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Research article

Adaptive variation in morphological traits of *Pinus patula* Schiede *ex* Schltdl. & Cham. seedlings

Variación adaptativa en caracteres morfológicos de plántulas de *Pinus patula* Schiede *ex* Schltdl. & Cham.

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Abstract

The seedling establishment stage of tree species is under strong selection pressures, so morphological traits of seedlings commonly show strong adaptive value and are relevant for genetic improvement purposes. The objectives were to determine the adaptive variation in morphological traits of *Pinus patula* seedlings and their relationships with the geoclimatic conditions at the seed's origin site. Germination capacity (*GC*), number of cotyledons (*NC*), cotyledon length (*CL*), and hypocotyl length (*HL*) were evaluated and correlated with geoclimatic variables during the 1991-2020 period at the progeny's origin sites. Genetic variation among families was wide; the greatest variation was observed in *GC* with average values ranging from 11 to 100 %. With the exception of *NC*, the correlation between morphological variables and latitude, longitude, mean annual temperature, temperature of the warmest month, beginning and ending dates of the frost-free period, snowfall, and extreme temperature ranged from -0.29 to 0.66. Seeds from sites further North and West, which were warmer and had a longer frost-free period, exhibited higher *GC*, *CL*, and *HL*. The first canonical function explained 77 % of variation among morphological and geoclimatic variables. The results help identify the geoclimatic factors that influence the adaptation of *Pinus patula* at early stages of development, thereby promoting the initial vigor of seedlings and their adaptation during the establishment phase.

Keywords: Germination capacity, canonical correlations, genetic differentiation, early evaluation, morphological traits, natural selection.

Resumen

La fase de establecimiento de las plantas leñosas está sujeta a fuertes presiones de selección, por ello las características morfológicas de las plántulas tienen un alto valor adaptativo y son importantes en los procesos de mejora genética. Los objetivos del presente estudio fueron determinar el valor adaptativo en características morfológicas de plántulas de *Pinus patula* y su relación con las condiciones geoclimáticas del sitio de origen de la semilla. La capacidad germinativa (*CG*), el número de cotiledones (*NC*), la longitud de cotiledones (*LC*) y la longitud de hipocótilo (*LH*) fueron evaluadas y correlacionadas con variables geoclimáticas del periodo 1991-2020 de los sitios de origen de las progenies. La variación genética entre familias resultó amplia; la mayor variación en *CG* registró valores promedio de 11 a 100 %. Con excepción del *NC*, la correlación entre las variables morfológicas con la latitud, longitud, temperatura media anual, temperatura del mes más cálido, fechas de inicio y término del periodo sin heladas, precipitación en forma de nieve y temperatura extrema varió de -0.29 a 0.66. Las semillas de sitios más al norte y al oeste, más cálidos y con mayor periodo libre de heladas, presentaron valores superiores de *CG*, *LC* y *LH*. La primera función canónica explicó 77 % de la variación entre variables morfológicas y geoclimáticas. Los resultados contribuyen a identificar los factores geoclimáticos que influyen en la adaptación de *Pinus patula* en etapas tempranas de desarrollo, para favorecer el vigor inicial de las plántulas y su adaptación durante la fase de establecimiento.

Palabras clave: Capacidad germinativa, correlaciones canónicas, diferenciación genética, evaluación temprana, rasgos morfológicos, selección natural.

Introduction

In Mexico, *Pinus patula* Schiede *ex* Schltdl. & Cham. is a conifer with a wide geographic distribution, found between 18° and 23°20′ N and 97° and 99° 45′ W (Vela, 1980), at altitudes between 1 800 and 3 100 m, with average annual rainfall >1 000 mm and average annual temperature between 10 and 20 °C (Rzedowski, 1978).

This pine is fast-growing, with high-quality wood that is easy to manage, and its natural populations are adapted to different environmental conditions (Dvorak et al., 2000). Provenance and progeny trials have contributed to the genetic improvement of the species by selecting seed sources and genotypes with greater growth and better adaptation to different planting sites (Escobar-Sandoval et al., 2018; Morales-González et al., 2013; Salaya-Domínguez et al., 2012).

Due to the long periods involved in the genetic improvement of forest species, associated with tree longevity and growth rates, the evaluation of progenies in the field requires periodic monitoring for up to 10 years or more (Adams et al., 2001; Badilla & Murillo, 2026). One approach to optimize this process is the use of early selection, which is based on using characteristics expressed in juvenile stages to predict performance at later ages (Adams et al., 2001; Vargas-Hernández & Adams, 1992). However, for this strategy to be efficient, the traits must have high heritability and be strongly correlated with adult performance (Badilla & Murillo, 2026; Farfán-Vázquez et al., 2002).

Greater germination capacity and initial seedling growth rate provide competitive advantages that can have a lasting effect on subsequent developmental stages (Christie et al., 2022). Furthermore, the initial growth phase after germination represents a vital stage in the life history of plants, subject to strong selection pressure (Larson et al., 2020) and critical for the establishment and subsequent development of individuals (Duncan et al., 2019; Leger et al., 2019), with significant adaptive value in the face of adverse factors (Barton et al., 2020; Metz et al., 2018; Welles & Funk, 2021).

Although studies exist on intraspecific variation and the adaptive value of characteristics in early plant stages (Caruso et al., 2019; Larson et al., 2020; Welles & Funk, 2021), there is very little information on woody species, and especially on *P. patula* (Pérez-Luna et al., 2024). More information is needed on the genetic variation in seedling traits, shaped by natural selection under specific geoclimatic conditions (Singh et al., 2015). Evaluating this variability is a key tool for identifying the seedling morphological traits with the greatest adaptive value, thereby reducing the risks of establishment failure and poor adaptation of plantations in a context of climate change (Christie et al., 2022; Hamann et al., 2000; Singh et al., 2015).

Extensive genetic differentiation is observed in natural populations of the *Pinus* genus in phenotypic traits such as seed size, germination capacity, and germination rate (Ghildiyal et al., 2009). Seed size can be associated with geoclimatic variables of the site of origin, including latitude, longitude, altitude, temperature, and precipitation

(Loha et al., 2006), and in turn significantly influence vigor and overall germination (Farahani et al., 2011; Hojjat, 2011; Rawat & Bakshi, 2011; Singh et al., 2015) and the initial growth of seedlings (Farahani et al., 2011; Loha et al., 2006; Rawat & Bakshi, 2011).

On the other hand, germination capacity is strongly influenced by abiotic factors such as temperature and water stress (George-Miranda et al., 2022), and can affect seedling quality during growth (Singh & Thapliyal, 2012; Wahid & Bounoua, 2013) and establishment at the planting site (Castoldi & Molina, 2014). Another relevant trait is the number of cotyledons, which exhibits a maternal effect associated with seed size (Callejas-Díaz et al., 2022). In *Pinus sylvestris* L., a greater number of cotyledons is related to greater height growth (Ulusan & Bilir, 2008). These characteristics are relevant in selection and genetic improvement processes both for their adaptive value at early ages and for their potential relationship with performance at later ages (Morales-González et al., 2013).

In this context, the objectives of this study were: (1) To determine the adaptive variation in germination capacity and initial morphological characteristics of *P. patula* seedlings from different regions of Mexico; (2) To analyze the correlation between seedling morphological variables and geoclimatic variables of the seed's origin site; and (3) To evaluate differences among families based on their initial development. The hypothesis is that germination capacity and initial morphological characteristics of seedlings vary among germplasm sources and are associated with the environmental conditions of the origin site.

Materials and Methods

Seed samples

The study included 59 seed lots from individual trees (open-pollinated families) from different regions within the species' natural distribution area: 28 families from the state of *Veracruz*, six from *Puebla*, 10 from the state of *Hidalgo*, and 15 from a second-generation asexual seed orchard (ASO) established in *Aquixtla*, *Puebla*, with materials originating from *Tlaxcala*, *Hidalgo*, *Puebla*, *Tamaulipas* and *Veracruz*. The geographic coordinates of the origin sites of the 59 families included in the study are shown in Table 1.

Table 1. Origin sites of the seed lots of *Pinus patula* Schiede *ex* Schltdl. & Cham.

Family	Latitude (N)	Longitude (W)	Elevation (m)
HS-15R	19°40'	98°05'	2 750
HS-64R	19°40'04.2"	98°05'0.0"	3 020
HS-10S	19°43'07.6"	98°00'07.2"	3 121
HS-12C	19°43'17.3"	97°59'49.2"	3 069
HS-117C	19°43'18.1"	97°59'51.1"	3 097
HS-23S	19°43'24.1"	97°59'33.8"	2 997
HS-34S	19°43'45.2"	97°59'17.7"	2 916
HS-36S	19°43'52.0"	97°59'25.3"	2 892
HS-58C	19°44'03.7"	97°59'08.2"	2 829
HS-37R	20°09'	98°10'	2 460
HS-02R	20°24'	98°25'	2 400
HS-17R	20°29'	98°28'	2 833
HS-25R	20°53'	99°13'	2 525
HS-72R	20°39'10.9"	98°40'02.5"	2 020
HS-10R	23°56'	99°28'	1 780

R2-43	18°38’03.3"	97°07’34.0"	2 445
R2-55	18°49’53.0"	97°17’12.4"	2 427
R3-12	19°45'15.4"	97°32'04.6"	2 484
R3-11	19°45'38.0"	97°30'53.4"	2 651
R3-09	19°45'53.0"	97°31'17.8"	2 548
R2-21	19°21’34.3"	97°07’52.9"	1 988
R2-23	19°21’59.8"	97°07’54.9"	2 096
R2-27	19°26’09.0"	97°05’30.3"	2 125
R2-25	19°26’16.0"	97°05’31.9"	2 141
R2-18	19°30’40.8	97°05’06.0"	2 824
R2-16	19°30’42.8"	97°05’14.8"	2 864
R2-14	19°30’55.1"	97°05’30.8"	2 912
R2-15	19°30’55.8"	97°05’48.3"	2 919
R2-20	19°31’09.1"	97°05’30.4"	2 908
R2-62	19°35’47.8"	97°01’45.1"	2 234
R2-06	19°37’46.8"	97°03’54.8"	2 362
R2-07	19°37’50.5"	97°03’57.9"	2 365
R2-04	19°38’23.4"	97°05’21.9"	2 405
R2-02	19°38’30.4"	97°05’07.9"	2 380
R2-01	19°39’14.0"	97°05’35.6"	2 378
R2-64	19°40’56.2"	97°01’50.5"	2 106
R2-63	19°43’11.2"	97°01’41.9"	2 357
R3-18	20°04'04.2"	98°06'20.3"	2 414
R3-24	20°04'14.1"	98°06'47.8"	2 364
R3-21	20°04'54.5"	98°06'32.2"	2 270
R3-72	20°12'58.3"	98°12'02.1"	2 208
R3-51	20°27'03.0"	98°28'07.3"	2 600
R3-53	20°27'19.1"	98°27'50.1"	2 547
R3-55	20°27'59.0"	98°28'16.4"	2 469
R3-57	20°28'02.5"	98°28'01.2"	2 453
R3-42	20°34'20.0"	98°31'07.1"	1 903
R3-47	20°34'27.8"	98°30'08.9"	2 064
R3-48	20°34'29.5"	98°34'29.5"	2 000
R3-46	20°34'31.2"	98°30'14.8"	2 067
R3-43	20°35'08.1"	98°31'10.4"	1 911
R3-35	20°37'27.8"	98°35'44"	2 037

R3-33	20°37'30.4"	98°36'07.5"	2 091
R3-32	20°37'36.7"	98°36'12.1"	2 089
R3-31	20°37'41.1"	98°36'15.4"	2 050
R3-27	20°39'55.7"	98°42'21.7"	2 129
R3-29	20°40'03.8"	98°42'15.7"	2 145
R3-66	20°55'01.9"	98°55'59.8"	2 137
R3-68	20°55'05.2"	98°55'48.2"	2 143
R3-67	20°55'05.4"	98°56'03.7"	2 192

Trial establishment

The trial was conducted in a greenhouse with a 180-micron plastic covering at the *Centro Nacional de Investigación Disciplinaria en Conservación y Mejoramiento de Ecosistemas Forestales*, *Cenid Comef* (National Center for Disciplinary Research in Conservation and Improvement of Forest Ecosystems) of *Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias*, *INIFAP* (National Institute for Research on Forest, Agriculture and Livestock); the average temperature was 21 °C, with an average relative humidity of 65 %.

For each family, 60 full seeds were used. The seeds were soaked for 24 h in distilled water with 5 % hydrogen peroxide. Subsequently, they were sown in rigid, black polyethylene tubes with internal root guides, measuring 4.8 cm in top diameter, 21 cm in length, and 170 mL, placed in 54-cell trays. Each tube was labeled with a key to the tree and its site of origin. The substrate consisted of a 60:20:20 mixture of Lambert® peat moss, Coarse® perlite, and Verlite® vermiculite, with the addition of 5 g L^{-1} of Multicote® (Israel) controlled-release fertilizer (18-06-12+Em) for eight months.

The experimental design was a randomized complete block design with five replicates per family and 12 seeds per experimental unit. During the study period, seedlings were watered with drinking water three times a week and Captan® WP (USA) fungicide (2 g L^{-1}) was applied once a week to prevent fungal attacks.

Evaluation of germination and morphological variables

For the purposes of this study, germination capacity (*GC*) was determined based on the number of seedlings that emerged from the substrate 30 days after sowing, considering that under natural conditions germination ends when the seedling emerges from the soil and becomes autotrophic (Bareke, 2018). To obtain the final germination percentage, the equation of the International Seed Testing Association (ISTA, 2024) was used, considering the number of emerged seedlings equivalent to the number of germinated seeds:

$$GC(\%) = \left(\frac{germinated\ seeds}{total\ number\ of\ seeds}\right) \times 100 \qquad (1)$$

Forty-five days after sowing, cotyledon length (*CL*, cm) and hypocotyl length (*HL*, cm) were measured using a Baco® graduated ruler, and the number of cotyledons (*NC*) was determined by direct counting. Of the 59 sown plots, 12 plots that did not germinate were excluded from the analysis; the other 47 plots germinated and provided information for the evaluated traits (*GC*, *NC*, *CL*, and *HL*).

Geoclimatic variables

Climatic normals for the 1991-2020 period were obtained from the latitude, longitude, and elevation of the origin site of each family using ClimateNA_v7.50 (Center for Forest Conservation Genetics, 2023).

Statistical analysis

The assumptions of normality and homogeneity of variances for the evaluated variables were verified using the Kolmorov-Smirnov and Levene tests, respectively. The variable *GC* did not meet the assumptions (p>0.10), so the Glimmix procedure was used for its analysis, with the binomial distribution link function, where the emerged plant was considered the success case (*i. e.*, with a value of 1) and the non-emerged plant was considered non-success (0). The variables *NC* (p<0.10), *CL*, and *HL* (p<0.09) were considered sufficiently robust with respect to the normal distribution, so the Mixed procedure of SAS® V9.2 (SAS Institute Inc., 2012) was used for them. The linear model used in both cases was:

$$Y_{ijk} = \mu + b_i + F_j + b_i F_j + e_{ijk} \qquad (2)$$

Where:

Y_{ijk} = Observation value on the *k*-th plant of the *j*-th family in the *i*-th block

μ = Population mean

b_i = Fixed effect of the *i*-th block

F_j = Random effect of the *j*-th family

$b_i F_j$ = Random effect of the interaction of the *i*-th block with the *j*-th family

e_{ijk} = Experimental error

The ANOVA results allowed for the estimation of average values per family for the evaluated variables. In the case of *GC*, the probability of success cases (*i. e.*, emerged seedlings) in each family automatically provided the *GC* value in decimal fractions.

To determine the adaptive value of the morphological variables of the seedlings, a correlation analysis was performed with the geoclimatic variables of the families' sites of origin. After removing redundant geoclimatic variables (r>0.9), that is, those with high correlation, one was excluded from the final analysis, leaving 15 for subsequent analyses. The variables that were not excluded were incorporated into a second Pearson correlation analysis with the morphological variables to determine possible interrelationships between the two groups of variables. The *GC* (expressed as a percentage for each family) was transformed using the logit function (Seiffert et al., 2024) to approximate a normal distribution before the correlation analysis with the geoclimatic variables. The geoclimatic variables of interest were: latitude (*LAT*), longitude (*LONG*), elevation (*ELEV*), mean annual temperature (*TMA*), mean temperature of the warmest month (*TMMC*), continentality temperature (*TC*=), mean annual precipitation (*MAP*), heat index (*IC*), day on which the frost-free period begins (*iPLH*) and ends (*tPLH*), snowfall (*PFN*), extreme temperature for the period 1991-2020 (*TEX*), Hargreaves reference evaporation (*Eref*), Hargreaves climatic moisture deficit (*DHC*), and mean annual relative humidity (*RH*). Subsequently, a canonical correlation analysis was performed between both groups of variables using the CANCORR procedure of SAS® V9.2 (SAS Institute Inc., 2012).

Results and Discussion

Means of morphological variables by family

Analysis of variance (ANOVA) indicated highly significant variation ($p<0.001$) among families for the variables evaluated (Table 2).

Table 2. Mean (±standard error) and extreme (minimum and maximum) values of germination capacity and morphological characteristics of *Pinus patula* Schiede *ex* Schltdl. & Cham. seedlings.

Trait	**General average**	**Extreme family values**	
		Minimum	**Maximum**
Germinative capacity (%)	55.7±0.8	11.0	100.0
Number of cotyledons	5.2±0.1	4.6	7.0
Cotyledon length (cm)	2.0±0.1	1.5	2.6
Hypocotyl length (cm)	2.5±0.1	1.9	3.1

The average number of cotyledon leaves varied by up to 2.4 leaves among families from different origin sites (Table 1). Eighty-one percent of the seedlings had five or six cotyledons, 15.4 % had four, and 3.8 % had between seven and eight cotyledons. The average values of *CL* and *HL* at the family level differed by 73 % and 63 %, respectively.

The low germination percentages in some families (both those excluded and those not excluded from the test), especially those from the state of *Veracruz*, may be the result of asynchrony in the periods of female receptivity and pollen dispersal, lack of pollen, or the isolation of the trees at the collection sites, with a small number of participating individuals, which generally leads to potential problems of inbreeding and reduced gene flow (Capilla-Dinorin et al., 2021; Juárez-Agis et al., 2006).

However, the low germination rates in some *Veracruz* families may also be a result of storing the seeds at room temperature for a year; whereas the ASO seeds, which showed higher germination rates, were collected during the same year the trial was conducted. In conifers, seed longevity and vigor depend critically on storage conditions and moisture content (Corbineau, 2024). Differences were observed between the two groups of seed lots (those stored at room temperature and those collected more recently), indicating a genetic effect combined with the physiological response to handling and storage conditions prior to germination.

Correlations between characteristics

GC, *CL*, and *HL* were significantly and positively correlated ($p<0.05$) with the latitude and longitude of the origin site (Table 3). Furthermore, *HL* showed moderate positive correlations ($p<0.05$) with *TMA*, *TMMC*, *tPLH*, and *TEX*, and moderate negative correlations ($p<0.05$) with *iPLH* and *PFN*. This indicates that seedlings obtained from seeds originating in warmer environments with longer frost-free periods tend to have larger hypocotyls (Ranade & García-Gil, 2021).

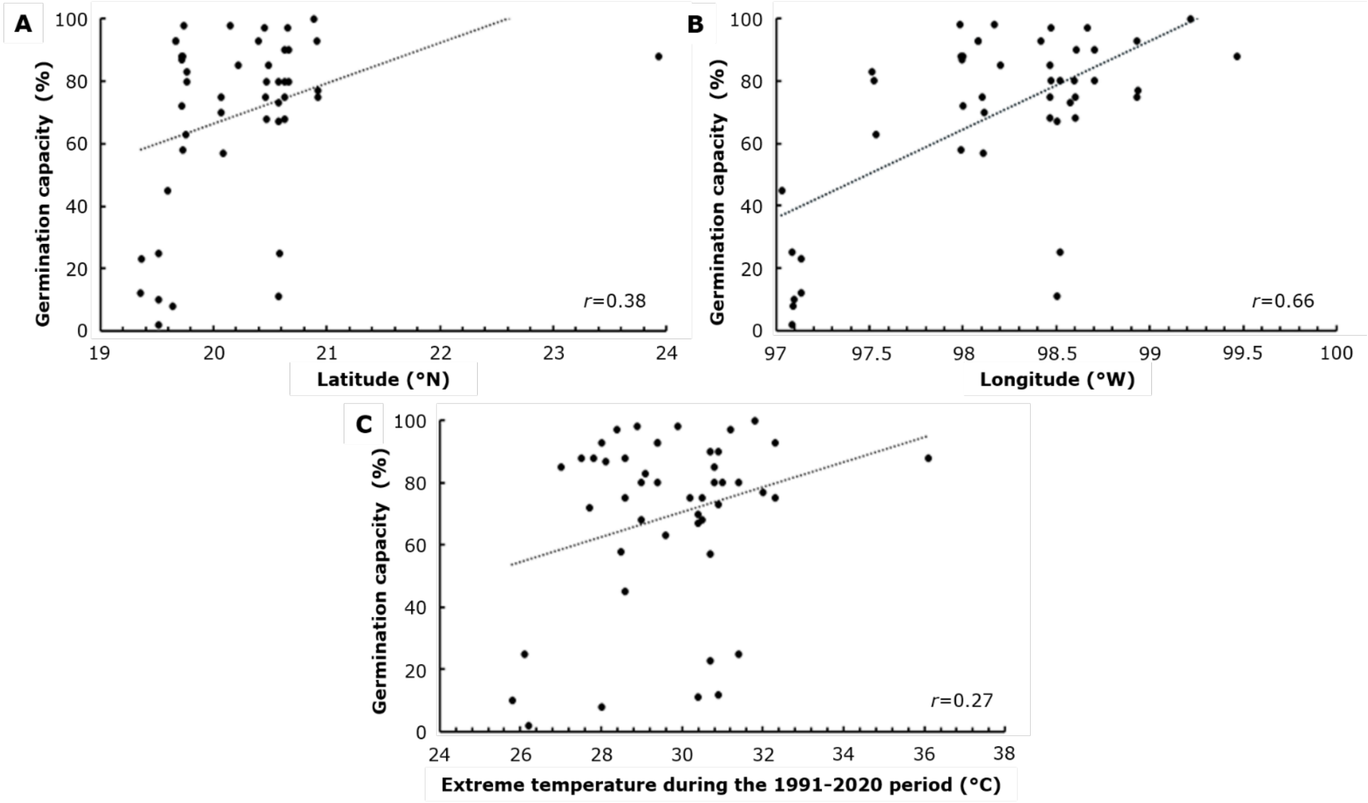
Table 3. Pearson correlation between progeny characteristics and geoclimatic variables.

CP	**Latitude**	**Longitude**	***TMA***	***TMMC***	***iPLH***	***tPLH***	***PFN***	***TEX***
GC	0.36**	0.64**	0.03	0.09	0.10	-0.02	-0.11	0.28*
NC	0.01	-0.09	-0.21	-0.19	0.21	-0.20	0.16	-0.17
CL	0.36*	0.52**	0.08	0.14	-0.04	0.09	-0.09	0.24
HL	0.30*	0.40**	0.31*	0.33*	-0.31*	0.33*	-0.29*	0.36*

CP = Progeny characteristics. *GC* = Germination capacity (%); *NC* = Number of cotyledons; *CL* = Cotyledon length (cm); *HL* = Hypocotyl length (cm); *TMA* = Mean annual temperature; *TMMC*= Mean temperature of the warmest month; *iPLH* = Day on which the frost-free period begins; *tPLH* = Day of the year on which the frost-free period ends; *PFN* = Snowfall; *TEX* = Extreme temperature from 1991-2020. *Significant at 0.05 and ** at 0.01.

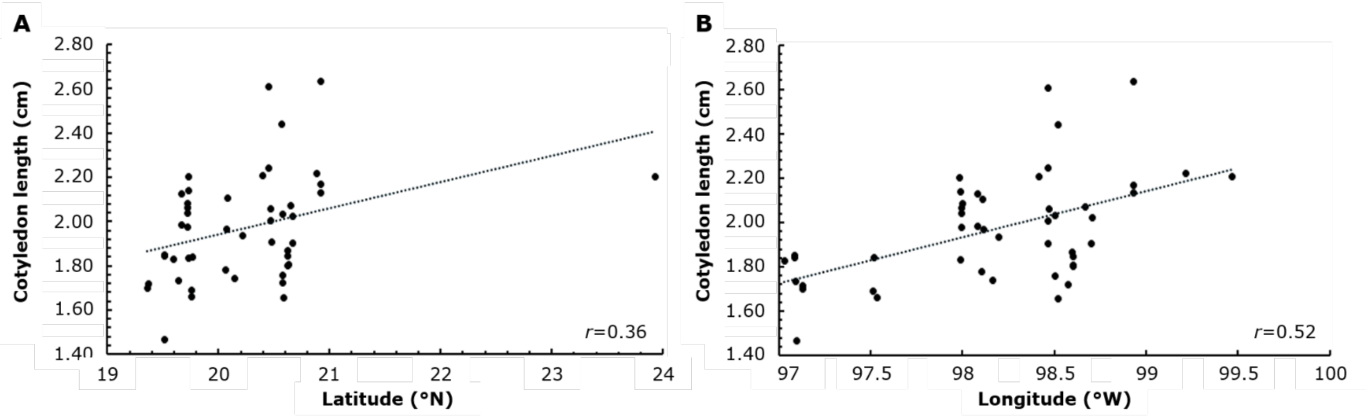
On the other hand, *GC* was weakly and positively, but significantly ($p<0.05$), associated with *TEX*, suggesting a slight (genetic) adaptation to extreme thermal conditions, related to differences in respiration and reserve consumption responses during handling and storage of seeds at different temperatures (Cai et al., 2025).

The observed trend toward higher *GC* and *CL* values in families distributed further North and West, located towards the *Sierra Madre Oriental*, can be interpreted as an adaptive response to specific thermal regimes (Figure 1A, 1B and 1C) and larger seedlings in *CL* (Figure 2A and 2B); in this regard, Cai et al. (2016) determined that seeds from populations with warmer climates grow faster, and that the function of cotyledons as storage during growth (Zhang et al., 2008) and photosynthesis are more important than the expansion of primary needles (Sasaki & Kozlowski, 1970). This is also due to a possible maternal effect, since seeds produced in cold environments have a lower germination capacity than those produced in relatively warm environments, as is the case with *Poa alpina* L. (Hermesh & Acharya, 1992).



A = Latitude; B = Longitude; C = Extreme maximum temperature during the 1991-2020 period.

Figure 1. Correlation between germination capacity (*GC*) with latitude, longitude and extreme maximum temperature during the 1991-2020 period of the origin site of *Pinus patula* Schiede *ex* Schltdl. & Cham. seeds.



A = Latitude; B = Longitude.

Figure 2. Correlation between cotyledon length (*CL*) and latitude and longitude of the seed origin site of *Pinus patula* Schiede *ex* Schltdl. & Cham.

Velasco-García and Hernández-Hernández (2024) mention that a longer frost-free period benefits *GC* in *Pinus oocarpa* Schiede *ex* Schltdl. These authors and Capilla-Dinorin et al. (2025) in *Pinus chiapensis* (Martínez) Andresen did not recognize a significant association of *NC* with the environmental variables at the site of origin, similar to that identified in the present work. But in the work with *P. chiapensis*, a significant, high, and positive association of *CL* with altitude was found, and a negative association with temperature and mean annual precipitation (Capilla-Dinorin et al., 2025), but they did not establish a significant association of *NC* with the environmental variables at the site of origin, similar to that obtained in the study described here.

Juárez-Agis et al. (2006) also concluded that the germination percentage of *Pseudotsuga menziesii* (Mirb.) Franco was higher in populations from higher latitudes, originating in Northern Mexico, compared to seeds from populations in the Central and Southern parts of the country. According to Rehfeldt (1993), geographic factors such as latitude, longitude, and elevation have a strong influence on natural selection in forest species, especially at early stages of development. Latitude is a relevant variable in the genetic differentiation among conifer populations in Mexico, given that these are mainly distributed along mountain ranges that extend in a North-South direction (Sáenz-Romero, 2004).

Canonical correlations

The first canonical function (F1) explained 77 % of the joint variation among the four plant characteristics and the 15 geoclimatic variables (r=0.83, p=0.001). The other three functions were not significant (Table 4).

Table 4. Values and statistical significance of the canonical correlations between progeny characteristics and geoclimatic variables of the seed origin site of *Pinus patula* Schiede *ex* Schltdl. & Cham.

Canonical function number	Canonical correlation	Adjusted canonical correlation	Approximate standard error	Squared canonical correlation	*Pr>F*
F1	0.88	0.83	0.03	0.77	0.001
F2	0.76	0.67	0.06	0.57	0.261
F3	0.52	0.31	0.11	0.27	0.898
F4	0.40	0.21	0.12	0.16	0.909

Germination capacity had the highest canonical coefficient, followed by *CL* (Table 5), indicating that an increase in the characteristic leads to an increase in the value of the integrated canonical function, while the coefficients for *NC* and *HL* are negative; that is, an increase in the characteristic value leads to a reduction in the value of the canonical function.

Table 5. Standardized canonical coefficients of progeny characteristics in the four functions (F1-F4).

Caracteristic	F1	F2	F3	F4
Germination capacity (%)	0.8585	0.6442	0.5566	-0.7008
Number of cotyledons	-0.1883	-0.1668	1.0686	-0.5769
Cotyledon length (cm)	0.2452	-0.4728	-0.2066	1.4012
Hypocotyl length (cm)	-0.1405	-0.8943	-0.1353	-0.883

In a siimilar way, in the case of geoclimatic variables, *TMMC* (8.11), *TEX* (-4.21), and *iPLH* (3.46) were the most important, although the weight or contribution of *TMMC* and *iPLH* to the canonical function is positive, while that of *TEX* is negative. This means that the progeny characteristics most sensitive to changes in the canonical function that maximizes correlations with environmental variables are *GC* and *CL*; while the climatic variables that most influence their respective canonical function 1 are *TMMC*, *TEX*, and *iPLH* at the progeny's site of origin.

Velasco-García and Hernández-Hernández (2024) mention that in *P. oocarpa*, trees from warmer sites were associated with lower seedling emergence; however, in the present study, the highest germination of *P. patula* occurred in seeds from warmer locations, which may be attributed to interspecific differences in adaptive strategies or in the evolutionary history of both species, as has been demonstrated for different functional traits in other woody species (Liu et al., 2022). However, explaining the origin of the differences in adaptive mechanisms during the initial growth phase of plants between *P. patula* and *P. oocarpa* is beyond the scope of this work, as it requires a much broader joint study.

Canonical coefficients are useful for identifying the most promising locations in the selection of germplasm collection sites with phenotypic traits of greater adaptive value (Blanco-Pastor et al., 2021), such as the initial vigor of the plants. Seedling characteristics associated with greater initial vigor, in addition to generating competitive advantages with positive impacts in later stages (Christie et al., 2022), have significant adaptive value during the plant establishment phase, when they are generally subjected to strong selection pressures from various factors (Barton et al., 2020; Larson et al., 2020; Welles & Funk, 2021), especially under current global warming conditions (Christie et al., 2022). Determining the degree of association between growth and environmental variables also allows for the selection of the best adapted individuals to specific environments and the improve their productivity (Singh et al., 2015).

Implications for genetic resource management

The significant variation among families in germination capacity and morphological characteristics of seedlings indicates genetic differentiation at the early stages of the *P. patula* life cycle. In conifers, these traits have adaptive relevance since they directly influence establishment, survival, and subsequent reproductive success, fitness components of these species (Rehfeldt, 1993; Sáenz-Romero, 2004). Correlations of seedling traits with geoclimatic factors such as latitude and temperature variables indicate that populations from warmer environments with longer frost-free periods exhibit greater vigor at early stages of development. This pattern can be interpreted as a product of natural selection favoring genotypes with greater initial growth in environments where the growth window is wide and the risk of frost damage is lower (Rehfeldt, 1993). The differences observed in *P. patula* may reflect historical processes of natural selection linked to the mountainous topography and North-South orientation of the Mexican mountain ranges, where small changes in latitude and elevation imply significant climatic contrasts.

The canonical F1 function confirms that the covariation between morphological traits and climate is, to some extent, of genetic origin, with adaptive value. The high contribution of *GC* and *CL* suggests that these traits concentrate a significant portion of the adaptive variance at initial stages of seedling establishment.

The effect of climatic factors, such as *TMMC* and *TEX*, suggests that genetic differentiation follows climatic gradients rather than solely geographic distances; that is, it shows evidence of local adaptation (Sáenz-Romero, 2004). However, some of the variation in germination capacity and initial size could include maternal effects, especially considering differences in seed quality and storage. In forest species, maternal effects can determine phenotypic expression at the juvenile level without necessarily implying genetic differences. The observed pattern partially coincides with that reported in other Mexican conifer species, such as *Pseudotsuga menziesii*

(Juárez-Agis et al., 2006) and *Pinus chiapensis* (Capilla-Dinorin et al., 2021, 2025), supporting the clinal differentiation hypothesis. However, interspecific discrepancies, such as those found in *P. oocarpa* (Velasco-García & Hernández-Hernández, 2024), show that evolution can differ between species even under similar environmental gradients.

Taken together, the results suggest that *P. patula* exhibits differential adaptation at early ages, mainly associated with geographic and thermal gradients. This pattern is consistent with models of natural selection in different environments, where selective pressure varies across the landscape, generating population differentiation.

Identifying the main geoclimatic factors that influence the adaptive value of plant morphological traits during their field establishment phase is extremely useful for guiding the most appropriate actions in managing the species' genetic resources, especially in the context of climate change. For example, this information is useful for locating suitable seed collection sites and for the correct use of germplasm in planting and reforestation programs, as well as for germplasm transfer in different geographic regions within the species' distribution area and for establishing germplasm production units for the species.

Conclusions

There is considerable variation among the evaluated progenies in seed germination capacity and seedling morphology. In particular, germination capacity, cotyledon length, and hypocotyl length have adaptive value, as they were significantly associated with some of the geoclimatic variables at the progenies' site of origin. The most important geoclimatic variables were latitude, longitude and extreme temperature during the 1991-2020 period.

The associations detected reflect both adaptive genetic differentiation and possible maternal effects. However, the differentiation in morphological traits with adaptive value at early stages of plant development is highly useful for establishing appropriate management measures for the species' genetic resources in the context of climate change, enabling plants to cope with more frequent and intense environmental stress events during the field establishment phase.

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Conflict of interest

There is no conflict of interest. Liliana Muñoz Gutiérrez declares that she did not participate in any stage of the article's editorial process.

Contribution by author

Araceli Hernández López: fieldwork and drafting of the first version of the manuscript; Liliana Muñoz Gutiérrez: research organization, fieldwork, and writing; J. Jesús

Vargas Hernández: data analysis, interpretation of results, and manuscript writing; Javier López Upton: manuscript writing and editing.

References

Adams, W. T., Aitken, S. N., Joyce, D. G., Howe, G. T., & Vargas-Hernández, J. (2001). Evaluating efficacy of early testing for stem growth in coastal Douglas-fir. *Silvae Genetica*, *50*(3-4), 167-175. https://pnwtirc.forestry.oregonstate.edu/evaluating-efficacy-early-testing-stem-growth-coastal-douglas-fir

Badilla, Y., & Murillo, O. (2026). Optimal age for selection in breeding clonal *Tectona grandis*. *Silvae Genetica*, *75*(1), 1-8. https://doi.org/10.2478/sg-2026-0001

Bareke, T (2018). Biology of seed development and germination physiology. *Advances in Plants & Agriculture Research*, *8*(4), 336-346. https://www.doi.org/10.15406/apar.2018.08.00335

Barton, K. E., Jones, C., Edwards, K. F., Shiels, A. B., & Knight, T. (2020). Local adaptation constrains drought tolerance in a tropical foundation tree. *Journal of Ecology*, *108*(4), 1540-1552. https://doi.org/10.1111/1365-2745.13354

Blanco-Pastor, J. L., Barre, P., Keep, T., Ledauphin, T., Escobar-Gutiérrez, A., Roschanski, A. M., Willner, E., Dehmer, K. J., Hegarty, M., Muylle, H., Veeckman, E., Vandepoele, K., Ruttink, T., Roldán-Ruiz, I., Manel, S., & Sampoux, J.-P. (2021). Canonical correlations reveal adaptive loci and phenotypic responses to climate in perennial ryegrass. *Molecular Ecology Resources*, *21*(3), 849-870. https://doi.org/10.1111/1755-0998.13289

Cai, H., Shao, J., & Shen, Y. (2025). Seed storability in forest trees: research progress and future perspectives. *Forests*, *16*(3), Article 467. https://doi.org/10.3390/f16030467

Cai, N., Xu, Y., Chen, S., He, B., Li, G., Li, Y., & Duan, A. (2016). Variation in seed and seedling traits and their relations to geo-climatic factors among populations in

Yunnan Pine (*Pinus yunnanensis*). *Journal of Forest Research*, *27*, 1009-1017. https://doi.org/10.1007/s11676-016-0228-z

Callejas-Díaz, M., Chambel, M. R., San-Martín-Lorén, J., Gea-Izquierdo, G., Santos-del-Blanco, L., Postma, E., & Climent, J. M. (2022). The role of maternal age, growth, and environment in shaping offspring performance in an aerial conifer seed bank. *American Journal of Botany*, *109*(3), 366-376. https://doi.org/10.1002/ajb2.1811

Capilla-Dinorin, E., López-Upton, J., Jiménez-Casas, M., & Pérez-Luna, A. (2025). Supervivencia y crecimiento inicial de *Pinus chiapensis* en gradientes ambientales de Puebla y Veracruz. *Ecosistemas y Recursos Agropecuarios*, *12*(3), Artículo e4739. https://doi.org/10.19136/era.a12n3.4739

Capilla-Dinorin, E., López-Upton, J., Jiménez-Casas, M., & Rebolledo-Camacho, V. (2021). Características reproductivas y calidad de semilla en poblaciones fragmentadas de *Pinus chiapensis* (Martínez) Andresen. *Revista Fitotecnia Mexicana*, *44*(2), 211-219. https://doi.org/10.35196/rfm.2021.2.211

Caruso, C. M., Maherali, H., & Martin, R. A. (2019). A meta-analysis of natural selection on plant functional traits. *International Journal of Plant Sciences*, *181*(1), 44-55. https://doi.org/10.1086/706199

Castoldi, E., & Molina, J. A. (2014). Effect of seed mass and number of cotyledons on seed germination after heat treatment in *Pinus sylvestris* L. var. *iberica* Svob. *Forest Systems*, *23*(3), 483-489. https://doi.org/10.5424/fs/2014233-05480

Center for Forest Conservation Genetics. (2023). *ClimateNA_MAP* (version 7.42) [Climate database]. University of British Columbia. https://climatena.ca/mapversion

Christie, K., Pierson, N. R., Lowry, D. B., & Holeski, L. M. (2022). Local adaptation of seed and seedling traits along a natural aridity gradient may both predict and constrain adaptive responses to climate change. *American Journal of Botany*, *109*(10), 1529-1544. https://doi.org/10.1002/ajb2.16070

Corbineau, F. (2024). The effects of storage conditions on seed deterioration and ageing: how to improve seed longevity. *Seeds*, *3*(1), 56-75. https://doi.org/10.3390/seeds3010005

Duncan, C., Schultz, N., Lewandrowski, W., Good, M. K., & Cook. S. (2019). Lower dormancy with rapid germination is an important strategy for seeds in an arid zone with unpredictable rainfall. *PLoS One*, *14*(9), Article e0218421. https://doi.org/10.1371/journal.pone.0218421

Dvorak, W. S., Hodge, G. R., Kietzka, J. E., Malan, F., Osorio, L. F., & Stanger, T. K. (2000). *Pinus patula*. In Central America and Mexico Coniferous Resources Cooperative (Ed.), *Conservation & testing of tropical & subtropical forest tree species* (pp. 148-173). College of Natural Resources. https://www.cabidigitallibrary.org/doi/full/10.5555/20003029405

Escobar-Sandoval, M. C., Vargas-Hernández, J. J., López-Upton, J., Espinosa-Zaragoza, S., & Borja-de la Rosa, A. (2018). Parámetros genéticos de calidad de madera, crecimiento y ramificación en *Pinus patula*. *Madera y Bosques*, *24*(2), Artículo e2421595. https://doi.org/10.21829/myb.2018.2421595

Farahani, H. A., Moaveni, P., & Maroufi, K. (2011). Effect of seed size on germination percentage in green gram (*Vigna radiata* L.). *Advances in Environmental Biology*, *5*(7), 1674-1679. https://www.aensiweb.com/old/aeb/2011/1674-1679.pdf

Farfán-Vázquez, E. de G., Jasso-Mata, J., López-Upton, J., Vargas-Hernández, J. J., & Ramírez-Herrera, C. (2002). Parámetros genéticos y eficiencia de la selección temprana en *Pinus ayacahuite* Ehren. var. *ayacahuite*. *Revista Fitotecnia Mexicana*, *25*(3), 239-246. https://doi.org/10.35196/rfm.2002.3.239

George-Miranda, S., Guillén, S., Viveros-Viveros, H., Montero-Nava, R., & Martínez y Pérez, J. L. (2022). Low germination rate of *Pinus hartwegii* seeds from trees growing at high elevations: Vulnerability to climate change? *Forest Ecology and Management*, *507*, Article 120001. https://doi.org/10.1016/j.foreco.2021.120001

Ghildiyal, S. K., Sharma, C. M., & Gairola, S. (2009). Environmental variation in seed and seedling characteristics of *Pinus roxburghii* Sarg. from Uttarakhand, India. *Applied Ecology and Environmental Research*, *7*(2), 121-129. https://doi.org/10.15666/aeer/0702_121129

Hamann, A., Koshy, M. P., Namkoong, G., & Ying, C. C. (2000). Genotype×environment interactions in *Alnus rubra*: developing seed zones and seed-transfer guidelines with spatial statistics and GIS. *Forest Ecology and Management*, *136*(1-3), 107-119. https://doi.org/10.1016/S0378-1127(99)00284-4

Hermesh, R., & Acharya, S. N. (1992). Influence of maternal plant environment and provenance on alpine bluegrass seed germination. *Canadian Journal of Plant Science*, *72*(3), 801-808. https://doi.org/10.4141/cjps92-096

Hojjat, S. (2011). Effects of seed size on germination and seedling growth of some Lentil genotypes (*Lens culinaris* Medik.). *International Journal of Agriculture and Crop Sciences*, *3*(1), 1-5. https://www.researchgate.net/publication/330159194_Effects_of_seed_size_on_germination_and_seedling_growth_of_some_Lentil_genotypes_Lens_culinaris_Medik

International Seed Testing Association. (2024). International Rules for Seed Testing. In International Seed Testing Association (Ed.), *International Rules for Seed Testing* (Chapter 2, i–2-44 (52)). International Seed Testing Association. https://www.seedtest.org/api/rm/9356SQF24TUK454/ista-rules-2024-02-sampling-final.pdf

Juárez-Agis, A., López-Upton, J., Vargas-Hernández, J. J., & Sáenz-Romero, C. (2006). Variación geográfica en la germinación y crecimiento inicial de plántulas de *Pseudotsuga menziesii* de México. *Agrociencia*, *40*(6), 783-792. https://www.agrociencia-colpos.org/index.php/agrociencia/article/view/509

Larson, J. E., Anacker, B. L., Wanous, S., & Funk, J. L. (2020). Ecological strategies begin at germination: Traits, plasticity and survival in the first 4 days of plant life. *Functional Ecology*, *34*(5), 968-979. https://doi.org/10.1111/1365-2435.13543

Leger, E. A., Atwater, D. Z., & James, J. J. (2019). Seed and seedling traits have strong impacts on establishment of a perennial bunchgrass in invaded semi-arid systems. *Journal of Applied Ecology*, *56*(6), 1343-1354. https://doi.org/10.1111/1365-2664.13367

Liu, L., Hu, J., Chen, X., Xu, X., Yang, Y., & Ni, J. (2022). Adaptation strategy of karst forests: Evidence from the community-weighted mean of plant functional traits. *Ecology and Evolution*, *12*(3), Article e8680. https://doi.org/10.1002/ece3.8680

Loha, A., Tigabu, M., Teketay, D., Lundkvist, K., & Fries, A. (2006). Provenance variation in seed morphometric traits, germination, and seedling growth of *Cordia africana* Lam. *New Forest*, *32*, 71-86. https://doi.org/10.1007/s11056-005-3872-2

Metz, J., Freundt, H., & Jeltsch, F. (2018). Stable germination behavior but partly changing seed-seed interactions along a steep rainfall gradient. *Basic and Applied Ecology*, *28*, 5-16. https://doi.org/10.1016/j.baae.2018.01.004

Morales-González, E., López-Upton, J., Vargas-Hernández, J. J., Ramírez-Herrera, C., & Gil-Muñoz, A. (2013). Parámetros genéticos de *Pinus patula* en un ensayo de progenies establecido en dos altitudes. *Revista Fitotecnia Mexicana*, *36*(2), 155-162. https://doi.org/10.35196/rfm.2013.2.155

Pérez-Luna, A., Prieto-Ruíz, J. Á., López-Upton, J., Madrid-Aispuro, R. E., & Salcido-Ruíz, S. (2024). Ensayos de germinación y producción de planta de procedencias-progenies de *Pinus patula*. *Bosque*, *45*(2), 257-269. http://dx.doi.org/10.4067/s0717-92002024000200257

Ranade, S. S., & García-Gil, M. R. (2021). Molecular signatures of local adaptation to light in Norway spruce. *Planta*, *253*, Article 53. https://doi.org/10.1007/s00425-020-03517-9

Rawat, K., & Bakshi, M. (2011). Provenance variation in cone, seed and seedling characteristics in natural populations of *Pinus wallichiana* A. B. Jacks (Blue Pine) in India. *Annals of Forest Research*, *54*(1), 39-55. https://doi.org/10.15287/afr.2011.96

Rehfeldt, G. E. (1993). Genetic variation in the Ponderosae of the Southwest. *American Journal of Botany*, *80*(3), 330-343. https://doi.org/10.1002/j.1537-2197.1993.tb13807.x

Rzedowski, J. (1978). *Vegetación de México*. Editorial Limusa, S. A.

Sáenz-Romero, C. (2004). Zonificación estatal y altitudinal para la colecta y movimiento de semillas de coníferas en México. En J. J. Vargas-Hernández, B. Bermejo-Velázquez & F. T. Ledig (Eds.), *Manejo de recursos genéticos forestales* (2da edición, pp. 65-77). Colegio de Postgraduados y Comisión Nacional Forestal. https://d1wqtxts1xzle7.cloudfront.net/40552297/Manejo_de_Recursos_geneticos_Forestales-libre.pdf?1449003820=&response-content-disposition=inline%3B+filename%3DManejo_de_Recursos_geneticos_Forestales.pdf

&Expires=1782167979&Signature=Nc740dY4zH8uudv6iql1JnYMA3GPGtYMD4so0CwEqPXReU4tYg0wwbMiQHikEvg-1EH~XqO1ceWVVHdStRPl9IhcM6q2TNSioH3n2pr-uHc5Qm35v6xlVeUiWNS0VNNHSWBphj41j6vrRKRrkPJIg9c~64kaTXOcnOUuTovh7GpyN13nObX4rdOF51QaH6WcdeRtAodsjJd-8MPelhjlxJ6veO3gGbYkeodz-y7UFS554dNd8iC~w~V2Dhdk1FWOKNK1G6fA21DxSXTMxlwCh3xhunQefQWmB2z0p29fPktd1ftZQv2pq-dbJQtZYovPaMmOy2~EaLhZ9K84~GEt8A__&Key-Pair-Id=APKAJLOHF5GGSLRBV4ZA#page=66

Salaya-Domínguez, J. M., López-Upton, J., & Vargas-Hernández, J. J. (2012). Variación genética y ambiental en dos ensayos de progenies de *Pinus patula*. *Agrociencia*, *46*(*5*), 519-534. https://www.agrociencia-colpos.org/index.php/agrociencia/article/view/973

SAS Institute Inc. (2012). *Installation and Maintenance instructions for SAS*$^{®}$ *9.2 installation kit for z/OS*$^{®}$ *Cartridges*. SAS Institute Inc. https://support.sas.com/documentation/installcenter/en/ikinstallcartii/63179/PDF/default/install_cart.pdf

Sasaki, S., & Kozlowski, T. T. (1970). Effects of cotyledon and hypocotyls photosynthesis on growth of young pine seedlings. *New Phytologist*, *69*(2), 493-500. https://doi.org/10.1111/j.1469-8137.1970.tb02445.x

Seiffert, S., Weber, S., Sack, U., & Keller, T. (2024). Use of logit transformation within statistical analyses of experimental results obtained as proportions: example of method validation experiments and EQA in flow cytometry. *Frontiers in Molecular Biosciences*, *11*, Article 1335174. https://doi.org/10.3389/fmolb.2024.1335174

Singh, O., & Thapliyal, M. (2012). Variation in cone and seed characters in blue pine (*Pinus wallichiana*) across natural distribution in western Himalayas. *Journal of Forestry Research*, *23*, 235-239. https://doi.org/10.1007/s11676-012-0246-4

Singh, O., Bordoloi, S., & Mahanta, N. (2015). Variability in cone, seed and seedling characteristics of *Pinus kesiya* Royle ex. Gordon. *Journal of Forestry Research*, *26*, 331-337. https://doi.org/10.1007/s11676-015-0036-x

Ulusan, M. D., & Bilir, N. (2008). Broad-sense heritability for seedling characters and its importance for breeding in Scots pine. *Süleyman Demirel University Faculty of Arts* *and Science Journal of Science*, *3*(2), 133-138. https://dergipark.org.tr/en/pub/sdufeffd/article/134649

Vargas-Hernández, J. J., & Adams, W. T. (1992). Age-age correlation and early selection for wood density in young coastal Douglas-fir. *Forest Science*, *38*(2), 467-478. https://doi.org/10.1093/forestscience/38.2.467

Vela, G. L. (1980). *Contribución a la ecología de Pinus patula Schl. et Cham*. [Publicación especial Núm. 19]. Instituto Nacional de Investigaciones Forestales.

Velasco-García, M. V., & Hernández-Hernández, A. (2024). Altitudinal genetic variation of *Pinus oocarpa* seedling emergence in the Southern Mountains, Oaxaca, México. *Seeds*, *3*(1), 1-15. https://doi.org/10.3390/seeds3010001

Wahid, N., & Bounoua, L. (2013). The relationship between seed weight, germination and biochemical reserves of maritime pine (*Pinus pinaster* Ait.) in Morocco. *New Forests*, *44*, 385-397. https://doi.org/10.1007/s11056-012-9348-2

Welles, S. R., & Funk, J. L. (2021). Patterns of intraspecific trait variation along an aridity gradient suggest both drought escape and drought tolerance strategies in an invasive herb. *Annals of Botany*, *127*(4), 461-471. https://doi.org/10.1093/aob/mcaa173

Zhang, H., Zhou, D., Matthew, C., Wang, P., & Zheng, W. (2008). Photosynthetic contribution of cotyledons to early seedling development in *Cynoglossum divaricatum* and *Amaranthus retroflexus*. *New Zealand Journal of Botany*, *46*(1), 39-48. https://doi.org/10.1080/00288250809509752