



Christian Wehenkel ^{1,*}, José Marcos Torres-Valverde ², José Ciro Hernández-Díaz ¹, Eduardo Mendoza-Maya ³, Artemio Carrillo-Parra ¹, Santiago Solis-González ⁴ and Javier López-Upton ⁵

- ¹ Instituto de Silvicultura e Industria de la Madera, Universidad Juárez del Estado de Durango, Durango 34120, Mexico
- ² Maestría Institucional en Ciencias Agropecuarias y Forestales, Universidad Juárez del Estado de Durango, Durango 34000, Mexico
- ³ Programa Institucional de Doctorado en Ciencias Agropecuarias y Forestales, Universidad Juárez del Estado de Durango, Durango 34000, Mexico
- ⁴ Instituto Tecnológico de El Salto, Durango 34942, Mexico
- ⁵ Postgrado en Ciencias Forestales Colegio de Postgraduados, Montecillo, Texcoco 56264, Mexico
- * Correspondence: wehenkel@ujed.mx; Tel.: +52-(618)-102-0873

Abstract: The distributions of the three Mexican spruces are fragmented, possibly leading to phenological, morphological and genetic differentiation, which is partly caused by local adaptation. In this study, we estimated for the first time the intra- and inter-specific phenotypic variation in 5641 seedlings from provenances of the three Mexican spruces. We examined (i) provenance-related differences in the seedling survival rate, diameter (D), height (H) and seed weight (SW) as quantitative traits, (ii) the association between the survival rate, D, H and SW and climatic and soil variables in the Picea provenances and (iii) (narrow-sense) heritability (within-provenance) based on D and H under the same nursery conditions, assuming that the response can be considered as a proxy for quantitative genetic differentiation between provenances. All Mexican spruce species differed significantly in H, and all eight provenances studied were significantly different in D and H, except for two neighboring provenances of *P. mexicana*. Very strong, significant correlations (up to $R^2 = 0.96$) were found between H, the survival rate and SW with respect to environmental factors of provenance/seed origin. Additionally, the heritability index explained a high percentage of the provenance-related variance. The use of germplasm for restoration in different sites and with different populations requires collecting seeds from numerous trees from as many provenances as possible, but should be carried out with caution owing to the apparently strong local adaptation in provenances of the Mexican spruces.

Keywords: Picea; Mexican spruces; quantitative genetic traits; genetic differentiation; provenance; heritability; nursery conditions; trans-specific trait; tree species conservation

1. Introduction

Provenance in forestry can be defined as the particular place where trees are growing naturally or the place of origin of any germplasm. The term provenance is generally applied to a tree population growing in a certain location and not to an individual tree [1]. Although the concept of "provenance" is commonly used at the species level, Gregorius et al. [2] developed an operational trait concept that, under specific conditions, allows for the measurement of variation in traits that can be observed in members of the same species and also in members of different species. This concept is based on research methods that can be adapted to a broader range of organisms without altering their traits. These traits, referred to as "trans-specific" traits, have been measured in several previous studies, e.g., [3–5]. Provenance–progeny trials enable the study of the genetic basis of quantitative traits and assessment of the degree of local adaptation [6–10]. In this context, heritability can be defined as the proportion of variance in phenotypic traits that can be attributed



Citation: Wehenkel, C.; Torres-Valverde, J.M.; Hernández-Díaz, J.C.; Mendoza-Maya, E.; Carrillo-Parra, A.; Solis-González, S.; López-Upton, J. Adaptive Trait Variation in Seedlings of Rare Endemic Mexican Spruce Provenances under Nursery Conditions. *Forests* **2023**, *14*, 790. https://doi.org/10.3390/f14040790

Academic Editor: Giovanbattista De Dato

Received: 16 March 2023 Revised: 3 April 2023 Accepted: 6 April 2023 Published: 12 April 2023



Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). to genetic variation in a provenance [11]. Several provenance trials have reported the heritability of quantitative traits in forest trees, such as tree height and diameter [12] and seed size [13–17].

Provenance trials are time-consuming and usually only provide a measure of phenotypic differences among populations under common conditions. However, no breeding experience is available, and provenance trials have not been carried out with the three rare, endemic and endangered Mexican spruces *Picea chihuahuana* Martínez, *P. martinezii* Patterson and *P. mexicana* Martínez (NOM-059-ECOL-2010, SEMARNAT, 2010) [18]. *P. chihuahuana* is only located in the Sierra Madre Occidental (SMOc) in the states of Chihuahua and Durango, Mexico (total cover ~300 ha). The 40 documented provenances of this species have between 21 and 5546 individuals (a total of approximately 42,600 mature trees), which are found in three geographical groups approximately 300 km apart [19,20]. Growing in an area of approximately 157 ha, *P. martinezii* only occurs in the Sierra Madre Oriental (SMOr) at elevations between 1800 and 2500 m in the four documented provenances in the state of Nuevo León, Mexico [18]. By contrast, *P. mexicana* occurs in three montane to subalpine sites above 3000 m, thriving in an area of approximately 173 ha; two provenances are in two of the highest peaks in the SMOr, at the border of the Mexican states of Coahuila and Nuevo León, and the third location is the highest peak in the SMOc, in the state of Chihuahua [21].

Given the high degree of isolation of the provenances of the three Mexican spruces (especially the isolation between these species), strong genetic differentiation and, respectively, a large genetic variation among the provenances have been observed and partly attributed to geographical (e.g., distance, relief, elevation), ecological and possibly pre- or post-zygotic barriers and time. Plastid, mitochondrial and nuclear sequences show that *P. mexicana* (a sister species of the more widespread *P. pungens* Engelm.), *P. chihuahuana* and *P. martinezii* are genetically distinct [22]. Moreover, isozyme analysis showed that the mean genetic differentiation (measured by the Fixation index, F_{ST}) for ten provenances of *P. chihuahuana* was 0.248 (i.e., 75.2% of the total genetic variation is within provenances and 24.8% among provenances), which is outside the range reported in most previous studies in conifers [23]. By contrast, the F_{ST} was 0.024 for two provenances of *P. martinezii* [24] and 0.069 for the three provenances of *P. mexicana* [25], i.e., higher than the average F_{ST} for spruces [23]. However, with SNP data, the F_{ST} was 0.027 for the four provenances of *P. martinezii* and 0.028 for the three provenances of *P. mexicana* [18].

Some of the genetic differentiation among these provenances may also have resulted from adaptation to the local climate and soil [20]. In this context, climatic variation across mountains often results in local adaptation to elevation, e.g., [26,27]; as it is closely correlated with key climatic factors, such as temperature and aridity [28]. Knowledge of possible local adaptation could be helpful in ex situ conservation programs for these three Mexican spruces. For example, as many genotypes as possible should be used for restoration and assisted migration to cope with climate change, but these genotypes should also be sufficiently adapted to the new locations [29,30].

In the present study, we estimated the intra- and inter-specific phenotypic variation in seedlings from eight provenances of the three Mexican spruces by applying the transspecific trait concept of Gregorius et al. [2]. More specifically, we examined (i) provenancerelated differences in the seedling diameter (D), height (H), survival rate and weight of 1000 seeds of parental trees (SW) as quantitative traits, (ii) the association between the survival rate, D, H and SW and climatic and soil variables in the *Picea* provenances and (iii) (narrow-sense) heritability (within-provenance) based on D and H in a common garden experiment under the assumption that the response can be considered as a proxy for quantitative genetic differentiation between provenances.

2. Materials and Methods

2.1. Study Site

The study was conducted between May 2019 and May 2020 in a nursery located in El Salto, Pueblo Nuevo, state of Durango, Mexico (23°47'11.72″ N, 105°21'55.18″ W) (https:// www.worldweatheronline.com/el-salto-weather-averages/durango/mx.aspx, (accessed on 8 April 2023)) with seeds from eight provenances: the largest of *Picea chihuahuana* (Pch) in the central part of its distribution area, situated in Guanaceví, Durango (mean annual temperature [Mat], 10.7 °C, and precipitation [Map], 740 mm), the four documented provenances of *P. martinezii* (Pma) from Nuevo León (Mat, 13.5 °C, and Map, 788 mm) and the three reported populations of *P. mexicana* (Pme) located in two different states in Mexico: one in Chihuahua and two in Coahuila (Mat, 9.3 °C, and Map, 858 mm) [20,21]. For each provenance, 10–30 dominant trees were randomly chosen, and 50–250 cones were collected from each (Table 1 and Figure 1). Although only one provenance of Pch was included and the trial thus did not meet the requirements of a species-level provenance trial, this provenance was an asset in the genus-level trial. Moreover, the Pch seed weight and survival and diameter and height growth of Pch seedlings have never been reported in previous studies.

Table 1. Location and population size of the eight provenances of three species of Mexican spruces under study and number of trees sampled (*N*); data of *Picea chihuahuana* from [20] and of *P. martinezii* and *P. mexicana* from [21].

Species	Code	Location Municipality, State	Population Size	Latitude (N)	Longitude (W)	Elevation (m)	N
	D 1 OD	Quebrada de los Durán,		a (2000/10//	10/000/50//	255 0	10
Picea chihuahuana	Pch-QD	Chiqueros, Guanacevi,	2628	26°08′48′′	106°22′53″	2570	10
Picea martinezii	Pma-AF	Agua Fría, Aramberri, Nuevo León	2769	24°02′17″	99°42′39″	1820	20
Pma-AA		Agua Alardín, Aramberri, Nuevo León	84,498	24°02′34″	99°44′04″	2120	30
	Pma-EB	El Butano, Ejido La Trinidad, Montemorelos, Nuevo León	1253	25°10′41″	100°07′37″	2180	30
	Pma-LE	La Encantada, Ejido La Encantada, Zaragoza, Nuevo León	712	23°53′24″	99°47′30″	2378	12
Picea mexicana	Pme-EM	El Mohinora, Ejidos El Tule y Portugal, Guadalupe y Calvo, Chihuahua	11,383	25°11′55″	100°21′52″	3113	30
	Pme-LM	La Marta, Felipe de la Peña, Arteaga, Coahuila	17,728	25°57′41″	107°02′32″	3494	29
	Pme-EC	El Coahuilón, Ejido Nuncio, Arteaga, Coahuila	2253	25°14′51″	$100^{\circ}21'17''$	3528	28

2.2. Determination of Climatic Variables

The climatic model developed [31] on the basis of thin plate spline (TPS) [32,33] and applied to Mexico [34] was used to estimate the values of 20 climatic variables in each location of the eight provenances of Mexican spruces. The point estimates of climate measures were obtained from a database managed by the University of Idaho (https://charcoal2.cnre.vt.edu/climate/ (accessed on 8 April 2023)), for which the geographical coordinates (latitude, longitude and elevation) were required as input data to predict the climatic variables in each location. The minimum, maximum and mean values of these climate values are listed in Table 2.



Figure 1. Locations of the eight provenances of the three Mexican spruces under study. *Picea chihuahuana* Quebrada de los Durán (Pch-QD); *P. martinezii* provenances of Agua Fría (Pma-AF), Agua Alardín (Pma-AA), El Butano (Pma-EB) and La Encantada (Pma-LE); *P. mexicana* provenances of El Mohinora (Pme-EM), La Marta (Pme-LM) and El Coahuilón (Pme-EC).

	Climatic Variable	Minimum	Maximum	Mean	SE *
Long	Longitude (degree)	-99.71	-107.04	-101.69	0.75
Lat	Latitude (degrees)	20.71	26.14	24.39	0.26
Elev	Elevation (m)	1820	3528	2644	223.00
Mat	Mean annual temperature (°C)	8.5	15.6	12.4	0.70
Map	Mean annual precipitation (mm)	649	1106	826	32.00
Gsp	Growing season precipitation, April to September (mm)	485	790	630	21.00
Mtcm	Mean temperature in the coldest month (°C)	3.7	11.6	8.5	0.80
Mmin	Mean minimum temperature in the coldest month (°C)	-5.9	4.5	1.1	1.00
Mtwm	Mean temperature in the warmest month (°C)	12.5	18.5	15.4	0.80
Mmax	Mean maximum temperature in the warmest month (°C)	19.4	25.6	23.0	0.83
Sday	Julian date of the last spring freezing (days)	39	184	89	14.22
Fday	Julian date of the first autumn freezing (days)	268	348	302	11.29
Ffp	Length of the frost-free period (days)	74	298	200	25.93
Dd5	Degree-days above 5 °C	1540	3873	2766	259.20
Gsdd5	Degree-days above 5 °C in the frost-free period	489	3408	2058	339.60
D100	Julian date when the sum of degree-days above 5 °C reaches 100	15	71	31.5	4.38
DD0	Degree-days below 0 °C (based on mean monthly temperature)	0	45	7.5	1.60
Mmindd0	Degree-days below 0 °C (based on mean minimum monthly temperature)	29	1162	316	91.84
Smrpb	Summer precipitation balance: (Jul + Aug + Sep)/(Apr + May + Jun)	1.29	4.77	2.39	0.32
Smrsprpb	Summer/Spring precipitation balance: (Jul + Aug)/(Apr + May)	1.26	13.14	4.84	1.32
Sprp	Spring precipitation (Apr + May) (mm)	26	129	94	11.36
Smrp	Summer precipitation (Jul + Aug) (mm)	163	486	275	20.57
Winp	Winter precipitation (Nov + Dec + Jan + Feb) (mm)	76	228	113	8.88

Table 2. Mean values of climate variable used for the environment–phenotype associations tests (* SE = standard error; data of *Picea chihuahuana* from [20] and of *P. martinezii and P. mexicana* from [21] for the time period 1961–1990).

The aforementioned climatic model estimates standardized monthly mean, minimum and maximum values of temperature and precipitation (e.g., mean annual precipitation (Map, mm), mean temperature of the warmest month (Mtwm, °C), Julian date of the first freezing date of autumn (Fday, days) and precipitation during the growing season (April-September; Gsp, mm), among others), which are based on data from weather stations in the northern states of Mexico, southern United States and the Caribbean countries for the period 1961–1990.

2.3. Determination of Edaphic Variables

In 2019, eight soil samples per provenance of *P. martinezii* and *P. mexicana* were collected to evaluate 27 edaphic variables (56 soil samples in total, 250 g each). The soil samples were randomly collected at a depth of 0–15 cm at the stem base of one spruce tree. Soil data for the *P. chihuahuana* provenance were taken from [20].

The following soil variables were considered: texture, density, concentration of calcium carbonate, pH and concentrations of potassium, magnesium, sodium, copper, iron, manganese, zinc and calcium in the soil, which were determined by the methods described by [35]. Phosphorus was determined by the method of [36]. Nitrate was determined by the method of [37], and the relative organic matter contents were measured by the method of [38]. Electrical conductivity was determined by the method described by [39]. Finally, the cation exchange capacity (CEC) was estimated on the basis of the ammonium acetate method (pH 8.5). The hydraulic conductivity was determined by the method of [40] and the percent of water saturation was measured by the method of [41]. These variables are listed in Table 3.

	Soil Variable	Minimum	Maximum	Mean	SE *
EC	Electrical conductivity (dS/m)	0.47	1.07	0.84	0.07
NO3	Nitrate (kg/ha)	86	628	261	63
Р	Phosphorus (mg/kg)	9.76	75.74	37.47	7.11
OM	Organic matter (%)	5.2	24.7	13.5	2.6
%CaCO ₃	Calcium carbonate (%)	0	1.18	0.28	0.20
%Sat	Percent saturation (%)	48.0	104.2	70.7	6.7
%Sand	Sand (%)	22.2	61.4	44.1	5.6
%Silt	Silt (%)	25.3	58	38.7	4.1
%Clay	Clay (%)	7.6	26.6	17.1	2.1
Den	Density (g/cm^3)	0.54	7.80	1.66	0.93
pН	pH	4.59	7.62	6.06	0.42
Ca	Calcium (mg/kg)	180	10,624	4784	1129
Mg	Magnesium (mg/kg)	123	528	263	49
Na	Sodium (mg/kg)	40.8	86.5	56.5	2.6
Κ	Potassium (mg/kg)	666	2475	1574	163
Fe	Iron (mg/kg)	31.2	521	234	52
Zn	Zinc (mg/kg)	3.0	118.1	19.7	14.9
Mn	Manganese (mg/kg)	18.9	171.7	59.0	17.5
Cu	Copper (mg/kg)	0.16	4.67	3.31	0.25
CEC	Cation exchange capacity (meq/100 g soil)	11.4	56.7	27.7	5.8
HC	Hydraulic conductivity (cm/h)	3.7	137.1	29.7	16.3

Table 3. Descriptive statistics for the 27 soil variables in provenance of *P. martinezii* and *P. mexicana* used for the environment–phenotype associations tests (* SE = standard error (sample = 56); data of *Picea chihuahuana* from [20] are not inserted in the table.).

2.4. Weight of 1000 Seeds, Survival and Growth Rate of Seedlings

The weight of 1000 seeds (*SW*, g) of each three randomly chosen parental trees per provenance was measured on a digital scale (Velab model No. VE-5000H, Mexico), and the mean weight was calculated for each provenance. We sowed 5641 seeds for evaluation of seedling survival and growth traits. A total of 93 seeds were from 10 *P. chihuahuana* trees; 2853 seeds were from 92 *P. martinezii* trees; and 2695 seeds were from 87 *P. mexicana* trees.

For common garden experiments, the seeds were first soaked in hydrogen peroxide (2%, v/v) for 24 h and were then sown in 170 cm³ plastic tubes containing a mixture of 60% peat moss, 20% agrolite, 20% vermiculite and 3 kg·m³ of a controlled-release fertilizer (Multicote[®]; 15% N + 7% P₂O₅ + 15% K₂O + 2 MgO + ME fertilizer). The tubes (containing seeds) were distributed in the 56 plastic trays, each with 98-hole plastic containers (7 × 14 cavities), in a randomized complete-block design. Provenance data-codes were maintained throughout the 12-month monitoring period; i.e., "species—provenance—seedling number—repetition".

Additionally, N-P-K Multicote[®] 08-25-17 soluble fertilizer (5.0%, v/v) was added once a week during two months of early growth of the seedlings. During the rapid growth phase, N-P-K Multicote[®] 20-09-20 soluble fertilizer (20%, v/v) was added once a week until six months of age. Finally, at the hardening stage, N-P-K Multicote[®] 04-25-40 soluble fertilizer (5.0%, v/v) was applied once a week until 12 months of age. Water was supplied by an automatic irrigation system three days/week. During the germination and growth of seedlings (first six months), a 720-gauge polyethylene plastic cover was used to protect the seedlings from ultraviolet rays, with no shading mesh. At the preconditioning stage (2 months), the seedlings were kept under a 50% light mesh shade, whereas, at the hardening stage (from month seven) the seedlings were kept outdoors.

Differences in growth of seedlings were evaluated monthly over a 12-month period by measuring basal diameter (at plant collar) (*D*, mm) with a digital Vernier scale of resolution tenths of a millimeter (AVEDISTANT, LCD6). The plant height at the apical growth bud (*H*, mm) was monthly measured with a flexometer to the nearest mm (Uline Accu-Lock,

H-1766). Survival rate was also determined at 12-month age, at which point 4753 seedlings were alive (Table 4).

Table 4. Descriptive statistics for seed traits and survival rate of each provenance of the Mexican spruces studied (* SW = weight of 1000 seeds, SE = standard error, NA = not available; ** PN = number of progenies evaluated).

Species	Provenance Code	SW (SE) * (g)	PN **	No. of Seeds Sown	Emerged Seedlings (%)	Survival after 12 Months (%)
Picea chihuahuana	Pch-QD	8.3 (NA)	NA	93	93.5	79.2
P. martinezii	Pma-AF	24.4 (0.013)	20	618	86.4	96.7
	Pma-AA	22.0 (0.0065)	30	930	90.8	97.6
	Pma-EB	23.0 (0.014)	30	930	89.5	93.5
	Pma-LE	20.0 (0.00027)	12	375	82.9	93.7
P. mexicana	Pme-EM	4.9 (0.00072)	30	929	95.5	87.6
	Pme-LM	5.1 (0.00072)	29	899	91.4	90.4
	Pme-EC	4.9 (0.003)	28	867	94.8	91.3

2.5. Classification by Cluster Analysis

To group the eight *Picea* provenances by seedling diameter, height and survival, we used the affinity propagation (AP) clustering technique, with the input preference to the quantile (q) = 1 of the input similarities [42] along with the k-means clustering algorithm (k-means) [43]. We also used the Calinski–Harabasz criterion (CHC) to determine the optimal number of clusters. CHC minimizes the within-cluster sum of squares and maximizes the between-cluster sum of squares. The highest CHC value is related to the optimal set. In this test, the optimal set can be identified by a peak on the linear plot of CHC values [44]. All cluster analyses were implemented using the "k-means" and "apcluster" packages [42,43], executed in the R free statistical software, version 3.2.3 [45].

2.6. Pairwise Multiple Comparisons of Mean Rank Sums and Spearman's Correlations

The median differences in survival rate and growth traits (D and H) among the three species, among the eight provenances of the three species and among the progenies within each provenance (Table 4) were tested using the non-parametric Tukey–Kramer (Nemenyi) test after corroborating a Tukey-distribution with the PMCMR package [46], implemented in R.

We used the Spearman's correlation (r_s) test [47] to analyze how survival rate, D, H and SW were related to the climatic and soil variables for each provenance (alpha = 0.025). First, we used the randomForest package in R [48] to detect which variables were most closely correlated with the growth traits. Spearman's correlations and their p values were then estimated in R [45]. Finally, some linear regression models (including R^2_{adj} , its p value, slope parameter (β) and intercept (α)) were created using the ggplot [49] package and lm function in R.

2.7. Heritability of Picea martinezii and Picea mexicana

To test whether provenance variation was significant, variance components were obtained using the PROC VARCOMP procedure and the restricted maximum likelihood method in the Statistical Analysis System software (SAS 9.0) [50].

To calculate the heritability and estimate the variance components, we used the MIXED procedure and the REML method, which are considered to be the most appropriate when the data are imbalanced [51], in SAS 9.0. The genetic control of each variable was evaluated using the equations described by [52]:

$$\begin{aligned} h_i^2 &= \sigma_A^2 / \left(\sigma_f^2 + \sigma_{bf}^2 + \sigma_e^2 \right) \\ h_f^2 &= \frac{1}{4\sigma_A}^2 / \left(\sigma_f^2 + \sigma_{bf}^2 + \frac{\sigma_e^2}{b} \right) \end{aligned}$$

where: h_i^2 = individual heritability; h_f^2 = family heritability; σ_A^2 = additive genetic variance = $3\sigma_f^2$; σ_f^2 = variance of families; σ_e^2 = variance of error; b = number of blocks (here b = 21).

A genetic determination coefficient of 3 was used to estimate additive genetic variance under the assumption that intra-class correlation in sibling families obtained by free pollination is 1/3 [53] and not 1/4 as in true half-sibling families [52].

3. Results

3.1. Provenance Differences in Quantitative Traits

Statistically significant differences between the provenances of the three Mexican spruces (*Picea chihuahuana, P. martinezii* and *P. mexicana*) in diameter and height were observed during the first 12 months after germination (Figure 2). However, the growth traits of some provenances were similar (Table 5). Differences in the seedling size of the provenances increased with age (Figure 2).



Figure 2. Monthly measurements of diameter (**a**) and height (**b**) growth traits of provenances of three Mexican spruces (June 2019—May 2020). *Picea chihuahuana*—only one provenance, Quebrada de los Durán (Pch-QD). *Picea martinezii* (Pma)—four provenances: Agua Fría (Pma-AF), Agua Alardín (Pma-AA), El Butano (Pma-EB) and La Encantada (Pma-LE). *Picea mexicana* (Pme)—three provenances: El Mohinora (Pme-EM), La Marta (Pme-LM) and El Coahuilón (Pme-EC).

Table 5. Absolute differences in mean diameter (*D*) and height (*H*) among the eight provenances of three Mexican spruces and respective *p*-values for differences in *H* and *D* (in brackets) (* Pro = provenances of: Pch-QD = *Picea chihuahuana*-Quebrada de los Durán, Pma-AF = *Picea martinezii*-Agua Fría, Pma-AA = *Picea martinezii*-Agua de Alardín, Pma-EB = *Picea martinezii*-El Butano, Pma-LE = *Picea martinezii*-La Encantada, Pme-EM = *Picea mexicana*-El Mohinora, Pme-LM = *Picea mexicana*-La Marta, Pme-EC = *Picea mexicana*-El Coahuilón.

Pro *	<i>D</i> (mm)	<i>H</i> (mm)	Pma-AF	Pma-AA	Pma-EB	Pma-LE	Pme-EM	Pme-LM	Pme-EC
Pch-QD	0.9	67	$5,50 \\ (2 \times 10^{-16} \\ 7.2 \times 10^{-14})$	$\begin{array}{c} 4,38\\(2\times10^{-16}\\9.2\times10^{-14})\end{array}$	$\begin{array}{c} 4,39 \\ (8.2\times 10^{-14} \\ 1.1\times 10^{-13}) \end{array}$	3,22 $(1.1 imes 10^{-7})$ $2.2 imes 10^{-5}$	$5,15(7.2 \times 10^{-14}0.003)$	$3, 3(1 \times 10^{-10}0.996)$	$3,4(1.1 \times 10^{-8}0.996)$
Pma-AF	1.4	117		1, 12 (0.008 0.001)	$1, 11 (1.1 \times 10^{-11} \\ 0.0006)$	$2,28 \ (2 imes 10^{-16} \ 7.9 imes 10^{-14})$	$0,35 \ (1.9 imes 10^{-5} \ 2 imes 10^{-16})$	$2,47 \ (2 imes 10^{-16} \ 2 imes 10^{-16})$	2,46 (2×10^{-16}) $2 \times 10^{-16})$
Pma-AA	1.4	105			0, 1 (0.0007 1.000)	$\begin{array}{c} 1, 16 \\ (5.9 \times 10^{-14} \\ 1.5 \times 10^{-11}) \end{array}$	1, 23 (0.7568 2×10^{-16})	$1,35 \ (1.8 imes 10^{-14} \ 2 imes 10^{-16})$	$1, 34 (2 \times 10^{-16}) 2 \times 10^{-16})$
Pma-EB	1.3	106				$\begin{array}{c} 1,17\\ (2.6\times10^{-9}\\ 6.8\times10^{-11})\end{array}$	1,24 (0.1625 $2 imes 10^{-16}$)	$\begin{array}{c} 1,36\\ (9.2\times 10^{-11}\\ 2\times 10^{-16})\end{array}$	$1,35 \ (6.5 imes 10^{-14} \ 2 imes 10^{-16})$
Pma-LE	1.2	89					2,7 (8.2 × 10 ⁻¹⁴ 0.172)	$0, 19 \\ (0.916 \\ 9.5 \times 10^{-14})$	0, 18 (1.00 $9.6 imes 10^{-14}$)
Pme-EM	1.4	82						$\begin{array}{c} 2,12\\ (6.6\times10^{-14}\\ 5.3\times10^{-13})\end{array}$	$2, 11 \ (1.2 imes 10^{-14} \ 5.8 imes 10^{-13})$
Pme-LM	1.2	70							0, 1 (0.681 1.000)
Pme-EC	1.2	71							,

The Calinski–Harabasz criterion (CHC) detected seven clusters based on the seedling survival rate, diameter and height (Figure 3a). Affinity propagation clustering also distinguished seven clusters (i.e., seven provenances) in the three *Picea* species studied, since Pme-LM and Pme-EC are in the same cluster (Figure 3b).



Figure 3. Grouping tests for the eight *Picea* provenances by seedling diameter, height and survival. Both the Calinski–Harabasz criterion (**a**) and the affinity propagation clustering technique (q = 1) (**b**) distinguished seven clusters. Pch-QD = *P. chihuahuana*—Quebrada de los Durán, Pma-AF = *P. martinezii*—Agua Fría, Pma-AA = *P. martinezii*—Agua Alardín, Pma-EB = *P. martinezii*—El Butano, Pma-LE = *P. martinezii*—La Encantada, Pme-EM = *P. mexicana*—El Mohinora, Pme-LM = *P. mexicana*—La Marta, Pme-EC = *P. mexicana*—El Coahuilón. In (**a**) each color represents a different cluster (group); in (**b**), the upper and left color bars indicate the groups, while the inner red-yellow scaled colors indicate the degree of similarity between provenances (the lighter, the more similar).

The Tukey–Kramer (Nemenyi) tests showed that all Mexican spruce species differed significantly in *H* and all provenances differed significantly in *D* and *H*, except for Pme-LM and Pme-EC (Table 5). However, there were no significant differences in the survival of species or provenances of the Mexican spruces.

3.2. Associations between Environmental Variables and Phenotypic Traits

Considering the eight provenances together, significant associations (p < 0.01) between H and the percentage of organic matter (O.M.) in the soil were observed ($r_s = 0.90$). Strong and significant correlations ($|r_s| > 0.9$, p < 0.01) were also observed between the survival rate and mean minimum temperature of the coldest month (Mmin), longitude (Long), length of the frost-free period (Ffp), Julian date of the first autumn freezing (Fday), summer precipitation balance (Smrpb), Julian date of the last spring freezing (Sday) and mean temperature of the coldest month (Mtcm). With regard to seed weight, strongly significant associations ($|r_s| > 0.9$, p < 0.01) were detected with elevation (Elev), mean annual temperature (Mat), mean temperature of the warmest month (Mtcm) and degree-days above 5 °C (Dd5) (Table 6). No significant associations between mean seedling diameter and environmental variables were found. Without considering Pch-QD, however, the association between H and the percentage of silt in the soil was also very strong and statistically significant ($r_s = -0.99$, p < 0.01). Figure 4 shows the linear regressions of seeding height with percentage of organic matter, seed weight with mean annual temperature and seedling survival with mean minimum temperature in the coldest month (°C) of seed origin.

Table 6. Spearman correlation (r_s) between mean seedling height (H, mm), survival (%) (SU) and weight of 1000 seeds (SW, g) with climatic and soil variables (var) ($\alpha = 0.025$) (* There was strong collinearity of seedlings height, survival and seed weight with respect to some climate variables and also with the percentage of silt (%Silt), organic matter and potassium in the soil ($r_s > 0.9$); O.M. = organic matter (%), Smrp = summer precipitation, Elev = elevation (m), Mmin = mean minimum temperature of the coldest month (°C), Long = longitude (m), Ffp = length of the frost-free period (days), Fday = Julian date of the first autumn freezing (days), Smrpb = summer precipitation balance (ratio), Sday = Julian date of the last spring freezing (days), Mtcm = mean temperature of the coldest month (°C), Mtwm mean temperature of the warmest month (°C) and degree-days above 5 °C).

	Phenotypes	Variables *	r _s	p Value
	Height	O.M.	0.90	0.0045
	Ū	Smrp	-0.83	0.011
		Elev	-0.83	0.015
		SW	0.78	0.027
	Survival	Mmin	0.98	0.00008
In du din a Dah OD		Long	-0.96	0.0001
Including Pcn—QD		Ffp	0.95	0.0011
		Fday	0.95	0.0011
		Smrpb	-0.92	0.0011
		Sday	-0.93	0.0022
		Mtcm	0.93	0.0022
		Mmindd0	-0.88	0.0022
		Height	0.81	0.021

	Phenotypes	Variables *	r _s	p Value
	Seed weight	Elev	-0.90	0.004
	0	Mat	0.90	0.0045
		Smrp	-0.87	0.0045
		Mtwm	0.90	0.0045
Including Pch—QD		Dd5	0.90	0.0045
		Map	-0.85	0.0072
		Smrsprpb	-0.84	0.0093
		Smrpb	-0.84	0.0093
		Height	0.72	0.027
	Height	%Silt	-0.99	0.00001
	0	Elev	-0.96	0.0027
		SW	0.89	0.012
		Mmax	0.85	0.016
		Potassium	0.85	0.016
		O.M	0.86	0.023
	Seed weight	Smrp	-0.954	0.0008
Excluding Pch—QD	-	Smrpb	-0.900	0.0056
-		Smrsprpb	-0.928	0.0067
		%Silt	-0.86	0.011
		Map	-0.89	0.012
		Mmax	0.85	0.016
		Mtcm	0.86	0.023
		Mat	0.86	0.023
		Elev	-0.86	0.023
		D100	-0.86	0.023

Table 6. Cont.



Figure 4. Cont.



Figure 4. Linear regression models of (**a**) seedling height with percentage of organic matter $(R^2_{adj} = 0.77, p \text{ value} = 0.0026, \text{ slope parameter } (\beta) = 2.24, \text{ intercept} = 58.54);$ (**b**) seed weight with mean annual temperature $(R^2_{adj} = 0.90, p \text{ value} = 0.0002, \text{ slope parameter } (\beta) = 3.23, \text{ intercept} = -25.68);$ and (**c**) seedling survival with mean minimum temperature of the coldest month (°C) $(R^2_{adj} = 0.75, p \text{ value} = 0.0035, \text{ slope parameter } (\beta) = 1.25, \text{ intercept} = 90.27)$ of seed origin; blue lines = mean values and grey area = 95% confidence level intervals for predictions; Provenances of Pch-QD = *Picea chihuahuana*—Quebrada de los Durán, Pma-AF = *P. martinezii*—Agua Fría, Pma-AA = *P. martinezii*—Agua Alardín, Pma-EB = *P. martinezii*—El Butano, Pma-LE = *P. martinezii*—La Encantada, Pme-EM = *P. mexicana*—El Mohinora, Pme-LM = *Picea mexicana*—La Marta, Pme-EC = *P. mexicana*—El Coahuilón.

3.3. Heritability (Within-Provenance) of Picea martinezii and P. mexicana Growth Traits

The medium to high within-provenance heritability values of the growth traits *D* and *H* and notable percentage of provenance variation relative to total variance for *Picea martinezii* and *P. mexicana* seedlings are shown in Table 7.

Species	Seedling Growth Trait	Percentage of Provenance-Related Variation *	h^2_{i}	h^2_f
Picea martinezii	Diameter	14.5	0.19 ± 0.55	0.64
	Height	13.4	0.21 ± 0.35	0.65
Picea mexicana	Diameter	8.1	0.47 ± 0.72	0.83
	Height	14.9	0.55 ± 0.60	0.85

Table 7. Heritability (within-provenance) of seedling diameter and height (growth traits) in *Picea martinezii* and *P. mexicana*. Individual (h_i^2) and family (h_f^2) heritability \pm standard error are shown (* relative to total variance).

4. Discussion

The study findings show significant (phenotypic) differences between the three spruce species considered, as well as between the provenances within the species, in seedling growth traits under the same environmental conditions (i.e., greenhouse) (Table 5, Figure 3). The differences in provenances could be caused by the high degree of spatial, ecological and temporal variation and possibly by the pre- or postzygotic isolation of these provenances and the divergent natural selection in heterogeneous environments, e.g., large differences in elevation, temperature and some soil conditions [20,28]. This selection has resulted in locally adapted plant genotypes [54]. It can be assumed that the observed growth differences will increase over time (Figure 2).

The strong correlations between the measured traits (height, survival rate and weight of 1000 seeds) with several climatic variables from the areas of seed origin indicate some degree of adaptation to local conditions that determines the variation in seedling growth in the spruce provenances considered. The prevailing climatic conditions in natural locations of the best-performing spruce (*P. martinezii*), particularly for the two best-performing provenances (AA and AF) (Table 5), were closer to climatic greenhouse conditions and, therefore, these provenances were probably best adapted (Table 6 and Figure 4). In addition, AA and AF (like all *P. martinezii* provenances) had a particularly high seed weight (*SW*) (Table 4) (see below), which also strongly promoted their faster initial growth in diameter and height (*H*) (Figure 2). *SW* is both a part of maternal effects [55] and a largely genetically controlled quantitative trait [17,55]. The high level of local adaptation is consistent with the high degree of genetic differentiation among the three spruce species and their provenances [18,22–24,30].

Other studies have also shown that adaptation is directly related to the climate gradient in the area where the species are distributed. For example, Rehfeldt [56] showed the adaptation of *Picea engelmannii* populations to heterogeneous environments. Oleksyn et al. [57] presented common garden evidence for elevational ecotypes and the cold adaptation of Picea abies. Islam and Macdonald [58] showed ecophysiological adaptations of Picea mariana and Larix laricina seedlings to flooding. Sáenz-Romero et al. [34] reported elevational-related genetic variation among *Pinus oocarpa* populations. Andersen et al. [59] observed differences in growth traits (number of secondary branches and seedling height), which were caused by differences in abiotic factors, in nine provenances of *Abies guatemalen*sis. Castellanos-Acuña et al. [60] showed that the mean temperature of the coldest month and an aridity index are strongly related to the genetic adaptation of Mexican tree species. In addition, Konôpková et al. [61] concluded that the Central European provenances of Abies alba from higher elevations, associated with wetter and colder conditions, demonstrated the greatest photosynthetic production and were less sensitive to moderate heat and dryness. Petrík et al. [62] found, in a study of 20 provenances of *Fagus sylvatica* in Europe, that saplings from hotter, drier environments showed the greatest growth in height, as we found in our study (Table 6).

Strong associations between seedling height and soil variables of seed origin were also detected (Table 6, Figure 4). Similarly, Pickles et al. [63] reported that the height of Douglas-fir seedlings was optimized after the transfer of seeds to drier soils, whereas

survival was improved when elevation transfer was minimized, and they concluded that soil biota interacts with biogeography to influence plant ranges. Macel et al. [54] found no evidence of adaptation to climate in the legume *Lotus corniculatus*, and only differences in number of fruits regarding soil origin, showing a weak indication of adaptation to soil conditions.

We observed strong associations between *SW* and *H* in relation to climatic and soil variables (Table 6), probably due to control by quantitative trait loci [17]. Similarly, the results of a provenance trial under nursery conditions with Ethiopian *Cordia africana* showed that *SW* was significantly and positively correlated with elevation and negatively correlated with mean annual temperature of seed origin [64]. Leal-Sáenz et al. [65] reported that *Pinus strobiformis* populations in more humid and warmer climates and growing in dense, shady forest stands had heavier seeds because larger seeds could provide greater resources for germination.

The medium-to-high within-provenance heritability values (Table 7), representing the proportion of phenotypic variation attributable to genetic variability within populations, also support the hypothesis of adaptation to local conditions for each provenance under study [20]. However, phenotypic plasticity, which enables species to cope with different environmental scenarios, can explain the complementary part of the growth differences [66,67]. Finally, environmental variation does not necessarily lead to adaptive variation and can also result in non-adaptive phenotypic plasticity [68]. According to the results obtained, the adaptation of provenances of the Mexican spruces to local conditions is more likely. Hence, the use of combinations of germplasm from different provenances for both in situ and ex situ activities should be carried out with caution. Thus, the conservation of current genetic pools should be prioritized, whereas the exchange of germplasm among provenances should be reserved for the genetic rescue of populations with a high extinction risk.

5. Conclusions

Applying the concept of trans-specific traits to the three Mexican spruce species makes local adaptation more visible than these traits only at the species level, probably due to the stronger isolation mechanisms and greater genetic distances among these species, and the different species' niches.

The study findings indicate the need to consider environmental conditions for future conservation actions and to analyze the relationships between the variation in environmental factors (such as precipitation and edaphic traits) and the growth patterns of tree species. This would enable the identification of favorable forest conditions and reforestation with seedlings of suitable species and origins for each site, considering the environmental setting. By considering the predicted future environmental conditions for each site to be reforested, increased survival rates can also be achieved by reducing the mortality due to the decoupling of plant requirements from the climates and soil in which they have evolved over long periods. Thus, reforestation programs for these species with isolated and fragmented populations should be more successful when seedlings from one provenance are planted in environmental conditions similar to those of the same provenance.

However, the very small ranges and habitats of these three endemic species and the very small sizes of provenances, along with the marked local adaptation detected, make both germplasm exchange among provenances and the ex situ conservation of genetic variation very difficult.

Author Contributions: Conceptualization, C.W.; methodology, C.W.; software, J.M.T.-V.; validation, C.W., J.C.H.-D. and A.C.-P.; formal analysis, J.M.T.-V. and J.L.-U.; investigation, J.M.T.-V.; resources, E.M.-M.; data curation, J.M.T.-V. and S.S.-G.; writing—original draft preparation, C.W.; writing—review and editing, J.L.-U., J.M.T.-V., J.C.H.-D., A.C.-P. and E.M.-M.; visualization, J.C.H.-D.; supervision, C.W.; project administration, C.W. and S.S.-G.; funding acquisition, C.W. All authors have read and agreed to the published version of the manuscript. **Funding:** This material is based on work supported by the Consejo Nacional de Ciencia y Tecnología of México (CONACYT) and the Comisión Nacional Forestal (CONAFOR). Moreover, CONACYT provided financial support to José Marcos Torres-Valverde for his master's studies (CVU No. 1004398).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Angélica Rocio Espinoza Delgado, Ana Maria Ibarra, Emma Lizbeth Espinoza Delgado, Ricardo Silas Sánchez-Hernández and Oscar Alfredo Díaz-Carrillo for assistance with the fieldwork.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Callaham, R.Z. Provenance research: Investigation of genetic diversity associated with geography. In *Unasylua*; Food and Agriculture Organization of the United Nations: Rome, Italy, 1963; Volume 18, 12p. Available online: https://www.fs.usda.gov/ research/treesearch/32867 (accessed on 7 April 2023).
- Gregorius, H.-R.; Bergmann, F.; Wehenkel, C. Analysis of biodiversity across levels of biological organization: A problem of defining traits. *Perspect. Plant Ecol. Evol. Syst.* 2003, *5*, 209–218. [CrossRef]
- 3. Wehenkel, C.; Bergmann, F.; Gregorius, H.R. Is there a trade-off between species diversity and genetic diversity in forest tree communities? *Plant Ecol.* **2006**, *185*, 151–161. [CrossRef]
- 4. Bergmann, F.; Gregorius, H.R.; Kownatzki, D.; Wehenkel, C. Different diversity measures and genetic traits reveal different species genetic diversity relationships: A case study in forest tree communities. *Silvae Genet.* **2013**, *62*, 25–37. [CrossRef]
- 5. Lamy, T.; Laroche, F.; David, P.; Massol, F.; Jarne, P. The contribution of species–genetic diversity correlations to the understanding of community assembly rules. *Oikos* **2017**, *126*, 759–771. [CrossRef]
- 6. Grattapaglia, D.; Silva-Junior, O.B.; Resende, R.T.; Cappa, E.P.; Müller, B.S.F.; Tan, B.; Isik, F.; Ratcliffe, B.; El-Kassaby, Y.A. Quantitative genetics and genomics converge to accelerate forest tree breeding. *Front. Plant Sci.* **2018**, *9*, 1693. [CrossRef]
- 7. Guries, R.P. Forest genetics and forest tree breeding. In *Introduction to Forest Science*; John Wiley and Sons Inc.: New York, NY, USA, 1990; pp. 98–118. [CrossRef]
- 8. Matyas, C. Climatic adaptation of trees: Rediscovering provenance tests. Euphytica 1996, 92, 45–54. [CrossRef]
- Kramer, K.; Degen, B.; Buschbom, J.; Hickler, T.; Thuiller, W.; Sykes, M.T.; de Winter, W. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—Range, abundance, genetic diversity and adaptive response. *For. Ecol. Manag.* 2010, 259, 2213–2222. [CrossRef]
- 10. Gömöry, D.; Longauer, R.; Hlásny, T.; Pacalaj, M.; Strmeň, S.; Krajmerová, D. Adaptation to common optimum in different populations of Norway spruce (*Picea abies* Karst.). *Eur. J. For. Res.* **2012**, *131*, 401–411. [CrossRef]
- 11. Wicherts, J.M.; Johnson, W. Group differences in the heritability of items and test scores. *Proc. R. Soc. B Biol. Sci.* 2009, 276, 2675–2683. [CrossRef]
- O'Brien, E.K.; Manzanec, R.A.; Krauss, S.L. Provenance variation of ecologically important traits of forest trees: Implications for restoration. J. Appl. Ecol. 2007, 44, 583–593. [CrossRef]
- 13. Roach, D.A. Variation in seed and seedling size in *Anthoxanthum odoratum*. *Am. Midl. Nat.* **1987**, 117, 258–264. [CrossRef]
- 14. Winn, A.A. Ecological and evolutionary consequences of seed size in Prunella vulgaris. Ecology 1988, 69, 1537–1544. [CrossRef]
- 15. Biere, A. Parental effects in *Lychnis flos-cuculi*. I: Seed size, germination and seedling performance in a controlled environment. *J. Evol. Biol.* **1991**, *4*, 447–465. [CrossRef]
- 16. Platenkamp, G.A.J.; Shaw, R.G. Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. *Evolution* **1993**, 47, 540–555. [CrossRef]
- 17. Guo, Y.; Gao, M.; Liang, X.; Xu, M.; Liu, X.; Zhang, Y.; Liu, X.; Liu, J.; Gao, Y.; Qu, S.; et al. Quantitative trait loci for seed size variation in cucurbits–a review. *Front. Plant Sci.* **2020**, *11*, 304. [CrossRef]
- 18. Wehenkel, C.; Vargas-Hernández, J.J.; Flores-López, C.; Quiñones Pérez, C.Z. Genética de las piceas en México. In *Las Piceas (Picea, Pinaceae) de México*; González-Elizondo, M.S., Wehenkel, C., Eds.; Comisión Nacional Forestal: Zapopan, Mexico, 2022; pp. 56–68.
- 19. Ledig, F.T.; Mápula-Larreta, M.; Bermejo-Velázquez, B.; Reyes-Hernández, V.; Flores-López, C.; Capó-Arteaga, M.A. Locations of endangered spruce populations in Mexico and the demography of *Picea chihuahuana*. *Madroño* **2000**, *47*, 71–88.
- Dominguez-Guerrero, I.K.; Mariscal-Lucero, S.; Hernández-Díaz, J.C.; Heinze, B.; Prieto-Ruiz, J.A.; Wehenkel, C. Discrimination of *Picea chihuahuana* Martínez populations on the basis of numerous dendrometric, climatic and edaphic traits and genetic diversity. *PeerJ* 2017, *5*, e3452. [CrossRef]
- Mendoza-Maya, E.; Gómez-Pineda, E.; Sáenz-Romero, C.; Hernández-Díaz, J.C.; López-Sánchez, C.A.; Vargas-Hernández, J.J.; Prieto-Ruíz, J.Á.; Wehenkel, C. Assisted migration and the rare endemic plant species: The case of two endangered Mexican spruces. *PeerJ* 2022, 10, e13812. [CrossRef]

- 22. Lockwood, J.D.; Aleksić, J.M.; Zou, J.; Wang, J.; Liu, J.; Renner, S.S. A new phylogeny for the genus *Picea* from plastid, mitochondrial, and nuclear sequences. *Mol. Phylogenet. Evol.* **2013**, *69*, 717–727. [CrossRef]
- 23. Ledig, F.T.; Jacob-Cervantes, V.; Hodgskiss, P.D.; Eguiluz-Piedra, T. Recent evolution and divergence among populations of a rare Mexican endemic, Chihuahua spruce, following Holocene climatic warming. *Evolution* **1997**, *51*, 1815–1827. [CrossRef]
- Ledig, F.T.; Bermejo-Velázquez, B.; Hodgskiss, P.D.; Johnson, D.R.; Flores-López, C.; Jacob-Cervantes, V. The mating system and genic diversity in Martinez spruce, an extremely rare endemic of Mexico's Sierra Madre Oriental: An example of facultative selfing and survival in interglacial refugia. *Can. J. For. Res.* 2000, *30*, 1156–1164. [CrossRef]
- 25. Ledig, F.T.; Hodgskiss, P.D.; Jacob-Cervantes, V. Genetic diversity, mating system, and conservation of a Mexican subalpine relict, *Picea mexicana* Martínez. *Conserv. Genet.* **2002**, *3*, 113–122. [CrossRef]
- 26. Clausen, J.; Keck, D.; Hiesey, W. Experimental Studies on the Nature of Species. I. Effects of Varied Environments on Western North American Plants; Carnegie Institution of Washington: Washington, DC, USA, 1940.
- 27. Kim, E.; Donohue, K. Local adaptation and plasticity of *Erysimum capitatum* to altitude: Its implications for responses to climate change. *J. Ecol.* **2013**, *101*, 796–805. [CrossRef]
- Anderson, J.T.; Wadgymar, S.M. Climate change disrupts local adaptation and favours upslope migration. *Ecol. Lett.* 2020, 23, 181–192. [CrossRef] [PubMed]
- Mendoza-Maya, E.; Espino-Espino, J.; Quiñones-Pérez, C.Z.; Flores-López, C.; Wehenkel, C.; Vargas-Hernández, J.J.; Sáenz-Romero, C. Propuesta de conservación de tres especies mexicanas de *Picea* en peligro de extinción. *Rev. Fitotec. Mex.* 2015, 38, 235–247. [CrossRef]
- Ledig, F.T.; Hodgskiss, P.D.; Krutovskii, K.V.; Neale, D.B.; Eguiluz-Piedra, T. Relationships among the Spruces (*Picea, Pinaceae*) at Southwestern North America. Syst. Bot. 2004, 29, 275–295. [CrossRef]
- Rehfeldt, G.E. A Spline Model of Climate for the Western United States; General Technical Report RMRS-GTR-165; US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2004. [CrossRef]
- Hutchinson, M.F. Continent-wide data assimilation using thin plate smoothing splines. In *Data Assimilation Systems*; Jasper, E.D., Ed.; Meteorology: Melbourne, Australia, 1991; pp. 104–113. Available online: https://www.researchgate.net/publication/247765 032_The_Application_of_Thin_Plate_Smoothing_Splines_to_Continent-Wide_Data_Assimilation (accessed on 7 April 2023).
- 33. Hutchinson, M.F. *ANUSPLIN*, Version 4.3; Centre for Resource and Environmental Studies: St Michael, Barbados; The Australian National University: Canberra, Australia, 2004.
- Sáenz-Romero, C.; Guzmán-Reyna, R.R.; Rehfeldt, G.E. Altitudinal genetic variation among *Pinus oocarpa* populations in Michoacán, Mexico: Implications for seed zoning, conservation, tree breeding and global warming. *For. Ecol. Manag.* 2006, 229, 340–350. [CrossRef]
- 35. Castellanos, J.Z.; Uvalle-Bueno, J.X.; Aguilar-Santelises, A. *Manual de Interpretación de Análisis de Suelos y Agua*; Instituto para la Innovación Tecnológica en la Agricultura: Celaya, Mexico, 2000; 226p.
- 36. Olsen, S.R. *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate (No. 939)*; US Department of Agriculture: Washington, DC, USA, 1954.
- 37. Baker, A.S. Colorimetric determination of nitrate in soil and plant extracts with brucine. J. Agric. Food Chem. 1967, 15, 802–806. [CrossRef]
- León, A.R.; Aguilar, A.S. Materia orgánica. In Análisis Químico para Evaluar la Fertilidad del Suelo; Aguilar, A., Etchevers, J.D., Castellanos, J.Z., Eds.; Publicación Especial No. 1; Sociedad Mexicana de la Ciencia del Suelo: Chapingo, Mexico, 1987; pp. 85–91.
- Vázquez-Alarcón, A.; Aguilar-Noh, A. Prácticas del Curso Química de Suelos; Universidad Autónoma Chapingo, Departamento de Suelos: Chapingo, México, 2020; 125p. Available online: https://www.academia.edu/41715851/QU%C3%8DMICA_DE_ SUELOS_MANUAL_DE_PR%C3%81CTICAS (accessed on 8 April 2023).
- 40. Mualem, Y. A new model for predicting the hydraulic conductivity of unsaturated porous media. *Water Resour. Res.* **1976**, *12*, 513–522. [CrossRef]
- 41. Herbert, V.F. Prácticas de Relaciones Agua-Suelo-Planta-Atmósfera; Universidad Autónoma Chapingo: Chapingo, Mexico, 1992; 167p.
- Bodenhofer, U.; Palme, J.; Melkonian, C.; Kothmeier, A. APCluster: An R package for affinity propagation clustering. *Bioinformatics* 2022, 27, 2463–2464. Available online: https://academic.oup.com/bioinformatics/article/27/17/2463/224402 (accessed on 7 April 2023). [CrossRef]
- 43. Hartigan, J.A.; Wong, M.A. Algorithm AS 136: A k-means clustering algorithm. Applied Statistics. J. R. Stat. Soc. Ser. C (Appl. Stat.) 1979, 28, 100–108. [CrossRef]
- 44. Legendre, P.; Legendre, L. Numerical Ecology; Elsevier Science B.V.: Amsterdam, The Netherlands, 1998.
- 45. R Core Team. *R: A Language and Environment for Statistical Computing;* R Foundation for Statistical Computing: Vienna, Austria, 2015. Available online: http://www.R-project.org/ (accessed on 7 April 2023).
- 46. Pohlert, T.; Pohlert, M.T. Package 'pmcmr'. R Package Version; R Foundation for Statistical Computing: Vienna, Austria, 2018.
- 47. Hauke, J.; Kossowski, T. Comparison of values of Pearson's and Spearman's correlation coefficients on the same sets of data. *Quaest. Geogr.* **2011**, *30*, 87–93. [CrossRef]
- Liaw, A.; Wiener, M. Classification and Regression by randomForest. *R News* 2002, 2, 18–22. Available online: https://CRAN.R-project.org/doc/Rnews/ (accessed on 7 April 2023).
- 49. Wickham, H.; Chang, W.; Wickham, M.H. Package 'ggplot2'. Computer Software Manual. 2013. Available online: http://cran.r-project.org/web/packages/ggplot2/ggplot2.pdf (accessed on 4 September 2019).

- SAS Institute. SAS/STAT Guide for Personal Computers; SAS Institute: Cary, NC, USA, 1985; 378p. Available online: https://books. google.com.mx/books/about/SAS_STAT_Guide_for_Personal_Computers_Ve.html?id=EY4pAQAAMAAJ&redir_esc=y (accessed on 7 April 2023).
- Stroup, W.W.; Milliken, G.A.; Claassen, E.A.; Wolfinger, R.D. SAS System for Mixed Models; SAS Institute: Cary, NC, USA, 2018. Available online: https://support.sas.com/content/dam/SAS/support/en/books/sas-for-mixed-models-an-introduction/68 787_excerpt.pdf (accessed on 7 April 2023).
- Falconer, D.S.; Mackay, T.F.C. Introduction to Quantitative Genetics; Addison Wesley Longman Limited: Harlow, UK, 1989. Available online: https://vulms.vu.edu.pk/Courses/GEN733/Downloads/Introduction%20to%20Quantitative%20Genetic-DS%20Falconer.pdf (accessed on 7 April 2023).
- 53. Sorensen, F.C.; White, T.L. Effect of natural inbreeding on variance structure in tests of wind-pollination Douglas-fir progenies. *For. Sci.* **1988**, *34*, 102–118. Available online: https://www.fs.usda.gov/research/treesearch/4986 (accessed on 7 April 2023).
- Macel, M.; Lawson, C.S.; Mortimer, S.R.; Smilauerova, M.; Bischoff, A.; Crémieux, L.; Dolezal, J.; Edwards, A.R.; Lanta, V.; Bezemer, T.M.; et al. Climate vs. soil factors in local adaptation of two common plant species. *Ecology* 2007, *88*, 424–433. [CrossRef]
- 55. Roach, D.A.; Wulff, R.D. Maternal effects in plants. Annu. Rev. Ecol. Syst. 1987, 18, 209–235. [CrossRef]
- 56. Rehfeldt, G.E. Adaptation of *Picea engelmannii* populations to the heterogeneous environments of the Intermountain West. *Can. J. Bot.* **1994**, *72*, 1197–1208. [CrossRef]
- 57. Oleksyn, J.; Modrzýnski, J.; Tjoelker, M.G.; Zytkowiak, R.; Reich, P.; Karolewski, P. Growth and physiology of *Picea abies* populations from elevational transects: Common garden evidence for altitudinal ecotypes and cold adaptation. *Funct. Ecol.* **2002**, *12*, 573–590. [CrossRef]
- 58. Islam, M.A.; Macdonald, S.E. Ecophysiological adaptations of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) seedlings to flooding. *Trees* **2004**, *18*, 35–42. [CrossRef]
- 59. Andersen, U.S.; Prado Córdova, J.; Nielsen, U.; Olsen, C.; Nielsen, C.; Sørensen, M.; Kollmann, J. Conservation through utilization: A case study of the vulnerable *Abies guatemalensis* in Guatemala. *Oryx* **2008**, *42*, 206–213. [CrossRef]
- Castellanos-Acuña, D.; Vance-Borland, K.W.; St. Clair, J.B.; Hamann, A.; López-Upton, J.; Gómez-Pineda, E.; Ortega-Rodríguez, J.M.; Sáenz-Romero, C. Climate-based seed zones for Mexico: Guiding reforestation under observed and projected climate change. *New For.* 2018, 49, 297–309. [CrossRef]
- Konôpková, A.; Pšidová, E.; Kurjak, D.; Stojnić, S.; Petrík, P.; Fleischer, P., Jr.; Kučerová, J.; Ježík, M.; Petek, A.; Gömöry, D.; et al. Photosynthetic performance of silver fir (*Abies alba*) of different origins under suboptimal growing conditions. *Funct. Plant Biol.* 2020, 47, 1007–1018. [CrossRef] [PubMed]
- Petrík, P.; Grote, R.; Gömöry, D.; Kurjak, D.; Petek-Petrik, A.; Lamarque, L.J.; Sliacka Konôpková, A.; Mukarram, M.; Debta, H.; Fleischer, P., Jr. The Role of Provenance for the Projected Growth of Juvenile European Beech under Climate Change. *Forests* 2022, 14, 26. [CrossRef]
- 63. Pickles, B.J.; Twieg, B.D.; O'Neill, G.A.; Mohn, W.W.; Simard, S.W. Local adaptation in migrated interior Douglas-fir seedlings is mediated by ectomycorrhizas and other soil factors. *New Phytol.* **2015**, 207, 858–871. [CrossRef]
- 64. Loha, A.; Tigabu, M.; Teketay, D.; Lundkvist, K.; Fries, A. Provenance variation in seed morphometric traits, germination, and seedling growth of *Cordia africana* Lam. *New For.* **2006**, *32*, 71–86. [CrossRef]
- Leal-Sáenz, A.; Waring, K.M.; Menon, M.; Cushman, S.A.; Eckert, A.; Flores-Rentería, L.; Hernández-Díaz, J.C.; López-Sánchez, C.A.; Martínez-Guerrero, J.H.; Wehenkel, C. Morphological differences in *Pinus strobiformis* across latitudinal and elevational gradients. *Front. Plant Sci.* 2020, 11, 559697. [CrossRef]
- 66. Núñez-Farfán, J.; Careaga, S.A.; Fornoni, J.; Ruiz-Montoya, L.; Valverde, P. La evolución de la plasticidad fenotípica. *Rev. Espec. Cienc. Químico-Biol.* **2003**, *6*, 16–24.
- 67. Bucholz, E.R.; Waring, K.M.; Kolb, T.E.; Swenson, J.K.; Whipple, A.V. Water relations and drought response of *Pinus strobiformis*. *Can. J. For. Res.* **2020**, *50*, 905–916. [CrossRef]
- 68. Ghalambor, C.K.; McKay, J.K.; Carroll, S.P.; Reznick, D.N. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **2007**, *21*, 394–407. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.