Discrimination of *Picea chihuahuana* Martinez populations on the basis of numerous dendrometric, climatic and edaphic traits and genetic diversity

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Background. *Picea chihuahuana*, which is endemic to Mexico, is currently listed as "Endangered" on the Red List. Chihuahua spruce is only found in the Sierra Madre Occidental (SMO), Mexico. About 42,600 individuals are distributed in forty populations. The populations are fragmented and can be classified into three distinct clusters in the SMO of the two States (south, center and north), each group separated by a distance of about 300 km. The total area covered *P. chihuahuana* trees is less than 300 ha. A recent study suggested assisted migration as an alternative to the *ex situ* conservation of *P. chihuahuana*, taking into consideration the genetic structure and diversity of the populations and also predictions regarding the future climate of the habitat. However, detailed background information is required to enable development of plans for protecting and conserving species and for successful assisted migration. Thus, it is important to identify differences between populations in relation to environmental conditions. The vitality and genetic diversity of populations, which affect vigour, evolution and adaptability of the species, must also be considered. In this study, we examined the *P. chihuahuana* tree community growing in fourteen different locations, with the overall aim of discriminating the populations and clusters of this species using 22 climatic, 27 edaphic and 15 dasometric variables and three genetic diversity indices. **Methods.** Each location was represented by one 50 x 50 m plot established in the center of the location in which was measured the climate, soil, dasometric and genetic variables. The putative neutral and adaptive AFLP were used to calculate genetic diversity. Multivariate discriminant analysis including cross-validation was considered to test for significant differences in variables in the southern, central and northern populations and locations of the *P. chihuahuana* tree community. Spearman's correlation test was used to analyze the relationships between genetic diversity, population size, and the climatic, soil and dasometric variables. **Results.** The discriminant analysis revealed 22 highly significant variables, which separated the southern, central and northern populations. The mean genetic diversity of *P. chihuahuana* was significantly correlated with the mean temperature in the warmest month. Genetic diversity of *P. chihuahuana* calculated with putative adaptive AFLP was not statistically significantly correlated with any environmental factor. Finally, no significant correlations were observed between any of the three genetic diversity indices and population size. **Discussion.** At least three different ecotypes of *P. chihuahuana* probably exist, as local adaptation may take place because of the different environmental conditions. Therefore, future reforestation programs should take into account these different ecotypes and environmental conditions.

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Abstract

Background. *Picea chihuahuana*, which is endemic to Mexico, is currently listed as "Endangered" on the Red List. Chihuahua spruce is only found in the Sierra Madre Occidental (SMO), Mexico. About 42,600 individuals are distributed in forty populations. The populations are fragmented and can be classified into three distinct clusters in the SMO of the two States (south, center and north), each group separated by a distance of about 300 km. The total area covered *P. chihuahuana* trees is less than 300 ha. A recent study suggested assisted migration as an alternative to the *ex situ* conservation of *P. chihuahuana*, taking into consideration the genetic structure and diversity of the populations and also predictions regarding the future climate of the habitat. However, detailed background information is required to enable development of plans for protecting and conserving species and for successful assisted migration. Thus, it is important to identify differences between populations in relation to environmental conditions. The vitality and genetic diversity of populations, which affect vigour, evolution and adaptability of the species, must also be considered. In this study, we examined the *P. chihuahuana* tree community growing in fourteen different locations, with the overall aim of discriminating the populations and clusters of this species using 22 climatic, 27 edaphic and 15 dasometric variables and three genetic diversity indices.

Methods. Each location was represented by one 50 x 50 m plot established in the center of the location in which was measured the climate, soil, dasometric and genetic variables. The putative neutral and adaptive AFLP were used to calculate genetic diversity. Multivariate discriminant analysis including cross-validation was considered to test for significant differences in variables in the southern, central and northern populations and locations of the *P. chihuahuana* tree community. Spearman's correlation test was used to analyze the relationships between genetic diversity, population size, and the climatic, soil and dasometric variables.

Results. The discriminant analysis revealed 22 highly significant variables, which separated the southern, central and northern populations. The mean genetic diversity of *P. chihuahuana* was significantly correlated with the mean temperature in the warmest month. Genetic diversity of *P. chihuahuana* calculated with putative adaptive AFLP was not statistically significantly correlated with any environmental factor. Finally, no significant correlations were observed between any of the three genetic diversity indices and population size.

Discussion. At least three different ecotypes of *P. chihuahuana* probably exist, as local adaptation may take place because of the different environmental conditions. Therefore, future reforestation programs should take into account these different ecotypes and environmental conditions.

Key words: tree species, conservation, cross-validation, linear discriminant function analysis

Introduction

Picea chihuahuana Mtz. (Chihuahua spruce), which is endemic to Mexico, is currently listed as "Endangered" on the Red List of the International Union for the Conservation of Nature and Natural Resources (IUCN, 2013) and in the official Mexican normativity on endangered species (NOM-059-SEMARNAT-2010) (SEMARNAT, 2010). This tree species grows at elevations between 2,150 and 2,990 m in areas with mean annual temperatures of 9-12 °C and precipitation ranging from around 600 mm to 1,300 mm (Sáenz-Romero et al., 2010).

Chihuahua spruce is only found in the Sierra Madre Occidental (SMO), Mexico. About 42,600 individuals are distributed in forty populations (Sánchez, 1984; Farjon, Page & Schellevis, 1993; Ledig et al., 2000; Wehenkel & Sáenz-Romero, 2012). The species is specifically located in the states of Chihuahua (in the municipalities of Bocoyna, Temosachi, Guerrero and Balleza) and Durango (in the municipalities of El Mezquital, Pueblo Nuevo, San Dimas, Canelas and Guanacevi) (Ledig et al., 2000). The populations are fragmented and can be classified into three distinct clusters in the SMO of the two States (south, center and north), each group separated by a distance of about 300 km (Mendoza-Maya et al., 2015). The total area covered Chihuahua spruce trees is less than 300 ha (Simental-Rodríguez et al., 2014). *Picea chihuahuana* is commonly associated with species of the genera *Pinus* and *Quercus,* and occasionally with species of the genera *Abies, Pseudotsuga, Cupressus, Populus, Juniperus* and *Prunus* (Gordon, 1968; Wehenkel et al., 2015).

Several factors threaten *P. chihuahuana* populations, including the low reproductive capacity resulting from high levels of self-fertilization and mating between closely related individuals (Ledig *et al.,* 1997). Harvesting, grazing and forest fires have also contributed to reducing the population sizes (Ledig *et al.,* 1997). Recent research has revealed problems of genetic erosion in one population (Wehenkel & Saenz-Romero, 2012).

Different approaches have been used to study populations of *P. chihuahuana* from the perspectives of ecology (Narváez, 1984; Ledig et al., 2000; Quiñones-Pérez, Silva-Flores & Wehenkel, 2012), genetic structure (Ledig et al., 1997; Jaramillo-Correa et al*.,* 2006; Wehenkel et al., 2012; Wehenkel & Saenz-Romero, 2012; Quiñones-Pérez, Sáenz-Romero & Wehenkel, 2014; Wehenkel, Sáenz-Romero & Jaramillo-Correa, 2015) and climate change (Ledig et al., 2010).

In a recent study, Mendoza-Maya et al. (2015) suggested assisted migration as an alternative to the *ex situ* conservation of *P. chihuahuana*, taking into consideration the genetic structure and diversity of the populations and also predictions regarding the future climate of the habitat. However, detailed background information is required to enable development of plans for protecting and conserving species and for successful assisted migration. Thus, it is important to identify differences between populations in relation to environmental conditions (Aguilar-Soto et al., 2015). The vitality and genetic diversity of populations, which affect vigour, evolution and adaptability of the species, must also be considered (Frankham, Ballou & Briscoe, 2002; Reed & Frankham, 2003). In this study, we examined the *P. chihuahuana* tree community growing in fourteen different locations, with the overall aim of discriminating the populations and clusters of this unique tree species. For this purpose we: i) determined 69 climatic, edaphic and dasometric variables (as proxies for tree health) and genetic diversity indices and tested them for any significant differences, to enable prediction of species distributions by linear discriminant function analysis, ii) identified suitable variables for separating populations, and iii) tested for correlation between genetic diversity, dasometric (health) and environmental factors. The results led to make proposals for *ex situ* conservation for *P. chihuahuana*.

Materials and methods

Study area

The study was conducted in 14 populations of *P. chihuahuana* located in several municipalities in the states of Durango and Chihuahua, Mexico (Table 1 and Figure 1). These populations were growing with 15 other tree species, mainly *Pinus strobiformis*, *Pseudotsuga menzesii* and *Populus tremuloides* (Simental-Rodríguez et al., 2014). Each location was represented by one 50 x 50 m (0.25 ha) plot established in the center of the population. Following Wehenkel et al. (2015), all trees with diameter at breast height (DBH) ≥ 7 cm were scored in regard to position, DBH, height and species affiliation. Within each plot, the number of trees of *Picea chihuahuana, Pinus strobiformis*, *Pseudotsuga menzesii and Populus tremuloides* with DBH < 7 cm were also recorded. Field experiments were approved by SEMARNAT, Mexico.

Determination of edaphological variables

In each location, a soil sample (250 g) was collected at a depth of 0 to 15 cm at the base of the stems of four *Picea chihuahuana* trees and at the base of four specimens of *Pinus strobiformis*, *Pseudotsuga menzesii* and *Populus tremuloides* (when present). The four soil subsamples for each species in each location were combined to make a 1,000 g sample (35 samples in total) for analysis of 27 edaphic variables. The texture (relative proportion of sand, silt and clay), water flow (cm/h), concentration of calcium carbonate ($CaCO_3$), pH ($CaCl_2$, 0.01 M), concentrations of K (ppm), Mg (ppm), Na (ppm), Cu (ppm), Fe (ppm), Mn (ppm), Zn (ppm) and Ca (ppm) in the soil were determined by the methods described by Castellanos, Uvalle-Bueno & Aguilar-Santelises (1999). Phosphorus (P) (ppm) was determined by the method of Olsen et al. (1954). Nitrate (NO_3) (kg /ha) was determined by the method of Baker (1967) and the relative organic matter (OM) contents were determined by the method of Leon & Aguilar (1987). Electrical conductivity (CE) (dS/m) was determined by the method described by Vazquez & Baptist (1993). Finally, the cation exchange capacity (CEC) and the relative proportions (%) of oxygen, hydrogen, Ca, M, K and Na in the CEC were estimated on the basis of the Ammonium Acetate Method (pH 8.5). The soil variables are described in Table 2.

Determination of climate variables

The climate model of Rehfeldt (2006), based on thin plate spline (TPS) of Hutchinson (1991, 2004), was used to estimate 22 climate variables in each population. This model yielded data from standardized monthly mean, minimum, and maximum values of temperature and precipitation from more than 200 climate stations in Chihuahua and Durango, for the period 1961-1990. Point estimates of climate measures were obtained from a national database managed by the University of Idaho (http://forest.moscowfsl.wsu.edu/climate/), for which the geographical coordinates (latitude, longitude and elevation) are required as input data. The variables considered included mean annual precipitation (mm), mean temperature in the warmest month (ºC), mean maximum temperature in the warmest month (ºC), Julian date of the first freezing date of autumn, and precipitation during the growing season (April to September) (mm). Climate variables are described in Table 3.

Determination of dasometric variables

Fourteen dasometric variables were considered as vitality parameters (Ledig *et al*., 2000) (Table 4). For each plot and for each of the four tree species (*Pinus strobiformis*, *Pseudotsuga menzesii, Populus tremuloides* and *Picea chihuahuana)* we estimated the basal area (G_{sp}), diameter at breast height (DBH_{sp}), height (H_{sp}), maximum diameter at breast height ($DBH_{max,sp}$), maximum height ($H_{max,sp}$). For each plot we also estimated the following variables considering together the all tree species per plot: total diameter at breast height (DBH_{tot}), total height (H_{tot}). Besides we registered the total maximum diameter at breast height for all tree species per location ($DBH_{max,tot}$) and total maximum height for all tree species per location ($H_{max,tot}$), according to Assmann (1970). We also estimated the total number of individuals of each of these four tree species per plot (N_{sp}), quadratic DBH of each of these four tree species per plot ($D_{g,sp}$), total number of individuals per plot (N_{tot}), basal area per plot (G_{tot}) and quadratic DBH per plot (D_g), according to Wehenkel *et al.* (2015).

Determination of genetic diversity variables

Needles were sampled from a total of 686 individuals of *Picea chihuahuana* trees in the fourteen populations (plots) studied (i.e. 17–53 individuals per plot), for determination of genetic diversity variables (Table 5). Needles and leaves from 129 individuals of *Pinus strobiformis* in ten locations (3-17 trees per plot), 63 trees of *Pseudotuga menzesii* in six locations (10–11 trees per plot) and 74 trees of *Populus tremuloides* in five locations (8-13 individuals per plot) were sampled for analysis of the genetic diversity of the *Picea chihuahuana* tree community.

The DNA was extracted using the DNeasy 96 Plant Kit (QIAGEN). The amplified fragment length polymorphism (AFLP) analysis was conducted according to a modified version of the protocol of Vos et al. (1995), described by Simental-Rodríguez et al. (2014). The restriction enzymes used were Eco RI (selective primer: 5'-GACTGCGTACCAATTCNNN-3') and Mse I (selective primer: 5'-GATGAGTCCTGAGTAANNN-3'). The primer combination E01/M03 (EcoRI-A/MseI-G) was used in the pre-AFLP amplification. Selective amplification was carried out with the fluorescent-labelled (FAM) primer pair E35 (EcoRI-ACA-3) and M63+C (MseI-GAAC). The AFLP products were separated in a Genetic Analyzer (ABI 3100), along with the GeneScan 500 ROX internal lane size standard (Applied Biosystems). Selection of the amplified restriction products was totally automated, and only strong and high quality fragments were considered. The size of the AFLP fragments was determined with the GeneScan® 3.7 and Genotyper® 3.7 software packages (Applied Biosystems). Binary AFLP matrices were created from the presence (code 1) or absence (code 0) at probable fragment positions. The quality and reproducibility of the analysis were verified according to Ávila-Flores et al. (2016).

The AFLP data were used to calculate three genetic diversity indices (Table 5): the modified frequency-down-weighted marker value (DW), percentage polymorphism (POLY) (Schönswetter & Tribsch 2005), and mean genetic diversity (v_2) were determined according to Gregorius (1978),

$$\mathrm{V}_{2,j} = \left(\frac{1}{N}\right) * \sum\left(\frac{1}{\sum p_{ij}^2}\right)$$

where p is the relative frequency of a variant from the i to the j locus. The value of DW is expected to be high when rare AFLPs are accumulated (Schönswetter & Tribsch 2005). In order to equalize dissimilar sample sizes, the values of the three diversity indices were multiplied by a correction term (N/(N-1)) (Gregorius, 1978).

The species richness variables ($\nu_{sp,0}$), Simpson index ($\nu_{sp,2}$) and number of prevalent tree species ($\nu_{sp,inf}$) were taken from Simental-Rodríguez et al. (2014) (Table 5).

The values of the three genetic diversity indices were also calculated for putative AFLPs under natural selection (outlier AFLP) detected in *Picea chihuahuana*. These outlier AFLPs were taken from Simental-Rodríguez et al. (2014) (Table 5).

Discriminant analysis

Discriminant analysis (Fisher 1936) including cross-validation was used to test for significant differences in 69 climatic, dasometric and soil variables and genetic diversity indices in the southern, central and northern populations and locations of the *Picea chihuahuana* tree community (taking into account the four species *P. chihuahuana*, *Pinus strobiformis*, *Pseudotsuga menziesii* and *Populus tremuloides*) (Table 1). The XLSTAT 2015.1 software was used to conduct the analysis. A discriminant function comprising a linear combination of the 35 variables that explained the highest level of variability was thus generated. The discriminant function was built up gradually by adding or removing variables that best separate the groups (of populations and locations).

The optimality criterion for the discriminant function was a maximum relation of the variance between the groups for variance within the groups. The eigenvalues and correlations between these 35 variables and factors of each group of factors were calculated. These coefficients revealed the influence of individual variables. The results of this multivariate method for distinguishing between groups were statistically examined by using the Wilks Lambda, Pillai's trace and Hotelling trace test variables. At least one mean vector is considered significantly different from the other when p is < 0.05. The rate of generation of false classifications was determined by a confusion matrix before and after cross-validation (Everitt & Dunn, 1991; Polit, 1996).

Spearman correlations

Spearman's correlation test (Hauke & Kossowski, 2011) was used to analyze the relationships between genetic diversity, population size (taken from Ledig et al. (2000)), and the climatic, soil and dasometric variables in the 14 populations and the locations of the *Picea chihuahuana* tree community. The test was implemented using R 3.2.3 statistical software (R Core Team, 2015). Bonferroni correction was conducted to calculate the new critical significance level (α* = 0.0007), by dividing the critical significance level (α= 0.05) by the number of comparisons (hypotheses) (m = 69) (Hochberg, 1988).

Results

Discriminant analysis

The discriminant analysis revealed 22 highly significant variables ($p<0.05$), which separated the southern, central and northern populations and locations of the *Picea chihuahuana* tree community (Tables 1 and 6). In the analysis of the whole *P. chihuahuana* tree community, only 15 relevant variables belonging to Factor 1 explained 99.9% of the variability. Nine of these variables are related to climate (Long, Elev, Mtcm, Mtwm, Mmax, D100, DD0, Smrpb and Sprp), five are soil variables (NO_3, Sand, Clay, Ca and %Mg) and one is a dasometric variable (G_{tot}). Four variables belonging to Factor 2 explained the other 0.1% of the variability: EC, pH, %H (soil variables) and FFP (a climate variable) (Table 6). When analyzing the 14 populations of *P. chihuahuana*, 99.82% of the variability was explained by Factor 1, which included 11 variables, nine of which are related to climate (Long, Elev, gsp, Mtcm, Mtwm, Mmax, DD0, Smrpb and Smrsprpb), one is a soil variable (Clay) and one variable is related to genetic diversity (v_2). No significant variables were found in Factor group 2 (Table 6, Figure 2). The confusion matrix after cross-validation revealed a rate of generation of false classifications of 33%. The southern, central and northern populations (*P. chihuahuana)* and the *P. chihuahuana* tree community are represented in Figs. 3 and 4, respectively.

The discriminant analysis of the *P. chihuahuana* tree community revealed the following (Table 7):

a) southern locations (S) are characterized by acidic soils with low concentrations of Mg, a long frost-free period and large basal area of the trees.

b) central locations (C) are characterized by moderate temperatures in the warmest month, slightly acidic soils with high concentrations of Ca and particularly of %Mg.

c) northern locations (N) are characterized by high temperatures in the warmest month, acidic soils and low basal areas of trees.

On the other hand, the discriminant analysis of three groups of *P. chihuahuana* populations indicated that (Table 7):

a) southern populations presented the highest levels of precipitation in the months April to September, low temperatures in the warmest month, low proportion of clay in soil, and low genetic diversity.

b) central populations are characterized by moderate levels of precipitation in the months April to September, moderate mean temperature in the warmest month, and a low level of genetic diversity.

c) northern populations are characterized by low levels of precipitation in the months April to September, high temperatures in the warmest month, a high percentage of clay in soils and a high level of genetic diversity.

After Bonferroni correction, the mean genetic diversity v_2 of *Picea chihuahuana* was significantly correlated with the mean temperature in the warmest month (ºC) (Mtwm) (p = 0.0002) (Table 8, Figure 5). Genetic diversity of *P. chihuahuana* calculated with putative adapted AFLP markers was not statistically significantly correlated with any environmental factor. Finally, no significant correlations were observed between any of the three genetic diversity indices and population size.

Discussion

The study's findings show that the southern, central and northern *Picea chihuahuana* populations and locations of the *P. chihuahuana* tree community are characterized by different climate and soil conditions. Eleven climate and nine soil variables were identified as important for separating the three groups and explained almost 100% of the variability (Table 6). However, the most important climate variables for differentiating the *P. chihuahuana* populations were the mean maximum temperature in the warmest month and the summer precipitation balance (Fig. 2). This is not a novel finding. Several authors have reported that the distribution of species and provenances depends both on the climate and the soil (e.g. Ellenberg 1996, Härdtle et al., 2004; Soberon & Peterson, 2005; Sánchez et al., 2007; Flores-Rentería et al., 2013).

The tree basal area (G_{tot}) was significantly lower in the northern locations of the *P. chihuahuana* tree community, in which the maximum temperatures (Mmax and Mtwm) were also highest (Table 6). Hence, the climate conditions strongly restricted biomass production and therefore the vitality of these locations. This was also observed by Ledig et al. (2010) who identified the northern locations as the first group that may be threatened with extinction in some climate change projections.

The genetic diversity across all AFLPs studied was found to be an important variable separating the three populations of *Picea chihuahuana* under study. It was significantly correlated with Mtwm (Tables 6 and 8, Figure 5), but not with the population size. By contrast, the genetic diversity among the putative adaptive AFLPs was not significantly related to other variables. The relationships observed were probably not determined by selection, but by differences in the degree of isolation, which would influence gene flow and genetic drift. The northern populations are much closer (about three km of mean distance between the 11 documented populations in the Municipality of Bocoyna, Chih., minimal 0.5 km, maximal 13 km to each other) to each other than the southern populations are (Ledig et al. 2000), which may lead to greater genetic exchange and a lower tendency for genetic drift and inbreeding and, thus, to a higher level of genetic diversity (Hamrick, Godt & Sherman-Broyles, 1992; Ledig et al., 1997).

Jaramillo-Correa et al. (2006) also found that the diversity of cpDNA in *P. chihuahuana* decreased from northern to southern areas (with the highest to the lowest Mtwm, respectively). These authors assumed that genetic drift, rather than selection, was the main factor determining the population diversity in Chihuahua spruce. Moreover, the observations of Ledig et al. (1997), based on isozyme analysis, also suggest the importance of drift and inbreeding in the recent evolution of this tree species.

Conclusions

Our findings have three important practical implications in relation to ex situ conservation: First, at least three different ecotypes of *Picea chihuahuana* probably exist, as local adaptation may take place because of the different environmental conditions. These differences are also indicated by genetic differences between the southern and northern populations (Ledig et al., 1997; Jaramillo-Correa et al., 2006; Quiñones-Pérez, Sáenz-Romero & Wehenkel, 2014). Therefore, future reforestations should only be established with seed sources from the same region. Second, there are no notable environmental and genetic differences within the groups (if a misplacement rate of 30 % means "no difference"). Thus, seed from different populations of the same ecotype could be mixed to improve the level of genetic diversity. Finally, the study revealed the special climate and soil conditions in the locations where *P. chihuahuana* is growing.

Measurement of these environmental variables may be useful for identifying suitable sites that are similar to those where the original stands are growing, which may help to improve the reforestation success. However, *Picea chihuahuana* grows in areas with special micro climate conditions that are not easily modelled with simple macro climate models (Aguilar-Soto et al., 2015), but that can be recorded at local weather stations. Importantly, it was noticed that almost all *Picea chihuahuana* populations are located on creeks or rivers and on north-east to north-west facing slopes (Ledig et al., 2000).

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Tables

Table 1. Locations of the *Picea chihuahuana* tree community under study

Group	Code	Property	Municipality	Location	Population size	Latitude N	Longitude W	Altitude m
northern	TN	El Ranchito	Bocoyna	La Tinaja	99	27º57´27"	107º46´13"	2,380
	RC	El Ranchito	Bocoyna	El Ranchito	217	27º57´20"	107º45´12"	2,414
	CV	El Ranchito	Bocoyna	El Cuervo	140	27º57´01"	107º46´18"	2,500
	TY	Los Volcanes	Bocoyna	Talayote	291	27º55´03"	107º49´01"	2,355
	TR	El Ranchito	Bocoyna	Las Troja	834	27º54´27"	107º45´17"	2,395
	VN	San Javier	Bocoyna	El Venado	3,364	27º45´41"	107º41´33"	2,311
center	LQ	El Caldillo y su anexo El Vergel	Belleza	La Quebrada	877	26º28´13"	106º21´51"	2,730
	PPR	Chiqueros	Guanaceví	Paraje Piedra Rayada	3,564	26º09´15"	106º24´17"	2,600
	QD	Chiqueros	Guanaceví	Quebrada de los Duran	2,628	26º08´48"	106º22´53"	2,570
	CB	Private property	Canelas	Cebollitas	172	25º05´55"	106º26´27"	2,450
southern	SJ	San José de las Causas	San Dimas	San José de las Causas	21	24º01´07"	105º47´56"	2,480
	SB	El Brillante	Pueblo Nuevo	Santa Bárbara	148	23º39´44"	105º26´20"	2,725
	ACH	Santa Maria Magdalena de Taxicaring	Mezquital	Arrollo del Chino	46	23º21´05"	104º43´05"	2,600
	LP	Santa Maria Magdalena de Taxicaring	Mezquital	La pista	919	23º19´52"	104º45´00"	2,685

Table 2. Descriptive statistics for the (climatic) variables: minimum, maximum and mean values and the standard deviations are shown for 17 observations per variable.

	Variable Climatic	Minimum	Maximum	Mean	Typical deviation
Long	Longitude	-107.817	-104.718	-106.703	1.064
Elev	Elevation (m)	2,311	2,730	2,509	132
Mat	Mean annual temperature (ºC)	9.70	11.90	10.80	0.50
Map	Mean annual precipitation (ºC)	700	1,350	905.9	218.9
Gsp	Growing season precipitation, April to September (mm)	520	941	658.0	150.5
Mtcm	Mean temperature in the coldest month (ºC)	3.8	7.3	5.0	1.0
Mmin	Mean minimum temperature in the coldest month (ºC)	-5.6	-1.3	-4.2	1.4
Mtwm	Mean temperature in the warmest month (ºC)	13.8	17.2	15.8	1.08
Mmax	Mean maximum temperature in the warmest month (ºC)	21.7	26.6	24.8	1.40
Sday	Julian date of the last freezing date of spring	126	163	151	10
Fday	Julian date of the first freezing date of autumn	266	295	281	9
Ffp	Length of the frost-free period	104	165	134	19
Dd5	Degree-days above 5 °C	1,873	2,593	2,275	178
Gsdd5	Degree-days above 5 ° C in the frost-free period	974	1,679	1,323	220
D100	Julian date the sum of degree-days above 5 ° C reaches 100	35	69	56	10
DD0	Degree-days below 0 °C (based on mean monthly temperature)	0	39	20	12
Mmindd0	Degree-days below 0 °C (based on mean minimum monthly temperature)	427	907	780	157
Smrpb	Summer precipitation balance: (Jul+Aug+Sep)/(Apr+May+Jun) (mm)	3.83	4.96	4.47	0.36
Smrsprpb	Summer/Spring precipitation balance: (Jul+Aug)/(Apr+May) (mm)	10.53	14.48	12.49	1.00
Sprp	Spring precipitation (Apr+May) (mm)	26	43	32	6
Smrp	Summer precipitation (Jul+Aug) (mm)	316	544	396	81
Winp	Winter precipitation (Nov+Dec+Jan+Feb) (mm)	100	326	172	62

Table 3. Descriptive statistics for the soil variables: minimum, maximum and mean values and standard deviations are shown (35 observations per variable).

	Soil variable	Minimum	Maximum	Mean	Typical deviation
EC	Electric conductivity (dSmol)	0.22	2.19	0.76	0.40
NO_3	Nitrate (kg/ha)	14.78	606.08	236.02	178.40
P	Phosphorus (ppm)	5.23	114.68	25.66	26.98
OM	Organic material (%)	3.35	26.80	9.33	4.62
$\%CaCO_3$	Calcium carbonate (%)	0.00	13.60	2.13	3.58
%Sat.	Percent saturation (%)	29.00	95.00	68.71	14.27
Sand	Sand (%)	49.26	75.26	62.92	7.99
Slime	Slime (%)	15.28	35.28	25.45	6.07
Clay	Clay (%)	7.46	17.46	11.63	2.84
Den	Density (gr/cm^3)	0.54	1.07	0.87	0.13
pH	pH	4.42	7.47	5.70	0.63
Ca	Calcium (ppm)	2340.00	6576.00	3985.20	1072.01
Mg	Magnesium (ppm)	144.00	942.00	380.40	148.48
Na	Sodium (ppm)	40.00	177.50	71.09	26.63
k	Potassium (ppm)	191.00	6225.00	1388.61	1270.31
Fe	Iron (ppm)	27.28	401.72	172.38	86.66
Zn	Zinc (ppm)	0.32	21.28	4.55	4.70
Mn	Manganese (ppm)	16.64	419.76	108.50	82.46
Cu	Copper (ppm)	0.16	1.06	0.41	0.23
% o.b.	Relative proportion of other bases in the cation exchange capacity (%)	0.00	38.70	20.14	8.70
%Ca	Relative proportion of Ca in the cation exchange capacity (%)	5.44	69.52	53.63	11.55
%Mg	Relative proportion of Mg in the cation exchange capacity (%)	0.69	15.06	8.47	2.48
%K	Relative proportion of K in the cation exchange capacity (%)	0.30	21.95	8.99	6.29
%Na	Relative proportion of Na in the cation exchange capacity (%)	0.06	1.76	0.87	0.35
%H	Relative proportion of H in the cation exchange capacity (%)	3.97	7.09	5.96	0.81
CEC	Cation exchange capacity (meq / 100 g soil)	20.77	392.46	46.54	60.99
HC	Hydraulic conductivity (cm/h)	0.27	60.98	19.99	15.65

Table 4. Descriptive statistics for the diversity variables: minimum, maximum and mean values and standard deviations are shown (17 observations per variable).

Diversity variable		Minimum	Maximum	Mean	Typical deviation
v_2	Mean genetic diversity	1.23	1.74	1.52	0.13
POLY	Percentage polymorphism	0.31	1.04	0.72	0.22
DW	Modified frequency-down-weighted marker value	0.04	0.57	0.24	0.18
$v_{2\ (\text{outlier AFLP})}$	Mean genetic diversity per outlier AFLP	1.07	1.78	1.46	0.27
$\text{POLY}_{(\text{outlier AFLP})}$	Percentage polymorphism per outlier AFLP	0.26	1.02	0.78	0.31
$\text{DW}_{(\text{outlier AFLP})}$	Modified frequency-down-weighted marker value per outlier AFLP	0.002	0.02	0.01	0.07
$v_{sp,0}$	Species richness	4.00	9.00	6.17	1.49
$v_{sp,2}$	Effective number of tree species	1.92	4.46	3.39	0.80
$v_{sp,inf}$	Number of prevalent tree species	1.49	3.00	2.31	0.46

Table 5. Descriptive statistics for the dasometric variables used: minimum, maximum and mean values and standard deviations are shown (17 observations per variable).

	Dasometric variable	Minimum	Maximum	Mean	Typical deviation
N_{sp}	Total number of individuals per tree species*	4.00	168.00	76.45	47.80
G_{sp}	Tree basal area per tree species (m^2/ha)	0.093	14.300	4.793	4.24
Dg_{sp}	Quadratic diameter at breast height per tree species (cm)	11.38	49.90	25.96	10.80
DBH_{sp}	Diameter at breast height per tree species (cm)	10.73	44.09	22.91	9.39
H_{sp}	Height per tree species (m)	8.25	23.58	14.09	5.63
$DBH_{max,sp}$	Maximum diameter at breast height per tree species (cm)	17.20	86.50	49.37	21.24
$H_{max,sp}$	Maximum height per tree species (m)	13.00	48.00	25.83	11.13
N_{tot}	Total number of individuals	152.00	736.00	366.06	133.34
G_{tot}	Tree basal area (m^2/ha)	13.70	53.28	22.05	8.76
Dg_{tot}	Quadratic diameter total (cm)	22.10	37.30	28.06	3.98
DBH_{tot}	Total diameter (cm)	17.90	32.90	24.01	3.68
H_{tot}	Total height among all tree species per plot (m)	9.70	17.90	14.10	2.22
$DBH_{max,tot}$	Maximum diameter at breast height total per plot (cm)	55.00	104.00	75.01	14.29
$H_{max,tot}$	Maximum height total among all tree species per plot (m)	23.30	48.00	34.61	7.39

Note: * the tree species were *P. strobiformis*, *P. menzesii* and *P. tremuloides* and *P. chihuahuana*.

Table 6. Eigenvalue of each factor group, variability explained by factor groups F1 and F2 including the 22 most important variables within the three factor groups ($p < 0.05$). The importance of the variable in the factor group increased with the correlation between variable and factor group.

Picea chihuahuana	Tree species community		Population	
	F1	F2	F1	F2
Eigenvalue	1,132,512	1141	95,360	168
Variability explication (%)	99.90	0.10	99.82	0.18
Relevant variable	**Variable / factor correlation**			
Long	-0.974		-0.972	
Elev	-0.707		-0.765	
Gsp			-0.782	
Mtcm	-0.758		-0.771	
Mtwm	0.796		0.861	
Mmax	0.932		0.950	
Ffp		0.485		
D100	0.740			
DD0	0.794		0.830	
Smrpb	0.911		0.908	
Smrsprpb			-0.847	
Sprp	-0.409			
EC		-0.547		
NO_3	0.342			
Sand	-0.528			
Clay	0.611		0.775	
pH		-0.500		
%H		0.447		
Ca	-0.436			
%Mg	0.419			
v_2			0.804	
G_{tot}	-0.518			

Table 7. Descriptive statistics for the most important conditions studied and for the genetic diversity (v_2) of the *Picea chihuahuana* populations and tree species community, respectively (growing season precipitation, April to September (Gsp), mean temperature in the warmest month (Mtwm), mean maximum temperature in the warmest month (Mnax), length of the frost-free period (Ffp), degree-days below 0 °C (based on mean monthly temperature) (DD0), clay, calcium (Ca), pH value (pH), relative ratio of Mg in the cation exchange capacity (%Mg), tree basal area of all tree species per plot (G_{tot})), mean and standard deviation (±).

Picea chihuahuana populations

Populations	**Gsp**	**Mtwm**	**Mmax**	**DD0**	**Clay**	**v_2**
North	557.50 ± 20.87	16.95 ± 0.25	26.25 ± 0.27	30.83 ± 5.00	14.46 ± 2.10	1.57 ± 0.02
Centre	650.00 ± 143.58	15.08 ± 0.38	24.23 ± 0.22	14.25 ± 7.08	9.96 ± 2.18	1.47 ± 0.03
South	860.75 ± 87.68	14.88 ± 0.87	22.95 ± 0.90	8.25 ± 9.29	9.46 ± 0.00	1.48 ± 0.04

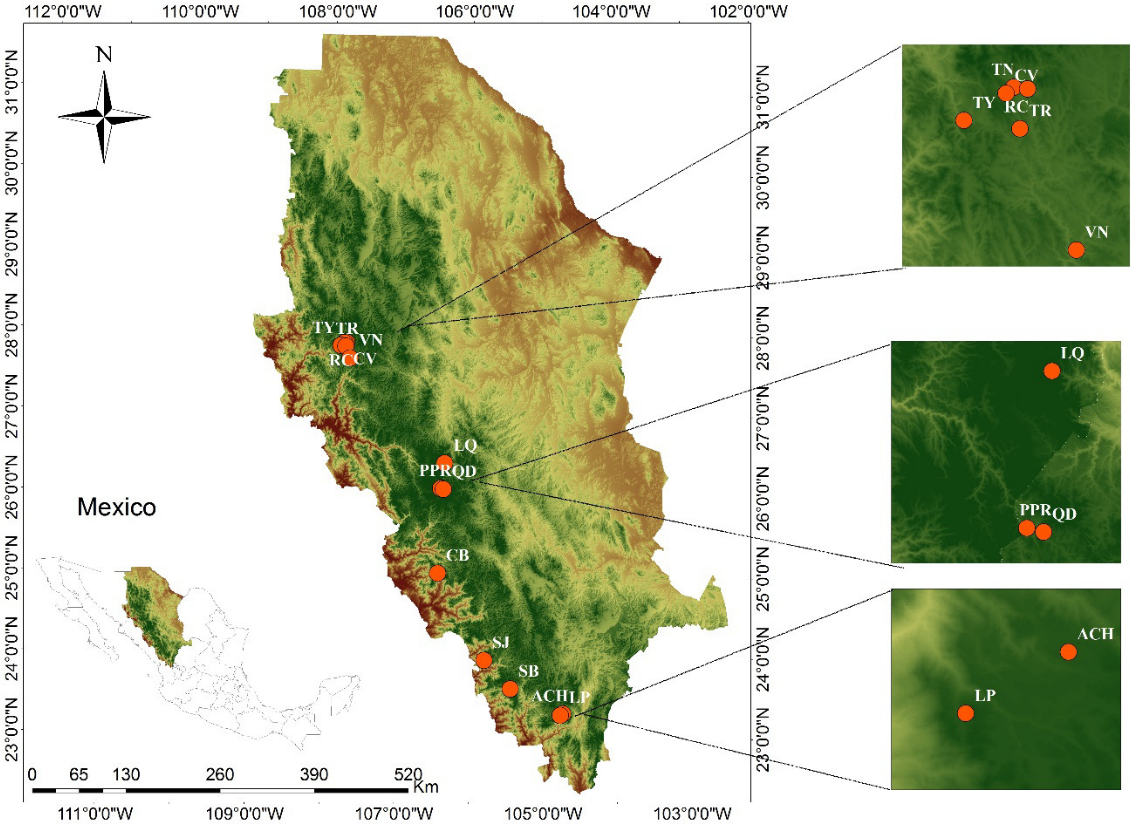
P. chihuahuana tree community

Locations	**Mtwm**	**Mmax**	**Ffp**	**pH**	**Ca**	**%Mg**	**G_{tot}**
North	16.96 ± 0.22	26.27 ± 0.24	137.07 ± 3.28	5.53 ± 0.43	3702.40 ± 911.28	9.03 ± 1.50	17.84 ± 2.27
Centre	15.08 ± 0.39	24.26 ± 0.23	122.25 ± 24.93	6.12 ± 0.69	4618.50 ± 1002.77	9.31 ± 2.61	22.38 ± 4.18
South	14.94 ± 0.86	23.01 ± 0.88	147.25 ± 18.21	5.39 ± 0.55	3565.50 ± 1131.66	6.13 ± 2.55	29.45 ± 15.29

Table 8. Correlation between genetic diversity (v_2) and climate and soil variables in the *Picea chihuahuana* populations and tree species community under study. $^+$ = significant after Bonferroni correction

***Picea chihuahuana* populations**		
Genetic diversity (v_2)		
	Spearman r	***p***
Long	-0.74	0.0027
Mtwm	0.83	0.0002^+
Mmax	0.70	0.0058
D100	0.68	0.0074
DD0	0.67	0.0088
Smrpb	0.69	0.0061
Smrsprpb	-0.68	0.0076
Clay	0.67	0.0091
Tree species community		
Mean genetic diversity (v_2)		
	Spearman r	***p***
K	-0.45	0.0063
%K	-0.46	0.0053

577 **Figures**



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580 Figure 1. Locations of the study populations: La Tinaja (TN), El Ranchito (RC), El Cuervo (CV),
581 Talayote (TY), Las Trojas (TR), El Venado (VN), La Quebrada (QD), Paraje Piedra Rayada
582 (PPR), Quebrada de los Duran (QD), Cebollitas (CB), San José de las Causas (SJ), Santa Bárbara
583 (SB), Arrollo del Chino (ACH), La pista (LP).

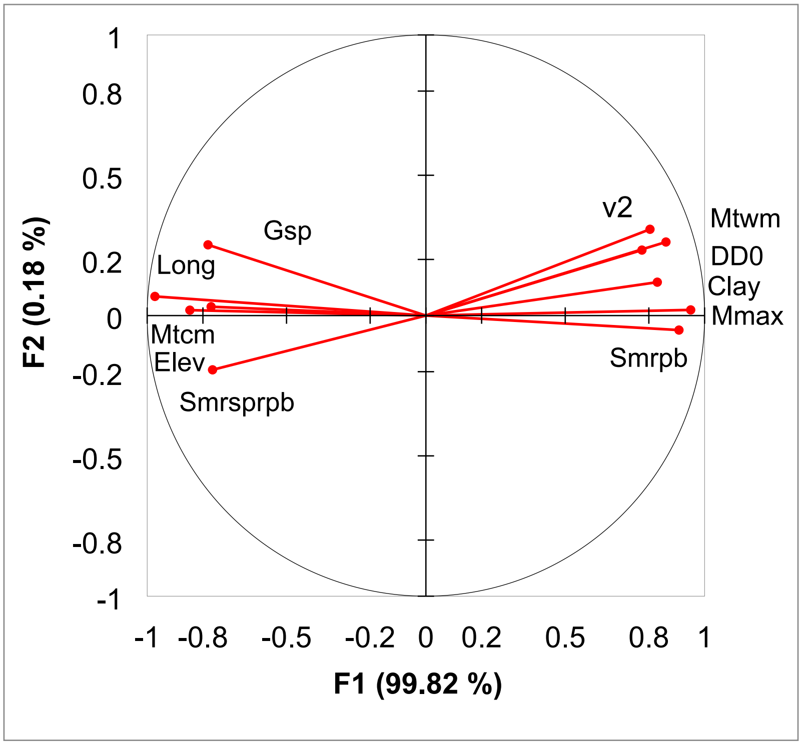

Figure 2. Most important variables distinguishing the three groups of populations of *Picea chihuahuana* and the correlation variables for the factor groups F1 and F2. For definitions of the variable abbreviations, see Table 2.

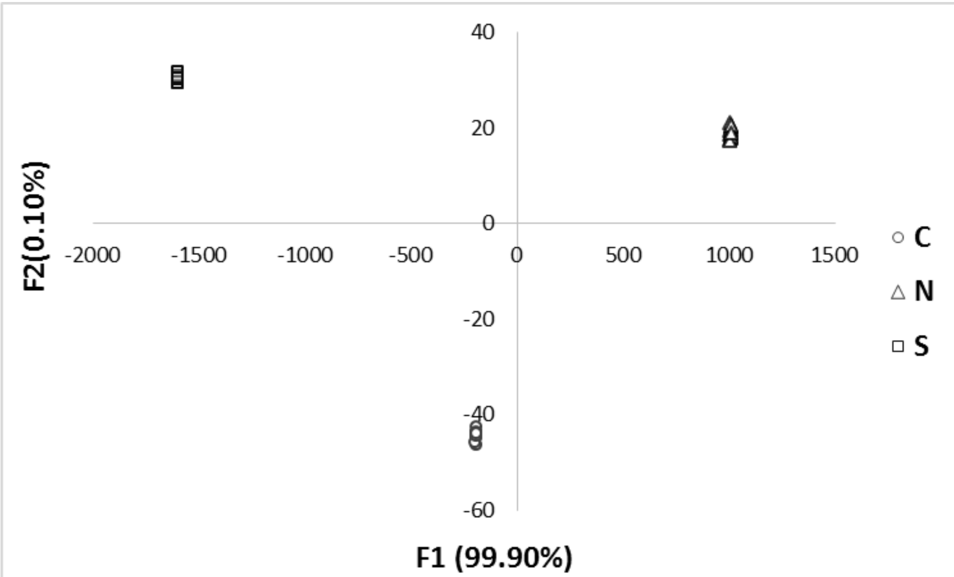

Figure 3. Discrimination of the 14 locations of the *Picea chihuahuana* tree species community on the factor axes extracted from the original explanatory variables; northern (N), central (C), southern (S) group of the *Picea chihuahuana* tree species community.

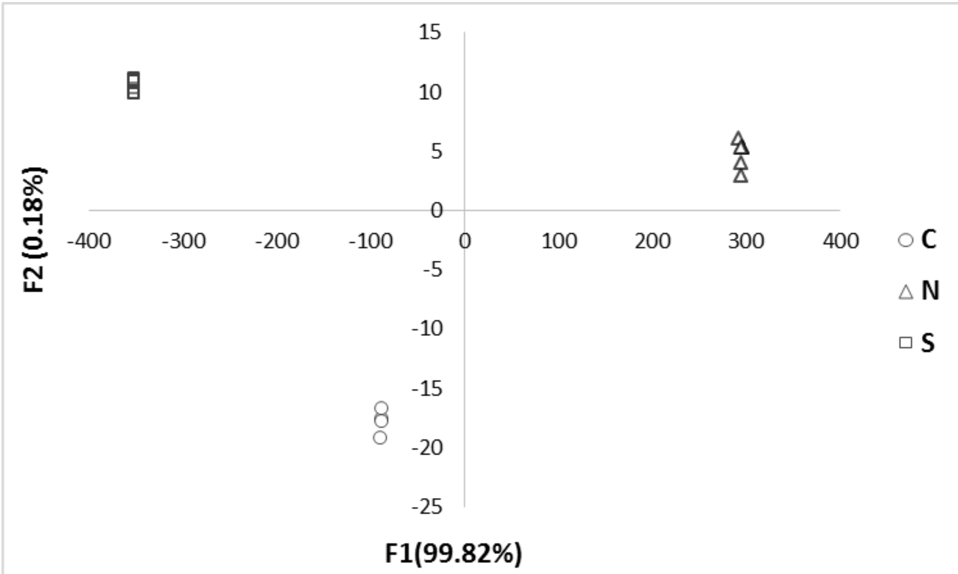

Figure 4. Discrimination of the 14 populations of *Picea chihuahuana* on the factor axes extracted from the original explanatory variables; northern (N), central (C), southern (S) populations.

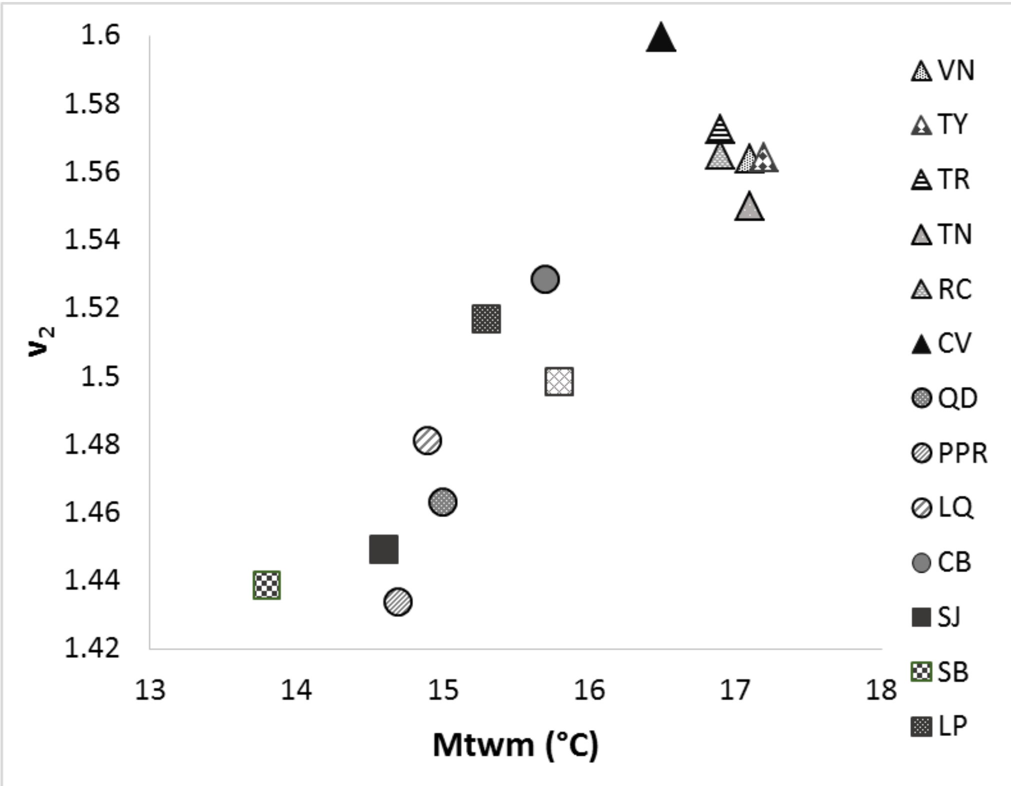

Figure 5. Relationship between genetic diversity (v_2) and mean temperature in the warmest month (Mtwm) in 14 populations of *Picea chihuahuana*: La Tinaja (TN), El Ranchito (RC), El Cuervo (CV), Talayote (TY), Las Trojas (TR), El Venado (VN), La Quebrada (QD), Paraje Piedra Rayada (PPR), Quebrada de los Duran (QD), Cebollitas (CB), San José de las Causas (SJ), Santa Bárbara (SB), Arrollo del Chino (ACH), La pista (LP); Triangles represent northern populations, circles represent central populations, squares represent southern populations.