Experimental Native Tree Seedling Establishment for the Restoration of a Mexican Cloud Forest

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Abstract

The cloud forests of Mexico have been degraded and severely fragmented, and urgently require restoration. However, progress with restoration has been constrained by a lack of information concerning the seedling ecology of native tree species. An experiment was therefore conducted to assess the influence of different environmental factors on the seedling survival and growth of four native tree species (Fagus grandifolia var. mexicana, Carpinus caroliniana, Symlocos coccinea, and Quercus acutifolia). The seedlings were established on three sites, in two contrasting environments: inside forest fragments and on adjacent agricultural land. Highly significant differences were recorded in seedling survival and growth among sites, environments, species, and interactions between these factors. Highest survival was recorded for Quercus, which uniquely among the four species displayed the same survival percentage inside and outside the forest. Survival of the other species was higher inside the forest. In contrast, growth rates of all four species were higher outside the forest. The most important cause of mortality outside the forest was desiccation, although significant seedling predation was also observed on two sites. Results indicate that all four species can be established successfully both within forest fragments and in neighboring agricultural areas, emphasizing the scope for forest restoration. However, the interactions observed between species, sites, and environments highlight the importance of accurate species-site matching if optimum rates of growth and survival are to be obtained. Quercus spp. have great potential for establishment on agricultural sites.

Key words: cloud forest, fragmentation, native tree species, restoration, seedling establishment, seedling survival, tropical montane cloud forest, Veracruz.

Introduction

The montane cloud forests of Mexico are of exceptional conservation importance, owing to their high species diversity and endemism (Challenger 1998). Most of the cloud forests that remain have been highly fragmented and degraded as the result of human activities, including clearing for agriculture, grazing by livestock, and the harvesting of trees for fuelwood and timber (Challenger 1998; Ramírez-Marcial et al. 2001; Williams-Linera 2002). In the Mexican state of Veracruz, the establishment of coffee plantations and the extraction of construction materials (mainly sand and volcanic gravel) have also been important causes of forest destruction. As a result, the forests of this area have been reduced to small patches surrounded by pastures, coffee plantations, old fields, and human settlements (Williams-Linera 2002).

Recent research into the impacts of anthropogenic disturbance on cloud forests in Veracruz has indicated that all remaining forest fragments continue to be disturbed, and that very few sites have any degree of protection (Williams-Linera 2002). Given the extent of forest degradation that has occurred, restoration should form part of the developing conservation strategy for the area. Opportunities for such restoration exist, because private landowners within the region are increasingly becoming interested in alternatives to agricultural land use, such as ecotourism. Potential approaches to restoration include assisting natural regeneration by protecting the site from further disturbances and by allowing natural successional processes, and accelerating natural colonization through artificial establishment of seedlings (Lamb et al. 1997; Holl et al. 2000).

Expanding of cloud forest fragments will require establishing native tree species on sites currently under some form of agricultural land use. In Mexico, reforestation programs have tended to focus on the use of exotic rather than native tree species (e.g., Eucalyptus spp. and Casuarina cunninghamiana from Australia and Pinus radiata from California, U.S.A.). The restoration ecology of Mexican cloud forests has received very little attention to date (Pedraza & Williams-Linera 2003; Ramirez-Marcial 2003). As a result, the use of native tree species for forest restoration has been constrained by a lack of knowledge about their requirements for propagation, survival, and growth.

The objective of the current investigation was to experimentally assess seedling survival and growth of four native...
tree species with different ecological characteristics, in two contrasting environments: within forest fragments and on adjacent areas of agricultural land. We tested the following hypothesis: The relative success of tree species inside and outside forest fragments would largely be governed by their shade tolerance and microenvironmental conditions. The experiment was performed by establishing seedlings in paired plots both inside and outside forest fragments, and by monitoring their success in terms of survival and growth over a period of 14 months.

Methods

Study Area

The investigation was undertaken in three forest fragments located in central Veracruz, Mexico, adjacent to agricultural lands. The vegetation in the area corresponds to tropical montane cloud forest or bosque mesófilo de montaña, sensu Rzedowski (1978). The sites were located between 1,340 and 1,500 m altitude in the Sierra Madre Oriental (Table 1a). The three study sites, Rancho Viejo, Xolostla, and Las Cañadas, were selected because they were situated inside private properties and their owners were interested in their conservation, making the sites safer for long-term experiments. The ecological characteristics of these forest fragments, including floristic diversity, soil characteristics, and disturbance regime, were described by Williams-Linera (2002). All three fragments are crossed by paths used by local people, who occasionally cut trees or gather fuelwood. Rancho Viejo is situated close to pastureland, whereas Xolostla is near a macadamia nut plantation and a cornfield. In Las Cañadas, livestock grazing occurred in the past within the immediate vicinity, but currently the site is being protected by its owner from disturbance.

Production of Seedlings

The selected tree species were Fagus grandifolia var. mexicana (gúichin, acailite), Carpinus caroliniana (pepinque), Symlocos cocinea (limoncillo), and Quercus acutifolia (encino). Carpinus and Symlocos were collected from forest around Xalapa as seeds; Fagus was collected as seedlings from the forest located in the Acatlan volcano, and the nursery of Xalapa municipality donated Quercus seedlings. Seeds were germinated on moist filter paper in the laboratory. All seedlings were transplanted into black plastic bags (12 × 20 cm) filled with a 50:50 mixture of soil from the nursery and potting compost. Mean seedling heights at the inception of the field experiment were 10 cm for Fagus, 80 cm for Quercus, and 20–25 cm for Carpinus and Symlocos.

To homogenize the growth conditions, seedlings were raised in a greenhouse with a clear plastic roof for 6 months before transplanting. The greenhouse was located in the Botanical Garden of the Instituto de Ecología, A.C. in Xalapa, at an altitude of 1,300 m in vegetation similar to that of the experimental sites. The plants were watered daily.

Seedling Establishment

At each of the three sites, seedlings were transplanted into eight 10 × 16-m experimental plots. Four of those plots were positioned randomly within a 1-ha parcel, in the forest interior at least 30 m from the forest edge. The other four plots were established outside the forest at a fixed distance (5 m) from the forest border, at a spacing of 3 m. Forty seedlings (10 of each species) were transplanted into each plot in a grid with 2-m spacing between adjacent seedlings. All seedlings (960 seedlings, 320 per site) were permanently numbered with metal tags, and their location was marked. The experiment therefore incorporated three forest sites and two treatments within each site (inside and outside). Two months after the onset of the experiment, plots located outside in Rancho Viejo were fenced with barbed wire to protect seedlings from livestock. It was not necessary to protect any of the other sites.

Measurements of Seedling Growth

Seeding height, stem basal diameter, and number of leaves were assessed for each seedling 1 month after transplanting. Seedling survival, cause of mortality (e.g., vertebrate or invertebrate predation, and desiccation), height, diameter, and number of leaves were subsequently monitored every 3 months for a period of 14 months. Diameter was measured with a digital caliper at the stem base and stem height was measured with a ruler, and all the leaves in each plant were counted. Survivorship was estimated as the proportion of seedlings surviving at each time interval. The change in growth over time was assessed by calculation of relative growth rate (RGR), which expresses growth in terms of a rate of increase in size per unit of initial size (Hunt 1990). The formula used to calculate RGR was the following:

\[ RGR = \frac{\log e H_2 - \log e H_1}{t_2 - t_1} \]

where \( H_2 \) and \( H_1 \) are the seedling height/diameter at different times (\( t_2 - t_1 \)). Leaf production was expressed as the number of leaves produced between the first and last period of observation. In all cases, increments were expressed over an interval of 14 months.

Microclimate

Microclimatic data were collected inside the forest, at five sampling points randomly placed in each 1-ha parcel, and outside the forest, at five points placed in the plots. Microclimatic conditions were measured on 1 day every month at around 1200 hours. The variables measured at each sampling point were air and soil temperature, relative humidity, gravimetric soil water content, canopy openness, and photosynthetically active radiation (PAR). Air temperature and relative humidity were recorded at 1.5 m
above soil level using a digital therm-hygro thermometer and psychrometer, respectively. Soil temperature was measured at 5-cm depth with a soil thermometer. Gravimetric soil water content was measured by calculating the difference in soil mass between fresh and dried soil. Soil samples (at 5-cm depth) were collected, transported to the laboratory in plastic bags, and weighed. Soil dry mass was obtained after drying for 72 hr at 105ºC in an oven. Percentage of canopy openness was evaluated with a spherical densiometer (Forestry Suppliers Inc., Jackson, MS, U.S.A.); estimates were made from four cardinal directions at the center point of each sampling point. Photosynthetically active radiation was measured using light-sensitive Proprint Sepia Diazo paper (Charrette Corp., Woburn, MA, U.S.A.). Paper sensors were constructed with 14 layers of paper and were collected 72 hr after being placed in the field. The paper was calibrated using integrated light values for 72 hr with light sensors (LICOR LI-190SA,

Table 1a. General characteristics of the study sites.

<table>
<thead>
<tr>
<th>Forest Fragment</th>
<th>Las Cañas</th>
<th>Xolostla</th>
<th>Rancho Viejo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m)</td>
<td>1,340</td>
<td>1,450</td>
<td>1,500</td>
</tr>
<tr>
<td>Latitude (N)</td>
<td>19º11'</td>
<td>19º32'</td>
<td>19º30'</td>
</tr>
<tr>
<td>Longitude (W)</td>
<td>96º59'</td>
<td>96º58'</td>
<td>97º0'</td>
</tr>
<tr>
<td>Area (ha)</td>
<td>40</td>
<td>6.6</td>
<td>19.8</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>16–27</td>
<td>12–33</td>
<td>31–35</td>
</tr>
<tr>
<td>Mean temperature (°C)</td>
<td>16.7 ± 0.71</td>
<td>19.1 ± 0.06</td>
<td>19.1 ± 0.06</td>
</tr>
<tr>
<td>Maximum temperature (°C)</td>
<td>23.0 ± 0.80</td>
<td>24.2 ± 0.75</td>
<td>24.2 ± 0.75</td>
</tr>
<tr>
<td>Minimum temperature (°C)</td>
<td>10.5 ± 0.71</td>
<td>13.9 ± 0.60</td>
<td>13.9 ± 0.60</td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>1,924</td>
<td>1,610</td>
<td>1,610</td>
</tr>
</tbody>
</table>

Characteristics of the study sites in central Veracruz, Mexico, where seedling transplant experiments were conducted. Climatic variables were obtained from the nearest meteorological station, and temperatures are means from December 1998 to March 2000.

Table 1b. Characteristics of the experimental locations (inside and outside of each forest fragment).

<table>
<thead>
<tr>
<th>Forest Fragment</th>
<th>Las Cañas</th>
<th>Xolostla</th>
<th>Rancho Viejo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (°C)</td>
<td>20.2 ± 0.24</td>
<td>23.8 ± 0.55</td>
<td>20.7 ± 0.42</td>
</tr>
<tr>
<td>Soil temperature (°C)</td>
<td>17.3 ± 0.29</td>
<td>20.4 ± 0.57</td>
<td>18.6 ± 0.25</td>
</tr>
<tr>
<td>Relative humidity (%)</td>
<td>65 ± 1.7</td>
<td>61 ± 2.7</td>
<td>72 ± 2.3</td>
</tr>
<tr>
<td>Soil water content (%)</td>
<td>27 ± 1.0</td>
<td>26 ± 1.1</td>
<td>25 ± 0.8</td>
</tr>
<tr>
<td>Canopy openness (%)</td>
<td>25 ± 1.5</td>
<td>100</td>
<td>11 ± 1.1</td>
</tr>
<tr>
<td>PAR (mmol m⁻² sec⁻¹)</td>
<td>1.26 ± 0.25</td>
<td>12.29 ± 3.25</td>
<td>1.15 ± 0.18</td>
</tr>
</tbody>
</table>

PAR, photosynthetically active radiation. Microclimatic variables recorded inside and outside of each forest fragment.

Table 1c. Soil characteristics.

<table>
<thead>
<tr>
<th>Forest Fragment</th>
<th>Las Cañas</th>
<th>Xolostla</th>
<th>Rancho Viejo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil pH</td>
<td>4.6</td>
<td>4.5</td>
<td>4.2</td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>14.3</td>
<td>16.4</td>
<td>21.8</td>
</tr>
<tr>
<td>Soil compaction (kg/cm²)</td>
<td>15.20</td>
<td>20.88</td>
<td>11.51</td>
</tr>
<tr>
<td>Bulk density (g/cm³)</td>
<td>0.73</td>
<td>1.23</td>
<td>0.82</td>
</tr>
<tr>
<td>N total (%)</td>
<td>0.55</td>
<td>0.70</td>
<td>1.09</td>
</tr>
<tr>
<td>P (p.p.m.)</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>K (cmol/kg)</td>
<td>2.30</td>
<td>5.23</td>
<td>0.33</td>
</tr>
<tr>
<td>Ca (cmol/kg)</td>
<td>4.81</td>
<td>2.12</td>
<td>3.97</td>
</tr>
<tr>
<td>Mg (cmol/kg)</td>
<td>2.08</td>
<td>1.40</td>
<td>1.79</td>
</tr>
</tbody>
</table>

Values are mean ± standard error.
Lincoln, NE, U.S.A.) connected to a data logger (LICOR 1000).

Data Analysis

Relative growth rate of height and stem diameter, and number of leaves for all seedlings per species per site and per treatment (inside and outside forest) were averaged within a plot. The data were tested for normality, and transformations were made when data were not normally distributed. Relative growth rate for height and stem diameter were square root transformed, height and number of leaves were log transformed, and survival percentages were arcsine transformed. Data were analyzed by an ANOVA of a split-plot design which is divided into the main-plot analysis and the subplot analysis. The main-plot analysis dealt with variation among the sites, and the subplot analysis with the effects of treatment (inside and outside the forest) and species. Each part had a separate measure of random variation; consequently, they were tested against the error for the section of the analysis in which they occurred. Microclimatic variables were analyzed using two-way ANOVAs. When significant differences were found, we used least significant difference to examine planned pair of means. All statistical analyses were performed using Minitab (Minitab Inc., State College, PA, U.S.A. Release 12.1, 1998).

Results

Site Characteristics

The three sites had similar climatic conditions and soil characteristics (Table 1b & 1c). The sites did not differ significantly in air and soil temperatures, relative humidity, gravimetric soil water content, or photosynthetically active radiation (PAR). However, canopy openness in Las Cañadas was greater than that in the other sites (one-way ANOVA, $F = 19.4$, $df = 2$, $p < 0.05$). Air and soil temperatures were consistently higher outside than inside the forest fragment ($F = 29.20$, $16.43$, respectively, $df = 1$, $p < 0.001$). Air relative humidity was higher inside the forest but the difference was statistically weak ($F = 3.33$, $df = 1$, $p = 0.07$), whereas soil water content was statistically similar inside and outside of the forest. Mean daily integral PAR values were lower inside than outside the forest ($F = 106.23$, $p < 0.0001$). Values for microclimatic variables are in Table 1b.

Seedling Survival and Growth

The proportion of seedlings that survived to the end of the experiment varied significantly among sites, treatment, and species (Table 2). Significant interactions were recorded between species $\times$ treatments, and species $\times$ site $\times$ treatment (Table 2). Survival of all species was relatively lower in Las Cañadas, particularly outside the forest, even for *Quercus* (83% outside the Las Cañadas forest fragment vs. 95–98% in the other sites). Survival was higher inside the forest; all species (with the exception of *Quercus*) showed a marked contrast in survival percentage between inside and outside the forest (Tables 2 & 3). *Quercus* was the species with the highest survival, followed by *Carpinus, Fagus,* and *Symplocos* (Table 3). *Quercus* differed from the other species in displaying the highest survival and the same survival percentage inside and outside the forest.

In Rancho Viejo, predation by cows, before the fences were installed, was one of the most important causes of mortality for the four species outside the forest, particularly *Fagus* and *Symplocos*. In Las Cañadas, predation by crickets caused high mortality outside the forest in *Carpinus, Fagus,* and *Symplocos*. In general, the most important cause of mortality was desiccation, which mainly occurred outside the forest.

Growth variables such as relative growth rate (RGR) for height and stem diameter, and number of leaves varied considerably among sites, treatments, and species. Significant interactions for all of the growth variables were also recorded between site $\times$ treatment, species $\times$ site, species $\times$ treatment, and species $\times$ site $\times$ treatment (Table 2).

*Quercus* and *Symplocos* were the species with the lowest RGR (in height and stem diameter). *Quercus* showed a mean RGR in height of 0.17 and 0.40 cm cm$^{-1}$ yr$^{-1}$ inside and outside the forest, respectively, followed by

Table 2. Split-plot model ANOVA results for the effects of site, treatment (closed and open canopy), and species on seedling survival, relative growth rate (RGR) in height and diameter, and number of leaves per seedling.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Survival (%)</th>
<th>RGR Height</th>
<th>RGR Diameter</th>
<th>F (No. of Leaves)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>2</td>
<td>15.63**</td>
<td>32.82**</td>
<td>54.69**</td>
<td>11.98*</td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>39.53**</td>
<td>69.90**</td>
<td>246.51**</td>
<td>53.97**</td>
</tr>
<tr>
<td>Site $\times$ treatment</td>
<td>2</td>
<td>0.89</td>
<td>14.59**</td>
<td>21.18**</td>
<td>8.21*</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>3</td>
<td>50.20**</td>
<td>75.50**</td>
<td>73.21**</td>
<td>41.83**</td>
</tr>
<tr>
<td>Species $\times$ site</td>
<td>6</td>
<td>0.92</td>
<td>5.24**</td>
<td>10.96**</td>
<td>3.72*</td>
</tr>
<tr>
<td>Species $\times$ treatment</td>
<td>3</td>
<td>8.68**</td>
<td>35.91**</td>
<td>17.72**</td>
<td>15.42**</td>
</tr>
<tr>
<td>Species $\times$ site $\times$ treatment</td>
<td>6</td>
<td>3.26</td>
<td>9.20**</td>
<td>11.09**</td>
<td>5.30**</td>
</tr>
</tbody>
</table>

*p < 0.01; **p < 0.001.
Symplocos with a mean of 0.44 cm cm⁻² yr⁻¹ inside and 0.48 cm cm⁻² yr⁻¹ outside the forest (excluding Xolostla where Symplocos displayed its highest growth rate). Carpinus (0.41 and 1.50 cm cm⁻² yr⁻¹) and Fagus (0.69 and 0.75 cm cm⁻² yr⁻¹) grew more rapidly outside than inside the forest (Table 3). After 14 months, Quercus and Carpinus reached the highest mean height (1.51 and 1.26 m, respectively), whereas Symplocos and Fagus reached a mean height of 0.35 cm (with the exception of Xolostla outside the forest, where Symplocos reached 1 m). It is important to note that at the beginning of the experiment the mean size of Quercus seedlings was larger than that of the other species. Quercus and Carpinus were the species with highest leaf production, both producing more than 200 leaves per seedling outside the forest, whereas Symplocos and Fagus produced no more than 50 leaves per individual, except at Xolostla (outside the forest), where Symplocos produced more than 300 leaves (Table 3).

Seedling growth and leaf production, for all of the species, were influenced by the site and the presence of a forest canopy. Seedlings growing outside the forest grew faster and produced more leaves than those growing inside the forest. The exceptions were Quercus in Rancho Viejo where apparently seedlings grew less rapidly outside the canopy because of predation by cows at the beginning of the experiment, and Symplocos and Fagus in Las Cañasadas, where seedlings grew more rapidly and produced more leaves inside the forest. Xolostla, inside and outside the forest, was the site where all the species grew most rapidly and produced more leaves (Table 3).

**Discussion**

Seedling survival was higher inside the forest fragments than in adjacent open areas (except for Quercus). This may be attributed to differences in microenvironmental conditions and other causes of mortality (such as herbivory and predation) between the locations. Outside the forest, increased isolation resulted in higher temperatures, lower relative humidities, and higher irradiance that clearly caused death of seedlings by desiccation. A higher survival of seedlings planted in a site with remnant trees compared with those planted in sites without any tree canopy has been reported in the same region (Pedraza & Williams-Linera 2003) and in a montane forest in Costa Rica (Holl et al. 2000). Also, seedling predation was clearly a factor influencing seedling establishment. Browsing by cattle outside the forest in Rancho Viejo was one of the most important causes of mortality on this site. Although many seedlings died as a result, those that survived grew rapidly after the plots were protected from livestock. In contrast, in an abandoned pasture restoration study, seedling resprouting after cutting by rabbits showed reduced growth (Holl & Quiros-Nietzen 1999). It is widely recognized that high tree seedling mortality can result from the effects of mammalian herbivores such as livestock, pocket gophers, and rabbits (Osunkoya et al. 1993; Boerner & Brinkman 1996; Holl & Quiros-Nietzen 1999; Pedraza & Williams-Linera 2003), and insect herbivores (Pedraza & Williams-Linera 2003). The current results provide evidence that primary tree species seedlings may
be attacked by insects associated with agricultural grasslands, when colonizing such habitats.

Differences in moisture availability may also account for the differences in seedling survival and growth outside and inside the forest fragments, at least in part. Water deficit has been reported as a major cause of seedling death of tropical trees in gaps (Turner 2001). Outside the forest, the lower air humidities recorded may have increased the rate of water loss from the seedlings and caused soil desiccation. *Fagus grandifolia* is known to be sensitive to low soil moisture, and seedlings of this species survive better under a moderate canopy than in open areas where the surface soil may dry out at depth (Fowells 1965). *Carpinus caroliniana* also reaches its optimum survival and growth in a continuously moist soil (Schopmeyer 1974), and it can grow well on the forest edge and in adjacent open areas when water is available (Pedraza & Williams-Linera, unpublished data). In contrast, many *Quercus* are known to be relatively resistant to drought, as a result of high water use efficiency, low stomatal conductances, and the production of a large taproot (Jones 1959; Osonubi & Davies 1981). This may account for the striking result obtained here, where uniquely among the species studied, *Quercus* seedlings survived equally well outside as inside the forest.

Seedling growth rates of all four species were higher outside the forest. This may be attributed to the effects of increased light availability. At the beginning of the experiment, the decrease of air moisture produced by the increasing solar radiation could have adversely affected seedling establishment. However, seedlings that survived desiccation took advantage of light availability. The importance of light for the growth of seedlings of tropical trees has been well documented (Turner 2001). For example, research on tree species in tropical forests has shown that growth rates increase when plants are growing in a large canopy gap (Ramos & del Amo 1992; Boot 1996) or on forest edges (Williams-Linera 1990; Sizer & Tanner 1999; Pedraza & Williams-Linera 2003) and decrease when plants are moved to a shaded environment (Parrish & Bazzaz 1982; Popma & Bongers 1991; Osunkubi et al. 1993; Van der Meer et al. 1998). However, the two relatively shade-tolerant species investigated here, *Fagus* and *Symlocos*, displayed the lowest survival rate in open areas. These results support those obtained in lowland tropical rain forests elsewhere in Veracruz, where shade-tolerant species displayed the lowest survival rate when planted in a large gap (Ramos & del Amo 1992).

*Fagus grandifolia* seedlings can survive beneath a dense canopy, but under such conditions their growth is slow (Fowells 1965; Canham 1990; Alvarez-Aquino & Williams-Linera 2002). In general, *F. grandifolia* is considered a species that reaches the canopy after alternating periods of release and suppression (Canham 1990). Seedlings of *F. grandifolia* var. *mexicana* 13–60 cm tall may range from 2 to 18 years in age, reflecting the duration of such suppression (Williams-Linera et al. 2000). Parrish and Bazzaz (1982) compared the responses of shade-tolerant and intolerant species on gradients of light, moisture, and nutrients and found that the mean niche breadth for seedlings of shade-intolerant species was higher than that for shade-tolerant species. The less shade-tolerant species considered here (*Carpinus* and *Quercus*) were more tolerant of the environmental conditions outside the forest, which suggests that they have higher potential for use in forest restoration programs. *Carpinus caroliniana* has been considered suitable for rehabilitation of deforested areas (Pedraza & Williams-Linera 2003), whereas *Quercus* spp. have been established under heavily disturbed conditions (Ramirez-Marcial 2003) in Mexican montane forests.

The results presented here indicate that seedlings of the four species considered can successfully be established in areas outside forest fragments, on agricultural land. All species could therefore be considered as candidates for restoration programs focusing on expanding the area of cloud forest in the region. In general, growth of the four species was faster in the open sites, indicating that all have potential for restoration if the factors causing seedling mortality can be addressed. However, the many interactions observed among species, sites, and experimental treatments highlight the importance of accurate species–site matching if optimum rates of growth and survival are to be obtained. The fact that survival of *Quercus* appeared to be relatively unaffected by growth environment highlights the particularly high potential of this species for restoration efforts in the region. Therefore, one approach might be first to establish stands of this species and then consider establishing individuals of more shade-tolerant species in the understory, once the canopy of *Quercus* has developed.

In general, species appropriate for planting in reforestation programs are selected on the basis of their high growth rates and utility to wildlife (Lamb et al. 1997). For conservation of forest tree diversity, selection should also target species that are more vulnerable to fragmentation because they are poorly adapted to the secondary forest environment, have small and isolated populations (Viana et al. 1997), or are rare or threatened with extinction (Lamb et al. 1997). In the current example, both *Fagus* and *Symlocos* are globally threatened taxa, which provides an important justification for their inclusion in restoration programs. Even though *Fagus* now has a very restricted distribution in the Sierra Madre Oriental in Mexico (Miranda & Sharp 1950; Williams-Linera et al. 2000), the current results indicate that it is able to survive and grow on cloud forest sites other than those on which it is currently present.

Further information is required on the autecology of these species and other constituents of the cloud forest flora to define their establishment requirements with more precision. In particular, analysis is required of the factors responsible for the relatively low survival recorded in some experimental sites. Although survival of transplanted seedlings of *Carpinus* and *Quercus* was high compared with that of natural established seedlings in temperate deciduous
forests (Streng et al. 1989; Boerner & Brinkman 1996), survival of shade-tolerant species (such as Fagus and Sym-
plocos) was low compared with that of natural established seedlings (Streng et al. 1989; Williams-Linera et al. 2000),
for reasons that remain unclear. Nonetheless, the experiment described here clearly demonstrates that these species
can be successfully established on agricultural land, indicat-
ing the potential for forest restoration in the region. Current
efforts are focusing on working in collaboration with local landowners to protect and expand the cloud forest frag-
ments that remain in the Xalapa region of Mexico.

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LITERATURE CITED

dynamics of Fagus grandifolia var. mexicana before and after a
mast year in a Mexican tropical montane cloud forest. Journal of

establishment and mortality in an Ohio deciduous forest complex.

Booth, R. G. A. 1996. The significance of seedling size and growth rate of
tropical rain forest tree seedlings for regeneration in canopy open-
ings. Pages 267–284 in M. D. Swaine, editor. The ecology of tropical
UNESCO. The Parthenon Publishing Group, Paris, France.

Canham, C. D. 1990. Suppression and release during canopy recruit-
ment in Fagus grandifolia. Bulletin of the Torrey Botanical Club

Challenger, A. 1998. Utilización y conservación de los ecosistemas terres-
tres de México pasado, presente y futuro. Conabio, Instituto de
Biológia UNAM Y Agrupación Sierra Madre, S.C. Mexico, D.F.

Fowell, H. A. 1965. Silvics of forest trees of the United States. USDA
Forest Service Agricultural Handbook no. 271. Washington, D.C.

to edge formation in a lowland tropical rainforest, Amazonia. Bio-
logical Conservation 91:135–142.

seedling dynamics in an East Texas floodplain forest. Ecological
Monographs 59:177–204.

Cambridge University Press, Cambridge, United Kingdom.

Van der Meer, P. J., F. J. Sterck, and F. Bongers. 1998. Tree seedling
performance in canopy gaps in a tropical rain forest at Nouragues,

restoration on forest fragments in the Brazilian Atlantic moist forest.
Tropical forest remnants. Ecology, management and conservation of
fragmented communities. The University of Chicago Press, Chicago,
Illinois.

Williams-Linera, G. 1990. Origin and early development of forest edge

Williams-Linera, G. 2002. Tree species richness complementarity, distur-
bance and fragmentation in a Mexican tropical montane cloud forest.

population of Fagus grandifolia var. mexicana at the Acatlan
Volcano, Mexico: structure, litterfall, phenology and dendroecology.