Ecology and Genetics of *Pinus strobiformis*

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Abstract—Extending from the Canadian province of Alberta to the Transverse Volcanic Plateau of Mexico, *Pinus strobiformis* is part of a species complex with two geographically adjacent, but nonsympatric, species, namely *P. flexilis* and *P. ayacahuite*. *Pinus strobiformis* is classified as being of least concern and at lower risk according to the guidelines of the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List (IUCN 2014). In Mexico, this frequent tree species is protected and included in Mexican Regulation NOM-059-2010. *Pinus strobiformis* appears to have broad environmental tolerances and fire resistance when mature. It is often found in mixed-conifer forests that are valuable summer habitat for big and small game animals, rodents, and game and nongame birds. At the large scale, analyses of spatial genetic structure of *P. strobiformis* indicated a very weak spatial distance–genetic distance relationship, probably resulting from a strong seed interchange, likely by birds, particularly the Mexican jay (*Aphelocoma wollweberi*), and from a continuous and broad geographic distribution of this tree species. The highest genetic diversity was found in the southern populations, indicating the recent colonization of the populations at the northern distributional limit. Recently, interest in *P. strobiformis* has increased due to the discovery of white pine blister rust (causal agent: *Cronartium ribicola*) in the Sacramento Mountains of New Mexico (USA).

DESCRIPTION

Pinus strobiformis, subgenus *Strobus*, section *Quinquefoliae* (Gernandt et al. 2005), is commonly called Mexican white pine, Arizona white pine, Chihuahuan white pine, southwestern white pine, pino blanco, pinabete, and pino enano. Extending from Alberta (Canada) to the Transverse Volcanic Plateau of Mexico, *P. strobiformis* is part of a species complex that includes two geographically adjacent, but nonsympatric, species, namely *P. flexilis* and *P. ayacahuite* (Farjon and Styles 1997; Moreno-Letelier and Piñero 2009), as well as other species such as *P. strobiformis* subsp. *veitchii*, and *P. stylesii* (Gymnosperm Database 2014) (fig. 1). The conservation status of *P. strobiformis* is classified as "least concern and lower risk" according to the guidelines of the International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species™ (IUCN 2014). In Mexico, this frequent tree species is protected and included in Mexican Regulation NOM-059-2010.

Pinus strobiformis is a native, evergreen conifer with an open, irregular crown. It can grow to 27 m tall with a diameter up to 1 m; the bark is thin, rough, and furrowed. Branches are long and horizontal to pendant. Needles are 6 to 10 cm long in fascicles of five. The cones are 7 to 25 cm long with reflexed, thick scales;

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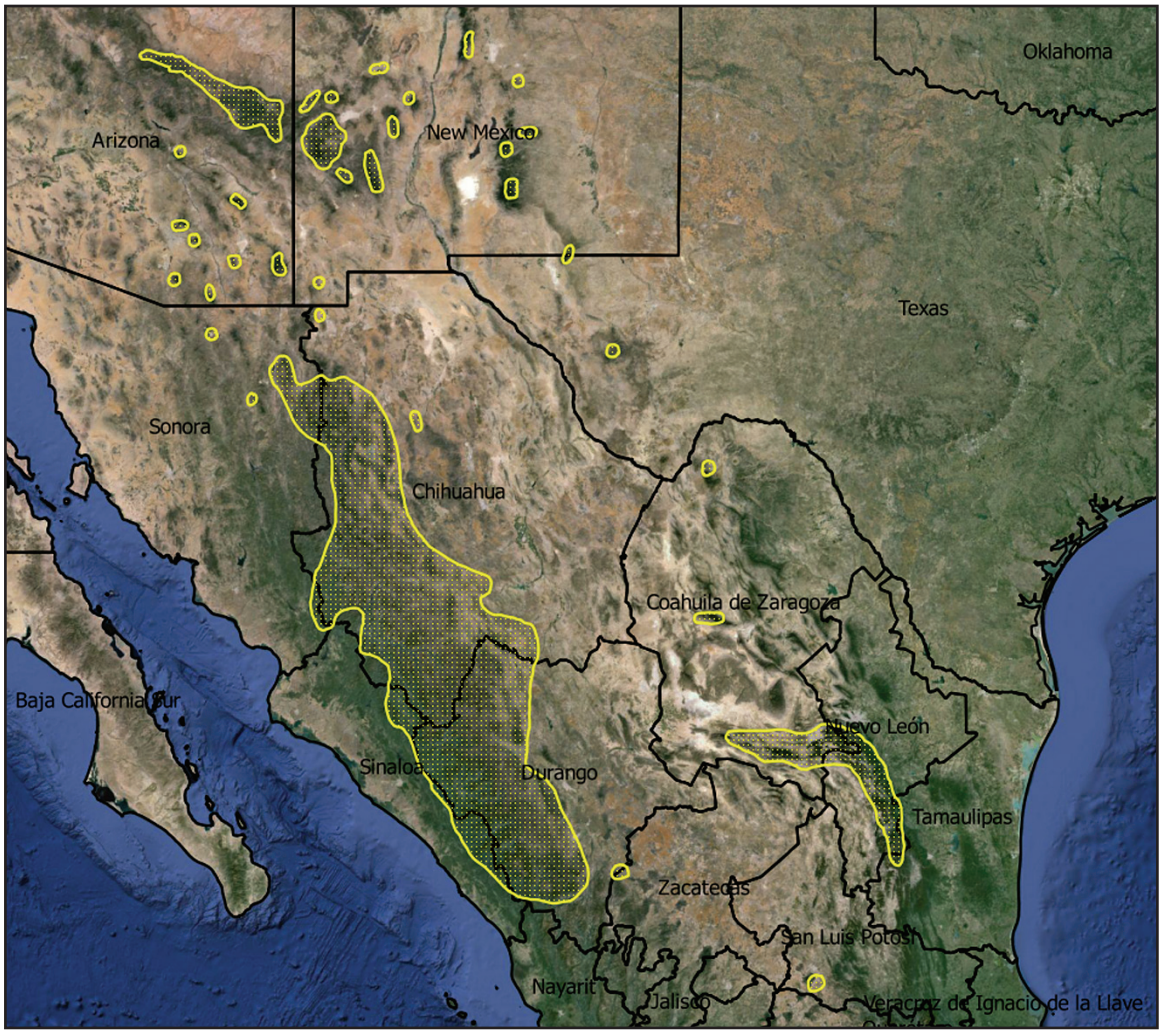

Figure 1—Natural range of *Pinus strobiformis* (from Little, E.L., Jr., 1971).

cones are dehiscent when mature (figs. 2 and 3). Seeds are essentially wingless and 10 to 12 mm long (Pavek 1993; Perry 1991).

DISTRIBUTION AND OCCURRENCE

Pinus strobiformis has a limited distribution. It occurs in the mountains of western Texas, New Mexico, Arizona, and southwestern Colorado (USA) (Jones 1974; Samano and Tomback 2003). It also extends along the mountains to central Mexico (Farjon and Styles 1997), ranging from northeastern Sonora to Western Chihuahua and Durango, northern Zacatecas, southern Coahuila, and central Nuevo Leon (U.S. Geological Survey 2006). The largest populations are found in Mexico (Pavek 1993). This species typically occurs in low densities in southwestern pine, mixed-conifer, and spruce-fir (*Picea* spp.-*Abies* spp.) forests (Stromberg and Patten 1991), which generally have been the subject of relatively few studies (Jones 1974).

This pine species is associated with several other pine species including *P. ponderosa*, *P. arizonica*, *P. leiophylla*, *P. engelmannii*, and *P. cembroides*. *Pinus strobiformis* also is associated with *Pseudotsuga menziesii*, *Populus tremuloides*, *Abies concolor*, *Abies bifolia*, *Picea pungens*, *Picea engelmannii*, *Juniperus deppeana*, *Cupressus arizonica*, *Arbutus arizonica*, and a variety of *Quercus* species. In Mexico, this tree species is associated with a wide variety of endemic Mexican species such as *Picea chihuahuana*, *Cupressus lusitanica*, *Abies durangensis*, *Abies vejari*, and *Abies religiosa* (Looney and Waring 2013; Simental-Rodríguez et al. 2014).

Figure 2—*Pinus strobiformis* trees (a and b) in Durango State, Mexico (photo: C. Wehenkel).

Figure 3—Female flowers (a) and cones (b) of *Pinus strobiformis* trees in Durango State, Mexico (photo: C. Wehenkel).

ECOLOGY

Pinus strobiformis appears to have broad environmental tolerances (Looney and Waring 2013) and fire resistance when mature (Dieterich 1983). It is widespread in mesic sites on ridges, slopes, and canyons of montane zones (Pavek 1993). These zones have a semiarid climate, with mild winters and warm summers. The average precipitation ranges from 487 to 1,143 mm per year. In its U.S. range, *P. strobiformis* typically grows at elevations ranging from 1,900 to 3,000 m above sea level (Pavek 1993). In Mexico, it is found at elevations from 2,200 to 3,600 m above sea level (Aguirre-Calderón et al. 2003; Fulé and Covington 1996).

The range of *P. strobiformis* is influenced by a variety of environmental factors, including elevation (Brady and Bonham 1976), moisture availability (Niering and Lowe 1984), and temperature (Laughlin et al. 2011). The species usually grows on moist, cool sites, where it is most likely to be dominant. It is preferentially located on dry rocky slopes in high mountains, or as a minor component in mixed-conifer forests. The species is found in sites with loamy soil textures ranging from shallow, gravelly loams to deep, sandy loams and stony silty clay loams (Pavek 1993). Depending on elevation, this species may occur on a variety of aspects and topographic settings (Looney and Waring 2013).

GENETICS

Moreno-Letelier and Piñero (2009) presented patterns of genetic variation between the taxa in the *P. strobiformis* complex by chloroplast haplotype (microsatellite) analysis, which supports the concept of significant distinctions between each of the taxa named here, and between the Sierra Madre Occidental, Sierra Madre Oriental, and Jalisco populations of *P. strobiformis* (Gymnosperm Database 2014). Two main genetic and geographic groups of *P. strobiformis* were separated by the Chihuahuan Desert. Little population differentiation and no isolation by distance within each of the two groups were found, suggesting genetic connectivity as a result of population expansions within these areas during glacial stages.

Quiñones-Pérez et al. (2014) observed a nonsignificant autocorrelation in fine-scale spatial genetic structure (SGS) using amplified fragment length polymorphism (AFLP), suggesting that the genetic variants of the tree species are randomly spatially distributed within sampled plots of 50 m × 50 m. On a larger scale, the SGS analyses of *P. strobiformis* also indicated a very weak spatial distance–genetic distance relationship, probably resulting from a strong seed interchange, likely by birds, particularly the Mexican jay (*Aphelocoma wollweberi*), and from a continuous and broad geographic distribution of this tree species (Looney and Waring 2013). The overall mean of genetic distances between *P. strobiformis* trees was higher than between *Picea chihuahuana* trees, *Populus tremuloides* trees, and *Pseudotsuga menziesii* trees in the rare Mexican *Picea chihuahuana* tree community.

Simental-Rodríguez et al. (2014) found no evidence that tree species diversity is related to adaptive AFLP structure and mean genetic diversity per AFLP locus of *P. strobiformis* at 12 locations in the *Picea chihuahuana* tree community on the Mexican Sierra Madre Occidental (in contrast to *Populus tremuloides*, *Picea chihuahuana*, and *Pseudotsuga menziesii*). As seen in Moreno-Letelier and Piñero (2009), the highest genetic diversity was found in the southern populations, indicating recent colonization of the populations at the northern distributional limit (Petit et al. 2003).

Villalobos-Arámbula et al. (2014) examined cross-species transferability and usefulness of six nuclear microsatellite markers developed in consubgeneric eastern white pine (*Pinus strobus*) with regard to ecologically and commercially important Mexican white pine species of conservation genetics concern: *Pinus chiapensis*, *P. flexilis*, *P. strobiformis*, *P. ayacahuite*, and *P. ayacahuite* var. *veitchii*. Four to six microsatellite loci were found to be polymorphic in different species.

MANAGEMENT CONSIDERATIONS

Pinus strobiformis is often found in mixed-conifer forests that are valuable summer habitat for big and small game animals, rodents, and game and nongame birds. As natural regeneration of clearcut mixed-conifer forests on south-facing slopes requires 50 to 100 years, these clearcut areas can be a valuable long-term forage resource for deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) (Pavek 1993).

This pine species is the principal host of Apache dwarf mistletoe (*Arceuthobium apachecum*). Infected trees have reduced growth and increased susceptibility to other infections, insects, and mortality (Hawksworth 1978; Walters 1978). *Pinus strobiformis* is infected by red ring rot and by root and butt rots (Walters 1978). Recently, interest in *P. strobiformis* has increased due to the discovery of white pine blister rust (causal agent: *Cronartium ribicola*) in the Sacramento Mountains of New Mexico (Hawksworth 1990). *Cronartium ribicola* is a potentially lethal introduced pathogen that threatens white pine species (Conklin 2004; Schoettle 2004; Zeglen et al. 2010).

Despite the research to date on white pine blister rust, there is insufficient information to predict how this disease will affect *P. strobiformis* in the future (Looney and Waring 2013). Other disturbances of *P. strobiformis* include fire (Danzer et al. 1996; Villanueva-Diaz and McPherson 1995), and climate change (Seager et al. 2007). A few studies reported effects of insects or animals on this species (Hawksworth et al. 2002).

Wood of *P. strobiformis* is soft, not resinous, and white with a slightly darker heartwood. It can be used for cabinetry, doors, and window frames. Crooked stems and coarse branches make it undesirable for lumber (Pavek 1993).

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