

17 **Abstract**

18 The Andes of Ecuador are known for their outstanding biodiversity but also as the region with
19 the highest deforestation rate in South America. This process is accompanied by accelerating
20 degradation and loss of environmental services. Despite an extraordinary richness in native
21 tree diversity, more than 90 % of all forest plantations established in Ecuador consist of exotic
22 species, primarily *Eucalyptus* spp. and *Pinus* spp. This is mainly due to the lack of
23 information about the autecological and synecological requirements of the native species.
24 The present study aims at providing basic knowledge on the early height development of
25 native species in comparison to exotics. 12,000 seedlings of exotic and native species were
26 planted in experimental trials at three sites of different successional stages: recently
27 abandoned pastures (*Setaria sphacelata*), bracken (*Pteridium arachnoideum*) and shrubs.
28 Results presented in this study refer to the status of the seedlings three years after planting.
29 Soil data were revealed from soil core analysis from a total of 1008 soil samples distributed
30 systematically over all plots. Soil chemical data derive from a subsample of 125 randomly
31 selected soil core sites. Soil properties in the study area emerged to be extremely
32 heterogeneous. More than 60 % of all plots presented two or more soil clusters. Soils in
33 general were very poor in plant available N. Soil heterogeneity affected extractable Mn and
34 Mg, dominating vegetation cover in turn affected Mn and P. Differences in soil properties had
35 a strong effect for *Eucalyptus saligna* and *Alnus acuminata*. Manual above ground weeding
36 showed species specific effects: *Tabebuia chrysantha* and *Heliocarpus americanus* showed
37 improved height growth, while that of *Cedrela montana* was reduced. There is evidence that
38 *Alnus acuminata* can compete in growth with exotic species. Early successional species and
39 exotics performed best on pasture dominated sites. Height growth of the mid successional
40 species *Cedrela montana* was facilitated by bracken fern under certain soil conditions, and
41 shrubs facilitated growth of *Tabebuia chrysantha*. The results indicate that reforestation with
42 native species in Ecuador is possible but requires intensive consideration of interactions with

43 soil properties and accompanying vegetation. Macroscopic soil core analysis can be a suitable
44 instrument for detecting small scale variation of soil properties. Nevertheless, a
45 characterisation of both small scale variation as well as variation on higher spatial scales, for
46 instance by aerial photographs, is essential for effective planning of reforestation measures in
47 the Andes.

48

49 *Key words: reforestation, native species, soil, site factors, competition, Andes, montane*
50 *forests*

51

52 **Introduction**

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

61 The deforestation cycle in the South Ecuadorian Andes is usually initiated by extraction of
62 high value timber species, resulting in an economical degradation of the forest value for the
63 land users. Similar to other areas in the tropics (Otsama et al., 1995; Hooper et al., 2002),
64 these forests are burned and converted into pastures for cattle raising (Mosandl et al. 2008).
65 Frequent burning of the pastures reduces germination, growth and survival of tree seedlings
66 (Hooper et al., 2002) and frequently leads to degraded landscapes, dominated by bracken fern
67 *Pteridium arachnoideum*. The introduced pasture grass *Setaria sphacelata* is frequently used

68 in our study area due to its high productivity (Rhoades et al., 2000; Makeschin et al., 2008).
69 Both grasslands and bracken are described to be major barriers for the establishment of tree
70 seedlings (Holl, 2002; Hartig & Beck, 2003; Griscom et al., 2007).

71 Tropical ecosystems are not only important refuges for biodiversity (Barthlott et al., 2005) but
72 play also an existential role for livelihood as indicated by the heavy deforestation (Stoian,
73 2005; Quang & Nato, 2008). Thus, the need for subsistence is a major driver for deforestation
74 (Davidar et al., 2007, Wunder, 2000; Lopez, 2006). The success of reforestation efforts
75 strongly depends on species that can fulfil the demands of the people and cope with the given
76 site conditions and predominant competing vegetation.

77 Today, about 90% of all forest plantations in Ecuador consist of introduced species (FAO
78 2006), mainly *Eucalyptus* spp. and *Pinus* spp. (*i.e.* *E. saligna*, *E. globulus*, *P. patula*, *P.*
79 *radiata*). This can be explained by the good availability of planting material, existence of
80 clear silvicultural management concepts, proven good productivity, but also the lack of
81 knowledge regarding the silvics of the native species (Stimm et al., 2008). It is known that
82 plantations with exotic species can facilitate secondary succession of native species
83 (Brockerhoff et al. 2008, Feyera et al. 2002). However, large-scale exotic plantations lead to
84 landscape homogenization (Lamb et al., 2005), and can even raise ecological problems, for
85 instance with soil properties (Islam et al. 1999), fire susceptibility, stability, diseases and low
86 diversity (Manchester & Bullock, 2000, D'Antonio & Meyerson, 2002, Lamb et al., 2005).

87 Unfortunately scientific studies on reforestation in Ecuador particularly with native species
88 are very sparse (Brandbyge & Holm-Nielsen, 1986, Knoke et al., in press). Therefore,
89 comparative studies with exotics and native species are of major importance. A special focus
90 has to be given to the synecological and autecological site requirements of the native species
91 as how a species accommodates itself to the environmental conditions at a given site is
92 keystone to ensuring low mortality and good growth performance. However, autecological

93 requirements depend strongly on soil properties, while synecological requirements depend on
94 the surrounding vegetation. Consequently, for best planting success both aspects must be
95 considered (Evans & Turnbull, 2004, Lamb et al., 2005).

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

107 While the successional stage of a site can easily be revealed from field surveys or satellite
108 imagery, it is much harder to consider the tremendous variation in the micro-site conditions as
109 they prevail in the Ecuadorian Andes. In Mid Europe macroscopic soil core analysis is a
110 proven valuable instrument for determination of suitable planting sites (Arbeitskreis
111 Standortskartierung, 2003). However, there is limited knowledge regarding if these techniques
112 can be transferred to the complex neotropical montane ecosystems.

113 For detection of synecological requirements, we established experimental reforestation trials
114 on abandoned pastures comparing exotic species with native species of different successional
115 status. These were planted on three sites along a successional gradient in the montane forest
116 ecosystem of Southern Ecuador. In the following text the term “successional status” will be
117 used for the planted trees, the term “successional stage” in turn will be used for the

118 surrounding vegetation. The autecological requirements and their interactions with
119 synecological requirements were detected by soil core analysis.

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

125

126 **Materials and Methods**

127 Study area

128 The field experiment was conducted from 2003 - 2006 at the research station “Estación
129 Científica San Francisco” at km 34 along the road from Loja to Zamora in South Ecuador.
130 The station is geographically located at 3° 58' 17.21" south, 79° 04' 44.08" west at an
131 elevation of 1840 m a.s.l. The study area is characterised by perhumid climatic conditions
132 with 2200 mm annual rainfall and a slightly drier season around November. Average
133 temperature is 15.3 °C with a very low annual fluctuation (1.2 °C) compared to the mean
134 daily fluctuation (11.1 °C) (Bendix et al., 2006). Two dominant groups of rocks were
135 identified for the study area: meta-siltstones/-sandstones/quartzites and slates/phyllites
136 (Makeschin et al., 2008). The key elements for distinguishing the rock types are Al, K, Mg,
137 Fe, Na, and Ca dependent from the mineral content. Makeschin et al. (2008) state that forest,
138 pasture and sites with secondary vegetation of the study area are comparable in a priori soil
139 mineralogy. Dominant soil types in the forest are Cambisols and Histosols (Wilcke et al.,
140 2008), those under pastures and secondary vegetation Cambisols, Podzols, Gleysols, whereby
141 podzolisation dominates gleyic processes under pastures (Bahr, 2007). The soils display a
142 high degree of small-scale heterogeneity (Wilcke et al., 2002). Natural disturbances like land

143 slides further increase the soil heterogeneity in the study area. (Wilcke et al., 2003).
144 Anthropogenic replacement ecosystems recovering from slash-and-burn can be stratified into
145 three major vegetation types (Martinez, 2008), which constitute a successional gradient from
146 pasture, bracken to the shrub stage (Hartig & Beck, 2003), according to hypothesis (2) and
147 (4). In each of these successional stages, four hectares were delineated for the establishment
148 of experimental reforestation plots (Aguirre, 2007):

- 149 a) “pasture”: 1800-2100 m a.s.l. (UTM coordinates 713475, 9560931), average
150 inclination of 53 % (6-90), aspect South, dominated by the grasses *Setaria sphacelata*,
151 *Melinis minutiflora*, *Axonopus compressus*,
- 152 b) “bracken”: 1850-2100 m a.s.l. (UTM coordinates 714299, 9561044), average
153 inclination of 69 % (10-90), aspect South, dominated by *Pteridium arachnoideum*,
154 *Ageratina dendroides*, *Baccharis latifolia*,
- 155 c) advanced successional stage “shrub”: 2000-2200 m a.s.l. (UTM coordinates 712269,
156 9560293), average inclination of 44 % (5-55), aspect South, dominated by *Ageratina*
157 *dendroides*, *Myrsine andina*, *Brachyotum* sp.

158 Study species

159 We selected tree species from three different ecological groups (hypothesis H 2). The
160 nomenclature follows Jørgensen and León Yanéz (1999). *Heliocarpus americanus* and *Alnus*
161 *acuminata* are fast growing species of early successional status in their natural habitat. The
162 mid successional species *Tabebuia chrsyantha*, *Juglans neotropica* and *Cedrela montana* are
163 characterised by a very high timber value. *Pinus patula* and *Eucalyptus saligna* as exotic
164 species are widely used for reforestation in Ecuador.

165

166

167 Experimental settings

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

174 Seeds of the exotic species were purchased from the local seed market; those of the native
175 species were collected in the adjacent primary forest from at least 10 dominant healthy
176 individuals with well developed crowns and straight stem forms and raised under semi-
177 controlled conditions in our experimental nursery in Loja (Stimm et al., 2008). The mean
178 temperature of 15° C corresponds closely to the environmental conditions of the reforestation
179 areas. After germination, the seedlings were transplanted into 560 cm³ polyethylene
180 containers with a substrate that consisted of a 2:1:1 mixture of mine sand, Páramo humus and
181 forest humus. Before planting to the field, all seedlings were subject to a two-month
182 hardening phase in the nursery.

183 In total, 336 plots were established, with 112 plots randomly distributed per successional
184 stage. On each plot of 10.8 x 10.8 m, 25 seedlings were planted between May and September
185 2003 with a spacing of 1.8 m and with 8 repetitions per species and treatment. In the present
186 study we present the growth data of 3 years after planting. Before planting herbs, grasses and
187 ferns were eliminated on all plots by machete, only woody vegetation was not removed. On
188 half of the plots this weeding treatment was repeated every 6 months for 2 years, the
189 remaining half was left as reference without further treatments (according to H1).

190 Consequently, the experimental design for the reforestation is: 7 species x 3 successional sites
191 x 2 weeding treatments x 8 repetitions = 336 plots.

192 Complementary to the planting trials we conducted a field survey of the respective site factors
193 (hypotheses H 3, H 4, and H 5). Therefore we extracted three soil samples per reforestation
194 plot using a soil core “Pürckhauer”. Every soil sample was extracted between four
195 surrounding tree seedlings at fixed positions within the plot, at distances of 0.9 m between soil
196 sample and plants. For each soil horizon the following parameters were recorded in the field,
197 applying the guidelines of Arbeitskreis Standortkartierung (2003): size (cm), texture, colour
198 by Munsell (Hue, Value and Chroma), stone content, root intensity, bulk density, and pH
199 (H₂O). Besides the soil core parameters, we registered also the site factors of inclination and
200 altitude for every soil sample. In total, we analyzed 1008 soil core samples (336 plots x 3 soil
201 core samples).

202 For further chemical analysis, 125 soil samples were extracted randomly from all mineral soil
203 horizons of the 1008 soil core sites by digging a soil pit for each sample. Soil samples were
204 oven-dried at 40°C. All samples were homogenized. CEC and pH were analysed on soil
205 fraction <2mm. C and N were analysed on ground soil material (smaller than 63µm).

206 Effective cation exchange capacity (CEC) was calculated by percolation with 0.5 N NH₄Cl-
207 solution at pH 4.3 as sum of exchangeable Ca, Mg, K, Na, Mn, Al, and Fe (see Lürer &
208 Böhmer, 2000). Base saturation was calculated as the proportion of charge equivalent of
209 extractable Ca+K+Na+Mg of the effective CEC. Plant available P was extracted by citric acid
210 after VDLUFA (1991). The concentrations of organic C and N were determined with a CHNS
211 analyzer. In order to detect whether different site clusters, based on macroscopic soil core
212 analysis, can reveal differences in chemical parameters (hypothesis H 4), an additional two-
213 factorial, univariate ANOVA was conducted separately for horizon A, B and subsoil. For
214 analysis of individual chemical soil parameters as dependent values we defined site cluster
215 (cluster 1-3) and vegetation units (pasture, bracken, shrub) as the two major independent
216 factors and analyzed the other chemical parameters as covariates.

217 Data processing

218 According to the top height approach, which is frequently used for characterisation of site
219 potentials (Sharma et al., 2002), we analyzed the growth of the highest plant out of the four
220 seedlings surrounding each of the soil core samples. This corresponds to the top height of the
221 25% highest plants. Additional parameters like root collar diameter, leaf area, etc. were
222 measured, too, but as the aim of the present study is to characterize the site potential for tree
223 growth we chose the top height approach.

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

231 In hypothesis H 3 and H 4 we wanted to investigate whether differences in macroscopic soil
232 parameters can reveal differences in height growth. Thus by conducting a cluster centre
233 analysis, the five factors resulting from factor analysis were clustered into three groups with
234 highest possible similarity of factor combinations within and highest possible differences
235 between the groups.

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

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

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

245

246 **Results**

247 **Management of aboveground competition (H 1)**

248 The multifactorial ANOVA (light ecology, vegetation cover, site cluster, weeding and
249 interactions) did not reveal any effect of aboveground weeding neither as independent factor
250 nor as interacting factor. However, on the species level, *Cedrela montana* reacted
251 significantly negatively to weeding as single independent factor ($p=0.015$); *Heliocarpus*
252 ($p=0.053$) and *Tabebuia chrysantha* ($p=0.055$) in contrast reacted positively (see Fig. 1).
253 Aboveground weeding of *Cedrela montana* interacts on a lower significance level with
254 vegetation cover ($p = 0.07$, Fig. 2) and with site cluster plus vegetation cover ($p=0.084$).
255 *Pinus*, in contrast, showed significant response only for the interaction vegetation
256 cover*weeding ($p=0.026$), but the effect is rather poor (Fig. 2). It is notable that weeding
257 under shrub cover had no effect for any species.

258

259 **Species-specific differences between successional sites (H 2)**

260 The vegetation cover had significant effects (Fig. 1) for the three species *Alnus acuminata*
261 ($p=0.001$), *Pinus patula* ($p<0.001$) and *Eucalyptus saligna* ($p<0.001$), with *Tabebuia*
262 *chrysantha* almost reaching the significance level ($p=0.054$). *Alnus* and *Pinus* behave like
263 typical early successional species with the significantly best height growth on the pasture site.
264 *Tabebuia chrysantha* showed the opposite behaviour, with best growth on shrub followed by

265 bracken and least on the pasture site. The exotic species *Pinus* and *Eucalyptus* are the only
266 species that reacted poorly on the bracken site, where in contrast *Heliocarpus* and *Juglans*
267 surprisingly showed the best height growth. However, vegetation cover in general had no
268 significant effect for the latter species.

269

270 **Soil core parameters as predictor for top height of planted trees (H 3)**

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

277 The differences between the soil core parameters were relatively small. The pH under shrub
278 (5.1 ± 0.03 , mean and STE) was slightly lower than under pasture (5.2 ± 0.01) and bracken
279 (5.3 ± 0.02). Cluster 3 is characterised by a slightly taller A-horizon and higher silt and clay
280 proportions in the first two horizons. Cluster 1 is slightly steeper and sandier than the others.
281 Cluster 2 is intermediate with all parameters with the exception of a slightly lower pH than
282 the other clusters (Table 2).

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

289

290

291 **Macroscopic soil core analysis as predictor for chemical soil properties (H 4)**

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

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

308

309 **Interactions between successional stage, site cluster and above ground weeding (H 5)**

310 It is notable that both, successional status of planted species and stage of surrounding
311 vegetation had a significant effect on the height growth of planted trees as single factors and
312 as well as interactions ($p < 0.001$). Exotic species performed significantly better than light
313 demanding species. Mid successional species performed in general worse than light
314 demanding species but significantly only on pastures. For exotic species and the light

315 demanding species the earliest successional stage “pasture” is by far the best environment.

316 However it is important to note that no species group showed significant differences between

317 the advanced successional stages “bracken” and “shrub”. In contrast to exotics and light

318 demanding species, mid successional species performed worse on pastures than on other

319 successional stages, but this effect was not significant.

320 Fig. 4 shows that exotic species perform significantly the best on pastures and site cluster 3,

321 which in contrast is the worst site cluster for the light demanding species on the pasture site.

322 This highlights the importance of deliberate matching of site conditions and successional

323 stage for successful reforestation. The differences between site clusters are relatively low for

324 the other successional stages and for the mid-successional species. Including “weeding” in the

325 analysis as an additional factor results in tremendous differences between the treatments. For

326 example, the best environmental setting for *Cedrela* ($p=0.84$, Fig. 5) is site cluster 1 in the

327 bracken stage without mechanical weeding (74.0 cm). However, in the bracken and pasture

328 stage cluster 2 also results in acceptable growth with 38.3 cm and 57.3 cm respectively.

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

330 species.

331

332 **Discussion**

333 *Above ground competition and performance of planted tree species (H 1)*

334 Suppressing weedy vegetation is recommended as one technique for assisting natural

335 regeneration (Shono et al., 2007). As small scale farmers in developing countries often cannot

336 afford the investment in chemical site preparation, manual weeding will continue to play an

337 important role, especially for reforestation measures by land users who depend on livelihood.

338 Grasses, bracken fern and many other competing plants survive manual above ground

339 weeding and resprout quickly (Hooper et al., 2002). Thus, the ecological effect of this
340 management technique on abandoned pastures is mainly limited to control of light conditions.

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

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

361 Davidson et al. (1998) found much better growth for *Heliocarpus americanus* in northern
362 Ecuador than did we. This can mainly be attributed to their initial herbicide treatment with

363 glyphosate prior to planting. Eckert (2006) showed clearly that tree growth in pastures is
364 much better after glyphosate treatment in comparison to mechanical weeding.

365

366 *Species-specific differences between successional sites (H 2)*

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

386 Some authors assume that bracken hinders reforestation (Humphrey & Swaine, 1997). Our
387 data show that this is not valid for our mid-successional species. In general, these species

388 performed similar or even better under bracken or shrubs in comparison to pastures (Fig. 2
389 and Fig. 5). Under cluster 1 conditions (high Mn, low P) *Cedrela montana* achieved best
390 height growth at the bracken site (high N, Mg, Mn, and low available P, Fig. 6). It is
391 surprising that the mid successional species could not profit more from the environmental
392 conditions at the shrub site. This can possibly be attributed either to the inferior shading
393 capacity of the shrubs compared to the dense cover of bracken (Humphrey & Swaine, 1997)
394 or to reduced nutrient supply in the soil due to higher plant uptake by the shrubs. External
395 factors like microclimate, which could not be included in the experimental settings as
396 covariables could also cause differences between the experimental blocks, which consist of
397 the three successional stages (Nepstad et al., 1990; Vieira & Nepstad 1994; Aide et al., 1995).
398 Thus, the influence of the dominating vegetation cover has to be discussed with caution.
399 The height growth of light demanding and exotic species at the shrub site was also not
400 convincing (Fig. 5) indicating that this site may be characterized by generally poorer
401 environmental conditions.

402 Pastures can be very competitive and cause high mortality and slow growth of tree species in
403 many cases (Otsamo et al., 1995, Pedraza & Williams-Linera, 2003). Despite higher root
404 competition on pastures, some tree species apparently grow better in grasses than under
405 shrubs. This can be explained by possible allelopathic effects of shrubs, differences in root
406 depths and fine root density (Gerhardt & Frederiksson, 1985; Sun et al., 1995; Holl, 1998).
407 Another reason could be the intensive C-dynamic under *Setaria* leading to high C contents in
408 comparison to other land use types (Rhoades et al., 2000; Makeschin et al., 2008).

409 It is well established that exotic species generally grow very fast, but some native species are
410 able to compete in survival and growth (González & Fisher, 1994; Islam et al., 1999; Wishnie
411 et al.; 2007) Thus, the good height growth of *Alnus* is in line with these findings. From
412 hundreds and thousands of tree species in Ecuador, broader experiences for reforestation

413 exists for only less than 10, mainly due to limited knowledge on seed ecology and plant
414 propagation (Stimm et al., 2008). Thus, success of reforestation efforts with native species in
415 Ecuador depends strongly on future research on these topics. Our data support the general
416 finding that early successional species perform better than mid-successional species in the
417 first years of plantation (Davidson et al., 1998). However, it must be recognized that site
418 conditions and surrounding vegetation are of major importance and adequate management
419 concepts to cope with these items are not yet available. Furthermore, the slower growth of
420 mid-successional species *Tabebuia* and *Cedrela* could be a temporal effect in the initial stage
421 of plantations. For instance, in long term reforestation trials in Puerto Rico, surprisingly many
422 merchantable tree species grew faster in the second 33-year period than in the initial 22 years
423 of observation (Silver et al., 2004). If the interactions between sites factors and the single tree
424 species are properly understood, the micro-environmental conditions at the shrub and bracken
425 stages could be used to facilitate the establishment of newly planted trees, especially from
426 later successional stages (Pedraza & Williams-Linera, 2003; Parrotta et al., 1997).

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

431

432 *Suitability of macroscopic soil core analysis for planning of reforestation measures (H 3, H*
433 *4)*

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

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

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

452 In our study we could identify some distinct species dependent effects between special site
453 clusters and the growth of young seedlings. For instance *Alnus*, *Cedrela*, *Tabebuia* exhibited
454 better height growth on site cluster 1, while *Eucalyptus* grew best on site cluster 3 indicating
455 species-specific requirements to environmental conditions. The results indicate that
456 parameters derived from soil core description could be used to estimate tree development on
457 abandoned pastures in neotropical mountain areas. However, this methodology requires
458 intensive statistical processing of the data and is actually effective only for some species,
459 although the results still suggest that this approach is a promising perspective for better
460 consideration of natives in future reforestation endeavours.

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

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

472 Studies of several authors confirm that P availability might be less problematic than N. For
473 instance, in a study by Haridasan (1985) *Eucalyptus grandis* performed well with available P
474 (46 ppm) and extractable cations comparable to our results. As Newberry et al. (2002)
475 reported, P did not limit growth of ectomycorrhizal trees on soils with extremely low
476 phosphorous supply. *Pinus radiata* plantations in Northern Ecuador were growing well on
477 soils with higher N values in the A-horizon (0.17-0.22 %) (Farley & Kelly, 2004).

478 Experimental reforestation trials with good performance of several native species on
479 Hydrandep soils were much higher in N (0.24%), only slightly higher in extractable cation
480 concentrations and much lower in Aluminium saturations (Davidson et al. 1998). Thus, in
481 comparison to those studies, low N values and high Aluminium toxicity in general could be
482 limiting factor for plant growth for our study region, rather than P or extractable cations. In
483 line with our findings of low base cations at the shrub sites, Slowcroft et al. (2004) show that
484 concentrations of extractable base cations and P can be affected rather by the vegetation type
485 than by the topographical position. These results support the hypothesis that early successional

486 stages are rather N limited, but they become more P-limited in later stages (Vitousek et al.,
487 1993; Herbert & Fownes, 1995; Newberry et al., 2002).

488

489 *Vegetation cover and site differences are independent factors for the success of reforestation*
490 *with native and exotic tree species (H 5)*

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

496 For the three major vegetation types, pastures, bracken and shrubs, there exist several possible
497 limiting factors for tree species. For instance, C4 plants generally have a better water use
498 efficiency than trees. Thus, *Setaria sphacelata* apparently has competitive advantages on the
499 sun exposed areas in comparison to forest species, especially the mid successional species
500 which are adapted to slight shading (Bazzaz & Picket, 1980). *Setaria* can store enormous
501 amounts of C due to its extended fine root system (Rhoades et al., 2000, Makeschin, 2008).
502 This rather advantageous effect for soil fertility, however, is combined with a negative effect
503 for the planted trees: Eckert (2006) has proven that root competition of this grass species is
504 one of the most important barriers for growth of reforestation species, especially for mid
505 successional species.

506 In our study the vegetation cover had significant effects on N and P-values. These typical
507 slash- and burn effects were also confirmed by Makeschin et al. 2008 for our study area: N
508 and P are strongly influenced by burning, accompanied by an increase of pH, resulting from
509 alkaline ashes which in turn reduces availability of P. Farley & Kelly (2004) showed that
510 forest plantations in Ecuador can effectively reduce N concentrations in the soil via nutrient

511 uptake and allocation processes in the biomass. Accordingly, differences of P under different
512 vegetation covers in the present study, could likewise have been caused by nutrient uptake
513 and reallocation.

514 N is generally considered to be a limiting factor in grasslands (Davidson et al., 1990;
515 Scowcroft et al. 2004). In general N values were very low in our study area, too. Thus, it
516 follows that proper N management could allow for better plant growth. For example,
517 intercropping nitrogen fixing trees with reforestation species may result in better performance
518 than initial fertilization (Carpenter et al., 2004). Our data support the findings of Murcia
519 (1997) that *Alnus* grows rapidly even in nitrogen-poor soils.

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

526 It is well known that vegetation cover can shape the site conditions via nutrient uptake, litter
527 fall, shading regimes and hydrological functions (Haridasan, 1985; Bruijnzell, 2004, Jobbagy
528 & Jackson, 2004). The latter authors show that grasses have lower Manganese cycling than
529 *Eucalyptus* and that vegetation cover alters the vertical distribution and bio-availability of
530 mineral elements. This could explain why Manganese is significantly different between
531 pastures, bracken and shrub in our study. On Gleysols, Mn deficiency is often combined with
532 P deficiency (Kreutzer 1970), and Mn mobilization and/or lateral Mn removal can be caused
533 by acidification and groundwater podsolization (Zech & Drechsel, 1991). Hydromorphy is
534 frequent, too, in our study area, but under the predominant steep slopes hydromorphic
535 processes are rather connected with percolating than groundwater. In the study area we can

536 find both processes for Mn-mobilization: podzolisation and reduction conditions (Makeschin
537 et al., 2008). Podzolization causes the complexation of Mn by fulvo acids; reduction
538 conditions in turn favour the transformation of non-soluble $Mn^{4+}O_2$ into soluble Mn^{2+} . Mn
539 can be discharged in both cases (Haubrich, unpublished data). These processes possibly could
540 explain differences in extractable Mn between the different site clusters. It is well established
541 that vegetation influences water content of soils via transpiration, and plant roots can produce
542 acids for better nutrient availability, which in turn affects Mn-mobility. This could be one
543 explanation of how site clusters and vegetation cover are interacting and thus influencing the
544 nutrient status of the soils.

545

546 **Conclusions**

547 Exotic species in Ecuador are generally considered to perform better than native species. In
548 our study *Alnus acuminata* was able to compete in height development with the exotics at
549 least in the first three years after planting. Reforestation trials with native and exotic species
550 in Costa Rica for instance revealed the enormous potential of several native species for
551 reforestation and restoration (Piotto et al., 2003, Wishnie et al., 2007). In Central America
552 experiences with native species started already several decades ago, while in Ecuador the
553 discussion has only recently started. Consequently, we assume that among the extremely high
554 number of 2736 tree species in Ecuador (Jørgensen and León-Yáñez, 1999) it is very probable
555 to find other and perhaps even more promising species. However, the crux is to identify the
556 best candidates for reforestation and to provide adequate knowledge on their seed ecology,
557 propagation and silvicultural requirements. As expected, mid-successional species performed
558 much slower than the exotics and light demanding species. However, if planted under
559 adequate environmental conditions the height development of such species improves. *Cedrela*
560 *montana*, for instance, showed acceptable development under bracken without above ground

561 weeding. Furthermore, the slow initial growth may be compensated for by their extremely
562 high timber value. Thus, from the economical point of view, mid-successional species could
563 be a very valuable contribution in a portfolio of species for reforestation purposes.

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

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

584

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590

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787 *Table 1: Correlation coefficients of site factors and corresponding principal components. Site*
788 *factors include plot based parameters (inclination, altitude) and horizon based parameters (A*
789 *and B horizon). The five extracted components were used for subsequent cluster analysis.*
790 *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

791

792 *Table 2: Differences of site factors between the site clusters 1-3 in the first two horizons (A*
 793 *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

794

Table 3: Differences in chemical soil parameters (mean \pm 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 $\mu\text{mol g}^{-1}$]. 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 [$\mu\text{g/g}$]	Al	Fe	Mn***	Ca	K	Mg*	CEC	BS [%]
1	A	5.4 \pm 0.54	0.26 \pm 0.04	21.3 \pm 1.41	38.2 \pm 15.7	71.6 \pm 25.5	1.12 \pm 0.16	0.23 \pm 0.27	6.5 \pm 5.0	1.45 \pm 0.65	1.92 \pm 1.35	90.1 \pm 20.1	13.0 \pm 9.7
	B	0.8 \pm 0.16	0.06 \pm 0.01	14.2 \pm 1.05	12.6 \pm 14.8	23.4 \pm 11.0	0.31 \pm 0.27	0.14\pm0.32A	1.0 \pm 0.8	0.68 \pm 0.29	0.27\pm0.15A	26.6 \pm 11.9	10.2 \pm 5.4
	Subsoil	0.4 \pm 0.03	0.04 \pm 0.00	10.8\pm1.72A	3.5 \pm 5.0	20.8 \pm 7.7	0.06 \pm 0.05	0.02 \pm 0.01	0.6 \pm 0.2	0.46 \pm 0.20	0.13 \pm 0.06	22.8 \pm 8.0	8.1 \pm 2.9
2	A	5.3 \pm 0.75	0.25 \pm 0.05	22.3 \pm 1.65	26.2 \pm 4.9	78.1 \pm 21.3	3.59 \pm 2.00	0.11 \pm 0.06	7.4 \pm 4.5	1.95 \pm 0.69	4.04 \pm 1.44	105.0 \pm 15.0	14.0 \pm 5.6
	B	0.9 \pm 0.10	0.08 \pm 0.01	12.8 \pm 1.15	10.0 \pm 9.5	26.7 \pm 9.6	0.23 \pm 0.18	0.09 \pm 0.15	0.9 \pm 0.8	0.82 \pm 0.31	0.39 \pm 0.43	30.0 \pm 9.6	9.9 \pm 5.6
	Subsoil	0.5 \pm 0.29	0.04 \pm 0.01	14.2 \pm 10.0	4.1 \pm 2.3	11.3 \pm 0.1	0.01 \pm 0.01	0.09 \pm 0.08	0.7 \pm 0.2	0.71 \pm 0.06	0.15 \pm 0.09	13.4 \pm 0.1	15.4 \pm 0.2
3	A	4.9 \pm 0.51	0.26 \pm 0.03	18.8 \pm 0.66	39.5 \pm 25.8	78.2 \pm 28.9	2.27 \pm 1.83	0.15 \pm 0.17	5.3 \pm 3.1	2.97 \pm 3.46	3.45 \pm 2.00	99.4 \pm 29.7	14.3 \pm 10.2
	B	1.1 \pm 0.19	0.08 \pm 0.01	12.4 \pm 0.70	9.7 \pm 14.5	32.6 \pm 14.1	0.23 \pm 0.29	0.07\pm0.14B	1.1 \pm 1.4	0.81 \pm 0.91	0.40\pm0.69B	36.7 \pm 16.1	8.2 \pm 4.8
	Subsoil	0.8 \pm 0.12	0.06 \pm 0.01	11.7\pm1.21B	6.3 \pm 8.2	22.4 \pm 9.5	0.18 \pm 0.25	0.04 \pm 0.06	0.8 \pm 0.7	0.87 \pm 0.60	0.51 \pm 0.91	25.6 \pm 9.8	11.7 \pm 5.5

Table 4: Differences in chemical soil parameters (mean \pm 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 $\mu\text{mol g}^{-1}$]. 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 ** [$\mu\text{g/g}$]	Al	Fe	Mn***	Ca	K	Mg	CEC	BS [%]
Pastures	A	5.2 \pm 0.49	0.26 \pm 0.03	20.8 \pm 0.94	45.9 \pm 26.5	65.7 \pm 23	1.46 \pm 1.2	0.14 \pm 0.20	7.8 \pm 4.3	2.84 \pm 3.8	2.79 \pm 1.6	87.9 \pm 20.5	17.4 \pm 11.1
	B	1.2 \pm 0.12	0.07 \pm 0.01	15.1 \pm 0.79	14.3\pm13.4A	30.1 \pm 14	0.24 \pm 0.2	0.03\pm0.05A	0.9 \pm 0.7	0.73 \pm 0.4	0.24 \pm 0.1	33.1 \pm 14.0	8.3 \pm 4.4
	Subsoil	0.7 \pm 0.15	0.05 \pm 0.01	12.6 \pm 1.61	8.0 \pm 9.0	20.2 \pm 7	0.09 \pm 0.2	0.01 \pm 0.01	0.9 \pm 0.7	0.68 \pm 0.5	0.16 \pm 0.1	22.8 \pm 7.2	10.3 \pm 4.9
Bracken	A	5.8 \pm 0.73	0.31 \pm 0.03	18.3 \pm 0.71	22.6 \pm 10.0	93.0 \pm 28	4.29 \pm 2.0	0.23 \pm 0.20	3.9 \pm 2.4	2.65 \pm 0.7	4.63 \pm 2.6	113.6 \pm 27.5	11.6 \pm 6.4
	B	0.9 \pm 0.09	0.09 \pm 0.01	10.3 \pm 0.59	5.1\pm6.2B	25.2 \pm 12	0.19 \pm 0.17	0.08\pm0.08A	0.5 \pm 0.5	0.94 \pm 0.4	0.48 \pm 0.4	28.2 \pm 12.1	9.6 \pm 4.7
	Subsoil	0.7 \pm 0.15	0.07 \pm 0.01	10.2 \pm 1.63	2.4 \pm 4.0	19.5 \pm 10	0.21 \pm 0.31	0.08 \pm 0.08	0.5 \pm 0.3	1.09 \pm 0.6	0.87 \pm 1.2	22.8 \pm 10.8	13.9 \pm 4.9
Shrubs	A	3.7 \pm 0.53	0.18 \pm 0.02	20.5 \pm 1.39	30.2 \pm 8.7	76.5 \pm 28	1.53 \pm 0.8	0.14 \pm 0.13	3.7 \pm 1.5	1.40 \pm 0.4	2.38 \pm 0.8	97.5 \pm 29.1	9.0 \pm 3.3
	B	0.8 \pm 0.33	0.06 \pm 0.02	11.4 \pm 0.76	7.7 \pm 15.4	32.8 \pm 13	0.32 \pm 0.4	0.15\pm0.29B	1.5 \pm 1.7	0.73 \pm 1.2	0.51 \pm 0.9	39.1 \pm 16.4	8.5 \pm 5.8
	Subsoil	0.7 \pm 0.19	0.05 \pm 0.01	13.7 \pm 2.08	9.3 \pm 10.6	25.1 \pm 11	0.14 \pm 0.1	0.02 \pm 0.01	1.5 \pm 1.1	0.36 \pm 0.1	0.18 \pm 0.1	28.0 \pm 11.4	10.3 \pm 6.8

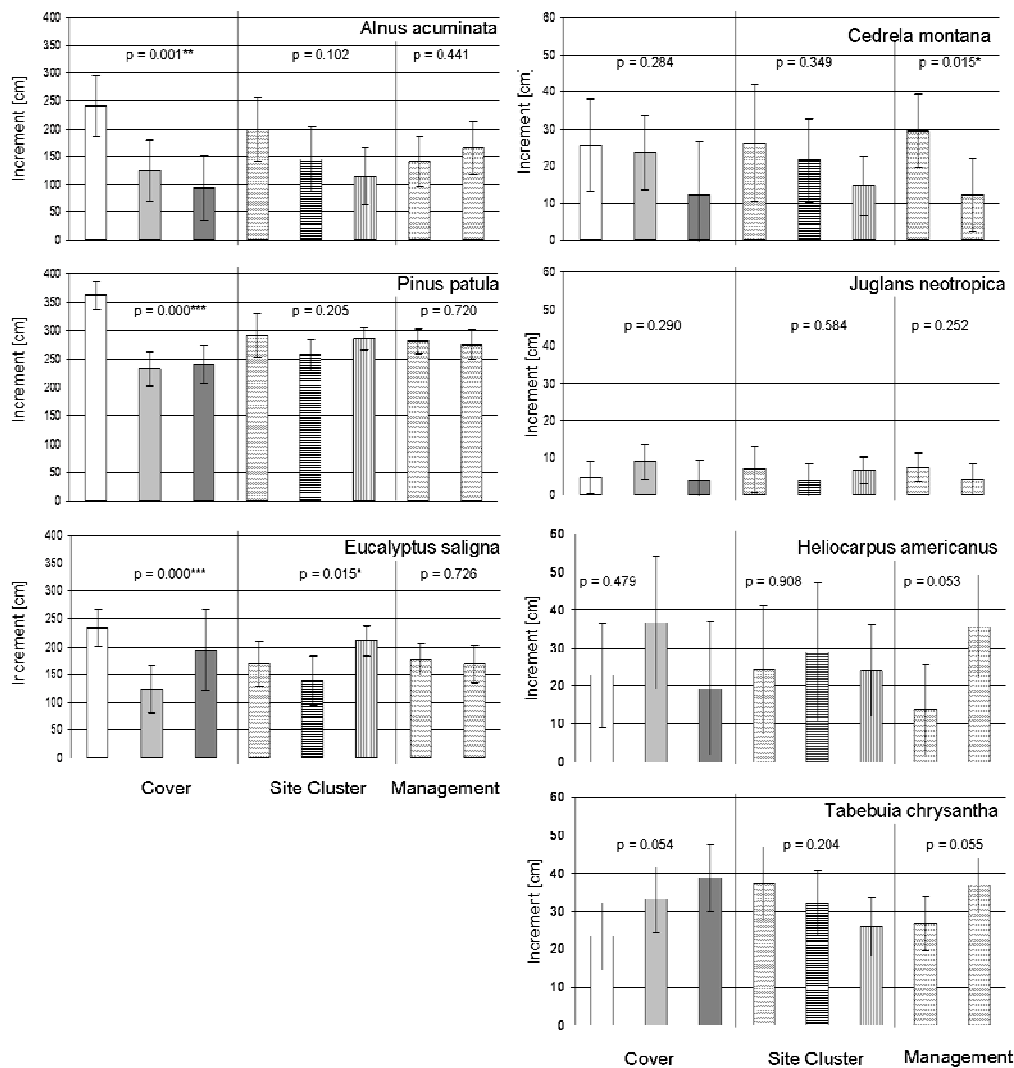


Fig. 1. Influence of competing vegetation cover on the growth performance of three year old seedlings from five native species (*Alnus acuminata*, *Cedrela montana*, *Juglans neotropica*, *Heliocarpus americanus*, *Tabebuia chrysantha*) and two introduced species (*Pinus patula* and *Eucalyptus saligna*). From left to right: pasture (white bars), bracken (bright grey), shrub (dark grey), site cluster 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 $p=0.95$.

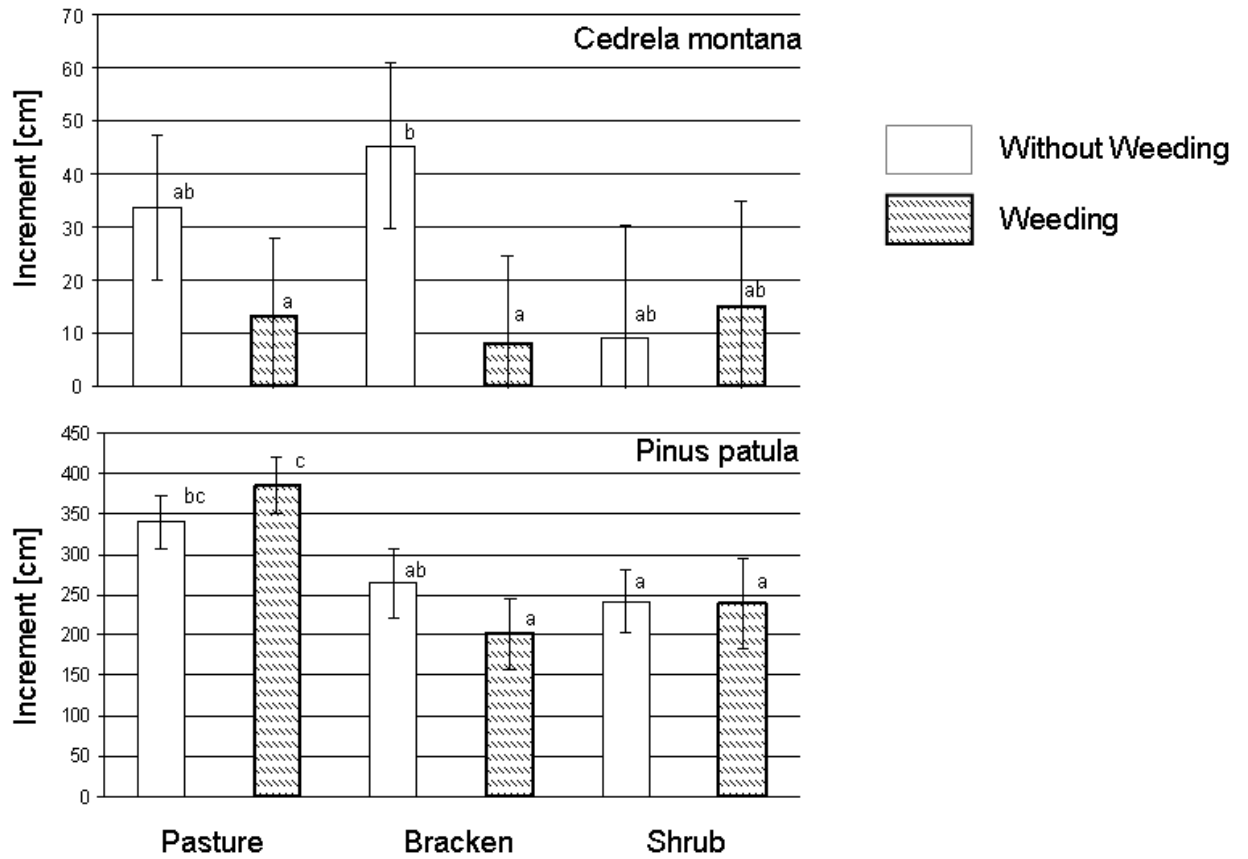


Fig. 2. Effects of interactions weeding*competing vegetation on growth performance for the 3 yr. old plants of *Pinus patula* and *Cedrela montana*). Different letters correspond to significant differences (confidence level $p = 0.05$).

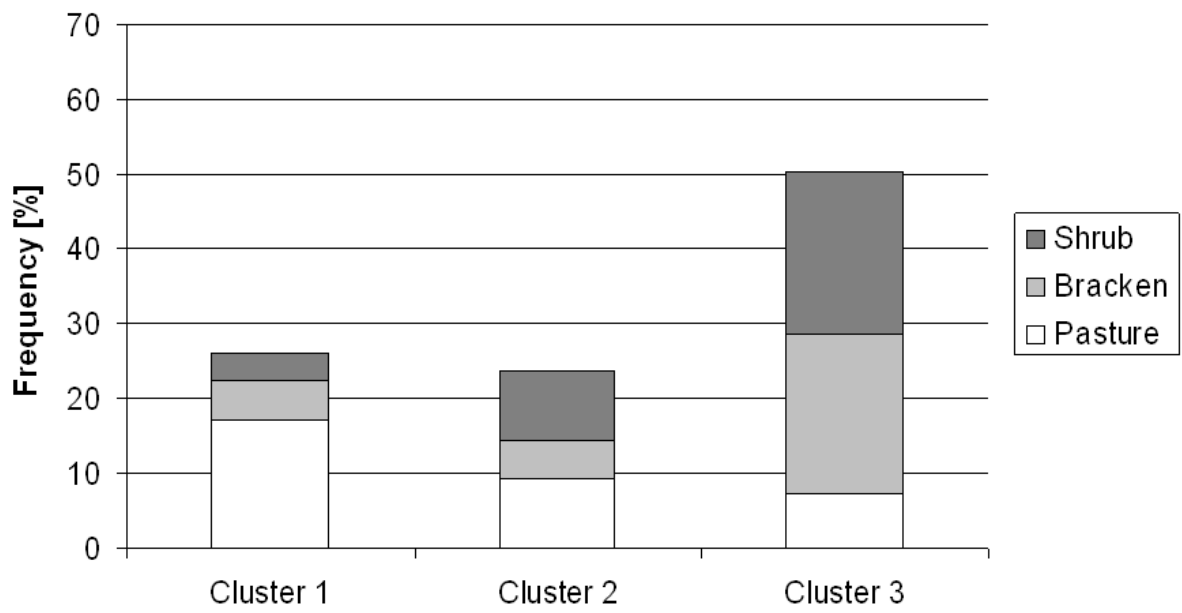


Fig. 3. Frequency of site clusters among sites with the dominant vegetation on experimental block “pasture” (white bars), “bracken” (light grey), “shrub” (dark grey), total = 100 %.

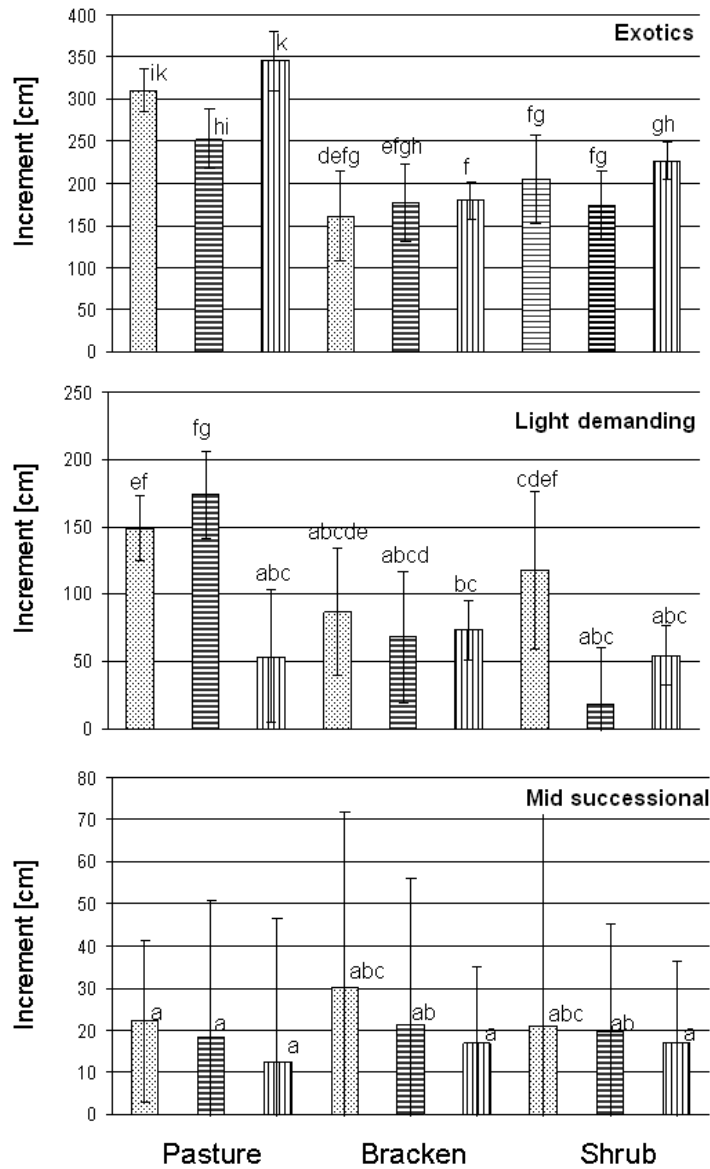


Fig. 4. Interaction (successional status*dominating vegetation*site cluster, ANOVA $p=0.003$) between successional status of planted seedling (from top to bottom), dominating vegetation on experimental block (x-axis) and site cluster 1 (squared), 2 (horizontally hatched) and 3 (vertically hatched) with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

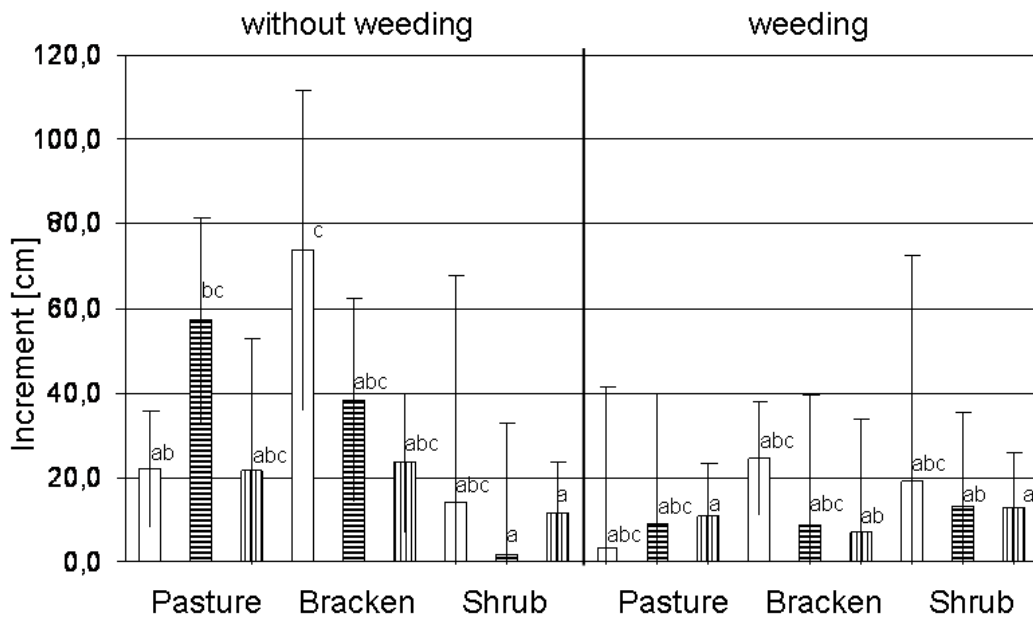


Fig. 5. Interactions for *Cedrela montana* (weeding*dominating vegetation*site cluster, ANOVA, $p = 0.084$) between dominating vegetation on experimental block (x-axis), site cluster (1= white bars, 2 = horizontally hatched, 3 = vertically hatched) and weeding of above ground vegetation (without and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