6 Variable success of native trees planted on degraded pasture in Costa Rica

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ABSTRACT

Native trees planted across a degraded 25-ha farm in southern Costa Rica in several experiments since 1993 varied at least 12-fold in success (growth and mortality). Depending on the experiment, our results showed that success can be affected by the tree species, seed mother tree, topography, and whether legume trees were part of the species mix. Historical use of each area on the farm during the 40 years after its deforestation also affected success. For example, areas that were bulldozed or heavily tracked by cattle exhibited poor success at reforestation. However, much of the variability depended on specific site and is still unexplained. Patchy occurrence of mycorrhizal fungi is a possible explanation for some of the variability in tree success. In the tree nursery, inoculation of mycorrhizal fungi into pot soil increased performance of native tree seedlings. One of our working hypotheses for the future is that improvement of mycorrhizal status in recalcitrant areas might increase re-establishment of trees and soil fertility to extremely degraded tropical soil.

INTRODUCTION

Foresters in Costa Rica began incorporating native tropical timber trees in reforestation schemes almost 20 years ago (Nichols & Gonzalez 1992, Haggar *et al.* 1998). More recently, experimental trials of various native species have produced preliminary results (Gonzalez & Fisher 1994). These results and continuing studies are important because tropical woods are becoming scarce, yet remain in demand. Also, many native trees are adapted to the environmental conditions of abandoned land and may perform better than

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exotics under such circumstances (Gonzalez & Fisher 1994). Furthermore, the tropical natives can serve many purposes other than timber production. Examples are restoration of wildlife habitat, erosion reduction, regeneration of soil fertility and improvement of watersheds.

This paper reports preliminary results of several experiments established between 1993 and 2000 on a degraded, eroded cattle pasture in southern Costa Rica. Tree growth and survival have varied greatly across the 25-ha farm. Although the pasture seemed homogeneously degraded when the experiments first began, experience revealed substantial underlying environmental heterogeneity. This heterogeneity explains some but not all of the variance in tree performance. Intentionally manipulated factors in our experimental designs also accounted for some of the variance. Such factors included tree species, seed mother, proximity of legume nurse trees, degree of erosion, topography, land-use history, and the nature of the soil mycorrhizal community. We report here our information to date on several of the factors explaining variability in tree performance. Understanding the factors affecting tree performance on tropical degraded land will help future restoration efforts as well as tropical plantation forestry.

MATERIAL AND METHODS

Our study site is a 25-ha farm in southwestern Costa Rica, 83°W, 9°N. Elevation is 1 050 m on the south Pacific slope. Mean annual temperature is 20°C, with 4 400 mm annual rainfall mostly between April and December. The site was "tropical premontane rainforest" (Holdridge 1967) before being cleared for agriculture in the 1950s. Much of the region is steep, subject to erosion, and inappropriate for annual crops or pasture. The Ultisols of the farm range from Typic Hapludults to Humic or Andic Hapludults (USDA system). Soils at the beginning of our experiments in 1993 were not compacted, bulk densities never exceeding 1.1 of cmg^{-3} even in the bottoms of cattle trails. Initial pHs before restoration ranged between 4.4 and 5.8, averaging 5.2. The soils of the region are acid, phosphorus-fixing and infertile—more so after erosion removes topsoil (Carpenter *et al.* 2001).

After growing coffee for about 20 years, approximately 20 ha of the 25 ha farm were converted to pasture in 1978 by planting exotic grasses for grazing. For the first experiment described below, 5 ha were fenced from cattle in 1993. Over the succeeding years, fences were built around each new experiment to exclude cattle. By the year 2000 about 15 ha had been planted in experimental plots.

Experiment 1—1993. *Terminalia amazonia* interplanted with legumes

We planted a native timber tree, *Terminalia amazonia* (Combretaceae), in eight experimental treatments to determine methods to improve growth and survival (Nichols *et al.* 2001). We planted tree seedlings in 3 × 3 m hexagonal arrays. Besides the unmanipulated control, treatments included:

- 10–30–10 fertilizer upon outplanting;
- *T. amazonia* interplanted with herbaceous legumes, either *Phaseolus vulgaris* or a mix of *Mucuna pruriens/Canavalia ensiformis* (Fabaceae);
- *T. amazonia* interplanted with arboreal legumes, either *Inga edulis* or *Gliricida sepium* (Fabaceae);
- *T. amazonia* interplanted with an equal mixture of the two legume trees to form three-species plots.

The experiment was a randomized block design with five replications of each treatment. Two of the five blocks were steep, one was flat at the foot of steep slopes, one was flat but cut by deep cattle trails and the fifth consisted of rolling hills. Each block contained eight experimental plots (one replication of each treatment), and each plot measured 24 × 26 m and contained 93 *T. amazonia*. The entire experiment consisted of 40 plots and over 3 700 *T. amazonia*.

At the beginning of the experiment in 1993 we took soil samples at 0–15 and 15–30 cm depth for each of the 40 plots and analysed pH, Olsen P, SOM, % Al saturation, CEC, NO_3, NH_4 and Ca to determine the initial soil fertility. We estimated the degree of erosion in each of the 40 plots based on depth of cattle trails and remaining topsoil. We characterised the topography of each plot as predominantly one of the following categories: ridge, slope, valley between slopes, or flat.

We collected *T. amazonia* seeds from 14 seed mother trees in the region around our site. We raised the seedlings in an on-site tree nursery till they reached 5 cm height and then outplanted them during September 1993. Seedlings were kept clear of weeds for the first two to three years.

Each year between 1993 and 2001 we measured the height to the tip of the tallest leader and diameter at breast height. In 2001 we also noted each death and scored each living tree along a rank of health: 1=very sick or dying, 2=sick, 3=normal, 4=exceptionally healthy.

We analysed height and DBH after four years (Nichols *et al.* 2001) and, here, after eight years in 2001, with Two-way ANOVA using SPSS. Here we also analyse survival and health data from 2001.

Experiment 2—1994. Tree species trials

We tested the relative abilities of seven tropical tree species to establish in our degraded pasture with no special treatment, only weeding when necessary during the first two or three years. In this experiment we included five natives as well as two exotics recommended by local foresters for our elevation. For each native species, we collected seeds during 1993–1994 from various provenances, and raised the seedlings in our nursery for several months. We purchased seedlings of the two exotics. The native species were *T. amazonia*, *Tabebuia ochracea* (Bignoniaceae), *Calophylum brasiliense* (Clusiaceae), *Cedrela odorata* (Meliaceae), and *Vochysia hondurensis* (Vochysiaceae). The exotics were *Pinus tecunumanii* (Pinaceae) and *Eucalyptus deglupta* (Myrtaceae).

From July to September 1994 we planted the seedlings in a randomized block design, 30 blocks across the entire farm, three individuals per species in each block. Each species was represented by a total of 90 trees. Planting pattern was a hexagonal array, each block measuring 18 × 9 m. We measured height annually and analysed growth and survivorship after five years (Bhasin 2000).

Experiment 3—1995. Fertilization of *Terminalia amazonia*

To determine if N, P, or K individually affects the growth of *T. amazonia*, we planted seedlings across a range of terrain in three randomized blocks with three levels of each mineral, for a total of nine treatments. We replicated each treatment three times in each block, giving 27 experimental plots per block (81 total plots). Each plot contained two experimental trees surrounded by six barrier trees, yielding 162 experimental trees and 486 barrier trees. The forms of fertilizer were ammonium nitrate for N (33 percent N), triple super phosphate for P (46% P_2O_5), and potassium chloride for K (60% K_2O). The concentrations were 0, 1×, and 2× the amount of each mineral recommended for trees.

We analysed growth annually for four years (Henriquez & Carpenter, ms in preparation). In 1999 we also took data on topography of each plot.

Experiment 4—1996. Mycorrhizal potential

As heterogeneity of tree growth and survival emerged in the above experiments, we suspected that mycorrhizal fungi might vary across the farm and cause some of this variability in success. Mycorrhizal communities are known to be related to history of land use and degree of erosion (Carpenter *et al.* 2001). We analysed soil fertility and mycorrhiza over a gradient of land mismanagement, ranging from the worst areas that had been bulldozed or especially heavily used by cattle, through moderately eroded areas, to secondary forest with 20 years of recuperation since the 1970s. In 1996 we selected eight sites that represented this gradient of land use and took three 1 kg soil samples from each site. A small subsample of this soil was used to measure pH, soil humidity, SOM (Walkley-Black method), and available P (Bray method). The remainder was used to culture mycorrhizal fungi to determine mycorrhizal inoculum potential. We harvested the cultures after two months, and counted and identified spores produced from each soil sample (Carpenter *et al.* 2001).

Experiment 5—2000. Mycorrhizal inoculation of six native species

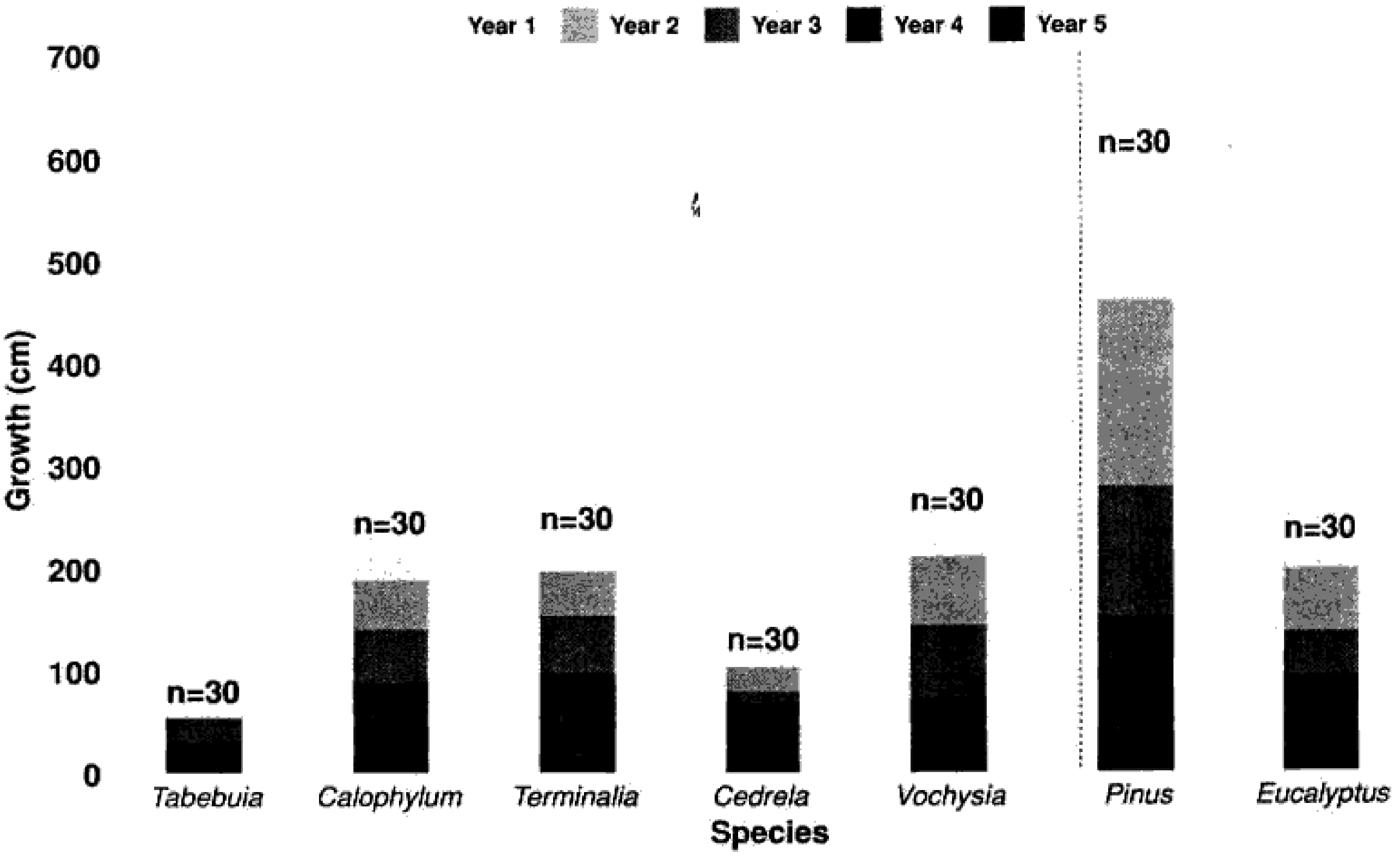
To determine the effect of mycorrhiza on six of the native trees with which we work, we selected three legume species and three non-legume species to raise from seed in 10 × 20 cm black plastic nursery bags in the tree nursery. The legume species were *Inga edulis, Dyphysa robinioides* and *Calliandra calothyrsus*; the non-legumes were *T. amazonia, C. odorata* and *Hieronyma oblonga* (family Euphorbiaceae). We established three blocks with 100 seedlings of each species in each block (one seedling per bag), half of which we inoculated with live mycorrhizal inoculum and half of which we inoculated with killed inoculum for controls. The entire experiment consisted, therefore, of 1 800 seedlings. We analysed growth at 3.5 and 6 months (Andonian 2001), and both growth and survival after 13 months (Zakhor unpublished ms, 2002).

RESULTS

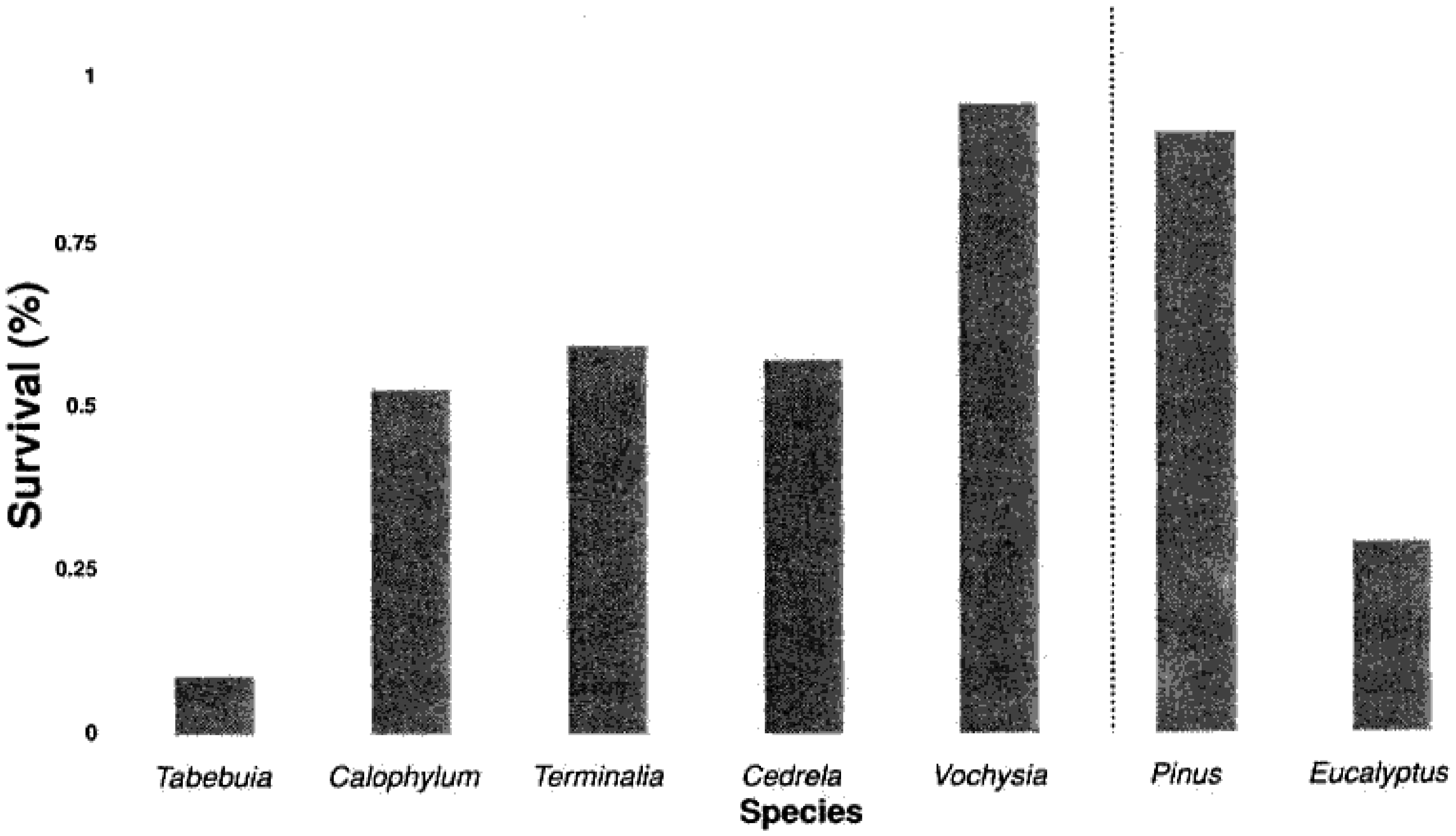
We present results not in chronological order but in the order in which they relate to one another.

Tree species trials (Experiment 2)

The different species included in our 1994 tree trial showed large differences in growth and survival, as expected (Figure 1). Survival was best in *P. tecunumanii* and *V. hondurensis* (above 90%) whereas almost all *T. ochracea* died. Spatial patterns of growth across the farm differed among species. Two species, *P. tecunumanii* and *C. brasiliense*, showed almost no spatial variation in growth across the farm, growing equally well in all areas. The only exception was that *C. brasiliense* died in one of the 30 blocks. In contrast, *T. amazonia* and *V. hondurensis* showed 4- to 5-fold differences in growth rates between their best and worst blocks. Mortality of *C. odorata* and *E. deglupta* was high in the same places where *T. amazonia* and *V. hondurensis* grew the worst, showing that these areas were stressful for four of the six surviving species.



A. Average incremental growth



B. Average survival

Figure 1. Growth from 1994 to 1999 and survival in 1999 of five native species of trees (left of vertical line) and two exotics (right of vertical line). A. Means of three trees per block averaged over 30 blocks for each species. B. Percent of the initial 90 trees of each species still alive in 1999. Species from left to right are *T. ochracea, C. brasiliense, T. amazonia, C. odorata, V. hondurensis, P. tecunumanii, E. deglupta.*

Table 2. Block effect on growth of *Terminalia amazonia,* shown by three significant Tukey subgroups ($p < .05$)

Block	Mean tree heights		
Eroded	326		
Steep 2	357	357	
Steep 1		373	
Hilly			422
Flat			440

Another important factor influencing performance of *T. amazonia* was seed mother, or provenance from which came the seeds. Seed mother affected height growth of progeny (14 different mothers, Two way ANOVA, mother $F = 13.1$, $p < .000$, no significant interaction between mother and block). The offspring of the best seed mother averaged 70% taller than those of the worst seed mother. We ranked the 14 seed mothers from worst to best performance of their offspring as represented by average height, survival and health rank. All three variables correlated positively with each other (Table 3), meaning that the mothers with the tallest offspring also produced offspring with higher survival and better health than those with the smaller offspring.

Table 3. Pearson correlation tests on performance ranks of offspring from 14 seed mothers of *Terminalia amazonia.* The rank order of all variables representing success correlated positively.

Comparison	Pearson correlation	Two-tailed p
Height rank vs. survival rank	.73	.003
Height rank vs. health rank	.78	.001
Height rank vs. survival rank	.86	.000

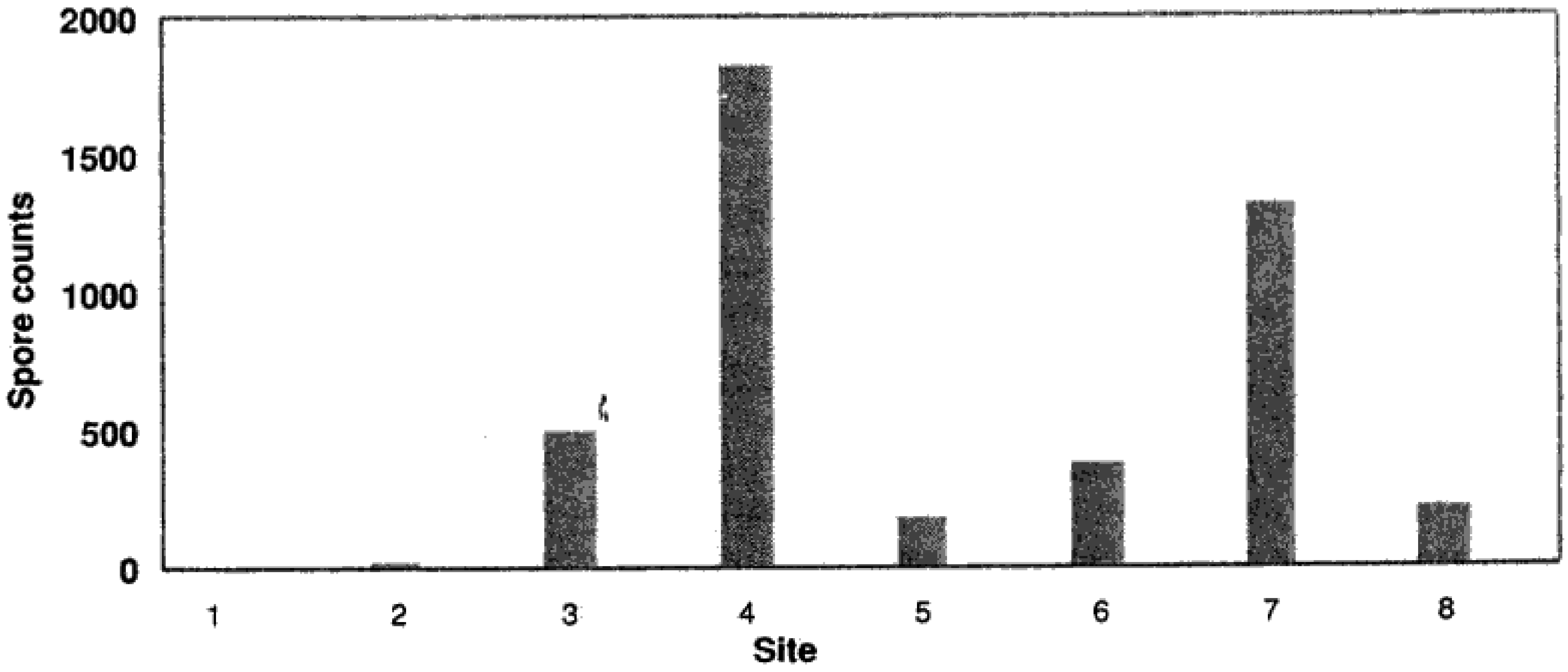
Fertilization of *Terminalia amazonia* (Experiment 3)

The experiment (#3) in which we fertilized *T. amazonia* with N, P, and K separately showed that none of these inorganic fertilizers had any significant effect on growth in any year. The first year's growth, 1995–1996, showed only a slight trend for effect of N ($p = .08$) but the overall analysis was not significant (GLM $F = 1.15$, $p > .33$). The trend disappeared in subsequent years. However, topography conspicuously affected growth. This experiment occupied three undulating ridges and valleys, with steep slopes between. Growth was best in the valleys and worst on the ridges.

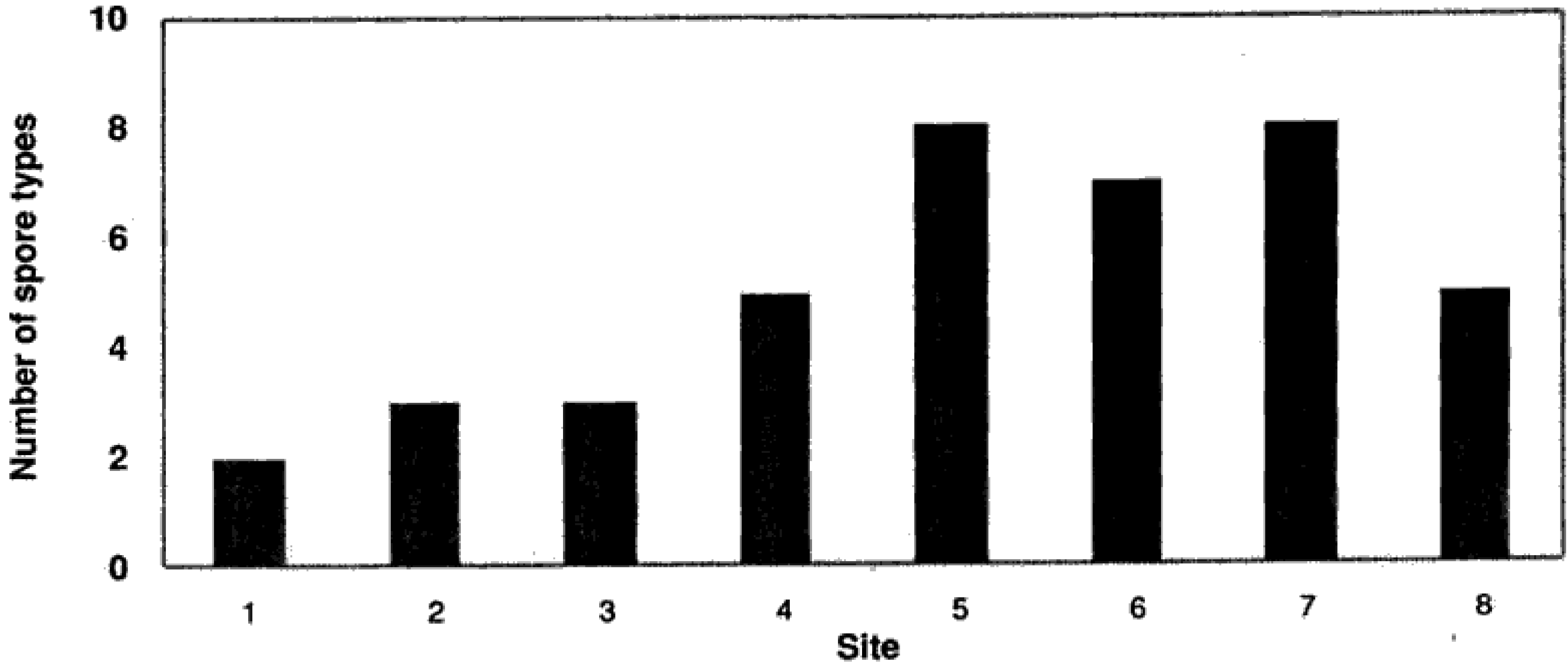
Mycorrhizal potential (Experiment 4)

Mycorrhizal inoculum potential did not correlate with degree of erosion except to approach zero in the two most deeply eroded sites (Figure 2A). One of these sites was the bulldozed site mentioned above. The other site was an area where cattle always had congregated when being herded off the farm, and was deeply cut by cattle trails. Neither of these sites contained rhizospheres of plants.

However, the *diversity* of mycorrhizal spore types was inversely related to degree of erosion ($p < .01$, Figure 2B), which in turn was negatively correlated with growth in Experiment 1.



A. Mycorrhizal inoculum potential



B. Spore diversity

Figure 2. Relationship between land management and mycorrhiza. Sites range from the most deeply eroded (1 and 2) to the least (8). A. mean mycorrhizal inoculum potential of soils from each site (n=3 samples per site). B. mean number of types of mycorrhizal spores cultured from these samples.

Mycorrhizal inoculation of six native species (Experiment 5)

Five of the six species inoculated with arbuscular mycorrhizal fungi in the nursery responded positively to inoculation (Table 4). All three species of legumes showed positive responses, either in growth (*I. edulis, D. robinioides*) or in survival (*C. calothyrsus*). Two of the three non-legumes showed increased growth (*H. oblonga*) or survival *C. odorata*) when inoculated. The other non-legume, *T. amazonia*, showed no response up to 13 months.

Results for *Terminalia amazonia*

Although *T. amazonia* did not perform the best in the tree trial experiment, it produces valuable wood and does grow well under some circumstances. What are those circumstances, and how can we grow it better?

First, to date, no evidence exists that would recommend fertilizing this species with inorganic fertilizer. Addition of P did not improve performance of 15 species of native trees on a P-fixing volcanic soil in Ecuador (Davidson *et al.* 1998). The lack of effect of 10-30-10 fertilizer in our 1993 experiment on *T. amazonia* was supported by our 1995 experiment in which we applied each mineral separately in two concentrations. Growth of this species was unrelated to any of the soil chemical factors measured at the beginning of the 1993 experiment, including N (Nichols *et al.* 2001). These negative results may also explain why this tree species does not seem to respond to inoculation with mycorrhizal fungi since the mutualism primarily helps plants obtain phosphorus. Perhaps this tree species simply has very low requirements for the macronutrients.

On the other hand, Nichols *et al.* (1997) found that performance of *T. amazonia* in plantations improved with soil nitrogen availability. Consistent with this result was the fact that we found interplanting *T. amazonia* with certain legume trees, especially *I. edulis*, improved performance of the former. The effect increased with time, which is not surprising as the impact of the nitrogen fixation of a legume tree probably increases as its biomass increases. We are now testing the impact of an organic form of nitrogen fertilizer, urea. The practice of interplanting this species with legume trees needs to be studied in more detail, including determining legume species to be used as well as optimal spacing of both timber tree and legume. The practice of using legume trees to "nurse" timber trees is not new. Various studies have shown their value (e.g. Kumar 1998).

Seed mother strongly affected performance, so plantations should definitely include a variety of provenances until genetic superiority can be selected.

Spatial heterogeneity of tree performance

Tree performance varied spatially in all field experiments. In tree trials, four of the six species that survived showed much greater growth in some areas than in others. In the fertilization experiment on *T. amazonia*, topographical effects may have swamped any fertilizer effects. And in the experiment testing the effect of legumes on *T. amazonia*, block effect explained twice as much variance in tree growth as did the experimental treatments. Blocking had originally been based upon topography and degree of erosion.

The very worst growth and survival occurred in areas that had been bulldozed or deeply cut by cattle trails in the past. Bulldozing has been shown to arrest succession in Brazil (Nepstad *et al.* 1991). In general, we found that growth was poor on ridges and on exceptionally steep and eroded slopes. Particularly problematic was poor performance on ridges, not just in *T. amazonia* but in all species except pine; yet ridges are not deeply eroded. Lack of moisture could explain this result in many regions of the world, but rainfall and humidity are so high in our site that this factor is unlikely to explain our patterns. We are currently examining the possibilities that ridges could be unusually compacted or devoid of mycorrhiza.

Growth was best on gentle slopes or in shallow valleys between slopes, which are both areas subject to less erosion. Also, valleys can capture runoff from steep slopes that might contain both nutrients and mycorrhizal inoculum. However, since many of our results showed no relationship between growth and availability of mineral nutrients,

nutrients may not be the most important factor. Topographical effects could instead be partly explained by heterogeneous occurrence of mycorrhizal communities.

Possible importance of arbuscular mycorrhizal fungi

In some studies, mycorrhizal fungi have been shown to aid regeneration of tropical forest trees (Alexander *et al.* 1992). Most neotropical trees are symbiotic with arbuscular mycorrhizal fungi rather than with ectomycorrhizal fungi. Tree species differ in their dependency on the relationship (Janos 1996). In some ecosystems the diversity of mycorrhizal fungi is an experimentally demonstrated factor increasing plant species diversity and plant productivity (van der Heijden *et al.* 1998).

In the most deeply eroded areas on our study site, both mycorrhizal inoculum potential and diversity of spore types are low. Even in less deeply eroded areas, spore type diversity decreases linearly with degree of erosion. Both mycorrhizal factors, diversity and density, could be important in tree growth, since most of the tree species that we tested showed positive reactions in the nursery to inoculation with a diverse inoculum. The lack of response of the one species (*T. amazonia*) may reflect premature testing. In other words, the relationship is a mutualism costing plants photosynthate in exchange for nutrients. In early growth, sometimes this cost exceeds or equals the benefit to seedlings, and no positive response in the trees can be detected for several months or even years (Ricardo Herrera, personal communication).

Alternatively, *T. amazonia* may need types of mycorrhizal fungi not included in our inoculum. Some plants are known to perform better with some types than with others (van der Heijden *et al.* 1998). Or, this tree species may simply not need the mutualism to do as well as it does in degraded land.

Still to be determined is the impact of inoculation in the field, and whether mycorrhizal communities destroyed by land mismanagement can be restored. The areas of exceptionally poor tree growth that had been bulldozed in the past or eroded to bedrock probably had their soil community completely removed. These sites contained no rhizospheres of any plants, so the fungi lacked any host material for colonization and subsequent propagule formation. These two sites also have subsequently failed to produce reasonable tree growth by any of the species we have so far tried. We currently have several experiments testing if mycorrhiza can be re-established in such areas, and if so, whether this feat results in improved tree growth.

CONCLUSION

At this point, we can make some recommendations for restoration practices as well as for future research:

- Choose your species carefully. Experiment with different possibilities for your site. Some species that would seem unsuitable, such as slow-growing late successional species, might actually do well in the most degraded areas.
- Consider planting pine in the most difficult areas to provide shade for other trees planted simultaneously or subsequently.
- Determine which nitrogen-fixing legumes can establish, because legumes can not only increase soil nitrogen but are also usually mycorrhizal and may re-establish soil communities.

- Inorganic fertilizer may be a waste of money and effort. Experiment with organics.
- Seed provenances of native species show variable performance; if the species you are using has not been selected for genetic superiority, use seedlings from several mother trees.
- Investigate nursery practices that yield superior performance once trees are outplanted. Examples might be to determine if collecting seeds at the peak of seed production in the field could improve later performance. Experiment with mycorrhizal inoculation in the tree nursery.
- Ridge tops may be recalcitrant. Try your hardiest tree species, perhaps pines. Investigate which characteristics of ridges differ from slopes and valleys and cause reduction in tree performance.
- The key to improving performance in extremely degraded areas in high rainfall areas is probably to slow erosion and increase soil organic matter. Increased SOM is associated with more mycorrhizal fungi as well as with organic forms of nutrients. Mulch if at all feasible.
- Research on the role of mycorrhizal fungi in reforestation of degraded lands is needed.

In sum, one should expect great spatial heteogeneity in tree performance, even if using a single hardy species. Improving the recalcitrant areas within the overall degraded landscape is one of our primary challenges.

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