduces availability of P. Farley and Kelly (2004) showed that forest plantations in Ecuador can effectively reduce N concentrations in the soil via nutrient uptake and allocation processes in the biomass. Accordingly, differences of P under different vegetation covers in the present study, could likewise have been caused by nutrient uptake and reallocation.

N is generally considered to be a limiting factor in grasslands (Davidson et al., 1990; Scowcroft et al., 2004). In general N values were very low in our study area, too. Thus, it follows that proper N management could allow for better plant growth. For example, intercropping nitrogen fixing trees with reforestation species may result in better performance than initial fertilization (Carpenter et al., 2004). Our data support the findings of Murcia (1997) that *Alnus* grows rapidly even in nitrogen-poor soils.

Bracken is able to recover burned areas and generates a closed canopy very quickly, preventing the establishment of a shade intolerant vegetation (Hartig and Beck, 2003). Our data confirm that this could also be a problem for the planted trees, because light demanding species and exotics were significantly smaller here than on the open pasture sites. However, for the height development of light demanding species, bracken apparently is not worse than the shrub stage. Mid-successional species are even favoured in this environment.

It is well known that vegetation cover can shape the site conditions via nutrient uptake, litter fall, shading regimes and hydrological functions (Haridasan, 1985; Bruijnzel, 2004; Jobaggy and Jackson, 2004). The latter authors show that grasses have lower Manganese cycling than *Eucalyptus* and that vegetation cover alters the vertical distribution and bio-availability of mineral elements. This could explain why Manganese is significantly different between pastures, bracken and shrub in our study. On Gleysols, Mn deficiency is often combined with P deficiency (Kreutzer, 1970), and Mn mobilization and/or lateral Mn removal can be caused by acidification and groundwater podsolisation (Zech and Drechsel, 1991). Hydromorphy is frequent, too, in our study area, but under the predominant steep slopes hydromorphic processes are rather connected with percolating than groundwater. In the study area we can find both processes for Mn-mobilization: podzolisation and reduction conditions (Makeschin et al., 2008). Podzolisation causes the complexation of Mn by fulvo acids; reduction conditions in turn favour the transformation of non-soluble $Mn^{4+}O_2$ into soluble Mn^{2+}. Mn can be discharged in both cases (Haubrich, unpublished data). These processes possibly could explain differences in extractable Mn between the different site clusters. It is well established that vegetation influences water content of soils via transpiration, and plant roots can produce acids for better nutrient availability, which in turn affects Mn-mobility. This could be one explanation of how site clusters and vegetation cover are interacting and thus influencing the nutrient status of the soils.

5. Conclusions

Exotic species in Ecuador are generally considered to perform better than native species. In our study *A. acuminata* was able to compete in height development with the exotics at least in the first

3 years after planting. Reforestation trials with native and exotic species in Costa Rica for instance revealed the enormous potential of several native species for reforestation and restoration (Piotto et al., 2003; Wishnie et al., 2007). In Central America experiences with native species started already several decades ago, while in Ecuador the discussion has only recently started. Consequently, we assume that among the extremely high number of 2736 tree species in Ecuador (Jørgensen and León-Yánez, 1999) it is very probable to find other and perhaps even more promising species. However, the crux is to identify the best candidates for reforestation and to provide adequate knowledge on their seed ecology, propagation and silvicultural requirements. As expected, mid-successional species performed much slower than the exotics and light demanding species. However, if planted under adequate environmental conditions the height development of such species improves. C. montana, for instance, showed acceptable development under bracken without above ground weeding. Furthermore, the slow initial growth may be compensated for by their extremely high timber value. Thus, from the economical point of view, mid-successional species could be a very valuable contribution in a portfolio of species for reforestation purposes.

In contrast to the findings of other authors, ours do not support the hypothesis that bracken hinders the establishment of native tree species in general. One soil cluster under bracken was even indicated as the best environment for mid-successional species. Exotic and light demanding species in contrast, performed better on the pasture plots, which indicates less susceptibility to root competition than to light competition. Thus, established young seedlings of light demanding species are shaded out under bracken, while bracken can be facilitative for the more shade tolerant mid-successional species which are more susceptible to higher vapour pressure deficits at open sites. Above ground weeding should be evaluated on the species level, as no general positive trends could be revealed neither for light demanding nor exotic species and no general negative trends were found for mid-successional species.

Soil properties revealed by soil core analysis showed significant effects on the height development of some tree species, in particular E. saligna and to a lesser extent A. acuminata. These differences were accompanied by differences in Mn and Mg status. However, significant interactions between soil cluster and dominating vegetation cover could be revealed for Mn, too. P was not affected by soil clusters, but only by vegetation cover. On more than 60% of plots more than two soil clusters could be identified. This extremely high small-scale heterogeneity is stunning. Large-scale site classification based on soil properties alone will hardly uncover all of the constraints for the establishment of tree seedlings. Thus, reforestation planning should imply site classification at different spatial scales including dominating vegetation cover.

Acknowledgements

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