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Research Article

Variación del crecimiento inicial y supervivencia de *Pinus hartwegii* Lindl. del Cofre de Perote, Veracruz

Variation in initial growth and survival of *Pinus hartwegii* Lindl. from *Cofre de Perote*, state of *Veracruz*

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Abstract

The initial growth of forest plants with a wide altitudinal distribution may differ depending on their origin. *Pinus hartwegii* has wide altitudinal distribution in the *Cofre de Perote* forest, located at the state of *Veracruz*, thus, it is necessary to know whether the altitude influences the growth of the species. The objective of this study was to evaluate at four separate ages the variation in base diameter, initial height and survival of *P. hartwegii* seedlings at four altitudes in the aforementioned place. Seeds collected at four altitudes (3 450-4 050 m) were germinated and a common garden test was established. The height and base diameter of the seedlings were evaluated at 9, 10, 11 and 12 months old, and survival at 13 months. Significant differences between altitudes were obtained (P<0.0001) for all variables at all ages. In the first assessment, the plants at extreme altitudes (the lowest and highest elevation) accomplished the tallest heights compared to those at intermediate elevation; at the oldest ages, the plants at the lowest elevation had the greatest heights, while the plants from the intermediate elevation (3 650 m) had the lowest height. The base diameter trend was similar to seedlings heights at advanced age, while survival was similar to height growth at early ages. Altitude has a significant effect on the growth of the *P. hartwegii* in *Cofre de Perote*.

Key words: Plant height, *Cofre de Perote*, base diameter, common garden test, altitudinal gradient, *Pinus hartwegii* Lindl.

Resumen

El crecimiento inicial de plantas forestales con amplia distribución altitudinal puede presentar diferencias dependiendo de su origen. *Pinus hartwegii* exhibe esa condición en el Cofre de Perote, Veracruz; por lo que es necesario conocer, si la altitud influye en el crecimiento de la especie. El objetivo del presente estudio fue evaluar en cuatro edades, de manera separada, la variación en diámetro basal, altura y supervivencia de plántulas de *P. hartwegii* en cuatro altitudes en el Cofre de Perote, Veracruz. Se germinaron semillas recolectadas en cuatro altitudes (3 450 a 4 050 m) y se estableció un ensayo en ambiente común. La altura y diámetro basal de las plántulas se evaluó a los 9, 10, 11 y 12 meses de edad, y la supervivencia a los 13 meses. Se obtuvieron diferencias significativas entre altitudes ($P<0.0001$) para todas las variables en todas las edades. En las primeras edades de evaluación, las plantas de las altitudes extremas (menor y mayor altitud) presentaron las alturas superiores a las de altitud intermedia; en las edades más avanzadas, las plantas de la cota altitudinal menor alcanzaron alturas mayores, y las de la altitud intermedia (3 650 m) registraron la altura más baja. La tendencia del diámetro basal fue similar a la de las alturas de las plántulas en edades avanzadas, mientras que la de la supervivencia fue similar a la de la altura en edades tempranas. La altitud tiene un efecto significativo en el crecimiento de *P. hartwegii* en el Cofre de Perote.

Palabras clave: Altura de planta, Cofre de Perote, diámetro basal, ensayo en ambiente común, gradiente altitudinal, *Pinus hartwegii* Lindl.

Introduction

The growth of forest tree species from sites distributed along altitudinal gradients exhibits differences associated with the elevation of their origin, as an adaptive response to environmental conditions (Skrøppa & Steffenrem, 2019).

Two main trends in forest plant growth are reported based on altitudinal variation. First, plants originating from seeds collected from sites located at the lower end of their altitudinal distribution exhibit greater growth than plants originating from seeds from sites at higher elevations, because plant growth at higher elevations is limited by the incidence of low temperatures (Bresson et al., 2011; Lopez-Toledo et al., 2017). In the second, plants originating from seeds from the middle part of the altitudinal distribution have a greater growth than plants from seeds from the extremes of distribution, because in sites with intermediate elevation, environmental conditions close to the optimum for the species predominate, while in sites located at lower elevations, plants may be subjected to water stress, since these elevations are the xeric limit for the species; however, in sites at higher elevations, low temperatures are the limiting factor for plant growth (Lopez-Toledo et al., 2017, Sáenz-Romero et al., 2006).

To identify these patterns of variation, it is necessary to measure plants with different altitudinal origins at an early age or at a later age in common environment trials, either in a nursery or established directly in the field (Berend et al., 2019). This ensures that plants with different altitudinal origins are exposed to the same environmental growth conditions, so that any differences that may arise can be attributed to genetic rather than environmental factors. These differences will be the result of adaptation to the different environments prevailing at their sites of origin (White et al., 2007). These types of studies allow for informed decisions regarding species and provenance selection and also serve as guides for seed movement in reforestation or restoration programs (Viveros-Viveros & Guillén, 2022).

Pinus hartwegii Lindl. is distributed in Mexico and Guatemala (Farjon et al., 1997). In Mexico, this species is present in 14 states, mainly in the Transversal Neovolcanic Axis (Hernández-Rivera et al., 2020); it dominates the upper limit of the altitudinal distribution of tree vegetation in Mexico and the world, as it is distributed at altitudes ranging from 3 000 to 4 200 m (Musálem & Solís, 2000). This makes it a key species for studying the effect of elevation and climate change on reproductive or adaptive traits, as some studies indicate that increased temperatures will affect high-mountain species (Astudillo-Sánchez et al., 2019).

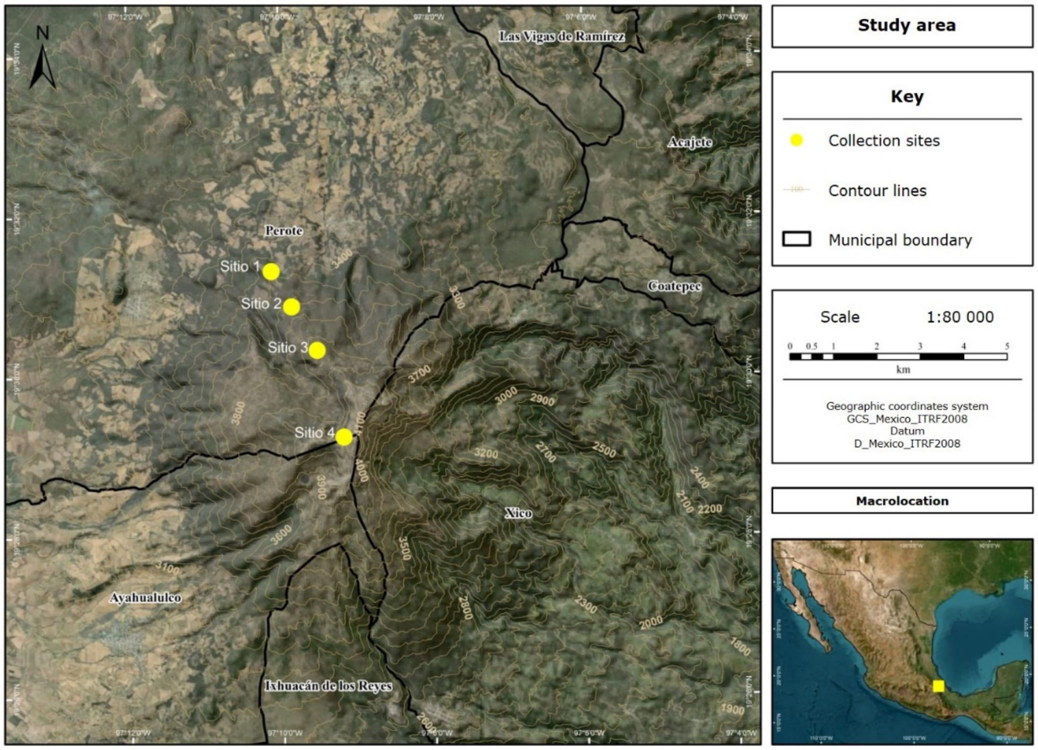
There is some evidence of adaptive altitudinal variation in height, base diameter, elongation rate, and dry weight of leaves, branches, and stems of seedlings at different ages in this species on *Pico de Tancítaro*, state of *Michoacán*. In these, it was observed that plants from lower elevation sites reached greater heights and base diameters than those from higher elevations (Loya-Rebollar et al., 2013; Viveros-Viveros et al., 2009).

However, there are no studies on the growth variation of the species across altitudinal gradients in other mountains in the country, except for the phenotypic variation of seeds at the *Zoquiapan* Experimental Station, State of Mexico (López et al., 2023). Based on the above, the objective of this study was to evaluate, at four separate ages, the altitudinal variation in base diameter, height, and survival of *Pinus hartwegii* seedlings originating from seeds from *Cofre de Perote*, state of *Veracruz*, Mexico. The hypothesis was that the initial growth and survival of *Pinus hartwegii* seedlings will vary with the altitude of origin of the collection sites. Furthermore, this variation will show a tendency for plants from lower elevations to have greater initial growth and survival than those from other elevations; or, for plants from intermediate elevations, to have greater initial growth and survival than those from other elevations.

Materials and Methods

Seed Collection and Processing

In December 2014 and January 2015, *P. hartwegii* seeds were collected from four sites along an altitudinal gradient in *Cofre de Perote*, state of *Veracruz*, from 3 450 to 4 050 masl. The separation between sites was 200 m in altitude; the last site corresponding to the upper limit of the tree vegetation (Figure 1). At each site, 15 trees with no evident presence of pests or diseases and with cones were selected; they were separated by at least 50 m to reduce possible inbreeding effects. Twenty cones were collected from each tree and transported to the Forest Research Institute of the University of *Veracruz*, in *Xalapa*, state of *Veracruz*, for seed processing and storage, and to establish the nursery trial. The cones were left to dry in the sun for a week on a patio with a cement floor. The seeds were extracted manually by dissecting the cones. Impurities and damaged seeds were removed manually.



Sitio = Site; Site 1: 3 450 masl; Site 2: 3 650 masl; Site 3: 3 850 masl; Site 4: 4 050 masl. *Las Vigas de Ramírez* = *Las Vigas de Ramírez* municipality; *Acajete* = *Acajete* locality; *Perote* = City of *Perote*; *Coatepec* = *Coatepec* municipality; *Xico* = *Xico* locality; *Ixhuacán de los Reyes* = *Ixhuacán de los Reyes* municipality; *Ayahualulco* = *Ayahualulco* municipality.

Figure 1. Geographic location of *Pinus hartwegii* Lindl. seed collection sites in *Cofre de Perote*, state of *Veracruz*, Mexico.

Assay establishment and assessed variables

In January 2015, four replications of 100 seeds were germinated per altitudinal site in 13×20 cm black polyethylene bags with a capacity of 1 L. The substrate used consisted of forest soil and mine sand in a 1:1 ratio.

Once the seeds had germinated, the seedlings were placed in the greenhouse of the Forest Research Institute of the University of *Veracruz*, located in the *El Haya* Ecological Park, on the old *Xalapa-Coatepec* highway at 19°31’12.6’’ N and 96°56’35.7’’ W, at 1 412 masl. The experimental design was completely randomized, with representation of the four altitudinal sites (treatments), eight seedlings per line (experimental unit), and six replications of each treatment, for a total of 192 observations. In the first three months, the plants were watered every other day, followed by twice-weekly irrigation.

Each plant's total height (cm) was measured using a 30-cm model H-6560 Westcott® metric ruler and its base diameter (mm) was measured using a digital vernier caliper (model CD-S6"C Mitutoyo®) at 9, 10, 11, and 12 months old. At 13 months, seedling survival was assessed by counting dead and live seedlings. The number of live seedlings in each line was used to estimate the survival rate per line using the following formula:

$$Survival\ (\%) = \left(\frac{Number\ of\ alive\ seedlings\ per\ replication}{Total\ number\ of\ seedlings\ \ per\ replication}\right)100 \qquad (1)$$

Statistical analyses

Statistical analyses were performed for each variable separately based on each age. To determine whether the data on total height and base diameter evaluated at the four aforementioned ages, as well as survival, met the principles of normality, a normality analysis was performed using the Shapiro-Wilk test using the UNIVARIATE procedure in the SAS statistical package version 9.4 (Statistical Analysis System [SAS], 2023).

The data on basal heights and diameters evaluated at four ages met the principles of normality ($P \geq 0.1504$). The data corresponding to the plant survival percentage did not meet the principles of normality ($P < 0.0001$), so an analysis of variance with generalized linear models was performed using the GENMOD procedure in the SAS statistical package version 9.4, following the Poisson distribution (SAS, 2023).

In the analysis of variance for variables that do not meet the principles of normality, more powerful models than traditional ones should be used; such as generalized linear models. In particular, the SAS GENMOD procedure allows for the adjustment of variables that do not have a normal distribution (Bandera & Pérez, 2018). For the height and basal diameter data at the four ages evaluated, the analysis of variance was performed using the GLM procedure of the SAS statistical package version 9.4, and multiple comparisons of means were performed using the Tukey test. To determine the contribution of the sites to the variance, the VARCOMP procedure, REML option, was used (SAS, 2023). The statistical model used was the following:

$$Y_{ij} = \mu + X_i + \varepsilon_{ij} \qquad (2)$$

Where:

Y_{ij} = Value of the j^{th} observation at the i^{th} altitude

μ = Overall mean

X_i = *i-th* altitude (m)

ε_{ij} = Experimental error

Results and Discussion

Differentiation at initial height

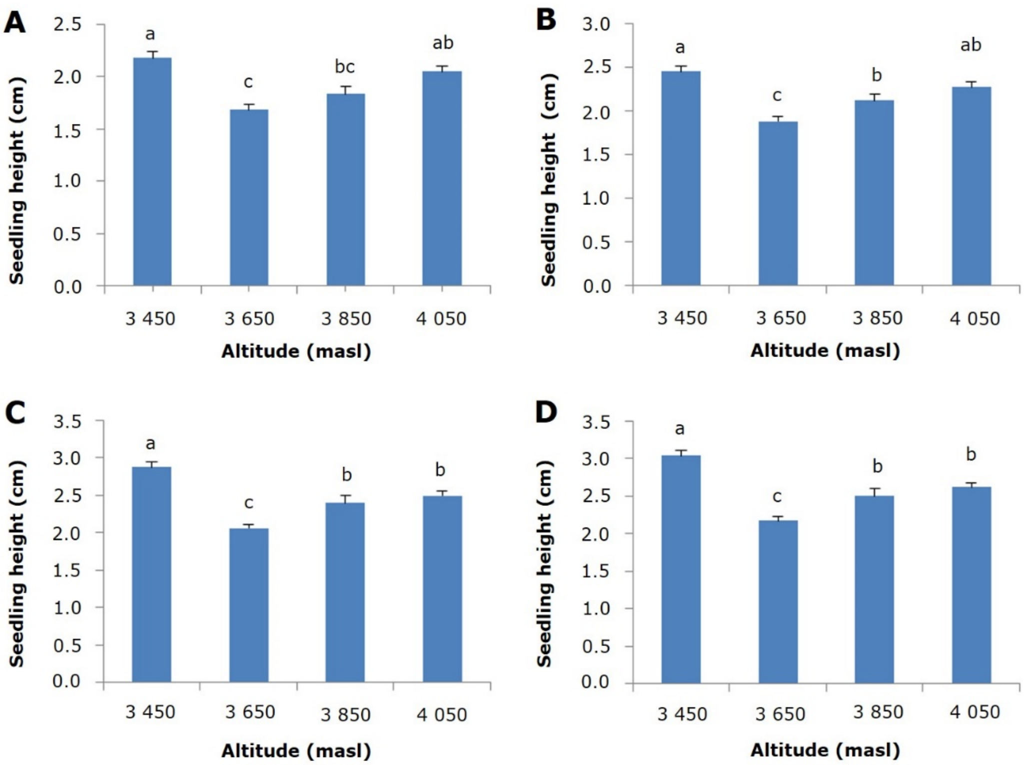
There were significant differences (P<0.0001) in total seedling height between the sites of origin of *P. hartwegii* seeds located at different altitudes in *Cofre de Perote*, state of *Veracruz*, at the four ages evaluated (Table 1). This was consistent with the total height at 7 and 18 months of age in plants of the same species from sites located along an altitudinal gradient on *Pico de Tancítaro*, state of *Michoacán* (Viveros-Viveros et al., 2009). Similar results have been described for other pine species with altitudinal gradient distributions; for example, Viveros-Viveros et al. (2005) determined differences between altitudinal sites for total height at 15 and 24 months of age in *Pinus pseudostrobus* Lindl. seedlings planted at two locations in the *Nuevo San Juan Parangaricutiro* forests of *Michoacán*. In a similar way, Ruiz-Talonia et al. (2014) recorded differences between altitudinal sites for seedling height at 18 and 24 months of age in *Pinus patula* Schltdl. & Cham. planted at two sites in *Ixtlán de Juárez*, state of *Oaxaca*. This demonstrates the importance of altitude in local adaptation for *P. hartwegii* and other pine species with similar gradient distributions (Martínez-Berdeja et al., 2019).

Table 1. Level of significance (*P*) of the analysis of variance and percentage contribution to the total variance of the height of *Pinus hartwegii* Lindl. seedlings from four altitudinal sites in *Cofre de Perote*, state of *Veracruz*, Mexico, evaluated at four ages.

Source of variation	9 months		10 months		11 months		12 months	
	P	**%**	***P***	**%**	***P***	**%**	***P***	**%**
Site	<0.0001	18.62	<0.0001	21.16	<0.0001	29.89	<0.0001	30.18
Error	----------	81.38	----------	78.84	----------	70.11	----------	69.82

The contribution of sites located at different altitudinal levels to the total variance for the total height of *P. hartwegii* seedlings ranged from approximately 18.6 to 30 %, and increased with age (Table 1). It was greater than that reported for the height of *Pinus patula*, *Pinus leiophylla* Schiede *ex* Schltdl. & Cham. and *P. pseudostrobus* seedlings (<10 %). In particular, the contribution at 12 months of age was similar to that recorded for *Pinus devoniana* Lindl. (39 %) (Castellanos-Acuña et al., 2013; Ruiz-Talonia et al., 2014). This indicates that in *P. hartwegii* altitudes contribute significantly to the genetic differentiation of populations for plant height (Viveros-Viveros et al., 2009).

P. hartwegii seedlings from sites at extreme elevations (lowest and highest) had the greatest average heights at 9 (2.176 cm and 2.047 cm, respectively) and 10 months (2.449 cm and 2.268 cm, respectively) of age; whereas sites at intermediate altitudes reached the lowest heights (Figure 2A and 2B). From 11 months of age, seedlings from the lowest elevation site (3 450 masl) reached a significantly greater height (2.871 cm at 11 months and 2.490 cm at 12 months) (Figure 2C and 2D) than the other sites. In contrast, those from the intermediate altitude site (3 650 masl) had significantly lower heights (2.063 cm at 11 months and 2.173 cm at 12 months), as well as at ages 9 and 10 months. At 11 and 12 months, the specimens from the 3 850 and 4 050 masl sites did not differ in height and were intermediate to those from the 3 450 and 3 650 masl sites (Figure 2A, 2B, 2C, and 2D).



A = 9 months; B = 10 months; C = 11 months; D = 12 months. The vertical bar represents the standard error, and different letters indicate significant differences between altitudes (P<0.05).

Figure 2. Average total heights of *Pinus hartwegii* Lindl. from four altitudes of *Cofre de Perote*, state of *Veracruz*, Mexico, at different ages.

The trend in altitudinal variation in height at 9 and 10 months of age was not as expected; based on results obtained with other forest species across altitudinal gradients, it was expected that plants from lower elevation sites would be taller than those from higher elevation sites, as was the case with *P. hartwegii* at *Pico de Tancítaro*, state of *Michoacán* (Viveros-Viveros et al., 2009) and *P. devoniana* (Castellanos-Acuña et al., 2013). Another possibility was that provenances from sites located in the middle of the altitudinal distribution might be taller than plants from sites at the lowest and highest elevations, as was the case with *Pinus oocarpa* Schiede *ex* Schltdl. (Sáenz-Romero et al., 2006). Therefore, the hypothesis initially proposed regarding the expected trend for the altitudinal variation in the height of *P. hartwegii* in *Cofre de Perote*, state of *Veracruz*, is rejected.

A similar trend to that observed at 9 and 10 months of age is reported for survival, height, and base diameter assessed at 18 months, as well as for height at 4 years old in *Abies religiosa* (Kunth) Schltdl. & Cham. (Cruzado-Vargas et al., 2020; Herrejón-Calderón et al., 2022). The trend in height at 9 and 10 months of age is likely explained by the fact that plants from sites at higher elevations are adapted to initiate growth as soon as they detect favorable temperature and humidity conditions. When these plants move to sites below their original elevation (where more favorable environmental conditions exist for their growth), the growth rate is more notable and the period is extended (Vitasse et al., 2013), allowing them to match the growth of plants at the lower elevation site and even surpass plants from intermediate sites (at least in the initial stage); however, at later ages, plants from lower elevations show greater growth potential, which is consistent with what has been recorded for *P. hartwegii* (Viveros-Viveros et al., 2009) and *P. devoniana* (Castellanos-Acuña et al., 2013).

Another possibility is that the trend observed at the first two evaluation ages (9 and 10 months of age) is the result of maternal effects (Vivas et al., 2015).

Differentiation in base diameter growth

Seedling base diameter showed significant differences (P<0.0001) among seed origin sites at the four ages evaluated (Table 2). This was consistent with the differences among sites located along altitudinal gradients for base diameter in *P. hartwegii* at 5.5 years of age at *Pico de Tancítaro*, state of *Michoacán* (Loya-Rebollar et al., 2013) and in *P. pseudostrobus* seedlings at 24 months of age planted in *Nuevo San Juan Parangaricutiro*, state of *Michoacán* (Viveros-Viveros et al., 2006).

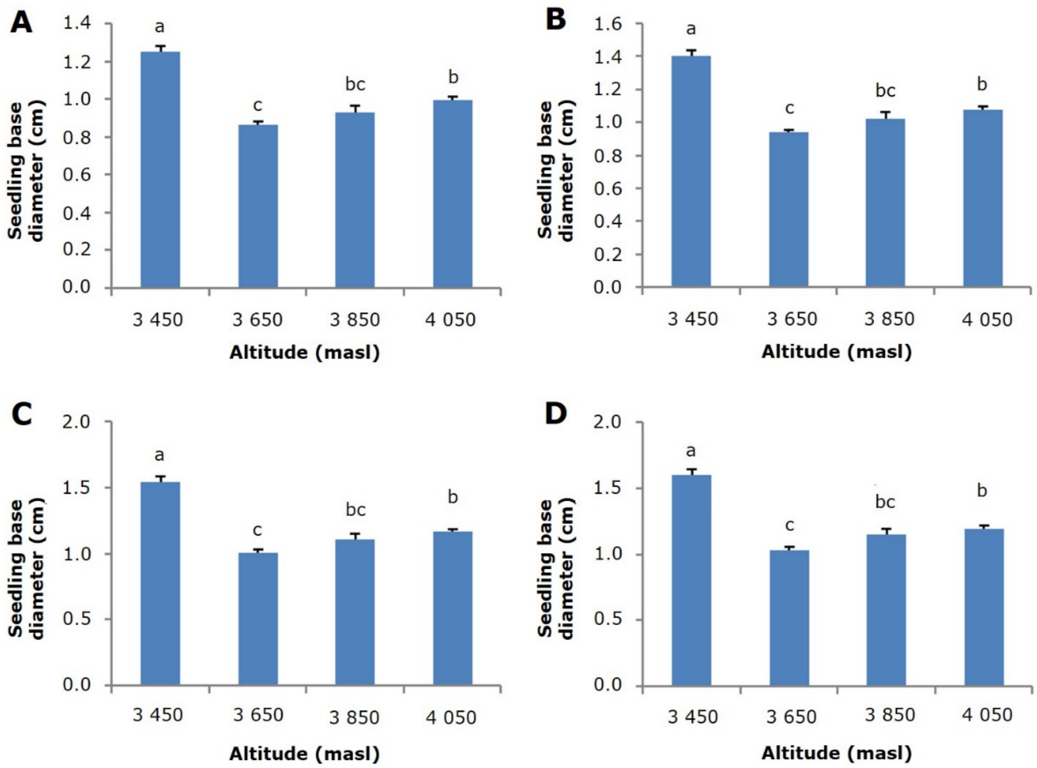
Table 2. Significance level (*P*) of the analysis of variance and percentage contribution of the site to the total variance in base diameter of *Pinus hartwegii* Lindl. seedlings from four altitudinal sites in *Cofre de Perote*, state of *Veracruz*, México, evaluated at four ages.

Source of variation	9 months		10 months		11 months		12 months	
	P	**%**	***P***	**%**	***P***	**%**	***P***	**%**
Site	<0.0001	45.99	<0.0001	47.56	<0.0001	47.48	<0.0001	45.79
Error	----------	54.01	----------	52.44	----------	52.52	----------	54.21

The contribution of altitudinal sites to the total variance in base diameter growth was high (>45 %) (Table 2) and was greater than the base diameter of *P. hartwegii* plants in *Michoacán* (23 %) (Loya-Rebollar et al., 2013). This indicates that in this species, altitude contributes significantly to the genetic differentiation of populations for base diameter, and is greater than that for plant height (Viveros-Viveros et al., 2009).

Plants from the lowest elevation site were distinguished by the largest base diameters at all ages evaluated (Figure 3A, 3B, 3C and 3D), while those from the intermediate site at 3 650 masl recorded the lowest values at all ages (Figure 3A, 3B, 3C and 3D);

plants from the 4 050 and 3 850 masl sites were found at intermediate height, although the latter did not differ from the 3 650 masl site. This is because plants from lower elevations, as part of their adaptation to sites where low temperatures are less limiting, tend to develop greater growth in base diameter (Bresson et al., 2011; Viveros-Viveros et al., 2009). Therefore, in this case, the initially planned hypothesis that greater growth in base diameter is expected in plants from the lower-elevation origin is accepted.



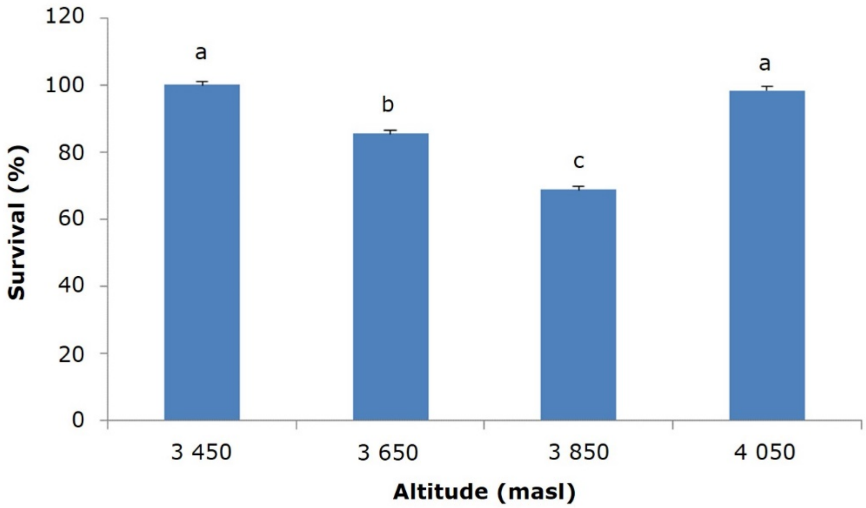
A = 9 months; B = 10 months; C = 11 months; D = 12 months. The vertical bar represents the standard error, and different letters indicate significant differences between altitudes (*P*<0.05).

Figure 3. Average basal diameters of *Pinus hartwegii* Lindl. seedlings from four altitudes in *Cofre de Perote*, state of *Veracruz*, Mexico, at different ages.

Differentiation in plant survival

P. hartwegii seedling survival differed significantly (*P*<0.0001) among seed origin sites. Furthermore, the percentage contribution of these sites to the total variance was high (75 %) for this variable at 13 months of age, and altitudinal sites were the largest contributor to the total variance. In a similar way, *A. religiosa* plant survival (at 18 months of age) also showed differences among sites located along an altitudinal gradient in the Monarch Butterfly Biosphere Reserve in the State of Mexico (Cruzado-Vargas et al., 2020).

The trend in survival variation was similar to that of seedling total height at 9 and 10 months; that is, plants from sites with extreme elevations (lower and higher elevations) had the highest survival, while intermediate populations had the lowest (Figure 4). Although this trend is not commonly verified, it is confirmed for specimens of *A. religiosa* from an altitudinal gradient (2 960 to 3 450 masl) in the Monarch Butterfly Biosphere Reserve in the State of Mexico (Cruzado-Vargas et al., 2020) and may be due to the fact that plants from the lower elevation site are better adapted to the more benign environmental conditions, particularly in terms of temperature and precipitation; while plants from seeds from the higher elevation site show a positive adaptive response to the prevailing better environmental conditions when moved well below their natural altitudinal distribution, at least temporarily (Vitasse et al., 2013).



The vertical bar represents the standard error, and different letters indicate significant differences between altitudes ($P<0.05$).

Figure 4. Average survival rates of *Pinus hartwegii* Lindl. seedlings at 13 months of age from four altitudes in *Cofre de Perote*, state of *Veracruz*, Mexico.

Conclusions

Altitude strongly influences the variation in survival and initial growth of *Pinus hartwegii* from *Cofre de Perote*. The response to height varies according to plant age; initially, specimens from extreme elevations performed better, but with age, those from lower elevations responded better. For base diameter and survival, the effect of altitude persisted with plant age; those from lower elevations showed greater growth in base diameter, and those from extreme elevations recorded higher survival rates.

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Conflicts of Interest

The authors declare no conflicts of interest.

Contribution by author

Héctor Viveros Viveros: planning and supervision of the experiment, statistical analysis, and writing of the document; Jesús Marin Hernández: conducting the experiment and writing of the document; Armando Aparicio Renteria: experimental supervision and document review; Diana Córdoba Rodríguez, Susana Guillén Rodríguez and César Ruiz Montiel: document review.

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