Review

Genetic diversity and conservation of *Picea chihuahuana* Martínez: A review

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The conservation of genetic diversity in tree populations is an essential component of sustainable forest management. *Picea chihuahuana* Martínez is an endemic conifer species in Mexico and is considered to be endangered. *P. chihuahuana* covers a total area of no more than 300 ha at the Sierra Madre Occidental, a mountain range that harbor a high diversity of tree species. There are 40 populations of the species that have been identified in the region, and it cannot be found elsewhere. These populations form clusters within gallery forests and are usually associated with eight other tree genera. The *P. chihuahuana* community is mostly well preserved. Owing to its remarkable characteristics and high conservation value, *P. chihuahuana* has been the subject of several studies aimed at learning more about the genetic structure, ecology and potential effects of climate change. However, the overall applicability of such studies is to confirm a dataset to develop management tools to help decision makers and to implement preservation and conservation strategies using genetic diversity. In this review, we summarize the studies carried out to date, emphasizing those concerning the most important aspects of the genetic diversity of the species. Although, genetic diversity in Chihuahua spruce is mostly moderate compared with other *Picea*, this species is unlikely to survive without help due to its small and isolated populations. Efforts should focus on the protection of populations displaying the highest degree of genetic variation because these populations have the greatest potential for adaptive evolution. Finally, continuous monitoring of size and genetic diversity of the current populations *in situ* is essential.

**Key words:** Pinabete, spruce, endangered species, heterozygosity, genetic variability, Sierra Madre Occidental.

INTRODUCTION

In a broad sense, genetic variability or genetic diversity is a basic component of biodiversity and it is defined as inheritable variations occurring in every organism, among individuals within a population and among populations within a species. Hence, knowledge and understanding of genetic diversity is of vital importance for evolutionary...
genetics, as well as for public health, productivity and sustainability of agricultural, livestock, fishing and forestry industries, domestication and biomedicine (Piñero et al., 2008). Historical biological processes, such as fragmentation, expansion of the geographical distribution and events such as genetic bottlenecks and other responses to climatic and geological changes, have altered genetic diversity and molded patterns of genetic differentiation among and within species and populations (Ledig et al., 1997; Schaal et al., 1998). These events can be detected in the genetic structure of many tree species due to their extended generation times (Newton et al., 1999). Conservation of genetic diversity in tree populations is an essential component of sustainable forest management. The abilities of trees and other forest species to evolve, resist and adapt to climate change largely depend on the genetic diversity within species (St. Clair and Howe, 2011). The Intergovernmental Panel on Climate Change (IPCC) estimates that global average temperature will increase about 1.8 to 4.0°C during the 21st century. An average increase in temperature of 3.7°C and a decrease in precipitation of 18.2% by the end of the century are predicted for Mexico (Sáenz-Romero et al., 2010). Furthermore, the extinction risk will increase for 30% of the world’s species (Intergovernmental Panel on Climate Change, 2007).

The study of genetic diversity can be applied to the following: a) evaluation of the responsiveness of populations and species facing environmental changes caused by anthropogenic activities; b) assessment of risks related to loss of species, populations and genetic resources; c) knowledge of the genetic richness and its geographical distribution; d) planning of exploitation and conservation strategies for populations, species and genetic resources; e) understanding the mechanisms, rate and causes of the loss of genetic diversity; f) assessment of risks produced in populations, native species and genetic resources of plants, animals and humans by introducing diseases, pests, invasive species and genetically improved varieties (Piñero et al., 2008). Until now, effects on genetic diversity originated by fragmentation, isolation and reduction of population size have been known theoretically. However, empirical data from natural populations of forest trees are relatively scarce. Wright’s theory suggests that the smallest populations without gene flow will lose genetic variability faster than larger populations because small populations are more susceptible to such loss due to genetic drift, endogamy depression and strong unidirectional selection, causing genetic erosion (Wright, 1969; Karron et al., 1988; Maxted and Guarino, 2006; Wehenkel and Sáenz-Romero, 2012). Locations displaying high genetic diversity probably represent the populations that are most adaptable to changes; therefore, these locations are the most suitable for focusing conservation efforts (Ledig et al., 2005). However, some simulation studies suggest that variability may not be lost as quickly as Wright’s (1969) model indicates and that selection of heterozygotes could delay the loss of alleles (Lesica and Allendorf, 1992). The study and interpretation of patterns of intraspecific genetic variation should be a priority for academic institutions, governmental and non-governmental organizations related to environmental conservation and sustainable natural resources management, in order to learn about dynamics, adaptation and evolution of the species (Ellstrand and Elam, 1993) and to contribute to the design of protection and conservation strategies for the species.

Studies of genetic diversity in Mexican plant species are scarce in relation to the number of studies on other aspects (e.g., ecological aspects) of the reported species in the country (CONAFOR, 2011). One exception to this is Picea chihuahuana Martínez of great value, because this spruce and two other congeners, Picea mexicana Martínez and Picea martinezii Patterson, are relics of the last glaciation, and the only representatives of the genus Picea located in southern latitudes in North America (Ledig et al., 1997; Ledig et al., 2000a). This species has been the subject of several investigations aimed at learning more about the ecology, genetics, potential and association with other species. However, the main aim of such studies has been to enable the design of preservation and conservation strategies (Sánchez and Narváez, 1990), as discussed further below.

GENUS PICEA

Picea is a mainly boreal genus and, depending on the taxonomy used, includes 31 to 50 species (Wright, 1955; Bobrov, 1970; Farjon, 2010). The genus Picea occurs in Europe, Asia, the Caucasus, Siberia, China, Japan, the Himalayas, North America and Mexico. The genus has evolved from primordial ancestors in the continental part of Northeast Asia (Youngblood and Safford, 2002). The Korean fir (Picea koraiensis Nakai) is probably the most primitive species of this genus. Most North American species probably arose due to the eastward migration and mutation of some fir species (Wright, 1955). Fossilized pollen is a source of reference data for interpreting changes experienced by boreal forests over time. This information has enabled reconstruction of the variation of geographical boundaries for boreal species in Western Europe and North America (Hansen and Engstrom, 1985). The most characteristic feature is the northward shift of some species at the end of the last glaciation. Boreal forest communities reached their present configuration during the last 5,000 years. Boreal forest boundaries were altered at the end of the last glacial period at very different speeds and in different ways for each species. This variability indicates that each species reacts differently to environmental changes and the introduction of a similar tree species contributes to interspecific variability in response to future environmental changes.
(Delcourt and Delcourt, 1987; MacDonald, 1992). Since the end of the last glaciation, there have been significant changes in the distribution of genetic diversity of some tree species. Because of this, future climate change due to global warming may cause a significant loss of genetic diversity in boreal plant species (Prentice et al., 1991). Other factors, such as deforestation and pollution, also endanger forest genetic diversity. These threats have affected the flora and fauna of the forests, as well as the habitats of various organisms. However, immediate loss of species is not the only danger, considering that many populations of the surviving species will disappear; because of this, much of the genetic diversity needed for the long-term survival and evolution of the species will be lost (Ledig, 1988).

A decrease during the Holocene warming (about 7,000 to 8,000 yr B.P. as suggest palynological evidence) in the number of Picea individuals in Mexico and their historical northward shift coincides with the interglacial global warming period (Ledig et al., 1997; Ledig et al., 2010). Recent studies indicate that Mexican endemic spruces are susceptible to climate change, because its suitable climate habitat will disappear too fast, and unless human assistance, they will not be able to reach (by natural means) the sites where it will occur at the remaining suitable climatic habitat, that in general will occur at distant places than the ones at present (Ledig et al., 2010).

The presence of genus Picea in Mexico’s subtropical and tropical latitudes (although at very specific sites, generally on high altitudes, northern aspect, humid sites near of creeks; Ledig et al., 2000a) is highly unusual, because these sites are much more southerly than the usual distribution of spruces in North America. The native spruces from Canada and USA do not include the rare Mexican P. chihuahuana Martínez, which is located in Northwest Mexico (Patterson, 1988).

**Picea chihuahuana** Martínez

This species is commonly known as Pinabete or Pinabete espinoso. According to a Mexican Official Standard (Norma Oficial Mexicana, NOM-ECOL-059-2010), this is an Endangered species and an endemic relict (Gordon, 1968; Narváez, 1984; García-Arévalo, 2008). However, before the official status of endangered was determined, Sánchez and Narváez (1983, 1990) already considered the very rare and fragmented species as Endangered, using as criteria the restricted distribution of the species, as well as its special ecological conditions, which are mainly related to specific soil and vegetation characteristics. Gordon (1968) and Mata (2000) reported that the main causes of the status of this endangered species was geographically isolated populations, irregular reproduction due to heterogeneous age distributions in populations, scarce natural generation, and clandestine cutting down of complete juvenile trees and tree crown tops for Christmas trees.

*P. chihuahuana* is also included in the list of Endangered taxa collected by the National Institute of Livestock, Forest and Agricultural Research (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, INIFAP) (Vera, 1990), and it is classified as Endangered according to the guidelines of the International Union for the Conservation of Nature and Natural Resources, IUCN Red List because “subpopulations are severely fragmented and there is an ongoing decline due to fires, logging and grazing. ... The number of mature individuals is uncertain but could be less than 2,500”.

Several factors lead to *P. chihuahuana* impoverishment, like reduction of its reproductive capacity due to high levels of self-fertilization and mating between closely related individuals. Harvesting, grazing and forest fires also contribute to reduction of population sizes (Ledig et al., 1997). However, currently wood logging is a marginal factor (Wehenkel and Sáenz-Romero, unpublished).

This species is usually associated with pines (*Pinus* spp.), oaks (*Quercus* spp.), and occasionally with species of the genera *Abies*, *Pseudotsuga*, *Cupressus*, *Populus-Juniperus*, and *Prunus* (Gordon, 1968; Narváez et al., 1983; Quiñones-Pérez et al., 2014); it is also sometimes associated with other species of the same genus, such as *Picea engelmannii* and *Picea pungens* (Gordon, 1968). Individual trees reach heights of up to 50 m in height and diameters up to 120 cm (Ledig et al., 2000a). Lower branches are almost horizontal, starting at 2 to 5 m in height, while higher branches are extended and somewhat raised, forming a conical crown (Gordon, 1968).

**Location of P. chihuahuana** Martínez

The existence of the species in Mexico was unknown before 1942. *P. chihuahuana* was first discovered in the State of Chihuahua in Northwestern Mexico (Martínez, 1953). The species was subsequently found in other locations in Chihuahua and Durango. The recent discovery of the species is indicative of their rarity and inaccessibility (Gordon, 1968). In Chihuahua, *P. chihuahuana* is located in the municipalities of Bocoyana, Temosachi, Guerrero and Balleza; in Durango, it is found in the municipalities of Pueblo Nuevo, El Mezquital, San Dimas, Canelas and Guanacevi (Ledig et al., 2000a) (Figure 1).

*P. chihuahuana* covers a total area of no more than 300 ha and it is located at least 40 sites along the Sierra Madre Occidental in Durango and Chihuahua states (Table 1) (Sánchez, 1984; Farjon et al., 1993, Ledig et al., 2000a; Wehenkel and Sáenz-Romero, 2012), and a minimum total of 42,600 individuals has been estimated (Ledig et al., 2000a); these sites are located at medium altitudes, ranging from 2,150 to 2,990 m a.s.l., with average temperatures from 9 to 12°C. The species probably grows in a precipitation range from 600 to 1,300 mm
considering the estimates obtained using a spline climate model (Sáenz-Romero et al., 2010).

This species is preferentially located in rough terrain areas on hillsides and canyons with slopes ranging from 35 to 80%. The species is also found at the margins of streams and rivers (Narváez, 1984). It is located in north facing areas, showing variations toward northwest and northeast (Narváez, 1984; Sánchez, 1984).

Importance and conservation of *P. chihuahuana* Martinez

Although, the endemic spruces are a minor element in Mexico's flora, they are potentially important from a scientific and conservational point of view. They represent a unique contribution to Mexico's biodiversity and, therefore, have a high value as a genetic resource (Ledig et al., 1997). *P. chihuahuana* occurs in some locations with the highest diversity of tree species at the Sierra Madre Occidental, recognized as a hot spot of species diversity (González-Elizondo et al., 2012). The habitat is a crucial aspect for the protection of this species (Ledig et al., 1997). The discontinuous distribution and variation in population sizes of *P. chihuahuana* provide an excellent opportunity to test the relationships between diversity and population size or degree of isolation (Ledig et al., 1997). Natural reproduction of *P. chihuahuana* has declined, probably by degradation in abiotic conditions, lack of regeneration and high proportion of seed loss caused by pests and inbreeding depression (SARH, 1993; Jacob, 1994; Ledig et al., 1997). Sánchez and Narváez (1990) were the first to propose some alternatives for protection, development and genetic improvement of *P. chihuahuana* by managing the distribution areas of the species, under a concept of botanical reserve.

*P. chihuahuana* has been used to measure genetic erosion because it is an excellent model for that purpose due to its small and isolated populations (Wehenkel and Sáenz-Romero, 2012). The species has been used to estimate the genetic potential of plant-plant interactions in
Table 1. Some populations of *Picea chihuahua*na in the states of Durango and Chihuahua.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Ownership</th>
<th>Municipality</th>
<th>Latitude (N)</th>
<th>Longitude (O)</th>
<th>Elevation (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Durango</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arroyo La Pista</td>
<td>Santa María Magdalena de Taxicaringa</td>
<td>Mezquital</td>
<td>23 ° 19'52&quot;</td>
<td>104 ° 45'00&quot;</td>
<td>2,685</td>
</tr>
<tr>
<td>Arroyo El Chino</td>
<td>Santa María Magdalena de Taxicaringa</td>
<td>Mezquital</td>
<td>23 ° 24'05&quot;</td>
<td>104 ° 43'05&quot;</td>
<td>2,600</td>
</tr>
<tr>
<td>Arroyo Las Lagunas</td>
<td>Private Property</td>
<td>Durango</td>
<td>23 ° 31'24&quot;</td>
<td>104 ° 31'20&quot;</td>
<td>2,775</td>
</tr>
<tr>
<td>Arroyo del Infierno</td>
<td>Ejido* El Brillante</td>
<td>Pueblo Nuevo</td>
<td>23 ° 29'40&quot;</td>
<td>105 ° 26'08&quot;</td>
<td>2,725</td>
</tr>
<tr>
<td>Faldeo de Cebollitas</td>
<td>Private Property</td>
<td>Canelas</td>
<td>25 ° 05'45&quot;</td>
<td>106 ° 26'35&quot;</td>
<td>2,450</td>
</tr>
<tr>
<td>Arroyo de Los Angeles</td>
<td>Ejido El Palomo</td>
<td>Guanaceví</td>
<td>26 ° 00'17&quot;</td>
<td>106 ° 18'14&quot;</td>
<td>2,990</td>
</tr>
<tr>
<td>La Estancia-Agua Amarilla</td>
<td></td>
<td>Guanaceví</td>
<td>26 ° 00'41&quot;</td>
<td>106 ° 27'13&quot;</td>
<td>2,580</td>
</tr>
<tr>
<td><strong>Chihuahua</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arroyo La Quebrada</td>
<td>Ejido El Caldillo y su anexo El Vergel</td>
<td>Balleza</td>
<td>26 ° 28'12&quot;</td>
<td>106 ° 21'51&quot;</td>
<td>2,730</td>
</tr>
<tr>
<td>Río Vinhueachí</td>
<td>Private Property</td>
<td>Bocoyna</td>
<td>27 ° 44'53&quot;</td>
<td>107 ° 41'58&quot;</td>
<td>2,160</td>
</tr>
<tr>
<td>El Pinabetal</td>
<td>Comunidad de San Elias</td>
<td>Bocoyna</td>
<td>27 ° 45'42&quot;</td>
<td>107 ° 41'35&quot;</td>
<td>2,305</td>
</tr>
<tr>
<td>Las Trojas</td>
<td>Ejido El Ranchito</td>
<td>Bocoyna</td>
<td>27 ° 54'27&quot;</td>
<td>107 ° 45'17&quot;</td>
<td>2,395</td>
</tr>
<tr>
<td>Napahuichi I</td>
<td>Private property: La Laja</td>
<td>Bocoyna</td>
<td>27 ° 54'53&quot;</td>
<td>107 ° 37'10&quot;</td>
<td>2,270</td>
</tr>
<tr>
<td>Napahuichi II</td>
<td>Private property: La Laja</td>
<td>Bocoyna</td>
<td>27 ° 54'47&quot;</td>
<td>107 ° 37'08&quot;</td>
<td>2,340</td>
</tr>
<tr>
<td>Talayote</td>
<td>Ejido Los Volcanes</td>
<td>Bocoyna</td>
<td>27 ° 55'03&quot;</td>
<td>107 ° 49'01&quot;</td>
<td>2,355</td>
</tr>
</tbody>
</table>

Ejido: Land owned and managed by local communities.

natural conditions (Quiñones-Pérez et al., 2014). Finally, *P. chihuahuana* is also of great importance because of its ecological, recreational and aesthetic value and as a refuge for wildlife (Sánchez and Narváez, 1990).

**Genetic diversity of *P. chihuahuana* Martinez**

Conifers in the family Pinaceae, which includes spruce, are categorized as strongly outcrossing (Schemske and Lande, 1985) with high levels of genetic diversity (Hamrick and Godt, 1989). Population bottlenecks accompanied by inbreeding depression and drift are usually invoked to explain the origin of low levels of genetic diversity. Because the Pinaceae have no self-incompatibility system, selfing is possible when numbers of breeding individuals are reduced, as in refugia or after colonizing events (Ledig et al., 2000b). The (spatial) analysis of genetic diversity in forest species can be estimated by using genetic markers and considering tree positions, the number of variants (polymorphism, polymorphism rate, proportion of polymorphic loci, abundance of genetic variants and average number of alleles or genotypes per locus), or the frequency of variants (effective number of alleles or genotypes, expected heterozygosity, *H*<sub>e</sub> and *Nei's genetic diversity*). Genetic diversity studies on the *Pinaceae* family in Mexico have focused on *Pinus*, followed by *Abies* and *Picea*. Thus, the genetic diversity of *P. chihuahuana* has only recently been studied (Ledig et al., 1997; Jaramillo-Correa et al., 2006) (Table 2).

In general, the average expected heterozygosity for *Picea*, estimated by isoenzyme electrophoresis, is *H*<sub>e</sub> = 0.11; the estimated value is below the average limit of genetic variation reported for most gymnosperms (0.17) (Hamrick et al., 1992). Comparing the above results (Table 2) with those reported by Hamrick and Godt (1996), *P. chihuahuana* displays moderate levels of genetic diversity (*H*<sub>e</sub>=0.093) within the observed range for conifers (*H*<sub>e</sub> from 0.055 to 0.131) even within a small geographic area. For example, allozyme analysis used to determine genetic diversity in other conifer species revealed an average *H*<sub>e</sub> of 0.19 (ranging from 0.07 for *Abies guatemalensis* to 0.39 for *Pinus lagunae*) (Aguirre-Plater et al., 2000; Molina-Freaner et al., 2001). These findings suggest the importance of drift and endogamy in the recent evolution of the species (Ledig et al., 1997).

The population’s mean heterozygosity of 0.111 expected for the Mexican Martínez spruce is lower than that reported for most other spruces and for conifers in general (Hamrick et al., 1992), but is higher than described for *P. chihuahuana*. The estimated genetic diversity in *P. mexicana* is higher than *P. chihuahuana* and than the average for long-lived, woody endemics, and it is similar to the average for outcrossing endemic plant species in general. This study suggests that *P. mexicana* is a genetically viable species and that threats
Table 2. Genetic diversity reported in some spruce species, including Mexican species.

<table>
<thead>
<tr>
<th>Specie</th>
<th>AL</th>
<th>P</th>
<th>He</th>
<th>Ho</th>
<th>H_{cpDNA}</th>
<th>H_{mtDNA}</th>
<th>Used Molecular Marker</th>
<th>Molecular Reference</th>
</tr>
</thead>
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<tr>
<td>Picea abies</td>
<td>-</td>
<td>-</td>
<td>0.371</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Allozymes</td>
<td>Lundkvist, 1979</td>
</tr>
<tr>
<td>Picea abies</td>
<td>-</td>
<td>-</td>
<td>0.250</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>RAPD</td>
<td>Jeandroz et al., 2004</td>
</tr>
<tr>
<td>Picea abies</td>
<td>-</td>
<td>-</td>
<td>0.545</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>SNPs</td>
<td>Heuertz et al., 2006</td>
</tr>
<tr>
<td>Picea abies</td>
<td>22</td>
<td>-</td>
<td>0.640</td>
<td>0.465</td>
<td>-</td>
<td>-</td>
<td>SSR</td>
<td>Tollefsrud et al., 2009</td>
</tr>
<tr>
<td>Picea asperata</td>
<td>10.89</td>
<td>100</td>
<td>0.426</td>
<td>0.400</td>
<td>-</td>
<td>-</td>
<td>SSR</td>
<td>Wang et al., 2004</td>
</tr>
<tr>
<td>Picea asperata</td>
<td>1.45</td>
<td>37.1</td>
<td>0.096</td>
<td>0.094</td>
<td>-</td>
<td>-</td>
<td>Allozymes</td>
<td>Luo et al., 2005</td>
</tr>
<tr>
<td>Picea asperata</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>0.37</td>
<td></td>
<td>mtDNA and cpDNA markers</td>
<td>Du et al., 2009</td>
</tr>
<tr>
<td>Picea breweriana</td>
<td>1.48</td>
<td>44.2</td>
<td>0.129</td>
<td>0.121</td>
<td>-</td>
<td>-</td>
<td>Isozymes</td>
<td>Ledig et al., 2005</td>
</tr>
<tr>
<td>Picea chihuahuana</td>
<td>1.37</td>
<td>27</td>
<td>0.093</td>
<td>0.073</td>
<td>-</td>
<td>-</td>
<td>Isozymes</td>
<td>Ledig et al., 1997</td>
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<tr>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>0.415</td>
<td>0</td>
<td></td>
<td>SSR</td>
<td>Jaramillo-Correa et al., 2006</td>
</tr>
<tr>
<td>Picea chihuahuana</td>
<td>-</td>
<td>75</td>
<td>-</td>
<td>-</td>
<td></td>
<td></td>
<td>AFLP</td>
<td>Wehenkel and Sáenz-Romero, 2012</td>
</tr>
<tr>
<td>Picea engelmannii</td>
<td>2.4</td>
<td>80</td>
<td>0.255</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Isozymes</td>
<td>Ledig et al., 2006</td>
</tr>
<tr>
<td>Picea glauca</td>
<td>3.03</td>
<td>-</td>
<td>0.344</td>
<td>0.342</td>
<td>-</td>
<td>-</td>
<td>Allozyme</td>
<td>O’Connell et al., 2006</td>
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<tr>
<td>Picea glauca</td>
<td>-</td>
<td>-</td>
<td>0.37</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>STS</td>
<td>Perry and Bousquet, 1998</td>
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<td>46.8</td>
<td>0.161</td>
<td>0.163</td>
<td>-</td>
<td>-</td>
<td>Allozymes</td>
<td>Godt et al., 2001</td>
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<tr>
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<td>-</td>
<td>-</td>
<td>0.78</td>
<td>0.71</td>
<td>-</td>
<td>-</td>
<td>SSR</td>
<td>Hodgetts et al., 2001</td>
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<td>-</td>
<td>0.345</td>
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<td>-</td>
<td>SSR</td>
<td>Rungis et al., 2004</td>
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<tr>
<td>Picea glauca</td>
<td>1.92</td>
<td>82</td>
<td>0.300</td>
<td>0.339</td>
<td>-</td>
<td>-</td>
<td>SSR</td>
<td>Namroud et al., 2012</td>
</tr>
<tr>
<td>Picea maritana</td>
<td>2.2</td>
<td>69.2</td>
<td>0.321</td>
<td>0.345</td>
<td>-</td>
<td>-</td>
<td>Allozymes</td>
<td>Isabel et al., 1995</td>
</tr>
<tr>
<td>Picea martinezii</td>
<td>1.9</td>
<td>82.1</td>
<td>0.321</td>
<td>0.345</td>
<td>-</td>
<td>-</td>
<td>RAPD</td>
<td>Isabel et al., 1995</td>
</tr>
<tr>
<td>Picea mexicana</td>
<td>1.39</td>
<td>31.9</td>
<td>0.111</td>
<td>0.104</td>
<td>-</td>
<td>-</td>
<td>Isozymes</td>
<td>Ledig et al., 2000b</td>
</tr>
<tr>
<td>Picea pungens</td>
<td>1.6</td>
<td>42.7</td>
<td>0.125</td>
<td>0.136</td>
<td>-</td>
<td>-</td>
<td>Isozymes</td>
<td>Ledig et al., 2002</td>
</tr>
</tbody>
</table>

AL=Number of alleles per locus; P= Percentage of polymorphic loci; He= expected heterozygosity; Ho= observed heterozygosity; H_{cpDNA} or mtDNA genetic diversity; RAPD= random amplification of polymorphic DNA; SSR= simple sequence repeats (microsatellites); AFLP=amplified fragment length polymorphism; SNPs= single-nucleotide polymorphisms; STS= sequence tagged site.

are primarily environmental (Ledig et al., 2002). Picea breweriana is at least as diverse as the endemic spruces of Mexico (P. chihuahuana, P. martinezii, and P. mexicana) (Ledig et al., 2005). Engelmann spruce is much more genetically diverse than the other spruce species. The higher genetic diversity of northern populations of Engelmann spruce may be a result of the wider distribution and larger populations, as well as introgressive hybridization with the transcontinental white spruce; but not in Southwestern populations with evidence of bottlenecks (Ledig et al., 2006). However, the estimated $H_{e}$ for Engelmann spruce was slightly higher than the average for woody species reported by Hamrick et al. (1992). The diversity of P. chihuahuana ($H_{c}$), estimated using chloroplast DNA markers, is much higher than that for mtDNA (Jaramillo-Correa et al., 2006), probably because of a much more active and wider gene flow by pollen dispersion than by seed dispersion. The latter authors found that none of the 16 P. chihuahuana populations surveyed was polymorphic for the mtDNA markers, while for cpDNA markers, 3 of the 16 stands surveyed were fixed for a particular chlorotype (Table 2).

In one study of P. chihuahuana, the degree of genetic erosion was evaluated in five populations located in the State of Durango (Figure 2) by comparing the genetic diversity using diameter classes. For this study, AFLP (Amplified Fragment Length Polymorphism) molecular markers were used and genetic diversity was quantified ($\delta_{h}$, Gregorius total differentiation were 0.183, 0.162, 0.150, 0.117 and 0.136, for each population, respectively as shown in Figure 2) (Gregorius, 1987; Wehenkel and Sáenz-Romero, 2012). The results revealed significant genetic erosion only for the smallest population, San José de las Causas (Wehenkel and Sáenz-Romero,
Therefore, if genetic diversity determined by AFLP loci reflects diversity in the whole genome, genetic erosion *per se* does not explain fragmentation and restricted distribution of *P. chihuahuana*, except in the smallest populations. In this case, genetic diversity would not be sufficient to prevent depression due to endogamy; also mutations could not compensate the loss of alleles as a result of genetic drift (Wright, 1938; Millar and Libby, 1991; Frankham et al., 2002; Bücking, 2003; Wehenkel and Sáenz-Romero, 2012).

In another study (Quiñones-Pérez et al., 2014), interactions between AFLP variants of *P. chihuahuana* and its two most dominant nearest-neighboring tree species were analyzed in five populations located in Durango, Mexico (Figure 2). The results show a statistically significant association between such genetic variants - at one AFLP locus in one *Picea* population - and two nearest-neighbor conifer species (*Picea chihuahuana* Martínez and *Pinus arizonica* Engelm.). The findings indicate that interactions between genetic variants and species diversity may be crucial in shaping plant communities. They also indicate the existence of interactions between different levels of diversity, e.g., between specific genetic variants of a single species and neighboring tree species. However, further studies are required for a better understanding of the possible roles that such asso-
Perspectives for management and conservation of P. chihuahuana Martinez

The maintenance of genetic variation is considered essential for long-term survival of the species. Consequently, the rate of loss of genetic diversity in isolated populations is a great concern for conservation and protection of rare or endangered species (Ledig et al., 1997). It is worth mentioning that small populations are more susceptible to extinction due to various factors such as demographic stochasticity, as well as environmental, genetic and natural catastrophes (Shaffer, 1981); this may apply to some P. chihuahuana populations. Therefore, the concept of minimum viable population (MVP) is appropriate, and it is widely applied for recovery and conservation management programs; this concept is also relevant in the IUCN Red List criteria for small and restricted populations (Traill et al., 2011). Thus, MVP is frequently defined as the smallest population showing a 95 to 99% chance of persistence in a given time period (Ewens et al., 1987). Calculation of the MVP allows the planning of management strategies for conservation of endangered species, as the case of Mexican spruces including P. chihuahuana (Mendoza-Maya et al., submitted). In a meta-analysis involving different species, the reported size of the minimum viable population was on average 4,169 individuals (Traill et al., 2011). Therefore, all populations, including P. chihuahuana, are unlikely to survive without help, because according to Ledig et al. (2000), the maximum size of a population of this species is only 3,564 trees (> 2 m in height) (Wehenkel and Sáenz-Romero, 2012).

Recent studies have shown that climate change will affect rare species such as P. chihuahuana. Therefore, the populations could be relocated by assisted colonization (Ledig et al., 2010; Ledig, 2012) to sites where it is predicted that the climate to which the populations are adapted will occur. Assisted colonization (also named assisted migration) need to be done at present, targeting sites will occur in suitable climate by year 2030 or so. That is, in order to have adult trees in the future, re-alignment to the climate for which they are adapted, aiming that those trees would be enough healthy to produce viable seed and thus they will be able to produce a new generation (that eventually might need to be relocated again, if climatic change would continue as predicted). Assisted colonization or migration need target a climate projection not too far away in time, because at present seedlings would be killed by frost damage (Loya-Rebollar et al., 2013). Although it could be argued that natural communities recipients of the population relocated could be altered, there are no reason to believe that natural plant communities will continue unaltered by climatic change. Worldwide evidence is emerging now of forest decline, sometimes massive, induced by climatic change (Allen et al., 2010; Mátyas, 2010; Alfaro et al., 2014). Thus, in our view, inaction imply larger risks than a proactive realignment of the populations to the climate for which they are adapted. Therefore, active conservation programs must be implemented to preserve P. chihuahuana. In a recent study, a management proposal for in situ and ex situ conservation of three Picea species from Mexico, including P. chihuahuana, was presented (Mendoza-Maya et al., submitted). This was based on the diversity and genetic structure of populations, as well as on projected climate scenarios for 2030, 2060 and 2090. Thus, the protection of eight P. chihuahuana populations, determined from the formula \( N_e = -984.58 + (36723 H_e) \) (Viveros-Viveros et al., 2010), was proposed for in situ and ex situ conservation. There are some indications of a requirement for a genetically effective population size (Millar and Libby, 1991) of 2,541 individuals to conserve a given average heterozygosity (\( H_e = 0.096 \)) in P. chihuahuana populations in the state of Chihuahua (Mendoza-Maya et al., submitted).

Some of the following actions could increase the population size:
1. ex situ conservation along with assisted migration in response to climate change,
2. increasing the size of the smallest populations by propagating individuals,
3. increasing the genetic diversity to restrain endogamy and to prevent the presence of extinction vortex,
4. protection of natural regeneration by acting against livestock, wildlife and forest fires,
5. establishment of artificial regeneration using reproductive local material gathered from well-selected sites in the population’s boundaries (but not within the population), and
6. elimination of competing vegetation (other tree species) in the vicinity of the particular population. Finally, continuous monitoring of size and genetic diversity of the current populations in situ is essential (Wehenkel and Sáenz-Romero, 2012).

Efforts should focus on the protection of populations displaying the highest degree of genetic variation because these populations have the greatest potential for adaptive evolution (Ledig, 2012).

Conflict of Interests

The author(s) have not declared any conflict of interests.

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