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Unlocking *Pinus ponderosa* (Douglas ex C. Lawson) potential: a comprehensive review of results from native and introduced areas

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Ponderosa pine (*Pinus ponderosa*) is one of the most valuable American pines growing naturally in the western and Pacific states of Arizona and California. Based on previously published research, its ecological valence makes this species suitable for introduction worldwide, including Europe. In Central Europe, climate change—the primary cause of significant dieback of native tree species, such as Norway spruce and Scots pine—has increased the need to explore new methods to ensure forest stand sustainability. Introducing previously overlooked tree species, such as ponderosa pine could help address this challenge. We reviewed 229 research sources to analyze *P. ponderosa*'s potential for utilization in new areas. The existing research from its native distribution range indicates ecological plasticity and strong resistance to drought and climatic extremes. Production parameters were evaluated in young European forest stands with a stand volume of 430 $m^3 \cdot ha^{-1}$ at the age of 45, pointing toward a promising use in the forestry sector. In European forestry, ponderosa pine's importance could grow due to its adaptability to warm and dry climates and tolerance of diverse soil conditions. Moreover, the extraordinary quality and texture of the wood, as well as ponderosa's biodiversity and ornamental functions, make the species destined to become part of future landscapes and forest ecosystems of Central Europe under changed climatic conditions. However, we also see challenges and scientific gaps associated with the management of ponderosa pine and its introduction to mixtures with native tree species without prior verification and silviculture recommendations.

KEYWORDS

silviculture, production, ecological valence, introduced tree species, climate change, ponderosa pine

1 Introduction

Global climate change represents a significant challenge for many sectors—and forestry has been one of the most threatened over the last few decades. Currently, forest ecosystems are facing an increasing rate of biotic and abiotic disturbances, be it increased mortality of native Central European tree species, primarily Norway spruce (*Picea abies* [L.] Karst.; Jandl, 2020; Knoke et al., 2021; Romeiro et al., 2022), or mass dieback of Scots pine (*Pinus sylvestris* L.; Rigling et al., 2018; Lemaire et al., 2022). Climate change may also disturb the wood supply chain by reducing the amount of high-quality wood for industry due to fluctuations caused by high wildfire occurrences or insect pest outbreaks (Rodríguez Silva et al., 2012; Vakula et al., 2015).

One option for afforestation in areas where forests have been disturbed, is to find alternatives to native tree species that no longer thrive under current climatic conditions. Moreover, the adaptation of forest ecosystems should be based on what the expected climate will be like in the upcoming decades. Therefore, the increase of non-native tree species proportions, such as those from North America or Asia (Brus et al., 2019) could be a part of a successful solution in Central European forests. According to Forest Europe (2015), non-native species occupy approximately 4.5% of European forest area (approximately 9.5 million ha). Many of them are critical for ensuring wood production in particular countries, e.g., *Pinus nigra* (J. F. Arnold), *Pinus contorta* (Douglas ex Loudon), or *Pinus radiata* (D. Don). However, significant differences remain in our understanding of the ecological aspects, as well as the quality and quantity of wood production. In particular, there is a lack of comprehensive knowledge about the potential of specific introduced tree species, especially regarding their resistance to extreme climatic conditions under ongoing climate change. For example, the potential of *P. nigra* in Europe has already been described by Vacek et al. (2023). The prospective management and use of lodgepole pine (*P. contorta*) in Europe was extensively described by Novotný et al. (2018).

Pinus ponderosa (Douglas ex C. Lawson) is another introduced pine species with considerable potential that has not yet been systematically evaluated in European conditions. This species is one of the most commercially used trees in North America, where it covers millions of hectares and provides high-quality wood (Oliver et al., 1990). Its ecological valence and economic value are why scientists, foresters, and the timber industry are paying more attention (Farjon and Styles, 1997). This growing interest is supported by the favorable mechanical and technological properties of the wood, such as good workability and sufficient strength and durability, making it a potential alternative to native conifers in Europe such as Scots pine (Kretschmann, 2010; Ross and Forest Products Laboratory, 2010). Geographically, *P. ponderosa* is native to areas from Canada to Central America (Price et al., 1998). It is also widespread in Western Europe and the Czechia (Pokorný, 1963), where it has been tested predominately in hilly areas. It is often planted in parks and woodlands as an attractive landscape feature (Hieke, 1994). However, planting it in standard forest stands is rare. The species prefers well-drained soils and a continental to subcontinental climate, and it is generally tolerant to drought and poor soil conditions (Farjon, 2010, 2021), which adds to its silvicultural appeal. Compared to regions in the Southern Hemisphere (Dezzotti et al., 2009; Mathias et al., 2023) the introduction of *P. ponderosa* in Europe is not expected to pose significant risks related to invasiveness or the spread of associated pests.

Systematic reviews describing *P. ponderosa*'s growth and production potential have only been performed in the area where it naturally grows (Krannitz and Duralia, 2004; Callaham, 2013). They are lacking for newly established stands in Europe with different soil and climatic conditions, which can be the main drivers for the successful growth of introduced tree species in non-native areas. Therefore, the objective of this literature review is to evaluate in detail the opportunities and risks of *P. ponderosa* cultivation in European forestry, based on the comparison of research results from native and non-native areas. The specific aims are to provide a detailed overview of (i) species description, (ii) taxonomy, (iii) distribution, (iv) ecology, (v) silviculture and production potential, (vi) wood properties, (vii) diseases and threats, and (viii) adaptation to climate change.

2 Materials and methods

This manuscript was prepared using information from research databases Scopus, Web of Science, and Google Scholar. The search covered a wide range of definitions and keywords related to *P. ponderosa*: *P. ponderosa,* taxonomy, cultivation, silviculture, growth, productivity, harvesting, use, and wood properties in both native and introduced distribution areas, i.e., European research and review articles, books, and conference proceedings were searched for in the study. Other sources, such as technical reports or dissertations, were also evaluated. A total of 229 references were included in this article – 137 research articles, 12 review articles, 28 books, 15 conference proceedings, and 37 other sources. In the past, *P. ponderosa* topics were rare, but with the increasing interest in this species since the mid-20th century, it was deemed unnecessary to establish a search window. The most recent manuscript was found in 2025, while the oldest was published in 1931. The selected manuscripts are from various countries worldwide, but most articles are from the United States.

3 Description of the species

Pinus ponderosa is not only one of the most important pine species in the U.S. in terms of forestry and timber industry, but also a symbol of the western part of North America. For example, *P. ponderosa* is the state tree of Montana (Kral, 1993). *P. ponderosa* is an evergreen monoecious tree species. It grows to a height of 50 m (83 m maximum) and a diameter of 120 cm (265 cm maximum) in its native distribution range. Taylor (2022) reports that the tallest *P. ponderosa* (*P. ponderosa* subsp. *benthamiana*) from the Sierra Nevada—Stanislaus National Forest—reaches a height of 83.66 m and is likely to be the tallest pine in the world.[1] In Europe, the tallest ponderosa pine reaches a height of 48.3 m with a diameter at breast height (dbh) of 161 cm in the United Kingdom, followed

1 http://www.ents-bbs.org

by a tree of 47.3 m in height with a dbh of 109 cm in Belgium.[2] The trunk is usually straight and sturdy. Branches are thick, usually 3–6 branches on a hinge, set to the trunk at an angle of 51°–56° from the top of the young trees. The bark on mature trees is vertically fissured, dark brown or dark gray to black. On old trees, it is already light yellow to yellowish brown, thick with broad stripes separated by shallow fissures. The tree forms a massive root system with a deep main root (taproot) (Oliver and Ryker, 1990; Callaham, 2013).

This pine species is characterized by three needles in the fascicle (Figure 1), but *P. ponderosa* subsp. *scopulorum* and *P. ponderosa* subsp. *readiana* often have only two. The needles are finely serrated and pointed, finely lined on all faces with vents. They are 13–25 cm long, yellow-green to blue-green, lighter and shorter at higher elevations and in xeric conditions. The needles rarely turn gray but are more likely to at higher altitudes and with the onset of winter. The needles are flexible and in bundles of three; they remain green for an average of 1.4–7.6 years, longer at higher altitudes (Callaham, 2013). The needles are enclosed at the base by sheaths of braces, which reach 10%–15% of their length in the first year (Helmers, 1943; Conkle and Critchfield, 1988; Callaham, 2013). *P. ponderosa* needles are toxic for pregnant cows, especially in the last trimester of pregnancy (Panter et al., 1990; James, 1999) due to labdane resin acid, ICA (Gardner and Panter, 1994).

On the oldest bundles, they leave a thick, dark brown to black sheath 4–8 mm long. The vegetative buds are covered with loosely appressed ovoid, sharp scales that are conspicuously lined with short brown hairlike projections. The scales are dark reddish-brown to light gray-brown, covered with resin in summer and occasionally in winter as well. Vegetative shoots are green or brownish-green and sticky, elongating once a year.

The production of cones in *P. ponderosa* typically starts at approximately 20 years old and can continue until the tree reaches a maximum age of 350 years. However, the superior seeds are produced by trees that fall within the 60–160-year-old range (Bonner and Karrfalt, 2008). The trees can live over 600 years (Youngblood et al., 2004) as OldList gives the oldest known *P. ponderosa* from measurements by Stan Kitchen from a drier climate in the Wah Wah Mountains. Using the cross-dating method, he counted 929 annual rings and estimated the final age at 941 years.[3]

The number of seeds in a cone varies from 50 to 70, depending on many abiotic and biotic factors, such as high temperature, precipitation, or insect pests, which can also affect seed growth and mortality (Krannitz and Duralia, 2004). Male cones borne in clusters of 5–30 are dark red or reddish-brown to reddish-purple, long-cylindrical, and 20–90 mm long. Male cones in the first year are 5–25 mm long, semi-double at the peduncle, initially red, then turning greenish-brown to gray, with short, appressed scales. Cones are either single or in clusters of usually 3–5, sessile, oblong-ovate-conical, 8–10–15 cm long, and 3–5 cm wide, and deciduous the following year after opening. The shield is flat-angled with a straight keel, while the umbilicus is conspicuously spiny (Conkle and Critchfield, 1988; Callaham, 2013).

The spines are usually erect, symmetrical, and straight to slightly curved at maturity. The color of the cones during the second summer ranges from apple green to reddish brown to dark purple. The cones are sessile, deciduous during the first winter after maturity, with a very short pedicel and a few basal scales that usually remain temporarily on the branch after the cone has fallen. The scales of the seed cones (134–159) are slightly concave, usually rounded at the apex. The apophysis is yellow to brown, shiny, and slightly raised along the transverse keel. The adaxial surface of the cones is slightly concave, dull yellow to reddish brown. The abaxial surface is dark brown, purple, or blackish (Farjon, 2005, 2021).

Pinus ponderosa produces seeds periodically, usually after mast years, and cone production is limited to a few or no cones (McDonald, 1992; Shepperd et al., 2006; Mooney et al., 2011). Generally, mast years occur from 3 to 8 years (Roeser, 1941; Fowells and Schubert, 1956; Larson and Schubert, 1970; Dahms, 1975). Seeds are dark brown or mottled, about two-thirds as wide as long, 4–5 mm × 6–8 mm in diameter, and are not translucent. Seed wings are 3.3–4.3 times the length of the seed, 16–25 mm long, thin, semi-transparent, light brown, sometimes dark brown, broadly striped in the middle or slightly below the middle, with a rounded apex (Pokorný, 1963; Pilát, 1964; Murphy, 1994; Farjon, 2001, 2010; Callaham, 2013). Individual morphological characteristics of *P. ponderosa* partially vary between subspecies (Callaham, 2013).

4 Taxonomy

Pinus ponderosa (Douglas ex C. Lawson), known as yellow western pine, was discovered by David Douglas in 1826 near Spokane, WA (Little, 1979), and was described by Lawson in 1836. The taxonomy of *P. ponderosa* has not been resolved due to differing opinions (Weidman, 1939; Wells, 1964a; Read, 1980; Kitzmiller, 1990; Lauria, 1991, 1996a, 1996b; Rehfeldt, 1993, 1999; Cregg, 1994; Farjon and Styles, 1997; Willyard et al., 2009, 2017, Willyard et al., 2021a; Callaham, 2013; Potter et al., 2013; López-Reyes et al., 2015). Provenance studies of *P. ponderosa* began in 1913 and have been described by numerous authors (Wells, 1964b; Read, 1980, 1984; Rehfeldt, 1986, 1990, 1991, 1993, 1999; Conkle and Critchfield, 1988). There have been a series of provenance studies to determine patterns of genetic variation in a broad north-south range extending from the Canadian border to nearly Mexico. Smith (1977), after studying xylem monoterpenes from 68 sites, divided *P. ponderosa* into five regional types with four transition zones. Critchfield (1984) demonstrated the close identity of *Pinus washoensis* H. Mason and Stockwell with Weidman's "North Plateau ponderosa pine."

- *Pinus ponderosa* Dougl. ex C. Lawson var. *ponderosa* is a typical heavy pine, ranging south from British Columbia, Idaho, Washington, Oregon, and northeastern California.
- Rocky Mountain ponderosa pine, *P. ponderosa* var. *scopulorum* Engelm. (1880), E. Murray (1982), elevated the subspecies in Montana and Wyoming, east of the Continental Divide and extending south through Utah, Colorado, and Nebraska into Arizona, New Mexico, Oklahoma, and West Texas to Mexico.
- Arizona pine, *P. ponderosa* var. *arizonica* (Engelm.) Shaw, growing in extreme southwestern New Mexico, southeastern Arizona, and adjacent northern Mexico.

2 https://www.monumentaltrees.com/
3 https://rmtrr.org/

FIGURE 1
Tree habitus, branch with cones, needles, and scales with the seed of *Pinus ponderosa* (Douglas ex C. Lawson).

Based on morphological data and climatic parameters, Callaham (2013) concluded that there are five subspecies of *P. ponderosa* in the western U.S. states and adjacent Canada (Figure 2):

- *Pinus ponderosa* subsp. *P. ponderosa*, Columbia ponderosa pine,
- *Pinus ponderosa* subsp. *critchfieldiana* Callaham, subsp. nov., Pacific ponderosa pine,
- *Pinus ponderosa* subsp. *scopulorum* (Engelm. and S. Watson) E. Murray, Rocky Mountain ponderosa pine,
- *Pinus ponderosa* subsp. *readiana* Callaham, subsp. nov., central High Plains ponderosa pine,
- *Pinus ponderosa* subsp. *brachyptera* (Engelm. and Wislizenus) Callaham, comb. nov., Southwestern ponderosa pine.

These subspecies of *P. ponderosa* closely match the geographic races proposed by Weidman (1939), the ecotypes proposed by Wells (1964b) and Haller (1965), the regions and zones proposed by Smith (1977), and the geographic clusters proposed by Read (1980, 1984).

However, according to Willyard et al. (2021a), based on nuclear genetics, there are only three subspecies of *P. ponderosa*:

- *Pinus ponderosa* subsp. *P. ponderosa* Douglas ex Lawson 1836,
- *Pinus ponderosa* subsp. *P. benthamiana* (Hartw.) Silba 2009,
- *Pinus ponderosa* subsp. *P. washoensis* (Mason & Stockwell) E. Murray 1982.

Mitochondrial studies suggest complexity within each subspecies, with mitochondrial haplotypes varying significantly across the species range (Potter et al., 2013; Willyard et al., 2021b). Molecular clock analyses (Lascoux et al., 2004; Potter et al., 2013) suggest that the separation of *P. ponderosa* and *P. scopulorum* occurred more than 250,000 years ago and that the separation may have persisted from the onset of the Glacial/Interglacial cycles at the Pliocene/Pleistocene boundary or even earlier, with the separation occurring when tectonism created the basin and range structure of central Nevada in what was formerly a montane plateau (Potter et al., 2013). In addition to taxonomy, recent research using state-of-the-art genetic methods has focused on the issue of advancing global climate change, both from an ecosystem perspective and from the perspective of management and its adaptation to ongoing processes (Skov et al., 2005; Xiaoyan et al., 2013; Rehfeldt et al., 2014; Jolly et al., 2015; McDowell and Allen, 2015; Mcdowell et al., 2016; Singleton et al., 2019; Willyard et al., 2021a).

5 Distribution

Geographically, *P. ponderosa*'s native range extends from Canada to Central America (Price et al., 1998). It is naturally distributed in western North America, from British Columbia to California and northern Mexico in the south and east to northwestern Nebraska, covering millions of hectares. The natural distribution of this species includes British Columbia, Arizona, California, Colorado, Idaho, Northeastern Mexico, Northwestern

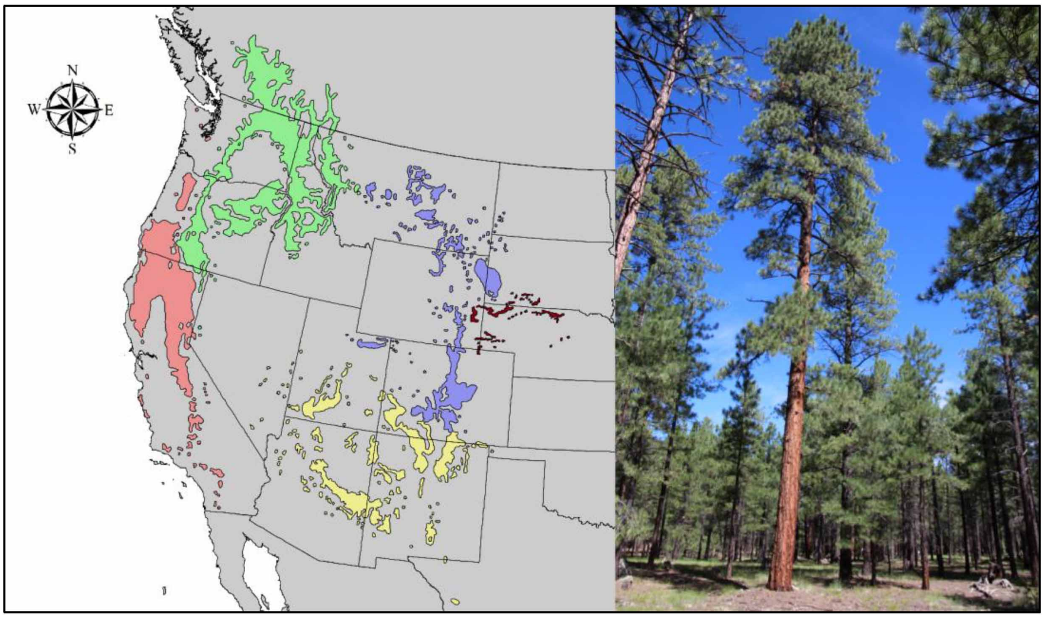

FIGURE 2
Distribution map of ponderosa pine according to Callaham (2013) with illustrated areas of the five main subspecies: *Pinus ponderosa* subsp. *P. ponderosa* (green), *P. ponderosa* subsp. *P. critchfieldiana* (red), *P. ponderosa* subsp. *P. scopulorum* (blue), *P. ponderosa* subsp. *P. readiana* (brown), and *P. ponderosa* subsp. *P. brachyptera* (yellow).

Mexico, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington, and Wyoming (Baker and Korstian, 1931; Meyer, 1938; Little, 1979; Thompson et al., 1999; Kolb et al., 2019).

Individual subspecies vary in their natural distribution:

- *Pinus ponderosa* subsp. *P. ponderosa,* Columbia ponderosa pine—southward from southern British Columbia, east of the Cascade Range in Washington, Oregon, and northeastern California, and eastward to the Continental Divide.
- *Pinus ponderosa* subsp. *P. critchfieldiana* Callaham, subsp. nov., Pacific ponderosa pine—from Puget Sound, Washington, southward to Southern California.
- *Pinus ponderosa* subsp. *P. scopulorum* (Engelm. in S. Watson) E. Murray, Rocky Mountain ponderosa pine—from the Continental Divide in Montana eastward to the Black Hills of South Dakota and southward into Utah and Colorado.
- *Pinus ponderosa* subsp. *P. readiana* Callaham, subsp. nov., Central High Plains ponderosa pine—restricted to Nebraska and adjacent areas in South Dakota, Wyoming, and Colorado.
- *Pinus ponderosa* subsp. *P. brachyptera* (Engelm. in Wislizenus) Callaham, comb. nov., Southwestern ponderosa pine—in Arizona, New Mexico, Oklahoma, and southwestern Texas, and, in all likelihood, extending into Mexico (Callaham, 2013).

The current distribution of *P. ponderosa* forests in its natural range is likely the result of its rapid expansion during the Holocene (Betancourt, 1986; Anderson, 1989).

In Europe, *P. ponderosa* was successfully introduced two centuries ago (Hermann, 1987). For example, in the Czechia, *P. ponderosa* was first noticed in 1827 (Pokorný, 1963) and first planted in 1845 in the Sychrov chateau park (Hieke, 1994). At the same time, ponderosa was also introduced in Great Britain, but recently, it has been used primarily as an ornamental plant and is rarely found in forest stands (Streets, 1961; Parrantt, 2020). On the other hand, it has been experimentally planted in forest stands in the Czechia (Poleno, 1985; Kaňák, 2004). Besides these two countries, *P. ponderosa* was introduced to many other European countries, e.g., Austria, France, Germany, Greece, Hungary, Ireland, Italy, Poland, Romania, Spain, and Sweden—in parks, arboretums, and forests (Tutin et al., 1968; Landry, 1978; Krauze-Baranowska et al., 2002; Dobignard and Chatelain, 2010; Stace, 2019). However, the total forest cover of this species has not yet been measured in Europe. *P. ponderosa* has also been introduced to other continents, such as Australia and Oceania, e.g., to South Australia and New Zealand (Weston, 1957; Burdon et al., 1991; Orchard et al., 1998), Asia, e.g., China (Gong et al., 1997), and South America, e.g., to Argentina (Bachmann, 1972; Broquen et al., 1998; Gyenge et al., 2012).

From the perspective of introduction into Europe and phytosanitary considerations, *P. ponderosa* is known to be susceptible to several pests and pathogens in its native range (McHugh et al., 2003; Fettig et al., 2007). However, these organisms are currently absent or not established in Europe, which minimizes the immediate risk of pathogen transfer associated with *P. ponderosa* introduction (Haffey et al., 2018). Ecologically, *P. ponderosa* thrives in environments differing from most native European pine species (Oliver et al., 1990; Caudullo et al., 2016), which may reduce competition and phytopathological impacts. Overall, while *P. ponderosa* does not currently pose significant phytosanitary threats in Europe, the potential for future pest or disease introduction via this species warrants ongoing surveillance and risk assessment.

6 Habitat and ecology

Pinus ponderosa has a wide ecological spectrum of environmental conditions where it can grow, which could be one reason for its successful introduction into new areas. It is a light-tolerant tree species that grows in forests and woodlands in predominately arid habitats (Farjon, 2001, 2010). It occurs from the lowlands to the mountains, reaching up to 3,200 m above sea level. Muir (1894) found it grows well on moist moraines, gravelly lake basins, arctic ridges, and arid lava covers. In the lower elevations of the mountainous west, these forests are adjacent to grasslands, pine-juniper woodlands, or chaparral (scrub). Their ecotone varies in width (Milo and Moir, 1986). In the higher elevations, *P. ponderosa* stands are usually next to mixed, mostly coniferous forests (Eyre, 1980).

Regarding habitat and vegetation, there are two types of *P. ponderosa* forests—xerophilous and mesophilous. In xerophilous (drier) forests, *P. ponderosa* occurs as a climax tree in predominantly monospecific stands and regenerates during the mid to late stages of its life cycle (Dick-Peddie, 1993; Moir and Fletcher, 1996; Moir et al., 1997). In mesophilous (wetter) forests, *P. ponderosa* is part of mixed conifer stands. Its regeneration occurs only during the early to mid part of the developmental cycle, although older trees may persist until the end of their life cycle (Johnson, 1993, 1994; Moir et al., 1997).

The average annual air temperatures in xerophilous forests range between 6°C and 9°C and precipitation between 480 and 600 mm, while in mesophilous forests, they are between 4°C and 7°C and 660–700 mm. In xerophilous forests, the driest periods are in May and June, and the understory vegetation, primarily grasses, is severely desiccated and flammable (Swetnam, 1990; Swetnam and Betancourt, 1990; Swetnam and Baisan, 1996). In mesic forests, drought does not usually occur during the growing season (Eyre, 1980; Johnson, 1994).

It grows on a wide range of soils, from stony and sandy on acidic rock to limestone and basalt. Soil types include podzols, rankers, rangelands, lithosols, cambisols, and volcanic cinder soils; loamy and sandy soils predominate (Brady and Weil, 1999; Hyndman, 1985; Kaye and Hart, 1998; Abella and Covington, 2006).

The xerophilous forests are dominated by pure stands of *P. ponderosa*, sometimes with small admixtures of oaks, junipers, and other pine species (*Quercus grisea*, *Quercus arizonica, Quercus emoryi*, *Juniperus* spp., *Pinus edulis*, *Pinus discolor*, *Pinus californiarum*). Mixed or intermixed woody species form the middle or bottom layer below *P. ponderosa* (Marshall, 1957; Fischer and Bradley, 1987; Bradley et al., 1992). In mesophilous forests, they usually form mixed stands. In the southern part of the range, it grows together with *Abies concolor* and *Pinus lambertiana*, while in the northern part, predominately with *Pseudotsuga menziesii* var. *glauca*. Locally, *Picea pungens*, *Pinus strobiformis*, and *Populus tremuloides* are also intermixed or interspersed (Jones, 1974; Bradley et al., 1992; Dick-Peddie, 1993; Johnson, 1993, 1994). The mixing of woody species varies among subregions. In California, *Calocedrus decurrens*, *P. menziesii*, *A. concolor*, and *P. lambertiana* are common. In Oregon, *P. contorta*, *A. concolor*, and *P. menziesii* grow, while *Larix occidentalis* and *Picea engelmannii* occur sporadically. In Washington and Idaho, *P. menziesii* and *A. concolor* are sometimes found, and in Montana, it is *P. menziesii* and *L. occidentalis* (Block and Finch, 1997).

The structure of *P. ponderosa* stands was initially open parkland, dominated by large, old trees, mostly of similar age, that are relatively fire tolerant (Weaver, 1943; Covington and Moore, 1994; Moore et al., 2004; Brown et al., 2015). Fires recorded in the old-growth tree rings have occurred every 8–15 years on average (Brown et al., 2015).

7 Silviculture and production

7.1 Reforestation and silviculture under wildfire threat

The cultivation of *P. ponderosa* has received considerable attention in western North America, as it is the most economically important tree on the continent (Fiedler and Arno, 2015). In California alone, approximately 280,000 ha of both private and National Forest lands are covered by such plantations (Zhang et al., 2019). Indeed, *P. ponderosa* is one of the best examples of the excellent adaptation of conifers to wildfire. Mature trees are not threatened by low-intensity fires due to their dense, fire-resistant boles. *P. ponderosa* forests, which are predominantly or co-dominantly composed of *P. ponderosa*, have long relied on wildfire as a crucial ecological disturbance (Korb et al., 2019). Historically, ponderosa stands were frequently dominated by low to moderate-severity surface fires, or mixed-severity fires that involved both moderate and high-severity crown fires (Brown and Cook, 2006; Iniguez et al., 2009; Scholl and Taylor, 2010; Sherriff et al., 2014). Moreover, as climate change continues, the incidence of fires worldwide increases. Wildfires play a critical role in *P. ponderosa* forests, both ecologically and economically (Swetnam and Baisan, 1996; Laughlin et al., 2004; Ouzts et al., 2015) due to their distribution in high fire-risk areas. Research indicates that the regeneration of *P. ponderosa* in post-fire areas is slow and not very effective, particularly during the first decade following a fire (Roccaforte et al., 2012; Ritchie and Knapp, 2014). Presumedly, the natural regeneration of ponderosa forests may even take a few decades (Bonnet et al., 2005; Haire and McGarigal, 2010), primarily because of large areas for regeneration with limited access to seed sources (Haire and McGarigal, 2010; Puhlick et al., 2012). Ponderosa seeds are relatively large and, therefore, do not disperse over long distances. They have a short lifespan (Howard, 2003). This phenomenon presents a danger to the forests in the Southwestern United States, as it may lead to their conversion into non-forested ecosystems (Savage and Mast, 2005; Dore et al., 2012; Roccaforte et al., 2012; Savage et al., 2013). This risk is becoming increasingly relevant due to the rising number of large-scale wildfires associated with climate change. Regeneration of ponderosa pine is severely limited beyond 150 m from a seed source, further hindering natural recovery (Haffey et al., 2018). On the other hand, with sufficient numbers of surviving mature seed trees, post-fire conditions—bare ground and open space—enable a successful natural regeneration of *P. ponderosa* (Howard, 2003; Oliver and Ryker, 1990).

The second, more promising option for reestablishing ponderosa forests is artificial regeneration (planting) (Schubert, 1970, 1974). However, Vickers et al. (2018) reported a lower survival rate of seedlings planted in West Texas in two periods—22%–34% after fall planting and 9%–25% after late-summer planting. The main reasons for the high seedling mortality were the occurrence of pocket gophers and drought. In Arizona and New Mexico, Ouzts et al. (2015) noticed the high variability of survival rates between research plots 5–8 years after artificial reforestation. The survival rate varied from 0% to 60%. Many authors offered options to improve the survival rate of ponderosa seedlings through different silvicultural methods and treatments, e.g., planting season (Vickers et al., 2018), irregular cluster planting designs (Vickers et al., 2018; North et al., 2019), selection of drought-adapted seed sources (Kolb et al., 2016), among others (Engeman et al., 1999; Pinto et al., 2011; Tricker et al., 2013; North et al., 2019).

However, competition from pioneer shrubs, such as *Arctostaphylos* and *Ceanothus* spp., may affect the seeds, seedling germination, and growth (McDonald and Fiddler, 2010; Zhang et al., 2013a). Therefore, it is essential to implement effective weeding control measures to enhance the survival rate of *P. ponderosa*. Reducing grass and shrub competition with herbicides can improve young trees' growth (Powers and Reynolds, 1999; Moore et al., 2023). Fertilization can be employed to increase the effect of weed control (Moore et al., 2023). However, fertilizing without initially removing competing plants may even be counterproductive in supporting weed growth (Zhang et al., 2022).

A great deal of attention has focused on stand management, particularly thinning intensity, which might reduce the negative impact of wildfire and improve the health status of managed forest stands (Covington et al., 1997; Waltz et al., 2014; Kalies and Yocom Kent, 2016). Many authors point out the need for tree reduction during the first thinning (Schubert, 1971; Ffolliott et al., 2000). Consequently, the stand ring base and volume will also change. Moreover, the natural regeneration was significantly reduced after the first thinning. This short-term management of density reduction may improve light conditions and influence the subsequent growth within the next 10 years after the thinning (Malchus and Ffolliott, 1999; Ffolliott et al., 2000). In xerophilous stands, natural regeneration was also severely reduced to minimize fire hazard (Gottfried and DeBano, 1990). These thinning operations produce a large volume of predominately small-diameter trees and woody by-products, such as wood chips (Hampton et al., 2008; Lowell et al., 2008). Contrastingly, managed dense stands of *P. ponderosa* are considerably less adapted to fire (Weatherspoon et al., 1992; Skinner and Chang, 1996). When fire does occur, it is likely to be highly destructive and destroy large areas of the stand. Since the mid-1970s, some forest managers have attempted to reintroduce low-intensity fire into this ecosystem, but their efforts have often been thwarted by the high cost of monitoring these fires (Swetnam and Baisan, 1996; Gutsell and Johnson, 1996; Laughlin et al., 2004; Waltz et al., 2014; Ouzts et al., 2015).

7.2 Production and productivity

In the early 1970s, an emphasis on timber production changed to a more holistic view of the natural resource management of *P. ponderosa*. In North America, where the species is native, production parameters vary greatly depending on altitude, habitat, or silvicultural interventions. For example, tree densities in old-growth *P. ponderosa* forests in Eastern Oregon and Northern California ranged from 58 to 1,853 trees·ha^{-1} and basal area from 18.9 to 30.9 $m^2 \cdot ha^{-1}$ (Youngblood et al., 2004). Research focusing on different types of treatment in Arizona showed that the control (unthinned) plots reached an average number of trees 3,160 per ha and a basal area of 47 $m^2 \cdot ha^{-1}$, while the heavily thinned stands had 70 trees, i.e., 7 $m^2 \cdot ha^{-1}$ (McDowell et al., 2006). The high production potential of this pine species was proven by a study by Zhang et al. (2013b) from Oregon and California, where periodic annual increment reached a respectable 18.7 $m^3 \cdot ha^{-1} \cdot yr^{-1}$.

Less information comes from non-native areas. In the Czechia, Podrázský et al. (2020) found above-average growth characteristics of *P. ponderosa* compared to seven other native and exotic pine species. In comparison, *P. ponderosa* reached the highest stand volume of 430 $m^3 \cdot ha^{-1}$ at age 45 years, while the lowest yield was calculated for *Pinus strobus*—112 $m^3 \cdot ha^{-1}$. High production potential (223 $m^3 \cdot ha^{-1}$) was observed in *Pinus jeffreyi* in the same study area. In a forest reclamation site on a former coal mine, *P. ponderosa* reached a 2% lower stand volume when compared to the average of the 12 tree species tested, including native and non-native ones (Vacek et al., 2021a). In another study from Czechia, the stand volume of *P. ponderosa* was 335 $m^3 \cdot ha^{-1}$ at the age of 50 years, which is 12% less than the native *P. sylvestris* but 53% more than, for example, *P. contorta* on the same site. Generally, *P. ponderosa* grows more slowly in the early years and can eventually overtake *P. sylvestris* in growth parameters (Pokorný, 1963). Production of *P. ponderosa* according to selected studies is summarized in Table 1.

8 Importance and use

8.1 Wood quality and utilization

Pinus ponderosa is a softwood (conifer) tree species. On the cross-section of the stem, its wood is divided into heartwood and sapwood. The heartwood is indicated by a light reddish-brown color, while the sapwood is from pale yellow to almost white (Ross and Forest Products Laboratory, 2010). Sapwood covers a relatively significant area of the cross-section (Domec and Gartner, 2003; Ross and Forest Products Laboratory, 2010). Domec and Gartner (2003) found that ponderosa sapwood covers 29-54-116 rings from young, mature, and old-growth trees at the trunk base. The juvenile wood may cover up to 30 rings in conifers and is characterized by somewhat poor wood properties and small sizes of anatomical elements (Panshin and Zeeuw, 1980). In pines, the wood properties exhibit an increase in their intensity from the pith to the bark (Zeidler et al., 2024). *P. ponderosa* sawtimber from the outer stem is known to be relatively lightweight and to have poor wood properties (Ross and Forest Products Laboratory, 2010).

The wood typically has straight grain and moderate shrinkage (Zeidler et al., 2024) showed that volumetric shrinkage for *P. ponderosa* was 14.4% for samples collected in the Czechia, while its native area showed 3.9% for radial, 6.2% for tangential, and 9.7% for volumetric shrinkage

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TABLE 1 **Overview of available publications related to *Pinus ponderosa* (Douglas ex C. Lawson) production parameters.**

Study	Country	Altitude (m a.s.l.)	Age (year)	DBH (cm)	Height (m)	Basal area ($m^2 \cdot ha^{-1}$)	Volume ($m^3 \cdot ha^{-1}$)	Density ($trees \cdot ha^{-1}$)	Climate classification
North America—native									
Youngblood et al., 2004	Oregon California	900–2,000	To 618	58.8–61.0	25.6–30.9	18.9–30.9		58–1,853	Csb
Hagmann et al., 2013	Oregon	1,270–2,300	Multi			8–14		38–72	Csb
Vaughan et al., 2019	Arizona	2,266	100	28.5–51.0		10.9–39.2		57–601	Csb
McDowell et al., 2006	Arizona	2,266	87	13.4–47.0	11.1–19.5	7–45		70–3,160	Csb
Robertson and Bowser, 1999	Colorado		214			25.8		241	Bsk
Negrón et al., 2008	South Dakota and Wyoming	1,814–1,827		21.1–22.8		22.0–26.3		583–630	Dfb
Zhang et al., 2013b	Oregon California	1,240–1,520	20–65	9.9–18.0		35.4–55.1		2,200–5,260	Dsb, Csb
Europe—introduced									
Forest Data Bank in Poland	Poland	300	88	40	21				Cfb
Insinna et al., 2007	Germany	14	112	50.2	28.8				Cfb
Podrázský et al., 2020	Czechia	300–345	35	37.0	18.2	49.4	430	460	Cfb
Vacek et al., 2021a	Czechia	440	48	15.1	10.6	35.6	183	2,000	Cfb
Zeidler et al., 2024	Czechia	430	50	23.6	13.7		335		Cfb
Australia and Oceania—introduced									
Burdon et al., 1991	New Zealand	300	28	34.6	16.0				Cfb
		375	29	29.3	14.4				Cfb
		500	28–29	22.5	9.5				Cfb

DBH, diameter at breast height; MAI, mean annual increment; Köppen climate type: Csb, warm-summer Mediterranean; Bsk, cold semi-arid; Dfb, warm-summer humid continental; Dsb, warm-summer Mediterranean continental; Cfb, oceanic.

(Ross and Forest Products Laboratory, 2010). The wood density of *P. ponderosa* in the native area of its distribution varied between studies, ranging from 380 to 464 kg·m^{-3} (Tsoumis, 1991; Alden, 1997; Vaughan et al., 2019, 2021). Similar results were obtained in Central Europe by Zeidler et al. (2024) who reported an average density of *P. ponderosa* growth on post-mining sites of approximately 426 kg·m^{-3}. In New Zealand, Ledgard and Belton (1985) observed slightly lower wood density: 361 kg·m^{-3}. The modulus of rupture of *P. ponderosa* wood also varied from a very low value of approximately 34 MPa (Mackes et al., 2005) to about 64 MPa (Alden, 1997), or even 65 MPa (Ross and Forest Products Laboratory, 2010), which corresponds to a modulus of elasticity ranging from 5.633 to 8.900 MPa (Alden, 1997; Mackes et al., 2005; Ross and Forest Products Laboratory, 2010). In the case of compression parallel to the grain, the average value for ponderosa is 36.7 MPa, and over four times lower compression perpendicular to the grain (Ross and Forest Products Laboratory, 2010). In Europe, Zeidler et al. (2024) noticed a lower average value for compression—26.2 MPa—which varied from 17.7 to 37.7 MPa.

Due to its high quality and large distribution in its native range, *P. ponderosa* wood is the most commercially important and versatile in western North America (Little, 1971, 1979; Safford, 2013; Western Wood Products Association, 2018). In the past, *P. ponderosa* wood was widely used for log cabin construction, lumber production, as firewood in mines, and to power steam locomotives (Meyer, 1938). Current uses include structural lumber, furniture lumber, miscellaneous cabinetry, firewood, log cabin construction (Western Wood Products Association, 2018), and, to a lesser extent, for pole production, mine timber, posts, or railroad crossties. The highest-quality wood is reserved for molding, blinds, doors, or even sashes. Low-grade wood is popular for making boxes and crates. Knotty *P. ponderosa* is often employed for interior woodwork. Its use is similar to Scots pine in Europe. The primary regions known to produce *P. ponderosa* are located in Oregon, Washington, and California. In addition, Idaho and Montana are considered other significant producing states (Ross and Forest Products Laboratory, 2010). In Europe, the potential of *P. ponderosa* is not yet recognized due to its sparse distribution. However, available studies have shown that compared to other pine species in Europe, it is not on par with Scots pine in similar habitats (Zeidler et al., 2024).

8.2 Other uses

The Nez Perce Indians harvested the inner bark to feed their horses in early spring when the forage was still buried deep under the snow. Cambium was scraped for food (often only in times of famine) by the Klamath, Sanpoil, Spokane, Colville, Okanogan, and Thompson-Nicola tribal nations. Seeds were also gathered for food. Most everyone ate the seeds, usually roasted, sometimes ground into flour. The pitch or sap was used by various tribes, including the Cheyenne, Flathead, Okanogan, Colville, Paiute, and Thompson-Nicola, for a wide variety of purposes, such as an ointment for sores, cuts, and earaches; to reduce inflammation of the eyes; to treat back pain or rheumatism. Decoctions of green needles have also been used for similar medicinal purposes. Many tribes used pitch as glue or putty. The Diegueño tribe made baskets from the needles, and the Karok and Maidu tribes made them from finer roots. The wood was used for 6,000 years in Indian dwellings to make hollowed-out canoes, and, of course, as fuel (Peattie, 1991; Schoenherr, 2017).

In Europe, *P. ponderosa* is also used for forest reclamation and soil improvement (Vacek et al., 2021a). For example, in the reclamation of former landfills, faster soil formation, low bulk density, higher porosity, pH, and nutrient levels were observed in *P. ponderosa* stands (Spasić et al., 2024). Cones are commonly used in handicrafts and decorations. This pine species is rarely used as Christmas trees due to its long needles; Scots pine is preferred instead (Johnson et al., 1997). *P. ponderosa* also has important scenic, recreational, and aesthetic values due to large tree sizes and low overstory density (Pokorný, 1963; Brown, 1984).

9 Risks and diseases

A serious threat to *P. ponderosa* is advancing global climate change, particularly in the Southwestern United States, where tree mortality has increased due to more frequent long-term droughts, warmer temperatures, and associated fire and insect attacks (Westerling et al., 2006; van Mantgem et al., 2009; Meddens et al., 2012; Xiaoyan et al., 2013; Allen et al., 2015; Cohen et al., 2016). In western North America, several species of *Dendroctonus*, particularly *Dendroctonus ponderosae*, *Dendroctonus valens*, and *Dendroctonus brevicomis*, are locally damaging in *P. ponderosa* stands, but are vital parts of the ecosystem. Their periodic outbreaks could potentially cause widespread mortality in mature forests over large areas, particularly in post-fire stands (McHugh and Kolb, 2003; McHugh et al., 2003; Fettig et al., 2007; Negrón et al., 2016). In California, they have caused significant mortality in these stands (Oliver, 1997). There is also a higher incidence of mistletoe (*Arceuthobium* spp.) in naturally weakened stands (Barrett and Roth, 1985; Filip, 2005; Abella and Denton, 2009).

Ponderosa seeds and cones can also be attacked by several insects, such as cone beetle (*Conophthorus ponderosae*), cone moths (*Dioryctria* spp. or *Eucosma* spp.), cone weevils (*Conotrachelus neomexicanus*), or cone bugs (*Leptoglossus occidentalis*), seed worms (*Cydia piperana*), and parasitic wasps or chalcids (*Megastigmus albifrons*) (Keefover-Ring and Linhart, 2010). These insects are only found on the *P. ponderosa* trees from the Colorado Front Range and display a tendency to limit their movements to only one or a few nearby trees (Bodenham and Stevens, 1981).

Major root diseases of *P. ponderosa* include *Armillaria ostoyae*, *Heterobasidion annosum*, and *Leptographium wageneri* var. *ponderosum*, which cause stunting to loss of growth, breakage or windthrow, and mortality. These root diseases are spread by contact with roots, aerial spores, or insect vectors, depending on the species of the root disease fungus. The trunk partially decays, mainly due to infection by *Phellinus pini*, *Fomitopsis officinalis*, and *Phaeolus schweinitzii*, but the post-decay is slowed by the highly resinous nature of the wood (Filip, 2001, 2005). The trunk disease is caused by *Endocronartium harknessii*, *Cronartium comandrae*, *Cronartium coleosporioides*, and *Cronartium ribicola*, which cause reduced tree growth and even death. Seedlings, young plants, and mature trees can also be affected (Allen, 1996; Filip, 2005).

Pine tree diseases are caused by *Mycosphaerella pini*, *Lophodermella concolor*, *Lophodermella morbida*, and

Lophodermium pinastri. These fungi regularly cause needle discoloration at 2–3 years old when environmental conditions are favorable for infection development. Recently, *P. ponderosa* has suffered from dieback caused by the microscopic fungus *Sphaeropsis sapinea* (Filip, 2005). Quail, squirrels, and many other wildlife species consume the seeds of *P. ponderosa* (Little, 1979). Introduced to New Zealand in 1865, *P. ponderosa* is considered an invasive tree species because of its negative impact on native communities (Burdon et al., 1991).

In general, the introduction of non-native species carries risks that may lead to their rapid spread and the displacement of native species from their natural ecosystems. Ponderosa pine does not have the status of an invasive species in most of the world, with the exception of some regions in the Southern Hemisphere, such as New Zealand (McAlpine and Howell, 2024; Mathias et al., 2023). The same phenomenon of treating ponderosa pine as an invasive species also occurs in Argentina, Australia, and Chile (Richardson and Rejmánek, 2004; Iglesias et al., 2022). In northwestern Patagonia, *P. ponderosa* has demonstrated invasive tendencies, with natural regeneration expanding beyond plantation borders at an average rate of up to 10 m per year, especially under disturbed conditions. Although factors such as dense ground vegetation, poor soils, and lack of mycorrhizal associations can hinder its spread, its potential to establish and persist in novel habitats has been clearly documented (Dezzotti et al., 2009). So far, no such evidence of spontaneous invasive spread has been reported from European countries.

10 Adaptation to climate change

The ability of *P. ponderosa* to adapt to different climatic conditions is the subject of anxiety and uncertainty, as well as prospects and expectations. In its natural range in the Southwestern United States, threatening climatic conditions can trigger damage to populations (Kolb et al., 2019; Davis et al., 2019). Foresters are particularly concerned about reduced growth rates due to warmer temperatures and decreased water availability, which can hinder tree growth and increase susceptibility to pests and diseases. Weakened trees are more vulnerable to insect and pathogen attacks. Climate change can also alter fire regimes—and changes in fire patterns disrupt the natural regeneration cycle of *P. ponderosa*. These situations raise the question about range shifts. As conditions become less suitable, *P. ponderosa* populations may migrate to higher elevations or latitudes. To mitigate these impacts, scientists and forest managers are investigating strategies such as assisted migration and drought-resistant genotypes (Dixit et al., 2020) including the increased adaptation to extreme environmental conditions by testing the survival or growth of seedlings with different phenotypes, which was conducted in Arizona (Dixit et al., 2021), but has not yet been evaluated under European conditions.

Pinus ponderosa is significantly more sensitive to changes in precipitation than temperature, making it challenging to predict its response to climate change, given the uncertainty surrounding future precipitation patterns (Kusnierczyk and Ettl, 2002). In regions such as central and southern Europe, where projected climate change is expected to involve greater increases in temperature than shifts in precipitation, this species may represent a suitable candidate due to its relative tolerance to rising temperatures (Carvalho et al., 2021; Ghazi et al., 2023). One of the options for adapting to climate change can be silvicultural practices (Vacek et al., 2023). From a management perspective, *P. ponderosa* trees in low-density plantations can withstand severe drought without substantial impact on their water relations, particularly in larger trees. In contrast, trees in high-density stands experience more pronounced drought effects on water relations, stem growth, and leaf area, likely resulting in lower growth resilience and prolonged drought impacts (Gyenge et al., 2012).

In contrast, in its non-native range of distribution, there are hopes for *P. ponderosa* to support or partially substitute local declining populations of native species, e.g., Norway spruce or Scots pine in Central Europe (Toth et al., 2020; Netherer et al., 2024), which originally had a temperate climate, but is now affected by climate change. In a wider introduction, it may be possible to rely in part on the research results reviewed so far. However, research on *P. ponderosa* from Europe is scarce. Podrázský et al. (2020) evaluated and confirmed the high production potential and growth stability of *P. ponderosa* compared to other tree species, including introduced ones. Similar observations were made by Insinna et al. (2006), who confirmed 60% higher productivity of *P. ponderosa* in comparison with Scots pine in dry growing conditions. High production is associated with biomass production and carbon sequestration, which plays an essential role in mitigating ongoing global climate change (Insinna et al., 2006; Berndes et al., 2016; Vacek et al., 2023). More recent tree-ring studies (Kerhoulas et al., 2017; McCullough et al., 2017; Fuchs et al., 2019; Fletcher et al., 2019; Arco Molina et al., 2024) indicate a decrease in radial growth due to ongoing climate change, but at the same time, they also show the adaptive capacity of *P. ponderosa* to cope with a drier climate. Based on the current knowledge, *P. ponderosa* looks promising in Central Europe, especially from the point of production value and, possibly, higher tolerance to climate extremes, particularly higher temperatures. The tolerance is determined by the adaptation to the climatic conditions in its original homeland, including the southern parts of North America.

When considering assisted migration and climate change adaptation, it is crucial to carefully evaluate and understand the ecological risks associated with species introductions (Probert et al., 2020). This includes assessing potential invasiveness, impacts on native biodiversity, and long-term ecosystem effects. Effective management involves ongoing monitoring and risk mitigation strategies to prevent unintended negative consequences (Meyerson and Mooney, 2007; Simberloff et al., 2013). A precautionary approach is necessary to balance the benefits of assisted migration with the protection of native ecosystems (Vitt et al., 2010).

Despite its potential, the limited research has focused primarily on incorporating *P. ponderosa* into mixtures of native species in newly planted forest stands. As described earlier, mixed forest stands are more resilient to climatic extremes, e.g., when precipitation and temperature have a greater effect on the growth of monospecific rather than mixed stands (Vacek et al., 2021b). There is a considerable scientific gap that needs to be addressed in future research on all introduced tree species, including *P. ponderosa*. The favorable production parameters, resistance, and ecology of *P. ponderosa* should provide new motivation for further verification of the production characteristics and other factors of existing stands, and particularly the motivation to establish new research-based forest stands with varying degrees of the admixture of this introduced tree species among native ones.

11 Conclusion

Native to North America, *P. ponderosa* exhibits a robust potential for cultivation in various climatic conditions throughout Europe due to its high adaptability. Previously published studies have shown that its ability to thrive in stressful environments, including extreme climate conditions, such as drought and poor soil stands, makes it a promising species in the context of ongoing climate change. Its resilience to drought periods and capacity to grow in diverse soil types suggest that it could be a suitable option for European reforestation projects, particularly in areas threatened by desertification or for forest reclamation. Low-density stands should be preferred in areas prone to severe drought, as this promotes growth resistance and stability of water conditions compared to high-density stands. However, *P. ponderosa* cultivation should be supplemented by a careful evaluation of its ecological impacts, including potential effects on native ecosystems, where we see limitations in studies already conducted, which focused on wood production characteristics. Monitoring its growth and adaptability under different conditions while assessing the risk of invasive behavior will be crucial. The potential for commercial forestry use of *P. ponderosa* in Europe is significant, especially given its high-quality timber, relatively fast growth, and positive effect on soil conditions. However, there have been no previous studies on silvicultural recommendations for mixtures with native tree species, highlighting another critical scientific gap. Therefore, the suitability of the species and its provenance for specific European regions requires further investigation, and more research is needed on its long-term impact on local biodiversity. If properly managed and implemented, ponderosa pine could contribute positively to commercial forestry and forest restoration efforts.

Author contributions

KT: Data curation, Formal analysis, Methodology, Writing – original draft. ZV: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. JCu: Conceptualization, Supervision, Validation, Writing – review & editing. SV: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. VB: Writing – original draft. AZ: Writing – original draft. VT: Validation, Writing – original draft. JG: Writing – original draft. JČe: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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