

PINUS ENGELMANNII CARR. IN NORTHWESTERN MEXICO: A REVIEW

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Abstract

Pinus engelmannii Carr., commonly known as real pine, Apache pine, Arizona long leaf pine and red pine, covers an area of about 2,450,000 ha in Mexico and extends along the Sierra Madre Occidental to the southwestern United States. It is one of the most important forest species in northwestern Mexico owing to its valuable wood properties, wide distribution and large timber volume harvested. It is widely harvested for lumber and also used in conservation and restoration programmes. The aim of this literature review is to provide a summary of relevant and current information about this species, its botanical classification, ecology, distribution, genetics, physiology, health, nursery reproduction, silviculture and management. Although the species is used in most conservation, restoration and commercial plantation programmes in northwestern Mexico, the available literature scarcely addresses many of the issues considered in this review. This indicates the need for further research to add to existing knowledge about *Pinus engelmannii* and thus improve the use and conservation of this important *Pinaceae* species in northwestern Mexico.

Key words: Apache pine, Pino real, Pine-oak forests, Reforestation programmes.

Introduction

Mexico is the main centre of diversification of pines (genus *Pinus*, family *Pinaceae*) and has more species than any other region of similar size in the world. Estimates of the number of pine species in Mexico have varied between 50 (Perry, 1991) and 47 (Farjon & Styles, 1997; Perry *et al.*, 1998), and as many as 69 taxa (species, subspecies and varieties) have been recognized (Eguiluz-Piedra, 1988). More recently, Gernandt & Pérez de la Rosa (2014) reported that 49 (41%) of the approximately 120 pine species in the world occur in Mexico.

Ideas regarding the preservation of forest resources in Mexico have changed in recent years, and emphasis has been placed on reforestation programmes and on restoration of forest ecosystems through actions aimed at preserving soil and water (Rodríguez-Trejo, 2008; Martínez-Salvador & Prieto-Ruiz, 2011). According to the 2025 Strategic Forest Plan for Mexico, sustainable forest development is a priority goal in the medium and long term, and the policies and programmes included in the plan prioritize the establishment of plantations for reforestation purposes (Comisión Nacional Forestal, 2011). As a result of these policies, various tree species, including Apache pine, were planted in an area covering approximately 220 thousand hectares in the period 2000-2011 (Prieto-Ruiz, 2015). However, only one year after establishment of the plantation, the annual average mortality rate was close to 45% as a result of various factors, in particular the deficient quality of the seedlings (Magaña-Torres *et al.*, 2007).

Apache pine (*Pinus engelmannii* Carr.) is, along with *P. arizonica* Engelm., *P. cooperi* C.E. Blanco and *P. durangensis* Martínez, one of the most commonly

occurring species of the *Ponderosae* group in the Mexican Sierra Madre Occidental (SMO) (Styles, 1993; González-Elizondo *et al.*, 2012). It is considered the dominant pine in the SMO (Ferguson *et al.*, 2013) and one the most common pine species in the state of Durango (Mexico) (González-Elizondo *et al.*, 2007, 2013; Silva-Flores *et al.*, 2014). Its distribution extends to the southwestern US. According to the National Forest Inventory 2004-2009 carried out by the Mexican National Forestry Commission, Apache pine covers an area of about 2,450,000 ha in Mexico; during this period, the mean stand density in the area was 39 trees (diameter > 7 cm at breast height) per hectare, and the maximum density was 794 trees per hectare (Comisión Nacional Forestal, 2009).

Pinus engelmannii is one of the most important timber species in Mexico (Rzedowski, 1981) owing to its valuable wood properties, wide distribution and the large volume of timber that can be harvested (Corral-Rivas *et al.*, 2004). It is widely harvested for lumber and also used in conservation and restoration programmes (García-Arévalo & González-Elizondo, 2003). It is also a potentially good source of bioactive phenolic compounds, as revealed by a study of the phenolic content and biological activity of needle extracts from several *Pinus* species (Sáenz-Esqueda *et al.*, 2010). Apache pine can reach quite large sizes and sometimes majestic trees emerge amidst smaller species that often include *Pinus ponderosa*, *P. arizonica*, *P. leiophylla* var. *chihuahuana*, *P. strobiformis* and *Pseudotsuga menziesii*; it is a very attractive species and because of its fire adaptation traits, appears to act as a keystone species in forest ecosystems (Earle, 2014).

Objective: The objective of this review is to summarize the available information about *Pinus engelmannii* in relation to its ecology, genetics, nursery, health, silviculture and management in order to facilitate the analysis and application of such information in scientific research and in governmental programmes.

Common names and description: *Pinus engelmannii* is known by the following common names: Apache pine and Arizona longleaf pine, in English (Earle, 2014; Tropicos, 2015), and pino real, pino real de tres hojas (Martínez, 1992) and pino rojo (García & Spellenberg, 2004), in Spanish.

Pinus engelmannii Carr. was originally named *Pinus macrophylla* by Engelmann in 1848. However, as the name had already been given to a different species by Lindley in 1839, the species was re-named *Pinus engelmannii* (Carriere, 1854). The epithet was given to honour George Engelmann (1809-1884), a prominent German-American botanist. The following names have also been applied to *P. engelmannii*, and are therefore synonyms: *P. apacheca* Lemmon; *P. latifolia* Sargent; *P. macrophylla* Engelmann; *P. ponderosa* var. *macrophylla* Shaw; *P. mayriana* Sudworth; *P. ponderosa* var. *mayriana* Sargent; *P. macrophylla* var. *blancoi* Martínez; *P. engelmannii* var. *blancoi* (Martínez 1948).

Botanical description: Trees up to 35 m, trunk straight, 25-100 cm diameter. Crown irregularly rounded, rather open, with sparse and very stout branches, the upper branches ascending, lower branches often descending and sigmoid, giving the tree a distinctive appearance (Fig. 1). Bark reddish to dark brown, deeply furrowed at maturity,

with elongate, scaly plates. Twigs stout, 1-3 cm thick, rough. Buds ovoid-conical, up to 2 cm long, resinous, with pale fringed scale margins. Needles, among the longest of any pine, in bundles of three, occasionally four or five, spreading-ascending to slightly drooping, grouped at the ends of branchlets; 20-43 cm long, stout, 1.4-2 mm wide and about 1 mm thick, dull green, with coarsely serrulate margins; all needle surfaces with stomatal lines; sheath 2-4 cm long, persistent, light brown in young specimens. Pollen cones cylindrical, ca. 25 mm long, yellow to brownish or reddish. Seed cones maturing in 2 years, not persistent, nearly sessile or on stout peduncles which persist on the branchlet together with the lower scales when the cone falls; cones lance-ovoid before opening, ovoid when mature (8-16 cm long, 6-12 cm wide), green or purple when growing, light brown when mature, moderately oblique with stoutly spined scales; apophyses rhombic, elongate, strongly raised toward cone base, sometimes curved, strongly cross-keeled, narrowed to a thick, curved, broadly triangular-based umbo. Seeds obovoid, 5-9 mm, with a wing 15-40 mm long (García & González, 2003).

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Fig. 1. Appearance of *P. engelmannii* in its habitat at Bayacora, Durango, Mexico.



Fig. 2. Two views of *Pinus engelmannii* seed cones.

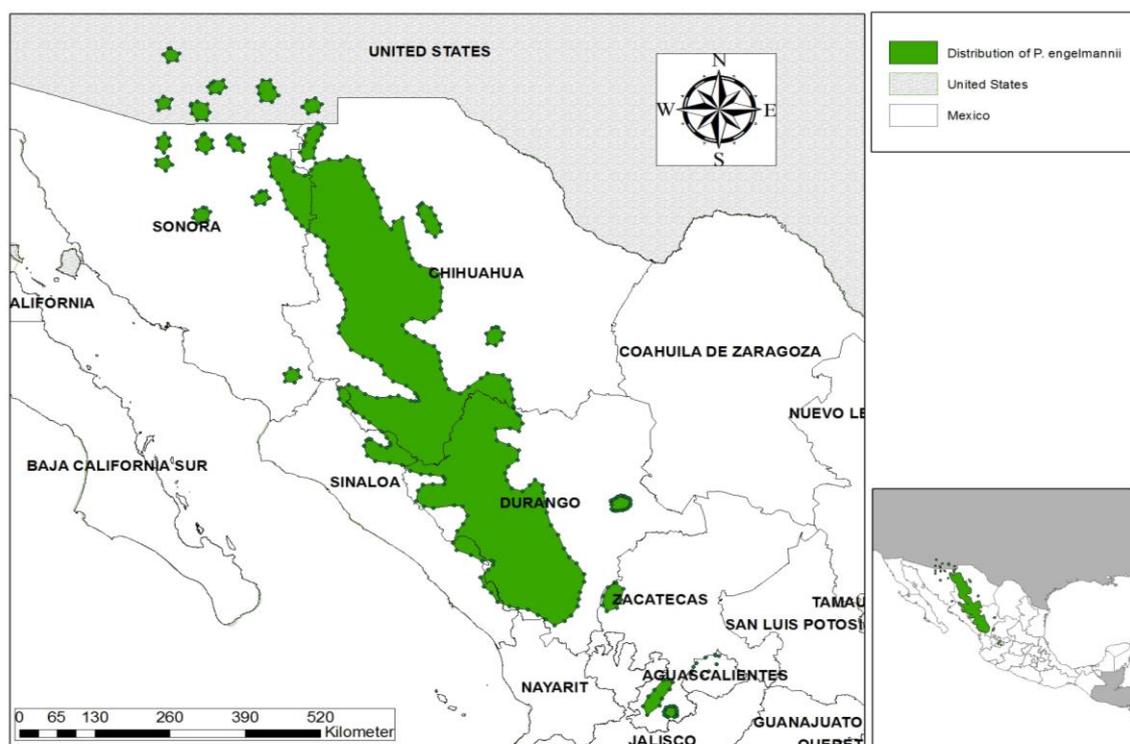


Fig. 3. Distribution of *Pinus engelmannii* in northwestern Mexico and the southwestern United States. Adapted from Little (1976). Freely available at: <http://esp.cr.usgs.gov/data/little/pinuenge.pdf> (accessed July 2015).

The appearance of *P. engelmannii* strongly resembles that of *P. palustris*, with its short-persistent, long leaves and in its tendency to form a grass stage. It has a deep taproot, as do *P. palustris* and *P. ponderosa* (Kral, 1993).

One variety, *P. engelmannii* var. *blancoi*, was described by Martínez (1948) on the basis of leaves that predominantly occur in fascicles of three and on the cones with smaller and wider, conspicuously spinose scales. These characters may represent variation in the species that is not of sufficient magnitude to warrant recognition of a variety (Perry, 1991; Farjon & Styles, 1997).

Yeaton *et al.* (1983) analyzed the variations in the morphological characteristics of *P. engelmannii* over an elevational gradient in Durango (Mexico). These authors used the needle number per fascicle to distinguish the varieties (*Pinus engelmannii* and *P. engelmannii* var. *blancoi*) and found that differences in needle number per fascicle represent clinal variation within the species: the needle number increased gradually with elevation and age. This was confirmed in the laboratory by germination of seeds from 5-needled pines and subsequent growth for 21 months under dry conditions, which produced predominantly 3-needled seedlings. However, Perry (1991) suggested that more detailed morphological studies and chemical analyses may reveal other significant differences.

Distribution and ecology: *Pinus engelmannii* is found in the Mexican states of Chihuahua, Durango, Sinaloa, Sonora and Zacatecas and a limited area in the mountains of SE Arizona and extreme SW New Mexico in the US (Fig. 3) (Little, 1976; Perry, 1991; Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 2015).

The species occurs on dry to moderately summer-warm open mountain slopes or plateaus ranging from 1250 to 3000 m, most abundantly between 2000 and 2500 m. It also grows on moist canyon slopes, ridges, valleys and streamside terraces, in poor rocky (volcanic) soils and in alluvial coarse sand/gravel or loamy sand (Farjon & Styles, 1997; Farjon, 2015). The soils in the sites where *P. engelmannii* grows are Leptosols ranging from shallow to deep and with the following characteristics: sandy clay, silty loam, clay texture; rocky; well drained structure; moderately acid (pH 5 to 6.8); and usually found in poor, rocky terrain and rocky outcrops (Natural Resources Conservation Service, 2015).

A study of about 59 seed stands of various Mexican pine species showed that only a few environmental variables strongly influence the distribution of 11 pine species and their different provenances (Wehenkel *et al.*, 2015). The soil variables are by far the most important, explaining about 51% of the variability. In particular, the acid and base levels in the soil followed by variables of extreme air temperature, such as the frost duration and intensity, define the ecological niche of Apache pine and the other ten pine species studied. *Pinus engelmannii* grows in a climate with a Julian date of the last freezing in spring of 136 ± 22 days and on soils of $\text{pH } 5.3 \pm 0.2$, with H^+ proportion of the cation-exchange capacity of $26.2 \pm 2.7\%$ and Mg concentration of 178 ± 70 ppm (Wehenkel *et al.*, 2015).

The climate where *P. engelmannii* develops is mild, with very variable annual rainfall, ranging from 500-1400 mm, and the best examples of these trees grow under annual precipitation levels of 600-900 mm, where the driest months are April, May and November (Martínez,

1992). The average temperature is 14°C, the minimum, -23°C and maximum, 42°C (Farjon *et al.*, 1997). In a study of the effects of climate and physiography on the density of trees and shrubs in northeast Mexico, Martínez-Antúnez *et al.* (2013) found that *P. engelmannii* occurred with a frequency of 17.85 (% plots) and a mean density of 7.04 (stems / ha) and a mean covariation of 0.22 with respect to 14 climate and physiography studied variables. Similarly, Martínez-Antúnez *et al.* (2015) estimated the density of conifers in relation to nine environmental variables and found that only the height above sea level (ASL) and the average temperature of the warmest month (MTWM) affected the density of *P. engelmannii*.

Other authors report that the species grows under climates ranging from semiarid with bimodal precipitation to temperate-subhumid with most precipitation falling in summer (Villa-Salas & Manon Garibay, 1980; Barton & Teeri, 1993). Another report describes the climate where the species grows as characterised by annual rainfall ranging from 400-700 mm increasing southward at elevations above 2,000 m where frost and snow are common in winter (Farjon, 2015). The species appears to be favoured by high levels of light (González-Elizondo *et al.*, 1993). Pollen dispersal is reported to occur in May (Arizona), although is likely to be dependent on elevation and can occur some weeks later at the highest elevations (Farjon, 2015).

Pinus engelmannii occurs in open mixed pine-oak forests. It also grows in pure, open stands, often associated with other species, mainly *P. arizonica*, *P. chihuahuana*, *P. cooperi*, *P. leiophylla*, *P. lumholtzii*, *P. strobiformis* and *P. teocote*, as well as with several species of *Arbutus* and *Quercus*. It grows in a wide array of ecological conditions ranging from dry, low-lying sites occupied by *P. chihuahuana* to moist ravines with mixed coniferous forest cover (González-Elizondo *et al.*, 2007, 2012, 2013). It has also been recorded to occur with *P. pseudostrobus* (Farjon, 2015).

A study of the composition and structure of the vegetation of La Michilía Biosphere Reserve in southern Durango (Mexico) (González-Elizondo *et al.*, 1993) revealed that *P. engelmannii* occurs in different types of sites: in intermountain valleys and streamside terraces it forms pure stands, sometimes with *Juniperus deppeana* in the understory; in plateaus and slopes it forms part of open communities with *P. chihuahuana*, *P. cooperi*, *P. leiophylla*, and/or *P. teocote*, often with *Arbutus* and *Quercus*; and in canyons and ravines it grows with *P. strobiformis* (cited as *P. ayacahuite*) and other pines, oaks and madrones. Villanueva-Díaz & McPherson (1995) studied the forest structure and determined age and size-class distributions for conifer communities in the Animas Mountains, New Mexico (US) and the Sierra Los Ajos, Sonora (Mexico). These authors found that higher elevations support pine communities dominated by *P. engelmannii*, *P. arizonica* (cited as *P. ponderosa* var. *arizonica*), *P. leiophylla* and *P. strobiformis* (cited as *P. ayacahuite*).

Márquez-Linares & González-Elizondo (1998) studied the forest composition and structure in a watershed in western Durango where *P. engelmannii* is associated with *Pinus teocote*, *P. lumholtzii*, *P.*

strobiformis (cited as *P. ayacahuite*), *Quercus sideroxyla*, *Q. laeta* and *Q. jonesii* (cited as *Q. coccolobifolia*). In 13 out of 235 sites studied by Márquez-Linares *et al.* (1999), also in western Durango, *P. engelmannii* was the dominant tree species, often associated with *P. teocote* and sometimes with *Quercus crassifolia*, *P. leiophylla* and *P. lumholtzii*.

In a transect survey on an elevational gradient between the city of Durango (2131 m) and El Salto (2556 m), both in the state of Durango, De León-Mata *et al.* (2013) observed two groups of vegetation associations. The tree species observed in most sites were *Quercus durifolia*, *Pinus leiophylla*, *P. engelmannii* and *P. teocote*. A plant association dominated by *P. engelmannii* and *Quercus laeta* and a second association between *Quercus durifolia* and *P. engelmannii* were identified in one site only.

In a dendrochronological reconstruction of long-term precipitation patterns in Basaseachic National Park, Chihuahua (Mexico), tree-ring samples from pine species including *Pinus durangensis*, *P. lumholtzii* and *P. engelmannii* were analyzed and cross-dated with existing chronologies. Ring widths were measured and non-climatic trends were removed from the data by application of mathematical models (Irby *et al.*, 2013). These authors concluded that those species are useful for reconstruction of past climate.

Wehenkel *et al.* (2011) estimated balanced structure areas in multi-species forests in the SMO, Mexico. It was found that *P. engelmannii* showed a balanced structure area of minimum 1.85 ha and maximum of 96.45 ha (average, 24.79 ha) in the forest region of Santiago Papasquiaro (Durango), typically in uneven-aged with tendency to even-aged forests.

Pinus engelmannii is adapted to low-intensity fire. Traits such as thick bark, self-pruning of dead branches (Rodríguez Trejo & Fulé, 2003) and "grass stage" seedlings enhance the fire tolerance of the species (Earle, 2014). The same source indicates that even in less frequently burned habitats, *P. engelmannii* appears capable of being a very effective competitor in the aftermath of severe fire. On the other hand, Barton (2002) found that pine seedlings were very rare after an intense fire in southwestern Arizona, especially the seedlings of *P. engelmannii*, in which, moreover, no sprouting occurred.

Keeley & Zedler (1998) included *Pinus engelmannii*, along with *P. ponderosa* and a few other species, among the pines whose life-history characteristics make them suitable for planting in environments with predictable stand-thinning fires. Furthermore, Wehenkel *et al.* (2012) found that *P. engelmannii* has one of the largest proportions of bark volume (0.200 - 0.236) of Durango pine species and that it probably prefers drier and warmer and thus more fire-prone habitats.

Nursery production: Nursery studies of *P. engelmannii* are relatively more abundant, probably because the variables to be measured are easier to control (Arriaga *et al.*, 1994; Prieto-Ruíz *et al.*, 2004; Prieto-Ruíz *et al.*, 2012a; Ávila-Flores *et al.*, 2014; Rosales-Mata *et al.*, 2015). In addition, *P. engelmannii* is the second most important species in nursery production in northwestern Mexico: it is commonly used in reforestation and

conservation programmes and, in recent years, also in commercial plantations (Mejía-Bojorquez *et al.*, 2011). Due to the ecological requirements of this species, few areas with a high potential for establishing commercial plantations have been identified in northwestern Mexico (Martínez-Salvador & Prieto-Ruiz, 2011).

Production of *P. engelmannii* nursery seedlings takes 10 to 12 months and generally involves the following material/steps: a) the containers used are polystyrene or rigid plastic trays usually with 77 cavities each of capacity 170 - 190 mL; b) the substrate comprises equal proportions of composted bark and peat moss, or a base mixture (55% peat moss + 24% vermiculite + 21% perlite); c) controlled release fertilizers are applied at doses of 3 to 5 kg/m³ of substrate. Soluble fertilizers in doses of 40 to 70 ppm of nitrogen are added at the establishment phase, 100 to 200 ppm in the fast growth phase and, 40 to 70 ppm during the preconditioning phase; d) preconditioning shades are removed two or three months before final field planting, and seedlings are exposed to direct sunlight; irrigation is also reduced and the potassium dose is increased at final planting (Prieto-Ruiz *et al.*, 2012b; Prieto-Ruiz *et al.*, 2013).

Genetic structure: The 47 pine species that occur in Mexico represent more than 42% of the known pine species in the world (Sánchez-González, 2008). Some taxa present in Mexico and the southwestern US are closely related since they belong to the *Ponderosae* subsection, such as *P. arizonica*, *P. cooperi*, *P. durangensis* and *P. engelmannii*, suggesting a common origin (Axelrod, 1986; Farjon & Styles, 1997; Hernández-León *et al.*, 2013). Migration occurring from the Rocky Mountains (USA) to Mexico may partly explain the diversity of pines in the region (Gernandt *et al.*, 2003).

Pinus subsection *Ponderosae* includes approximately 17 tree species distributed between western Canada and Nicaragua. In a phylogenetic analysis of the group, Gernandt *et al.* (2005, 2009) used multiple accessions for all widely recognized species from 3.7 kb of CpDNA sequence (matK, trnD-trnY-trnE spacer, chlN-ycf1 spacer, and ycf1). These authors found that the western Mexican species *P. cooperi* and *P. durangensis* have identical CpDNA sequences to one or more accessions of *P. arizonica* and *P. scopulorum*, and these taxa are all closely related to clades of *P. engelmannii* - *P. devoniana*.

In a study of 59 seed stands of 11 pine species in Durango, Wehenkel *et al.* (2015) reported that the AFLP diversity of Apache pine was very similar to that of other pine species, except *Pinus cembroides*, *P. discolor* and *P. oocarpa*. The genetic diversity was lower in populations of *P. engelmannii* exposed to prolonged cold periods in their range of distribution.

Natural populations of conifers, especially pines, display high crossover rates, typically 90% or more, with some exceptions: *Pinus radiata* (74%), *P. leucodermis* (77%), *P. engelmannii* (73%) and *P. maximinoi* (65%) (Vargas-Hernández *et al.*, 2004). One of the species reported to hybridize with *P. engelmannii* is *P. ponderosa* Laws. (Pavek, 1994), with up to a quarter of the seeds produced being viable (Conkle & Critchfield, 1988).

However, the range of distribution of *P. ponderosa* is very widely separated from that of *P. engelmannii*.

In a study using Amplified Fragment Length Polymorphism (AFLP) markers and morphological traits, Ávila-Flores *et al.* (2016) demonstrated introgressive hybridization between *P. engelmannii* and other pine species in eight seed stands of the species in Durango and examined how hybrid proportion is related to mean genetic dissimilarity between trees in these stands. These authors concluded that natural pairwise hybrids are very common in the studied stands. Therefore, both morphological and molecular approaches must be used to confirm the genetic identity of forest reproductive material.

Bustamante-García *et al.* (2012b) analyzed seed production potential and efficiency in three *Pinus engelmannii* seed stands in the state of Durango. Ten trees, separated by a minimum distance of 50 m, were selected in each stand; ten cones were collected from each tree and were air-dried to loosen the scales before analysis to determine the productive potential, number of developed seeds, ovule abortion in the first and second year of development and infertile upper and lower scales. In each stand, 400 seeds were chosen at random and examined by X-ray analysis to measure full seed dimensions and insect damage. Germination tests were carried out to determine the speed and capacity of germination. The stand with the highest potential yielded a total production of 171.9 seeds per cone and 143.7 fully developed seeds per cone.

Health: In the nursery, *P. engelmannii* is susceptible to damping off (Comisión Nacional Forestal, 2012). In its adult state, it is susceptible to colonization by southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) (Pavek, 1994) and is a principal host for other dwarf mistletoes, including *Arceuthobium globosum* subsp. *globosum*, *A. rubrum*, *A. vaginatum* subsp. *vaginatum* and *A. verticilliflorum* (Hawksworth & Wiens, 1996).

During cone production, *P. engelmannii* is susceptible to attack by insects such as *Conophthorus apacheae* Hopkins, a member of the *Scolytidae* family. This species has been reported as a cone borer in *P. engelmannii*, and mature larvae and pupae have been found in the cones (Álvarez-Zagoya & Márquez-Linares, 1998). *Leptoglossus occidentales* Heidenman, a member of the *Coreidae* family, has also been reported; nymphs and adults cause damage to cones and are responsible for loss of cone crops in this species (Cibrián-Tovar *et al.*, 2008). The larvae of *Cydia latisigna* Miller, a species of the family *Tortricidae* (Lepidoptera), also feed on the seeds of *P. engelmannii* (Perry, 1991).

In relation to infestation of cones and seeds of *P. engelmannii* Carr., Bustamante-García *et al.* (2012a) found that the main factors affecting seed quality were poor pollination and attack by pests, especially by *Leptoglossus occidentalis* Heidemann. These authors found that this insect is the main causal agent of damage during seed development.

Silviculture and management: Resource management modelling requires estimation of timber diameter. This can be predicted by diverse probabilistic functions (Maldonado-Ayala & Nívar Cháidez, 2002). In a study carried out in an Apache pine plantation, the parameters of the Weibull distribution were estimated and predicted using the attributes of the stands under study. The use of hypothesis testing procedures demonstrated that the predictive models efficiently mimicked the diameter structures of forest stands used for model fitting, as well as those of *P. engelmannii* stands used to validate the models (Maldonado-Ayala & Nívar Cháidez, 2002).

Similarly, Corral-Rivas *et al.* (2004) tested seven algebraic difference equations used to develop site index models for *P. engelmannii* and four other pine species of the forest region of El Salto, Durango. The best results were obtained with an algebraic difference equation, derived from the base model of Hossfeld IV. On the basis of this analysis, the Cieszewski and Bella polymorphic equation was recommended for all five pine species. This is a polymorphic function and it is base-age invariant with multiple asymptotes.

In a more recent study, Martínez-Salvador *et al.* (2013) examined the influence of physical variables on the productivity of *P. engelmannii* in the south of Chihuahua (Mexico). These authors used site index (SI) models to identify the influence of soil, climate and topography on growth. The SI models were fitted by the Schumacher equation and the guide curve with information from trunk analysis, using tree height and age data. Canonical discrimination analysis was carried out in order to identify multivariate differences in the productivity levels, and analysis of variance was conducted to detect differences among the variables studied. The authors concluded that the use of SI models enabled definition of levels of productivity in the distribution of *P. engelmannii* and identification of the variables most closely related to site productivity (soil depth, slope, vertical dissection, temperature maximum and minimum). These data may be very useful for constructing spatial models of forest productivity in northwestern Mexico.

Final considerations: Despite having conducted an extensive literature search, we found little information about *Pinus engelmannii*. Although this is a timber species of high commercial value and is widely used in reforestation for conservation and restoration programmes in northwestern Mexico, information is still scarce or even absent in relation to some aspects of this species.

Although we found some information regarding the physiology, genetics and forest management of the species, further research on these topics is clearly needed. We found relatively more studies and information about ecological aspects, nursery management and pest and disease control. There does not seem to be any consensus regarding the intraspecific variation and the interspecific taxonomy of *P. engelmannii*, and more detailed morphological, chemical and molecular studies are required for a better understanding of these aspects.

This review has helped to identify specific areas of research on which to focus for more efficient management of *P. engelmannii*, one of the most important and abundant forest species in northwestern Mexico.

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