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Seedlings Performance of Two Conifer Species in Disturbed Alpine Areas in Central Mexico

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Abstract. Growth performance and survival was evaluated for *Pinus ayacahuite and Pinus rudis* on three disturbed areas in the volcano Ajusco. The pines species were planted in all three areas, including the fir-pine forest. In 1994 and 1998 measurements of the growth and survival were made in 3 000 seedlings in 50 plots of 400 m^2 each. Comparison of growth and survival of *Pinus rudis* and *Pinus ayacahuite* indicated that a large proportion of the variation in these traits was accounted for type of locality, which in turn is a function of the microclimate variation provide by the slope exposures. The lowest values of growth and survival were found in pine forest, which, in comparison to pine-fir forest, is located at higher elevations and unprotected from winter dry winds and frost. The results showed that microclimatic variation has a profound effect in the performance of each species. This study shows the importance of carrying out a careful assessment of the revegetation practices in the region.
Key words: artificial regeneration; *Pinus ayacahuite; Pinus rudis;* disturbed forest regeneration

Sumário. Foi realizado um estudo para avaliar o sucesso de duas espécies de resinosas (*Pinus ayacahuite* e *Pinus rudis*) que foram plantadas em três áreas degradadas do vulcão Ajusco. Em 1994 e 1998 instalaram-se 50 parcelas de amostragem, em cada uma das amostragens 3000 árvores foram avaliadas em termos de crescimento e de sobrevivência. Os resultados do estudo revelam que o tipo de localidade é determinante no comportamento do crescimento e da sobrevivência destas espécies. Assim também foi relevante salientar a necessidade de avaliar as práticas de repovoamento nestas áreas degradadas afim de recomendar os tipos de espécies mais adequadas.
Palavras-chave: regeneração artificial; *Pinus ayacahuite*; *Pinus rudis*; regeneração em áreas degradadas

Résumé. Une étude a été menée afin d'evaluer le succès d'un reboisement en tenant compte de la croissance et de la survie de deux espèces: *Pinus ayacahuite* et *Pinus rudis*, plantées dans trois localités perturbées du volcan Ajusco. En 1994 et 1998 ont éte réalisées des mesures de la croissance et de la survie sur 3000 jeunes plantes provenant de 50 placettes de 400 m^2. La comparaison des résultats de cette étude permet de voir que la variation de la croissance et de la survie est liée au type de localité. Cette étude révèle aussi l'importance d'évaluer les travaux de reboisement afin de recommender les meilleurs espèces à utiliser dans la région.
Mots clés: régénération artificielle; *Pinus ayacahuite; Pinus rudis;* regénération de la forêt perturbée

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Introduction

In the Mexican's temperate forests usually selective silvicultural systems are used to give rise to the natural regeneration. An important percent of these forests are located in mountain sites and therefore, the laws avoid the use of clear cutting systems with the aim to reduce the risk of erosion (SEMARNAP, 1988). Nevertheless, another factors of disturbance are present, for instance, the fire. The wildfire is rare, the farmers induce a high percent of the fires recorded every year in the forest, in order to obtain a new grow of green grass for the cattle and sheep. Consequently, extensive areas in natural regeneration process are destroyed every year (PRONARE, 2001).

The elevation in these highlands restricts the use of many trees, making viable only a handful of species (see, MARTÍNEZ, 1948). The wish and the necessity to speed up the natural regeneration process is the fundamental reason for the use of artificial regeneration methods (ACKZELL, 1993). This is particularly important in highly perturbed environments, where natural regeneration is inadequate due to the fact that adult trees and the natural regeneration are lost continuously by disturbance agents, such as fire (MARGOLIS and BRAND, 1990). Because of increasing population pressure, natural forests in Mexico are prone to damage by diverse disturbance agents (LANDA *et al.*, 1997). In consequence, an ambitious reforestation program has been undertaken in large areas of the country, such as central Mexico (PRONARE, 2001).

In this study the growth and survival of two conifer species established by planting nursery-raised seedlings was examined on three disturbed areas in the Ajusco volcano, originally conducted by selective silvicultural system. These areas showed differences in orientation, elevation and microclimate. The aim of our study was to analyze the response of these species to different levels of environmental stress (e.g. frost and desiccation) found in each of the areas used in the reforestation program, as a mean to explaining their effect on seedling/ /sapling establishment. The study would thus provide useful information for future species selection and early management practices.

Materials and methods

Area description

Three disturbed areas 25 km south of Mexico City (figure 1) (19º12'N lat. and 99º 15'W long) and located at elevations between 3200 and 3340 m from northeast to northwest slopes of the Ajusco volcano were examined in 1994 and 1998. The artificial regeneration employing two species naturally occurring in the region (*Pinus ayacahuite* and *Pinus rudis*) was carried out in the summer of 1993 by the Mexico City government. We did not have control over the decision to plant these species or the areas reforested. We simply attempted to evaluate the result of these practices after the fact. The natural environmental conditions in these three areas were different. Areas 2 and 3 were found in forests naturally dominated by *Pinus hartwegii*. Although the altitude of both areas was similar, their exposition was different. Locality 2 was exposed to dry, cold winter winds (north-west slopes), while locality 3 was only partially exposed to those winds (north slope). Locality 1, on the other hand, was located at a lower altitude, on the northeast slope of the volcano, in the ecotone of the *Abies religiosa* and *Pinus hartwegii* forest. Compared to areas 2 and 3, this one was more humid and with deeper soils, and was protected by the slopes of the volcano against the winter westerly winds. The general characteristics of all studied areas are shown in Table 1.

Both geographic and topographic features determine the climate of the region. Summer rainfall at this altitude is determined by trade winds from the Gulf of Mexico that result in orographic precipitation on the mountains (DEL RÍO, 1962). Mean monthly temperatures range from -3º to 22ºC. The dry season lasts from November to March when polar, dry northwesterly winds are common. The climate of the region is classified as sub-humid temperate with winter rainfall lower than 5% of the yearly total (GARCÍA, 1978).

Natural vegetation

Pinus hartwegii forest

This forest is the most important in the area, it has a wider altitudinal distribution (3300-3960 m) than *Abies religiosa* (see below), and present even in small areas at all three localities. It was delimited at the northeast, southeast and east by fir-forests forming a sharp ecotone where the two forests showed very little overlap. Total yearly rainfall ranges from 700 to 1200 mm. Soils were shallow and stony, slightly acidic (pH=5.6-5.9) with a low rate of degradation of organic matter (Table 2). During the winter these forests are heavily influenced by the cold, dry northwesterly winds. Tree density is low [15-25 trees/ha after fires], and there is no crown overlap; trees are not usually taller than 20 m. This plant community is characterized by an association of 45 species, mostly grasses and ruderal shrubs (RZEDOWSKI, 1954). As found by MADRIGAL (1967), through the estimation of plant charcoal down to 1.8m in the soil, fires in this forest are frequent.

Abies religiosa forest

This forest is found on a narrow altitudinal belt (3200-3500 m), more or less surrounding the Ajusco volcano on three sides (north, east, and south). This forest type was only found in study area 1. Total yearly rainfall is higher than 1000mm. Clay-sandy soils are deep and slightly acidic (pH=5.3-6.1), with a moderate content of organic matter, nitrogen and phosphorus (Table 2).

Under natural conditions fir forests in Mexico show a tight, closed canopy, with trees about 40m tall. In the study area, however, selective logging during the first two-thirds of the last century created an open canopy that allows light to reach the forest floor in multiple forest gaps [60-380 trees/ha]. The understory is therefore composed of about 95 shrub and herb species, including several rhizomatous herbs that form a well-defined ground herb layer. The tall canopy, together with the herb layer and the accumulation of litter favor water retention and determine a more humid atmosphere throughout the year, as compared to the pine forest. As ultimate cause, the fir forest seems to owe its presence to the protection offered by the volcano's topographic features, which protect it against cold, dry winter winds.

Table 1 - Study areas

Characteristic	Area 1	Area 2	Area 3
Elevation (m)	3200	3300	3340
Exposition	NE	NW	NE
Surface (ha)	25	20	15
Nº of Plots	15	20	15
Temperature (°C)*	<12	<10	<10
Rainfall (mm)†	900-1200	700-1200	700-1200
Natural species	3,4	4	4
Planted species	1,2	1,2	1,2

* Temperature = mean annual temperature
† rainfall = mean annual rainfall
Species: 1 = *Pinus ayacahuite*; 2 = *Pinus rudis*; 3 = *Abies religiosa*; 4 = *Pinus hartwegii*

Table 2 - Physicochemical characteristics of soil at Ajusco volcano (mean values)

Area	Fine fraction (%)	Water holding capacity (%)	pH	Total N (%)	Total P (%)	K (meq/100)	Total C (%)	Organic matter (%)
1	33	53.6	5.9	0.93	0.32	0.33	21.60	10.4
2	16	49.8	5.9	0.47	0.24	0.27	24.33	6.9
3	26	51.1	5.7	0.67	0.22	0.38	26.99	12.3

Area 1 : fir and pine forest, area 2 and 3 : pin forest. The values are derived from the average of three replicates on each area.

Description of the species used in the artificial regeneration

<u>*Pinus ayacahuite*</u>

P. ayacahuite is a common, though not very abundant species in the mountain ranges of Mexico and Central America (MARTINEZ, 1948). It does not form large pure stands. At elevations below 3500 m, *P. ayacahuite* usually mixes with *Abies religiosa*, particularly in ravines and gorges, or in humid, protected, and fresh areas with annual rainfall above 1000 mm. Its wood is appreciated by furniture and paper industries. The tree is also planted for sale as a substitute for Christmas trees.

<u>*Pinus rudis*</u>

It is distributed along the high mountains (2200 to 3300 m) from Mexico to Guatemala. It is usually found in cold areas; in dry soils its growth is rather poor. It cohabits in Central Mexico with several species such as *P. montezumae, P. hartwegii,* and *A. religiosa*. Taxonomic classification places *P. rudis* next to *P. hartwegii*, and some authors consider them to be the same species (e.g. MIROV, 1967). It usually cohabits with *A. religiosa* and *P. ayacahuite* (MADRIGAL, 1967). *P. rudis* is able to grow in areas with poor soils where it replaces *P. montezumae* (MIRANDA, 1941).

During the first years of life this species grows very slowly, forming stunted, tufted saplings. Adult trees can reach up to 25 m. This species is also used by the paper industry.

General characteristics of seedlings

Seedlings were raised in a tree nursery located 20 Km Northwest of the Ajusco volcan, at an elevation of 3200 m. Seeds were collected from stands situated in this area, within Desierto de los Leones National Park (figure 1). Seedlings were produced in plastic bag containers (8 x 15 cm). They were transplanted to the field during the rainy season when they were 18 months old. In the planting, it was tried to avoid any damage of the roots when the containers were removed.

Soil and planting practices

The area was cleared of herbs, stumps and standing dead trees. Planting holes were dug along topographic level curves. Soil and water holding practices were carried out for steeply sloping ground. Therefore, to contain runoff and sediment, Gradoni technique was used in planted areas according to level curves and check dams were built in ravines reducing the streams energy to erode and transport sediment. An average of 1500 seedlings/ha was planted. No fertilizers, insecticides or fungicides were applied, and seedlings were not artificially watered. The herb layer was manually removed in 1993 and 1994.

Data collection

In 1994 we randomly selected a total of fifteen 400 m² plots in each locality. At locality 2, where the lower density of mature trees and poorer natural regeneration was observed, we added 5 more plots.

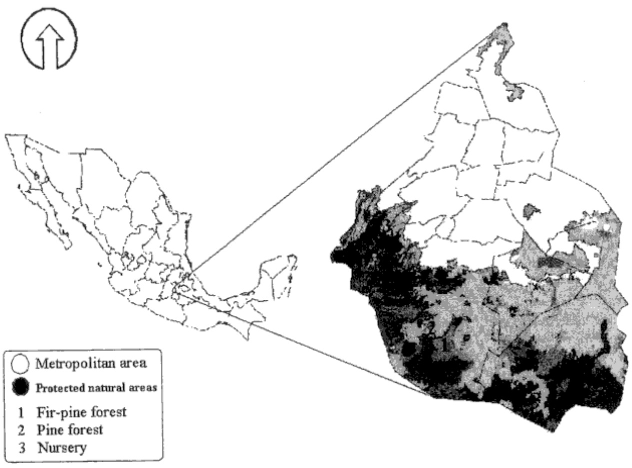

Figure 1 - Study areas and nursery where seedlings were raised.

We assessed the results of this plantation during the winter of 1994 and 1998, that is one and five years after planting. Approximately 3000 seedlings were studied in every survey. Within each plot all planted trees were recorded for total height, diameter at 0 –diameter 0-, 15, 30, 45 and 60 cm height, height increment between internodes (the distance between internodes allowed us to estimate the total height of the tree a year before the survey), and survival. Basal area was calculated considering diameter at ground level and individual volume was estimated using the general equations (HUSCH *et al*., 1982):

$$v = \frac{1}{3}\left(g_b h\right) \quad \text{(1) cone}$$

$$v = \frac{h}{3}\left(g_b + \sqrt{g_b g_c} + g_c\right) \quad \text{(2)cone frustum}$$

where: v = volume ; g_b = Stem basal area or cross-sectional area at base; g_c = cross--sectional area at top; h= tree or section height;

The small stem of seedlings was not perfectly cylindrical or conical in shape. Thus, when trees measured more than 15 cm in height, the stem volume was estimated throughout equation 2 (cone frustum) using circumference data recorded at 15, 30, 45 and 60 cm of height. For the top of the stem of these trees, and when trees were smaller than 15 cm, volume was estimated using equation 1 (cone).

Soil analysis

In 1997, three sample soils inside each locality were obtained. The sample was taken at 0-20cm depth. Physicochemical analysis were carried out using standard procedures: soil texture was measured by hydrometer, pH in a 1:2 (v/v), soil: water suspension, organic matter by wet oxidation methods (WALKLEY, 1946), available P by the Bray II method, total N by the Kjeldahl method, available K by atomic absorption spectrophotometry, and total C by the lost of weight by ignition method (TABATABAI and BREMNER, 1990).

Data treatment and statistical analysis

Analysis was carried out comparing growth and survival of *P. ayacahuite* and *P. rudis* among all three areas. Development was assessed through height, basal area and volume increments.

Diameter and total height were obtained during the surveys of 1994 and 1998, total height in 1993 and 1997 were determined by measuring internodes (whorls). Therefore height increment was known, but basal area and volume increments were unknown. Non-linear models were used to find the relationship between total height and diameter at ground level (diameter 0) in 1994 and 1998. Using this relationship, we estimated diameter 0, knowing total height, in 1993 and 1997. With this information, basal area and volume were also calculated for 1993 and 1997 and, using the difference between these years and 1994 and 1998, respectively, we were able to determine increments on these variables. Twenty mathematical models (HUANG *et al*., 1993) were tested. The selected models were fitted as global models (all areas together) and individual models (areas separated). The fitted models were assessed, compared and selected according, inasmuch as possible, to all of the following criteria: a good qualitative behavior - a theoretical curve passing in the best position among the observed values - (SALAS *et al.*, 1993), small mean square error and lack of tendency in residuals (by visual inspection of plots).

Before fitting the models the data set was divided into two groups, using a random algorithm programmed in PASCAL. 80% of the data were used to fit the models with the NLIN procedure from SAS, and the remaining 20% to validate them with an UNIVARIATED SAS procedure. The method employed for the minimization of the sum of the squared deviations in the NLIN procedure was the Gauss-Marquardt (SAS institute, 1988).

As mentioned above, because stems are not conical, the volume in 1994 and 1998 was estimated employing both equations 1 and 2 on each individual tree. However, because we only had information on diameter 0 and total height for 1993 and 1997, volume was calculated employing equation 1 and corrected by the following procedure. First, we fitted a simple linear regression between volume estimated by both equations 1 and 2 and volume estimated by equation 1 only, in 1994 and 1998. We then used this relationship to calculate the volume that should have been obtained with equations 1 and 2 in 1993 and 1997, for this purpose, two groups of trees were also composed to fit and validate the non-linear regression.

Once the height, basal area and volume increments were obtained, comparisons were made among localities (by species), by one-way analysis of covariance ($P<0.05$) using SAS procedure GLM (SAS Institute, 1988). Covariance sharpens the analysis of variance on a variable *y* (e.g. height increment) by utilizing a related variable x, called a covariate (e.g initial height, 1993). Pounds lost, height increment is linearly related to initial height, pounds overweight at the beginning of the study. By combining the regression of *y* on *x* with the analysis of variance on *y*, the within-treatment variability is reduced, making it more likely that treatment differences will be detected (SAS, 1998). The additive model for the analysis of covariance is:

$$Y_{ij} = \mu + \alpha_i + \beta(x_{ij} - \bar{x}..) + \varepsilon_{ij}$$

μ: The true overall mean for all studies of this type involving the specified treatments.

α_i: The deviation due to the *ith* treatment after allowance for the relationship of *y* to *x*.

β: The true common slope of the a regression lines

x..: The overall average of the covariate for the observations in the study

ε_{ij}: A random effect for the *jth* element in the *ith* treatment group.

RITCHIE *et al.* (1993) has shown, that height increment in seedlings (or any increment for that matter) is influenced by variation in initial height (size). Consequently, initial height, basal area and volume, were entered as covariates and variation was modeled in terms of locality. Increments were sqrt(y), $\log_{10}(y)$ or $(y)^{exp}$ transformed depending on the case, where –y- was each one of the three variables analyzed. A Tukey tests for mean comparisons were also applied. Survival was analyzed using one-way analysis of variance (SAS Institute, 1988) previous $\arcsin((\%)^{1/2})$ transformation.

Results

Soil

The most favorable soil conditions were found in the fir-pine forest (area 1). This soil had the highest values of fine particles, water holding capacity and the highest values of pH, total N and total P. In contrast, areas 2 and 3 presented the opposite pattern, being clearly the lowest value of pH and the highest value of organic matter (Table 2). In the fir-pine forest the physicochemical features of soils were not homogeneous, since the most favorable values were observed at the hill base, followed by the mid-slope and the hill top values.

Basal diameter assessment

Global and individual models

Out of 20 different equations, we selected model 1 proposed by WATTS (1993) and model 2 of Johnson--Schumacher proposed by BUDFORD (1986) (see HUANG *et al*., 1992). These models are, respectively:

$$\text{diameter } 0 = \left[\frac{(K * h)}{(h+1)+(b * h)}\right] \qquad (3)$$

$$\text{diameter } 0 = K * \exp^{\left(-b/h\right)} \qquad (4)$$

where: diameter 0: diameter at ground level; h: total height of tree; K, b= parameters.

Both models gave similar results. Other equations gave also acceptable results, but because they contained more parameters we decided to keep these simplest models.

The results of these fittings are shown in Table 3. Because the described curves for global and individual models allowed us to reject the hypothesis that both curves were identical, it was necessary to adjust the models individually in almost all areas for each species. Furthermore the lowest values of the mean square errors indicated a better fit when the models were adjusted by locality, than when the models were fitted considering all the areas together. An example of one adjusted curve to the data set and its residuals is presented in figure 2.

Table 3 - Fitted models to estimate diameter 0 at ground level

Year	Species	Locality	model	df	MSE	$K \pm \sigma_k$	$b \pm \sigma_b$
1994	1	1	3	353	0.01531	0.3888±0.0237	0.002214±0.0000
1994	1	2,3	3	248	0.05755	0.4763±0.0515	0.002486±0.0014
1994	2	1	3	208	0.03972	0.3827±0.0312	0.09839±0.0017
1994	2	2	3	108	0.07925	0.3594±0.0810	0.01010±0.0072
1994	2	3	3	140	0.06220	0.5098±0.0467	0.00548±0.0010
1998	1	1	4	115	0.1164	2.6961±0.1794	43.4610±4.4825
1998	2	1	4	175	0.1656	2.8487±0.1715	32.8729±0.0809
1998	2	2,3	3	162	0.0599	0.3532±0.03395	0.0193±0.00134

Species : 1= *Pinus ayacahuite* ; 2= *Pinus rudis.*

Assessment of the regression analysis to correct volume estimations

The simple regression analysis performed showed good results in terms of fit and general approach to correct the volume calculated with equation 1 (Table 4). This allowed us to estimate the "correct volume" as would have been jointly estimated by equations 1 and 2, such as we have done if data on diameter at different heights for 1993 and 1997 were available. An example of one adjusted curve to the data set is presented in Figure 2.

Table 4 - Fitted models to estimate diameter0 at ground level

Year	Species	Locality	df	MSE	$K \pm \sigma_k$	$b \pm \sigma_b$
1994	1	1-3	507	22.5134	2.9946±0.2961	0.9302±0.0193
1994	2	1-3	521	3.3153	0.4314±0.0929	0.8658±0.1550
1998	2	1	135	225.7209	4.1201±1.2978	1.0719±0.0069
1998	2	2-3	162	2.0060	0.2690±0.1160	1.3200±0.0045

Species : 1= *Pinus ayacahuite*, 2= *Pinus rudis*

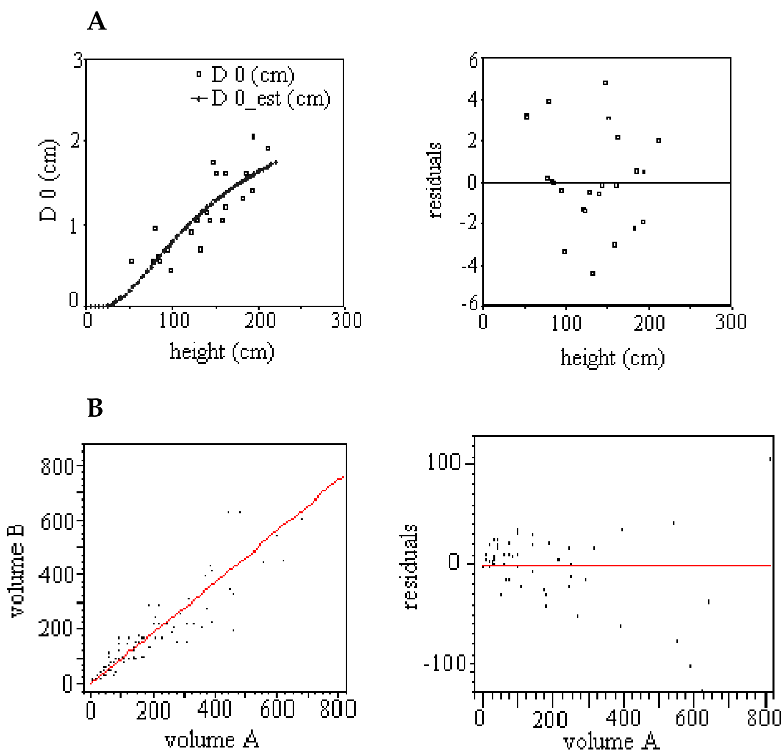

Figure 2 - **(A)** Example of non-linear model fitted to estimate diameter at ground level (D 0) from data on total height. Models, values of parameters and statistical analysis are show in table 3. **(B)** Example of regression employed to correct volume estimated by two methods. See text for explanation

Covariance analysis for the increments

First survey

Significant differences in height and volume (but not basal area) increment were found among the three localities as observed on *P. ayacahuite* and *P. rudis* during the interval 1993-1994 (Table 5). For both species, the largest height increments were found in area 1 and the lowest in area 3 (Table 6). The increment in basal area in *P. ayacahuite* was larger in localities 2 and 3 (Figures 3 and 4) than in locality 1. In localities 2 and 3 *P. ayacahuite* showed the "bottle brush" symptom, i.e. stunted terminal growth with shortened needles, large density of needles (number per unit length of shoot), browning or loss of needles, cessation of growth and even death. This behavior was not frequently found in area 1. Stunted growth was also observed in *P. rudis*: this species had its highest value of basal area increment in locality 1, and the lower height and volume increments in the first sampling period than *P. ayacahuite* in locality 1 (Table 6, Figures 3 and 4).

Second survey

Because all *P. ayacahuite* seedlings in areas 2 and 3 had died by 1998 (Figure 4d), the covariance analysis was only performed on *P. rudis*. The increments behavior of *P. rudis* in this second survey was similar to that observed in the first one. The effect of locality was highly significant for height, basal area and volume increments (Table 5). According to our results, two groups can be formed: group one consisting of areas 2 and 3, with the lowest increment values (pine forests), and group two consisting of locality 1, with the highest values for all studied increments (fir-pine forest). Although trees planted in areas 1 and 2 had similar initial height and diameter, it was obvious that height and basal area increments were lower in locality 2. In general, areas 2 and 3 had the poorest development in height, basal area and volume (Figures 3 and 4).

Table 5 - Results of the analyze of covariance

Source	Variable	Year	df	MSE	F	P
Locality	Log_{10} (Stature increment)	1994	2	45.920	168.1	0.0001
(Pinus	Sqrt (Basal area increment)		2	0.235	1.914	0.1489 ns
ayacahuite)	Sqrt (Volume increment)		2	4.496	2.995	0.0500
Locality	Sqrt (Stature increment)	1994	2	344.100	1439	0.0001
(Pinus	(Basal area increment) $^{0.3}$		2	0.076	1.97	0.1409 ns
rudis)	Sqrt (Volume increment)		2	22.71	34.94	0.0001
Locality	(Stature increment)	1998	*	*	*	*
(Pinus	(Basal area increment)		*	*	*	*
ayacahuite)	(Volume increment)		*	*	*	*
Locality	Sqrt (Stature increment)	1998	2	6.017	4.115	0.0170
(Pinus	(Basal area increment)$^{0.1}$		2	0.138	7.869	0.0005
rudis)	Log_{10} (Volume increment)		2	6.711	10.01	0.0001

Table shows the effect studied e.g. locality, for the conifer response variables (increments). ns: not significant

* Analyze of covariance it was not performed to *P- ayacahuite*, because survival was negative on sites 2 and 3

Table 6 - Mean values for variables studied

Source of variation	Area	h 93 (cm)	h 94 (cm)	BA 93 (cm^2)	BA 94 (cm^2)	V 93 (cm^3)	V 94 (cm^3)	Δh (cm/año)	ΔBA (cm^2/año)	ΔV (cm^3/año)	Mortality (%)
1994											
P. ayacahuite	1	27.19	34.78	0.43	0.69	3.89	11.18	7.59 a	0.26 ns	7.29 a	7 a
	2	28.31	29.82	0.65	1.45	5.84	17.37	1.51 b	0.80 ns	11.53 b	78 b
	3	31.79	36.04	0.66	1.37	6.54	15.49	1.48 c	0.71 ns	8.95 b	89 c
P. rudis	1	8.49	13.83	0.33	0.92	1.33	5.25	5.34 a	0.59 ns	3.92 a	13 a
	2	8.70	8.73	0.28	0.74	1.21	2.65	0.03 b	0.46 ns	1.44 b	59 b
	3	2.95	2.96	0.31	0.48	0.90	0.82	0.01 c	0.17 ns	0.08 b	50 b
1998											
P. ayacahuite	1	53.28	65.90	4.41	6.15	103.97	159.80	12.62	1.74	55.83	72 a
	2	0	0	0	0	0	0	0	0	0	100 b
	3	0	0	0	0	0	0	0	0	0	100 b
P. rudis	1	28.55	39.23	2.98	5.14	55.16	114.72	10.68 a	2.16 a	55.56 a	39 a
	2	15.13	21.94	0.30	2.41	1.96	42.45	6.91 ab	2.11 ab	40.49 a	84 a
	3	11.40	16.51	0.29	1.61	1.35	26.36	5.11 b	1.32 b	25.01 b	69 b

Increments shown were reconverted from the transformations used in the analysis of covariance to original units. Values with different letters showed significant differences, in the analysis of variance ($p<0.05$)

Variation in mortality

First survey

The analysis of variance indicated that locality had a strong effect on survival of both *P. ayacahuite and P. rudis*. *P. ayacahuite* had 7% mortality in area 1, but around 80% in areas 2 and 3; its global mortality was 58%. Mortality of *P. ayacahuite* was higher in pine forest, particularly in area 2, where even *P. rudis* showed high mortality (59%). Mortality for *P. rudis* was 50% in locality 3 and 13% in locality 1 (Tables 6 and 7; Figure 4).

Second survey

The statistical analysis showed significant differences among areas for both species (Tables 6 and 7). Five years after planting mortality was very high, particularly in areas 2 and 3. These areas were not favorable to *P. ayacahuite* where it did not survive, while in locality 1 its mortality reached 70%. Out of that 70% an unknown proportion of seedlings died as a result of further disturbance, such as logging and grazing. *P. rudis* was the most tolerant species in all-environmental conditions. Despite this, mortality reached 84% in area 2 (Table 7; Figure 4). Globally *P. ayacahuite* underwent 90% mortality and *P. rudis* 64%.

Discussion

Our results indicate that differences in environmental conditions at each locality had a strong effect on growth and survival of the studied species. Features such as exposition, elevation, soil characteristics, microclimate and forest type differentially limited the success of introduced trees. The highly seasonal pattern of rainfall and temperature in the area (GARCÍA, 1978), particularly in regard to variation in soil moisture and wind direction, could be the major factors influencing survival in the dry, cold winter season.

Our analyses of species performance are essentially based on two interrelated measures: (i) the comparative response in growth of the two species along a gradient where conditions worsen during the winter from fir-pine forest to pine forest, and (ii) the comparative analysis of the survival of these two species. As expected, growth and survival during the first year after planting was influenced by the nursery and planting practices. Because planting was carried out during the rainy season with healthy 18-month old trees, most likely this reduced water stress and growth and survival during the first year were promissory. However, the severe winter conditions in the following years were not equally tolerated. Thus, the second survey allowed us to follow and more clearly determine the fate of these plantations.

Physical environment

The most favorable soil conditions for plant growth were recorded in the fir-pine forest. This is reflected by the high proportion of fine particles in soil, water holding capacity. A higher degradation of organic matter is observed in the locality 1, revealed by the content of organic matter measured in these soils and by the slightly lower value of pH. The low N, P total values found in the soils in the areas 2 and 3 could be explained by the fact of these areas were exposed to lower temperatures, suggesting lower decomposition rates and slow nutrient release (e.g. GARKOTY and SINGH, 1995; MICHELSEN *et al.*, 1996). In the locality one, plants growth showed an assimilation of the nutrients from soils. Nevertheless, the level of nutrients is not depleted.

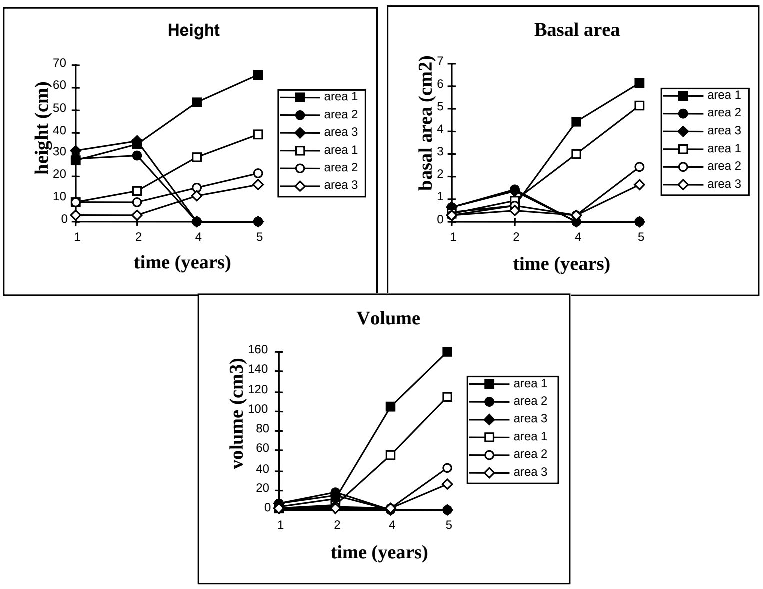

Figure 3 - Growth curves of *Pinus ayacahuite* (solid symbols) and *Pinus rudis* (open symbols) at three areas at the Ajusco volcano, Mexico

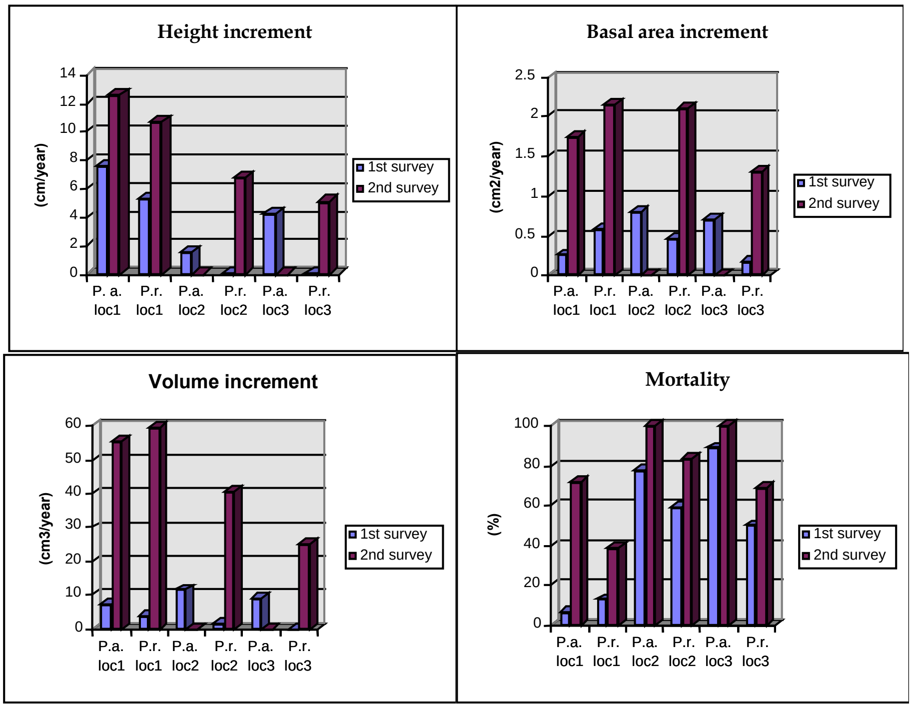

Figure 4 - The response of *P. ayacahuite* (P.a.) and *P. rudis*, in (a,b,c) growth and mortality is affected by locality

Table 7 - Results of analyse of variance for mortality

Source	Year	df	MSE	F	P
Locality (*P. ayacahuite*)	1994	1796	0.2780	712.92	0.0001
Locality (*P. rudis*)	1994	1217	0.5239	99.67	0.0001
Locality (*P. ayacahuite*)	1998	1803	0.1761	163.46	0.0001
Locality (*P. rudis*)	1998	1259	0.4511	111.64	0.0001

A good evidence of the environmental differences among studied areas was the dissimilar growth and survival recorded in the two forest types. Like in other studies (e.g. CHAUDRAY *et al.*, 1996) this was correlated with differences in environmental conditions among the studied areas. As reported for other species (e.g. MESSIER, 1993; ASHTON *et al.*, 1997), our results show differences in the regeneration niches of the species studied (see for example, MARGOLIS and BRAND, 1990). KOZLOWSKI *et al*

(1991) indicate that water availability, as estimated by rainfall, is perhaps the most important environmental factor determining not only species composition and distribution, but also circumference growth and wood production. This factor seems crucial for three of the species used in this revegetation program.

Species development

P. ayacahuite

Results confirmed that this species performs better, and is thus restricted to humid and protected places. Therefore, this species cannot cohabit with *P. hartwegii* in the open forests like those in localities 2 and 3. In these localities, and for the first survey, *P. ayacahuite* showed a growth delay, possibly due to water stress, which was also reflected in high mortality. No individuals of this species survived after five years in these two areas. The most probable was the low humidity and high desiccation caused by winds during the dry season. LARSON (1969) observed, for example, that one-year old *P. ponderosa* seedlings suffered very high transpiration levels and died, during the occurrence of dry and strong winds and despite the high humidity of the soil. Similarly, HAASE and ROSE (1993) observed as we did in this study in areas 2 and 3, that seedlings had shorter branches, a greater number of needles per unit of leader, yellowing, wilting and "bottle brushing" symptoms, growth cessation and finally death. Locality 1, however, which was protected from the cold westerly winter winds by the volcano slopes and by the fir forests, provided conditions closer to those found in its natural habitat (MIRANDA, 1941). In this respect, it is important to mention that ROJAS *et al* (1988) showed that, under experimental conditions, *P. ayacahuite* is highly susceptible to water regime and substrate.

Pinus rudis

P. rudis presented the lower height growth than *P. ayacahuite* in the locality 1. This species frequently has a stunted growth, which delays its development in comparison to the other species studied. This species was able to prosper in all areas. *P. rudis* is a low--temperature tolerant species, but water deficit at these localities may still affect its growth and survival. It is possible that the low values of height, basal area and volume increments in areas 2 and 3 were also a consequence of the acclimation process undergone in them. MARGOLIS and BRAND (1990) explained that under water deficit conditions in many seedlings of conifers species, stomatal closure can occur to prevent excessive transpiration and, as a consequence, the photosynthetic activity and biomass production are reduced. In this way a balance between water absorption surface and transpiration area is reached (KOZLOWSKI and PALLARDY, 1997). Rojas *et al.* (1988) indicated that under such conditions *P. hartwegii*, a species closely related to *P. rudis*, reduced its dry mater production by 25%, in comparison to artificially watered seedlings.

Since genetic variation is closely related to the environmental gradients under which each species is found, these results imply that populations are physiologically specialized for relatively small segments of the environmental gradient (LINHART, 1995; REHFELDT, 1985). Thus, although *P. rudis* has an extensive geographic range in Mexico, it does not have broad ecological amplitude. In consequence, variation in population attributes, as a consequence of differences in provenance, must be considered in reforestation practices. The lack of data on early growth of this species does not allow comparison with other studies.

Conclusions

Our results proved that area features have a strong effect on development and survival of *P. ayacahuite* and *P. rudis*, these species had different growth behavior and they need distinct environmental conditions to grow. Therefore, it is not possible to grow *P. ayacahuite* at high elevations, in open forests exposed to dry winds as observed in *P. hartwegii* forests. In contrast, *P. ayacahuite* has well developed in humid fir-pine forests.

P. rudis showed the highest global survival between the species studied, however mortality is remarkable in areas 2 and 3. This species also showed a characteristic growth delay of seedlings in comparison with *P. ayacahuite*. For this reason, it could be advantageous to determine not only which are the genotypes that could survive in these environmental conditions, but have a better development. Species and provenances used in the plantations of the areas 2 and 3 were not adequate, more attention must be done in genetic material employed in these practices, for example, it seems that *P. rudis* coming from seeds of Desert de los Leones National Park is not able to survive and growth satisfactory in environmental conditions found in these areas, it could be more adequate to reforest these places with *P. hartwegii*.

In a favorable environment, such as the one found at the fir-pine forest, protected by the Ajusco volcano slopes, planted species showed notable development and survival. The different growth behavior between the studied species was evident. At least, in this early growth phase, the highest height, basal area and volume increment values were recorded in *P. ayacahuite*.

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