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Early growth of native and exotic trees planted on degraded tropical pasture

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Abstract

Our goal was to assess the potential of two exotic and five native tree species in reestablishing trees to degraded land in the humid tropics of southern Costa Rica. Our study site was deforested in the 1950s. Steep topography and high rainfall led subsequently to severe erosion, which exposed nutrient-poor, acid, unproductive subsoil. Our site is typical of many tropical overgrazed pastures that have been established in high rainfall areas on ultisols worldwide. Restoration of useful trees to such lands is difficult when erosion is severe.

We established 30 experimental blocks in 1994 across our study site that varied in topography and degree of erosion. We analyzed survival over 7 years and height after 3 and 7 years. *Pinus tecunumanii*, non-native to Costa Rica but native to Central America, was the outstanding performer with best growth and survival among all blocks. Several of the Costa Rican natives, all considered valuable for timber, survived and grew moderately well (*Vochysia guatemalensis*, *Terminalia amazonia*, *Calophyllum brasiliense*).

We assessed the effect of erosion on survival and growth. Survival and/or growth negatively correlated with degree of erosion in five of the seven species. *P. tecunumanii*, an ectomycorrhizal species, survived and grew uniformly well and independently of erosion. *T. amazonia* survived better but grew worse on more eroded sites.

These results suggest the following recommendations for projects that attempt to restore trees to tropical degraded cattle pastures similar to our site:

- areas that have suffered less extreme erosion could be planted successfully with three of the native species studied here: *V. guatemalensis*, *T. amazonia*, or *C. brasiliense*, perhaps in mixtures;
- *P. tecunumanii* is suitable for planting on the most deeply eroded, bare areas and therefore might ameliorate hostile micro sites more quickly than other species;
- our results suggest that the pine should be tested as a site-preparing species by intermixing seedlings of more shade loving species two or more years after planting the pine;
- a system of crop rotation might be sustainable, planting pine as a rapidly growing frequently harvested species and interplanting more slowly growing but more valuable species.

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Keywords: *Terminalia amazonia*; *Vochysia guatemalensis*; *Calophyllum brasiliense*; *Pinus tecunumanii*; *Tabebuia ochracea*; *Cedrela odorata*; *Eucalyptus deglupta*; Degraded pasture; Tropical reforestation; Tree plantations; Costa Rica; Tropical restoration

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43 **1. Introduction**

44 Large areas of deforested and degraded land exist in
45 the humid tropics (NASA, 2003). In the decade of the
46 1990s approximately 0.38% per year of the worlds
47 forests were converted to other land uses. Some land
48 reverts to forest, but the net annual loss of forest
49 approaches 0.22% (FAO, 2001). The annual rate is
50 much higher in many developing countries, where
51 some 200 million ha of forest are estimated to have
52 been lost in the period 1980–1995 (FAO, 1997).
53 About 350 million ha of previous forest are unlikely
54 to regenerate spontaneously, including 155 mil-
55 lion ha in the Americas (ITTO, 2002). Common soil
56 problems in the deforested tropics include aluminum
57 toxicity, low pH and phosphorous fixation (Fisher,
58 1995). Many such areas are difficult to reforest even
59 with current methods of intervention. In our project,
60 we hope to provide information for developing meth-
61 ods of rehabilitating land that is on the verge of
62 abandonment.

63 At a given site in the humid tropics, either “exotic”
64 or native tree species may perform better. Among the
65 commonly planted exotics are various tropical pines,
66 *Eucalyptus* spp., *Tectona grandis*, *Gmelina arborea*
67 and some *Acacia* species. Annandale and Keenan
68 (1999) studied a range of species in tropical northern
69 Queensland, Australia. They tested *Eucalyptus pellita*,
70 *E. grandis* × *E. tereticornis*, *T. grandis*, *Acacia man-*
71 *gium*, and several provenances of *Cedrela odorata*, as
72 well as *Pinus caribea* var. *hondurensis*. On their
73 degraded lowland tropical site, the pine achieved by
74 far the best growth after 10 years.

75 Interest in establishing plantations of native species
76 has grown in recent years (Gonzalez and Fisher, 1994;
77 Montagnini, 2000; Piotto et al., 2002). Although,
78 some native species (e.g. members of Meliaceae)
79 may be less broadly adapted and more susceptible
80 to native pests, others may be well suited to particular
81 conditions such as low levels of soil nutrients char-
82 acteristic of degraded land (Nichols et al., 1997).

83 Our general aim was to find species with potential to
84 rehabilitate tropical sites similar to our degraded
85 pasture in southern Costa Rica. Our specific objectives
86 were to

- 87
- evaluate the performance of seven tree species
89 planted on degraded land;

- evaluate the impact of land erosion on seedling
growth and survival of each species; 91
- recommend potential combinations of methods to
better rehabilitate such sites. 93

2. Materials and methods 94*2.1. Study site* 95

The study site is a 25 ha farm in southwestern Costa 96
Rica, 20 km south of the town of San Vito de Coto 97
Brus, 83°W longitude, 9°N latitude. Elevation is 98
1050 m on the south Pacific slope, where the terrain 99
frequently intercepts heavy fog. Mean annual tem- 100
perature is 20 °C. Annual precipitation averages 101
4400 mm, most falling between April and December 102
with peaks in May and October. In the Holdridge 103
system of life zones (Holdridge, 1967) the site was 104
“humid premontane tropical rainforest” before clear 105
cutting for coffee in the 1950s. This region of Coto 106
Brus is characterized by steep rugged terrain not 107
appropriate for crops or pasture because of thin topsoil 108
and vulnerability to erosion (Laurent, 1992). Never- 109
theless, the area has been settled and intensively 110
cropped for half a century. 111

In 1976, the area was partly converted from coffee 112
to different uses. Some areas of the study site were 113
kept in coffee for 10–20 more years. Most of the rest 114
was converted to cattle pasture about 1978 by planting 115
grass species *Paspalum micay*, *Brachiaria* sp and 116
Melinis minutifolia (Poaceae). 117

In the 1970s, the pasture produced twice as much 118
beef as it did by 1990. By 1990, the land showed 119
serious signs of overgrazing, with barren, deeply 120
incised cattle trails occupying about 50% of the land 121
surface area. The three most deeply eroded areas on 122
the farm had cattle trails up to 2 m deep. The largest of 123
the areas was completely bare, lacking even grass 124
roots. 125

Soils on the farm are acid, phosphorous-fixing and 126
infertile—more so after erosion removes topsoil (Car- 127
penter et al., 2001). The soils are influenced by the 128
presence of a major volcano (Volcan Baru) 40 km to 129
the east in Panama and others farther north in Costa 130
Rica. The current USDA system classifies the soils as 131
ultisols, from typic hapludults to humic or andic 132
hapludults. The range of clay is 17–26%, silt 133

Table 1
Scientific names, common names, origin, wood density of seven tropical tree species

Scientific name	Family	Origin	Density of wood (g/cm ³)	Planting size	No. seed mothers
Natives					
<i>T. ochracea</i> (Cham.) Standl.	Bignoniaceae	Honduras–Brazil	0.85	6 cm seedling	2
<i>C. brasiliense</i> (Camb.)	Clusiaceae	Neotropics	0.72	33 cm seedling	8
<i>C. odorata</i> L.	Meliaceae		0.59	21 cm seedling	7
<i>T. amazonia</i> (Gmel.) Excell	Combretaceae	Mexico–Brazil	0.61	39 cm seedling	3
<i>V. guatemalensis</i> Donn. Smith	Vochysiaceae	Central America	0.37	30 cm seedling	10
Exotics					
<i>E. deglupta</i> Blume	Myrtaceae	New Guinea	0.49	54 cm seedling	Unknown
<i>P. tecunumanii</i> (Schw.) Equiluz et Perry	Pinaceae	Mexico–Central America	0.53	48 cm seedling	Unknown

134 19–28% and sand and sand-sized particles 48–64%.
135 Physical structure is good—even at the bottom of the
136 cattle trails values for bulk density do not exceed 1.

137 2.2. Tree species

138 We selected seven species for assay (Table 1),
139 including two non-native species, *E. deglupta* and *P.*
140 *tecunumanii*. These two species were included in local
141 reforestation projects by Costa Rican foresters at the
142 time our study began in 1994. *P. tecunumanii* is among
143 the best known of the neotropical pines and consider-
144 able research on its genetic improvement has been
145 done (Hodge and Dvorak, 1999; Dvorak et al., 2000,
146 2001).

147 Among the five native species were two “climax”
148 hardwood species expected to grow relatively slowly,
149 *Calophyllum brasiliense* (family clusiaceae) and
150 *Tabebuia ochracea* (Bignoniaceae). The other three
151 are “long-lived pioneers”: *Vochysia guatemalensis*
152 (Vochysiaceae), an early successional species with
153 low density but usable timber; *Cedrela odorata*
154 (Meliaceae), well-known as a high-value timber;
155 and *Terminalia amazonia* (Combretaceae), which pro-
156 duces attractive wood used for many purposes.

157 Recent years have seen several studies of *Vochysia*
158 species both in natural forest (Herrera et al., 1999;
159 Vera et al., 1999; Herrera and Alvarado, 2001) and in
160 plantations (Gonzalez and Fisher, 1994; Montagnini,
161 2000; Carnevale and Montagnini, 2002; Moulart
162 et al., 2002). There have been increasing attempts
163 to understand and develop the genetic potential of
164 species in the genus (Cornelius and Mesen, 1997;
165 Gonzalez and Fisher, 1998, 1997; Mesen and Corne-

lius, 2000). Other studies have identified *Vochysia* 166
spp. as species that can tolerate strongly acid soils, 167
accumulate Al and grow well in soils with moderately 168
high exchangeable Al and low exchangeable base 169
cations (Perez et al., 1993). 170

T. amazonia is also known as *T. amazonica*, 171
although, the former spelling is preferred (CABI 172
database 1995–2003). Earlier generations of foresters 173
developed the silviculture of *T. amazonia* (Marshall, 174
1939). Its use as a plantation species has increased in 175
recent years in humid areas of Costa Rica (Nichols and 176
Gonzalez, 1992; Gonzalez and Fisher, 1994; Nichols, 177
1994; Nichols et al., 1997, 2001; CAB International, 178
2000; Montagnini, 2000; Piotta et al., 2001; Torres 179
and Lujan, 2002; Ugalde et al., 2002; Fonseca and 180
Chinchilla, 2002). This species ranges widely from 181
Mexico through the Caribbean and Central America to 182
Brazil and occurs on a wide variety of soils. Its 183
moderately dense wood is yellow, often with reddish 184
streaks and is highly versatile, being used for general- 185
purpose construction and furniture. 186

187 2.3. Nursery procedures

188 We attempted to obtain seeds from several mother 188
trees in case seed viability and seedling performance 189
varied between provenances. Between 1993 and 1994 190
we located variable numbers of mother trees of four of 191
the five natives (Table 1) in local forests and farms and 192
collected seeds directly from their canopies by using 193
climbing gear. These seeds were sown in germination 194
beds and transplanted into black plastic nursery bags. 195
We inoculated each nursery bag with mycorrhizal 196
fungi by inserting about 10 cm³ of soil gathered from 197

198 under the mother trees into the top layer of potting soil.
 199 We fertilized the seedlings about 2 weeks after trans-
 200 plantation to the nursery bags. A local nursery man-
 201 aged by the organization for tropical studies provided
 202 seedlings from eight mother trees of *C. brasiliense*
 203 located in our region.

204 We also used material from local nurseries for the
 205 two exotic species. We obtained seeds for *E. deglupta*
 206 from the local high schools forestry project. Another
 207 local nursery provided seedlings of *P. tecunumanii*.
 208 These had been inoculated with soil from a healthy
 209 plantation of this pine species to provide the appro-
 210 priate mycorrhizal fungi. In the cases of *E. deglupta*
 211 and *P. tecunumanii* the number of mother trees was
 212 therefore unknown (Table 1).

213 Seedling size varied among species but in general
 214 did not reflect time in the nursery. For example,
 215 seedlings of *T. ochracea* were small when out planted
 216 (Table 1) but spent more time in the nursery than any
 217 other species.

218 2.4. Experimental design

219 In July–August 1994, we established 30 experi-
 220 mental blocks to capture the various terrains and
 221 degrees of erosion across the farm (Fig. 1). Terrain
 222 is extremely heterogeneous changing over short dis-
 223 tances from flat ridge tops, to steep (20–45°) slopes
 224 to flat areas at the foot of slopes to gentle valleys or
 225 rolling hills. Terrain and degree of erosion were
 226 homogeneous within each block. All blocks occupied
 227 overgrazed cattle pasture.

228 All seedlings were planted 3 m apart (Fig. 2). Loca-
 229 tion of the plot for each species within the array was
 230 determined randomly for every block. Each species was
 231 represented by one plot per block and three individuals
 232 per plot (different seed mothers where possible) for a
 233 total of 90 trees per species in the experiment.

234 2.5. Measurements and analysis

235 We measured seedling height after out planting in
 236 1994 and annually through 2001, noting seedling
 237 deaths. Once trees were over 122 cm tall, we measured
 238 dbh. For each species we calculated 7 years survival,
 239 means of height and diameter for each plot and volume
 240 according to the index $(0.298 \times (\text{dbh}/100)^2 (\text{height}/$
 241 $100))$ (Hayward, 1987).

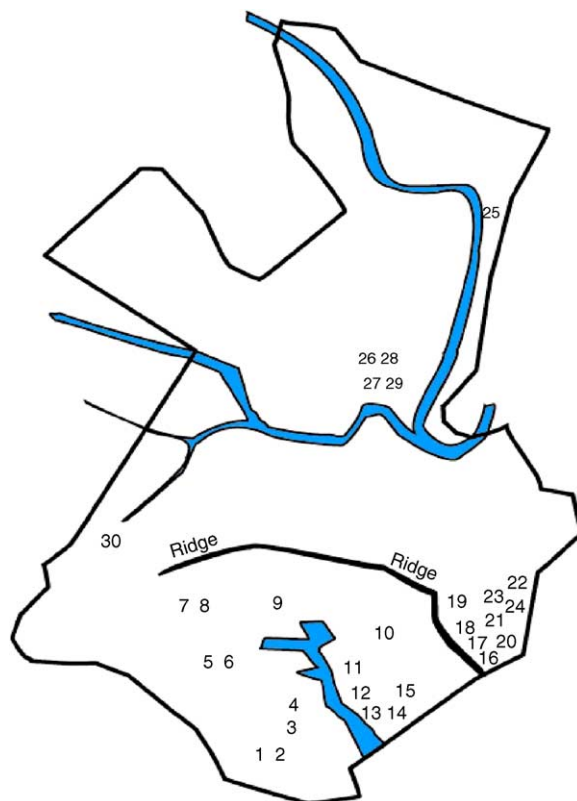


Fig. 1. Map of the 25 ha farm with 30 experimental blocks indicated. Placement of the blocks captured different degrees of erosion and terrains across the farm.

242 We estimated the degree of erosion in each block in
 243 August 1997, using depth and expanse of cattle trails
 244 to assign an index from 1 to 10. These signs of erosion
 245 do not change on this degraded farm for years because
 246 natural succession proceeds slowly. First, we observed
 247 the range of erosion in the 30 blocks by locating the
 248 least and most eroded blocks. We chose 1 as the index

```

V V V A A A
  O O O B B B
P P P T T T
  E E E X X X
  
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Fig. 2. Planting pattern within a single block. Different letters indicate different species, three seedlings per species. The plots for each species were assigned at random in each block. X indicates a plot with no seedlings planted for this experiment; these plots also were assigned locations randomly.

249 for the one block that showed the least erosion.
 250 Although, no topsoil remained in this block, it con-
 251 tained a well-formed B horizon and only shallow cattle
 252 trails. In contrast, an index of 10 represented the most
 253 eroded blocks of the 30. These blocks were eroded to
 254 the parent material and some contained cattle trails
 255 2 m deep. The values 5–6 represented average erosion
 256 between these extremes. Each of four observers scored
 257 the blocks independently from 1 to 10. The four values
 258 were consistent for a majority of the blocks. We later
 259 averaged the four values from each block to obtain the
 260 index of erosion for that block.

261 We applied the univariate general linear model in
 262 SPSS to test differences in growth rates between
 263 species and post hoc Tukeys ($\alpha = 0.05$) to differenti-
 264 ate groups. We used Pearson's rank correlation to
 265 determine the relationship between erosion and per-
 266 formance. We did not apply statistics to survival rates
 267 because the treatments (species) were replicated only
 268 three times within a block.

269 3. Results

270 3.1. Species survival after 7 years

271 By 2001 average survival differed greatly among
 272 species (Fig. 3). Highest mortality occurred in *T.*
 273 *ochracea* and *E. deglupta*. At the other extreme were
 274 survival rates of about 90% in *P. tecunumanii* and *V.*

guatemalensis. Approximately half the seedlings sur- 275
 276 vived of *C. odorata* and *C. brasiliense*.

3.2. Growth at 3 and 7 years 277

278 We analyzed growth in the top five surviving species, eliminating from consideration *T. ochracea* and 279
 280 *E. deglupta*. Heights after 7 years of growth differed significantly among species (Table 2). 281

282 Plotting heights in increments (Fig. 4) suggest that growth may be slowing in both *T. amazonia* and *C.* 283
 284 *odorata*. In contrast, growth rates appear to be stable in *C. brasiliense*, and to be accelerating in *V. guatema-* 285
 286 *lensis* and *P. tecunumanii*. Although, the pine and *V. guatemalensis* had similarly high rates of survival, *P.* 287
 288 *tecunumanii* had superior growth, achieving a mean height of over 10 m in 7 years. This growth rate 289
 290 significantly exceeded that of all other species and is accentuated when shown as calculated volumes at 291
 292 the end of 7 years of growth (Fig. 5).

3.3. Relationship of survival and growth to erosion 293

294 The tree species differed in how survival related to erosion (Table 3). For *E. deglupta* and *C. odorata* the 295
 296 correlation was significantly negative, with higher mortality on more eroded sites. For *T. amazonia* the corre- 297
 298 lation was significantly positive, with higher mortality on less eroded sites. Mortality did not correlate sig- 299
 300 nificantly with erosion for the remaining species.

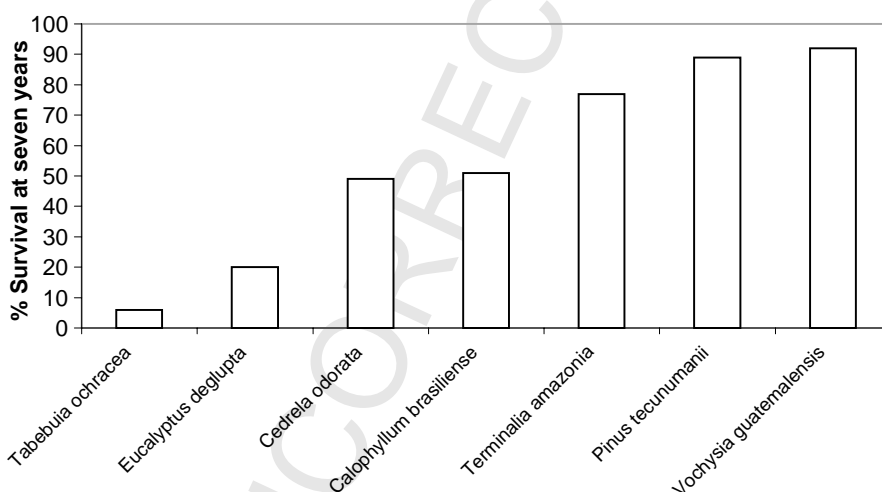


Fig. 3. Percent survival after 7 years in the field, based on the initial 90 individuals planted per species.

Table 2
One-way ANOVA with species as the factor

Source	Type III sum of squares	d.f.	Mean square	F	Significance
(A) Variable is tree height at 7 years					
Species	31246562	4	7811640	156.3	0.000
Error	15795539	316	49986		
Species		<i>n</i>	Mean	S.E.	
(B) Variability (S.E.) in tree height (cm) at 7 years					
<i>C. odorata</i>		44	224.3	32.9	
<i>P. tecunumanii</i>		79	1054.6	30.4	
<i>T. amazonia</i>		69	302.3	26.9	
<i>V. guatemalensis</i>		83	421.4	23.7	
<i>C. brasiliense</i>		46	386.1	20	

Adjusted R^2 is 0.660.

301 Growth negatively correlated with our index of
302 erosion in all species except *P. tecunumanii*
303 (Table 3). Fig. 6 shows the variability in erosion
304 and overall tree mortality and growth across all 30
305 blocks. Tree performance was exceptional in Block
306 21, where the erosion index was third-lowest of the 30
307 blocks and the terrain is a shallow valley.

308 4. Discussion

309 4.1. Relative performance of species for reforestation 310 projects

311 Clearly, we would not recommend using species or
312 methods with poor survival. We recommend against

using *T. ochracea* or *E. deglupta* in deeply eroded
ultisols. *T. ochracea* may be better adapted to shaded
conditions on the forest floor than to open pasture.
Although, seedlings grew in the nursery for 6–7
months, they remained small in above-ground stature
by out planting time. Small size may have been a
factor in their poor survival.

E. deglupta naturally occurs on tropical alluvial
flats with fertile well-drained soils (Eldridge et al.,
1994). We doubt that typically degraded soils will
support good growth of this species. In fact, local
foresters now recommend against planting this species
in degraded areas of Coto Brus.

In contrast, the pine and most of the other four
natives have potential for reforestation of degraded
land.

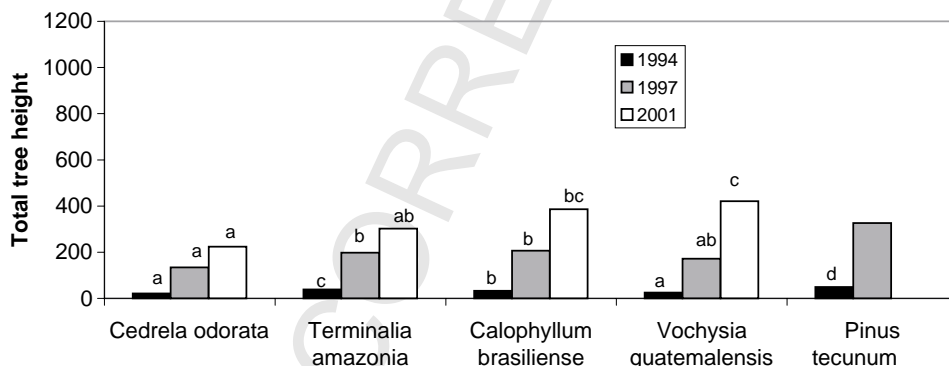


Fig. 4. Tree heights at three points in time: at initial out planting in 1994, after 3 years of growth and after 7 years of growth. Data for the five best-surviving species are shown. Letters indicate significant differences between species within a year, $\alpha = 0.05$.

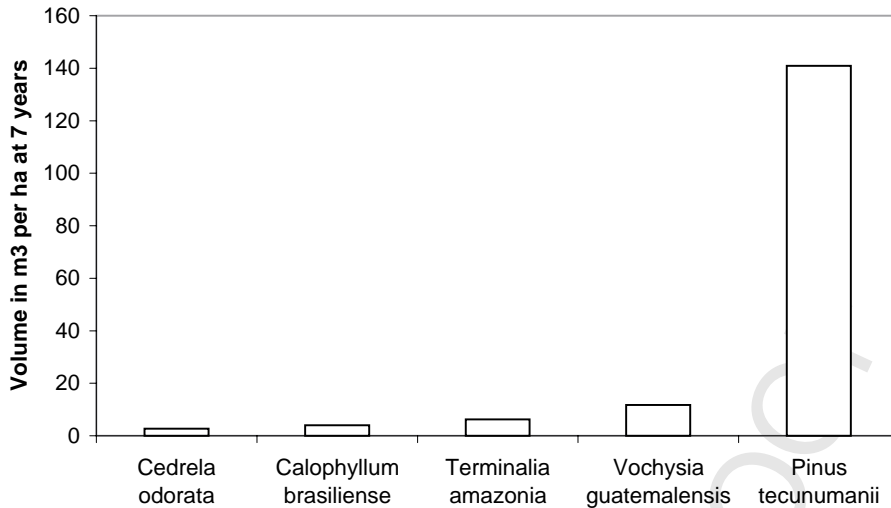


Fig. 5. Volumes in m³ per ha for each species after 7 years of growth, calculated as $[0.298 \times (\text{dbh}/100)^2(\text{height}/100)]$. The superior volume of pine was partly a function of large diameters.

329 4.2. Reforesting eroded tropical land: goals and 330 recommendations

331 Reforestation projects on degraded sites may have
332 different objectives, among them to:

- 333
1. reduce erosion;
 2. reestablish a variety of native species;
 - 337 3. establish economically viable commercial planta-
338 tions;
 - 339 4. combine two or more of the above goals.

340 First, land that is severely eroded and bare, with no
341 roots, continues to erode. Erosion control involves
342 protecting the soil with vegetation cover and root

343 systems. If a projects reforestation goal is to reduce
344 erosion as quickly as possible on extremely degraded
345 sites, *P. tecunumanii* likely would be the best candi-
346 date among the seven species we tested. This species
347 alone grew in parent material where not even grasses
348 succeeded over the 7 years period of the project. Its
349 survival and growth were even independent of the
350 magnitude of the erosion.

351 If the goal, however, is to reestablish a variety of
352 natives, the soil cannot be too degraded. None of the
353 natives assayed here grew when planted on soil eroded
354 to the C horizon. In areas with remnant B horizon, our
355 results suggest that a combination of *V. guatemalensis*,
356 *T. amazonia*, *C. brasiliense* and even *C. odorata* would
357 work.

Table 3
Correlations of 7 years survival and tree height with erosion index

Species	Survival		Height	
	<i>r</i>	One-tailed (<i>p</i>)	<i>r</i>	One-tailed (<i>p</i>)
<i>E. deglupta</i>	-0.66	<0.001	n/a	
<i>C. odorata</i>	-0.45	0.006	-0.57	<0.001
<i>T. amazonia</i>	0.33	0.04	-0.42	0.01
<i>T. ochracea</i>	-0.25	0.09	n/a	
<i>P. tecunumanii</i>	-0.23	0.11	0.05	0.25
<i>V. guatemalensis</i>	-0.16	0.2	-0.74	<0.01
<i>C. brasiliense</i>	-0.12	0.26	-0.44	0.015

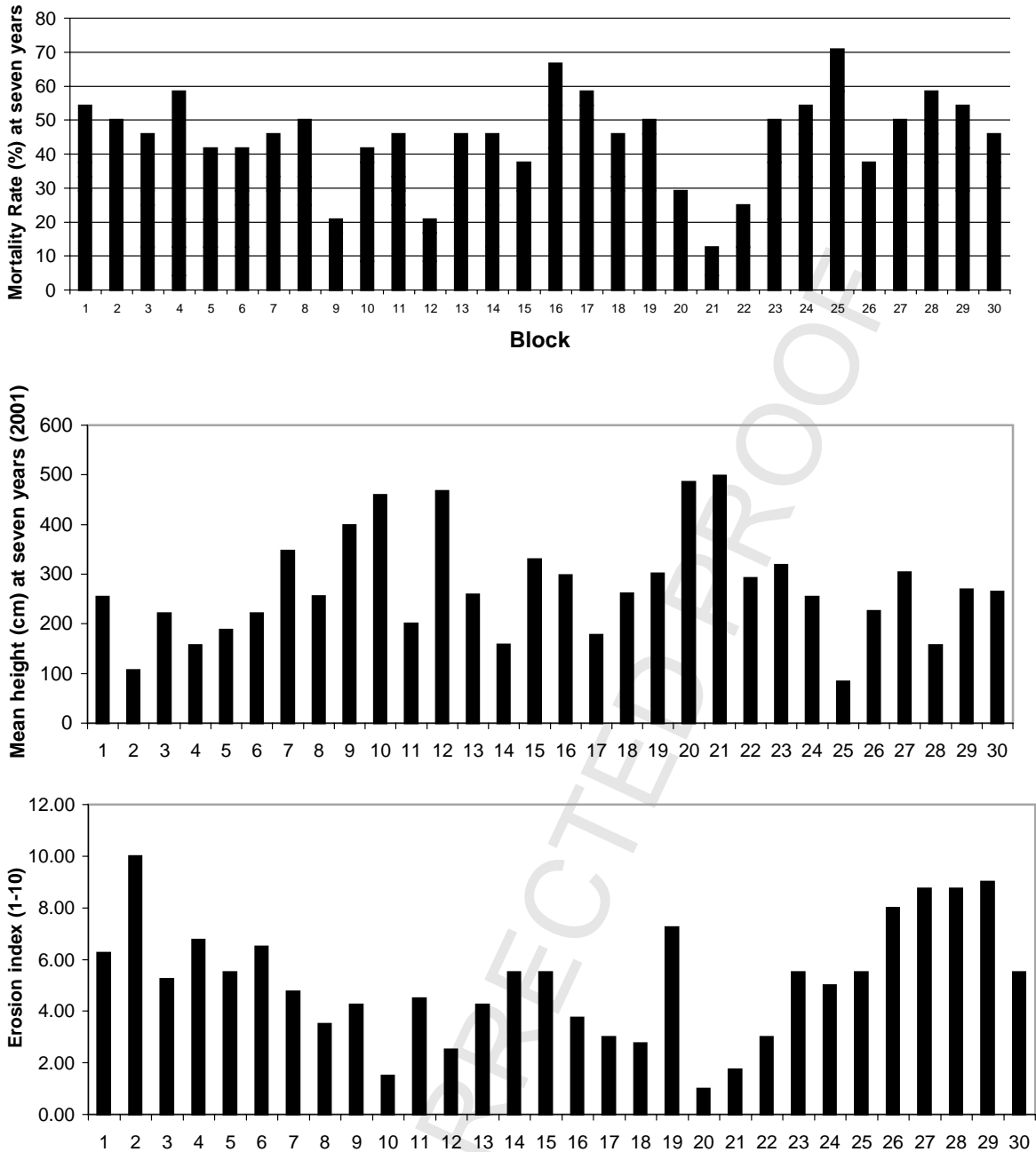


Fig. 6. Means of three variables indicated for all 30 plots—top: mortality rate at 7 years after out planting, for all tree species; middle: mean height after 7 years of growth, averaged across all species; bottom: average.

358 Planting pine initially might prepare a badly
 359 degraded area for later planting or regeneration of
 360 native species. A method of intermixing seedlings of
 361 shade loving species 2 or more years after planting the

pine might be more successful than planting such
 native species directly onto degraded sites. Relative
 to bare eroded pasture, microclimates under any trees,
 including pine, are less severe. Pine might also sup-

362
 363
 364
 365

- 366 press competition from weeds and grasses by shading
 367 the surface. Lugo (1997) discusses this use of exotic
 368 plantations in the introduction to a journal issue
 369 (Forest Ecology and Management, No. 99, 1997)
 370 dedicated to the topic of facilitating natural forest
 371 establishment through plantations, in which examples
 372 from around the world are provided. Articles specifi-
 373 cally documenting the use of pines to regenerate native
 374 forest include (Geldenhuys, 1997; Keenan et al., 1997;
 375 Loumeto and Huttel, 1997; Oberhauser, 1997). In our
 376 project *P. tecunumanii* established well enough in less
 377 than 3 years to provide perches for seed dispersing
 378 bats and birds.
- 379 The third goal above is more directly economic. If
 380 the goal is to produce a commercial plantation with a
 381 fast rotation time, pine was the only viable species of
 382 the seven, especially on the most degraded sites.
 383 However, some landowners prefer to use native tree
 384 species in plantations. Among the natives *V. guate-*
 385 *malensis* showed the best survival and growth. *Vochy-*
 386 *sia* species (*V. guatemalensis* and *V. ferruginea*) are
 387 common as seedlings in many early successional
 388 forests in much of the lowland areas of neotropical
 389 rainforest.
- 390 However, the cut timber of *Vochysia* spp. and the
 391 trunks of live trees are apparently quite susceptible to
 392 termite attack (Nichols and Gonzalez; 1992; Gallatin,
 393 personal communication). Therefore, rotations for
 394 timber production should probably be short (10–20
 395 years). Perhaps these species are best employed like
 396 pine to capture sites by growing quickly, reducing
 397 erosion and shading out grasses and other weeds.
- 398 *C. brasiliense* is a widespread native neotropical
 399 species that is attractive and has moderately valuable
 400 wood. Although, it survived well and grew moderately
 401 in our study, in another nearby area (Loik and Holl,
 402 1999) it appeared to tolerate full sunlight poorly. A
 403 review of the silvicultural literature (CAB Interna-
 404 tional, 2000) found that this species is generally
 405 considered to be better adapted to partial shade than
 406 to open conditions. Some studies suggest that this is
 407 not unusual: many later successional stage trees grow
 408 better in partial shade (6–42% of full irradiance) than
 409 in full sun (Agyeman et al., 1999). One possible
 410 forestry strategy might be to moderate a badly
 411 degraded site with pine or *Vochysia* before planting
 412 *C. brasiliense*. The faster growing species could pro-
 413 vide a harvest on a short rotation cycle, while *C.*
brasiliense could serve as a long-term investment
 for the landowner.
- 4.3. Possible role of mycorrhizal fungi in tree
 performance
- Why was the pine more successful than any of the
 other species, most of which were native and pre-
 sumably adapted to local conditions? First, a pasture
 where the original forest was removed over 50 years
 ago is obviously different from the understory of
 native rainforest. Our species adaptations may no
 longer be relevant.
- Second, pines perhaps did best because they are
 ectomycorrhizal. Pine seedlings do not survive if not
 inoculated, and nursery technicians usually inoculate
 them appropriately. Therefore, we can assume that the
 appropriate fungi had colonized our pine seedlings
 before out planting. Most native neotropical species
 are endomycorrhizal (Janos, 1996), having relation-
 ships with arbuscular mycorrhizal fungi (hereafter,
 “AMF”). Conceivably our techniques for inoculating
 the native tree species with AMF were less adequate.
 AMF improve phosphorous nutrition in their host
 plants when growing in P-deficient soils (O’Neil
 et al., 1991; Cooperband et al., 1994).
- Finally, the native tree species with the poorest
 growth in our site may need specific types of AMF.
 Shepherd et al. (2003) did find AMF in our slowest
 growing natives, *T. ochracea* and *C. odorata*. How-
 ever, to date, identification of fungi has been done at
 the generic level. On going analysis will show whether
 different tree species contain different fungal species.
 Such information in the future might help explain the
 poor performance of some natives and offer clues
 about how to use AMF to aid reforestation in the
 tropics.
- 4.4. Effect of erosion on performance
- The correlation analyses based on our erosion index
 could not determine causation. However, they did
 suggest that erosion had a strong negative impact
 on both survival and growth of most species. Erosion
 not only reduces the mineral fertility of the soil, but
 also changes its physical structure and biological
 community. Carpenter et al. (2001) showed that the
 number and diversity of AMF spores are low on the

458 most eroded sites on this farm. Scarcity of natural
 459 inoculum could account for poor performance on the
 460 deeply eroded sites. At our site Andonian (2001)
 461 experimentally inoculated AMF spores into nursery
 462 bags with germinating seedlings. Inoculation im-
 463 proved performance in five of six species. DNA
 464 analysis of fungi in root samples was consistent with
 465 the nursery results (Shepherd et al., 2003). Eleven of
 466 12 species were colonized by AMF, including four of
 467 the five native species of the present report.

468 *T. amazonia* was the odd species in both the nursery
 469 experiment and the DNA analysis, neither responding
 470 to inoculation (Andonian, 2001) nor containing AMF
 471 in the field. Interestingly, *T. amazonia* also was the
 472 only species for which survival increased with increas-
 473 ing erosion. This species grows well despite low levels
 474 of soil phosphorous (Nichols et al., 1997) even though
 475 it is not mycorrhizal. In contrast, grass and weeds do
 476 not grow well in extremely eroded areas on this study
 477 site. Perhaps *T. amazonia* survived better the worse the
 478 erosion because of less competition from other vege-
 479 tation. Also, all other native species in the study are
 480 endomycorrhizal and would suffer from lack of AMF
 481 in deeply eroded areas. So, besides the benefit of lower
 482 competition, *T. amazonia* would not have suffered
 483 inhibition due to lack of AMF. Nevertheless, growth
 484 of this species declined with erosion, so overall per-
 485 formance was poor despite better survival in deeply
 486 eroded blocks.

487 5. Conclusions

488 For rehabilitation of extremely eroded pasture sites
 489 similar to the one in this study, *P. tecunumanii* could
 490 establish vegetative cover relatively quickly. This
 491 species also might produce usable timber rapidly,
 492 but more time is necessary to establish the economics
 493 of this pine. Foresters should consider *V. guatemalen-
 494 sis* and possibly *T. amazonia* and *C. brasiliense* if
 495 native species are desired.

496 We saw a clear relationship between our erosion
 497 index and tree performance of most species. Only pine
 498 performed independently of the degree of erosion. The
 499 negative impact of erosion may relate to effects on soil
 500 biota, a possibility that we are currently investigating.
 501 Methods that reduce erosion are probably important
 502 for establishment of tree seedlings.

Finally, future work should test the ability of pine to
 prepare a site for later planting of other species.
 Studies should pursue the possibility that restoring
 soil AMF communities could facilitate tree restoration
 in severely eroded areas. This paper reports a long-
 term experiment, which we plan to continue measur-
 ing in the future, as rankings could change among the
 species over time.

Uncited references

Davidson et al. (1998), Hofer (2002), Marques and
 Joly (2000), Prokopy (2001), Sullivan et al. (1998).

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