Journal of Forest Science, 68, 2022 (9): 329–343 *Review*

https://doi.org/10.17221/101/2022-JFS

Pinus contorta Douglas ex Loudon and climate change: A literature review of opportunities, challenges, and risks in European forests

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Citation: Vacek S., Vacek Z., Cukor J., Podrázský V., Gallo J. (2022): *Pinus contorta* Douglas ex Loudon and climate change: A literature review of opportunities, challenges, and risks in European forests. J. For. Sci., 68: 329–343.

Abstract: Lodgepole pine (*Pinus contorta* Douglas ex Loudon) was distributed from its natural range in western North America to different destinations, primarily to Europe (Scandinavia, British Islands), South America (Chile, Argentina), and New Zealand. It is used for its superior timber production and resistance to environmental conditions. This literature review paper consists of 150 references and presents a summary of research results dealing with the lodgepole pine potential in general with a specific focus on Europe from 1910 to 2022. It summarizes the importance, taxonomy, biological and ecological characteristics, site requirements, production and silviculture, risks and pests, as well as the potential of this tree species for forestry and the wood industry in relation to global climate change. *Pinus contorta* also has a considerable potential in Central Europe, especially at extreme sites with strong anthropogenic impact and in polluted regions. This tree species is very resistant to climatic factors and extreme events compared to other coniferous tree species. Moreover, its annual increment reached from 3 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ on reclamation sites to 18 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ in favourable environmental conditions. On the other hand, caution must be taken for possible invasive behaviour outside its natural range. Its importance can increase with ongoing climate change and the decline of native tree species.

Keywords: distribution area; lodgepole pine; silviculture; threats; timber production

Lodgepole pine (*Pinus contorta* Douglas ex Loudon) is a fast-growing conifer tree species native to western North America (Farjon, Filer 2013). It has a very broad ecological valence and is planted extensively in North and South America, Europe, and New Zealand due to its considerable silvicultural timber production value and for erosion control on forest lands (Svoboda 1976; Ledgard 2001; Richardson, Rejmánek 2004; Sullivan et al. 2020). Because of its climate and air-pollution resistance and pioneer character, it is often used in the reforestation of air-polluted areas and in the reforesta-

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Supported by the Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, and the Ministry of Agriculture of the Czech Republic (No. QK22020045).

tion of reclamation areas after coal mining, etc. (Kaňák 1988, 1999; Kuznetsova et al. 2009; Novotný et al. 2018; Vacek et al. 2021). Because of its hardiness, flexibility, and low maintenance, *Pinus contorta* is also very suitable for urban ornamental plantings (Poleno 1985).

Even outside its natural range, *Pinus contorta* is a significant forest species, especially in Europe in extreme environments (Kaňák 1988, 1999; Čáp et al. 2018). In Central Europe, only the best provenances of *Pinus contorta* can match the local Scots pine (*Pinus sylvestris* L.) in growth, both in acidic habitats and on nutrient-poor sands (Fulín et al. 2017) as well as in beech-oak stands (Kantor 1980). In Northern Europe, *Pinus contorta* was widely planted because it showed faster growth and higher yield compared to native Scots pine (Karlman 1981).

In recent years, Scots pine stands in Europe have been growth declining and dying as a result of climate change and more frequent droughts (Rebetez, Dobbertin 2004; Vacek et al. 2016; Buras et al. 2018). The stands are additionally being attacked by fungal pathogens such as *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton or *Cenangium ferruginosum* Fr. (Zahradník 2014). Therefore, various pine species are being considered that could replace Scots pine stands under conditions of advancing global climate change. Prospective tree species, especially in more extreme habitats, include *Pinus contorta* (Fulín et al. 2017; Novotný et al. 2017). It is particularly remarkable in forestry use due to its resistance to abiotic and biotic factors (drought, to name one) and also for its pioneer nature in colonizing anthropogenically disrupted areas (Dimitrovský 2000). The resistance of some *Pinus contorta* populations to air pollution is the result of long-term evolutionary adaptation (Begon et al. 1990) in their natural ranges where volcanic activity had been abundant (Lotan et al. 1985; Lotan, Critchfield 1990; Kaňák 2001; Sullivan et al. 2020).

This literature review of 150 references aims to assess the opportunities, challenges, and risks of *Pinus contorta* stands in European forests with a focus on ongoing climate change in the time period 1910–2022. Our specific objectives were to consider (*i*) the taxonomy and description of *Pinus contorta*; (*ii*) its range of distribution; (*iii*) habitat and ecological requirements; (*iv*) silviculture and production; (*v*) the value and use of timber; and (*vi*) threats, predators and risks of this tree species.

TAXONOMY

Lodgepole pine (*Pinus contorta* Douglas ex Loudon) is divided into three varieties (Farjon 2017; Auders, Spicer 2012; Eckenwalder 2013), while according to other authors (Businský 2008; Businský, Velebil 2011), they fall into three subspecies with allopatric occurrence: shore pine (*Pinus contorta* subsp. *contorta* Douglas ex Loudon), lodgepole or doghair pine [*Pinus contorta* subsp. *latifolia* (Engelm.) Critchf.], Sierra lodgepole pine [*Pinus contorta* subsp. *murrayana* (Grev. & Balf.) Engelm.]. Some authors (Bartolome 1983; Wheeler, Critchfield 1985; Klinka 2002; Preston, Braham 2002) also distinguish a separate variety of Bolander beach pine [*Pinus contorta* var. *bolanderi* (Parl.) Critchfield], which is not accepted in more recent monographs and is considered part of the complex *Pinus contorta* subsp. *contorta* (Farjon, Filer 2013). Lodgepole pine and Banksian pine (*Pinus banksiana* Lamb.) are morphologically similar and hybridize where their ranges overlap, most notably in western Canada (Critchfield 1980; Krajina et al. 1982).

The morphological differentiation of the subspecies is dispersion-statistical in nature, making a determination in the wild often problematic and unreliable in cultures outside of provenance-defined plantings (Businský, Velebil 2011). The species is difficult to distinguish from the closely related *Pinus banksiana* Lamb., with which it naturally hybridizes in the Rocky Mountains in Canada (Eckenwalder 2013). Crossbreds between *Pinus contorta* and *Pinus banksiana* created in the USA by controlled pollination for plantation production are named *Pinus murraybanksiana* (Farjon 2010). Successful hybridization has also been achieved with *Pinus virginiana* Mill. (Klinka 2002). Auders and Spicer (2012) described a total of 14 cultivars of *Pinus contorta*. These cultivars were described from an ornamental viewpoint in park landscaping by Hieke (1994).

AREA OF DISTRIBUTION

Pinus contorta is native to western North America. *Pinus contorta* subsp. *contorta* grows from southern Alaska along the Pacific coast to northern California, Queen Charlotte, and Vancouver Islands. *Pinus contorta* subsp. *latifolia* has the largest range of the subspecies listed, growing across the Rocky Mountains from the Yukon, British Co-

https://doi.org/10.17221/101/2022-JFS

lumbia, Washington, and Oregon into northern Utah, and from Alberta to Colorado. Additionally, disjunct populations of this subspecies are found in Canada in the Northwest Territories and Saskatchewan, and in the USA in South Dakota. *Pinus contorta* subsp. *murrayana* occurs naturally in Oregon's Cascade Mountains, the Sierra Nevada, and the eastern Siskiyou Mts., while isolated populations are located in the mountains of southern California and Baja California, Mexico. Bolander beach pine (*Pinus contorta* var. *bolanderi*) occurs only in small areas in California (Critchfield 1980; Kartesz, Meacham 1999; Farjon, Filer 2013).

Pinus contorta-dominated forests cover about 6 million ha in the USA and about 20 million ha in Canada. The range of this species is limited to 64° N latitude in the north (Yukon Territory) and approximately 31° S latitude in the south (Baja California) (Klinka 2002).

The vertical distribution of *Pinus contorta* is from sea level to 3 900 m a.s.l. (Little 1979; Lotan, Critchfield 1990). This pine species has been widely planted, primarily for commercial purposes, and its exotic distribution includes Sweden, Iceland, the United Kingdom, Ireland, Russia, Central Europe, the Baltics, New Zealand, Turkey, Argentina, and Chile (Krajina et al. 1982; Watt 1987; Elfving et al. 2001; Ledgard 2001; Peña et al. 2008; Kuznetsova et al. 2009; Fedorkov, Turkin 2010; Juntunen 2010; Langdon et al. 2010; Jansons et al. 2013; Sullivan et al. 2020).

The reproductive capacity of natural populations of *Pinus contorta* is well adapted to climate change, which also explains the ability of this species to thrive well outside its natural range (Lew et al. 2017). From the management point of view, it is important to secure and plant a suitable subspecies or provenance when climate change is expected over the next 50–100 years. On the other hand, climate change may encourage the invasion of *Pinus contorta* into natural forests in suitable environments (e.g. Sweden), where it competes with *Pinus sylvestris* (Sykes 2001).

DESCRIPTION OF THE SPECIES

Pinus contorta trees of straight and evenly tapering shape reach to 41 m tall and 111 cm diameter at breast height (DBH; American Forests 1996). However, the different subspecies of *Pinus contorta* have distinct morphological features (Lotan, Critchfield 1990; Farjon 2010). *Pinus contorta* subsp. *contorta* are short (maximum 10–14 m) trees (sometimes shrubs) with crooked, irregular trunks and umbrella-shaped, branchy crowns. The needles are short and narrow, with many pores. The cones often point backward toward the tree trunk and open after seed ripening. *Pinus contorta* subsp. *latifolia* are tall trees of 15–22 m, sometimes reaching 30–35 m, maximum 48 m. The needles are long and of medium thickness. The cones are hard and heavy, asymmetrical, and remain unopened on the tree (serotinous). *Pinus contorta* subsp. *murrayana* is an alpine species of slower growth. It reaches a height of 20–25 m, occasionally up to 40 m. The needles are broad; the cones are subsessile, backward-pointing, and symmetrical. They open after maturing (Farjon 2010).

These subspecies and varieties differ in tree longevity, size, form and branching, needle size, shape, and structure, cone shape and serotiny, the timing of reproductive events, seed size and germination behaviour, resin composition, and in the presence of parasites and predators (Critchfield 1980; Wheeler, Guries 1982; Lotan, Critchfield 1990). In all subspecies, branches are usually thick, crooked, and relatively short. Evergreen needles occur in bundles of two and are 3–6 cm long (Little, Critchfield 1969). They are usually twisted, stiff, sharply pointed, and dark to yellowish green (Farrar 1995). The bark is relatively thin, usually finely scaled, sometimes longitudinally furrowed, and orangey-brown to grey in colour. The root system is generally shallow, so it is prone to windthrow on exposed sites (Lotan, Critchfield 1990). Ecto- and endomycorrhiza occur on the roots (Minore 1979).

Male and female strobili of *Pinus contorta* are separately on the same tree in this monoecious species (Lotan, Critchfield 1990). Female strobili most often on the apical end of main branches in the upper crown and male strobili occurring on older lateral branches of the lower part of crown (Pilát 1964). Female strobili reddish purple in colour are 10–12 mm long. They develop in whorls of two to five. Male strobili are yellow to yellow-orange in colour and occur in clusters at the base of new shoots and they are 8–14 mm long (Lotan, Critchfield 1990). Male or female dominance can often be found on individual pine trees (Lotan 1990). Cones vary from short and cylindrical to egg-shaped, 3–6 cm long. They are purplish brown in colour, stemless in small clusters, and usually closed on the tree for 10–20 years (Schopmeyer 1974; Satterlund 1975; Critchfield 1980).

Pollen generally matures from mid-May to mid-July according to the given environmental conditions (altitude, climate, stand canopy, etc.). For example, pollen shedding in forest stands in Northwestern Washington (150 m a.s.l.) was observed in May 12, while in Northern Utah (2 190 m a.s.l.) it was July 12 (Lotan, Critchfield 1990). However, it is most often the second and third week of June. The seed strobili mature from August to October and more than a year after pollination. Inland forms and high-altitude forest stands evidently mature earlier than coastal forms or low-altitude forest stands (Lotan, Critchfield 1990). Cone maturity is indicated by a change in colour from purplish green to light brown (Burns, Honkala 1990). Seeds are 3–4 mm in size with a papery wing and are predominately wind-dispersed. Seeds have been recorded at distances ranging from 30 m to 8 km from their source (Ledgard 2001; Langdon et al. 2010).

Pinus contorta is a very prolific seed producer with a short maturation period reaching in less than 10 years. In its natural range, it produces abundant seed crops every 3–4 years (Lotan, Perry 1983). However, good crops can be expected in range from 1- to 3-year intervals with light crops in the intervening years (Lotan, Critchfield 1990). In New Zealand, it produces cones annually, with abundant crops at irregular intervals (Ledgard 2001). In New Zealand and Chile, fertility has been reported in 5-year-old trees (Ledgard 2001; Peña et al. 2008). In Argentina, natural regeneration of *Pinus contorta* first occurs at the tree age of 12 years (Sarasola et al. 2006). Complete seed crop failures occur at an altitude of around 2 800 m a.s.l. (Lotan, Perry 1983). Seed dispersal is usually relatively poor, with seeds typically remaining within 100 m from the parent tree. However, prevailing winds, thermal effects, or snow transport can disperse pine seeds over much longer distances (Lotan, Critchfield 1990). For example, Peña et al. (2008) documents that one pine individual was found 1 200 m from the seed source in Chile.

Ledgard (2001) stated that precipitation substantially influences the quantity of seed production, with high precipitation reducing fertility. Seed germination is usually very good. Teste et al. (2011) reported that over 15 years, seed germination declined from initial 98% at maturity to 50%.

Some *Pinus contorta* cones are serotinous (closed). Serotinous cones are rare in populations of *Pinus contorta* subsp. *murrayana*; most populations of *Pinus contorta* subsp. *contorta* have non-serotinous cones and *Pinus contorta* subsp. *latifolia* and *Pinus contorta* var. *bolanderi* have predominately serotinous cones (Despain 2001). In Oregon, USA, where the non-serotinous cone habitus predominates, seed dispersal ranges from about 35 000 to over 1.2 million per ha (Dahms 1963; CABI 2019).

Most seeds are dispersed by wind after the cones open or break in autumn during warm and windy weather. Germination of *Pinus contorta* is good if climate and seedbed are favourable conditions (Lotan, Critchfield 1990). Seeds have little need for stratification and almost 100% of seeds germinate very quickly at optimal temperature and humidity (Critchfield 1980). Germination is best on bare soil without vegetation cover and with a small layer of raw humus. The survival and planting of seedlings are limited by drought and frost. In mountain areas, the survival of pine seedlings on bare mineral soil is usually very low due to winter frost (Ledgard 2001; Fajardo, Piper 2014). At low light intensity, the potential for natural regeneration of pine is very low while regeneration occurs only in the canopy gaps. Natural regeneration is favoured in open areas, especially after forest fires. The initial rate of height growth is high, reaching more than 50 cm·year^{-1} after the third vegetation season on productive sites. In dense forest stands, *Pinus contorta* has a high capacity for self-reduction, and its spatial requirements for the canopy are low. Light conditions under mature stands with closed canopy are relatively good, reflected in the well-developed ground vegetation. Growth of trees slows down after about 80–120 years and the trees usually live less than 300 years (Klinka et al. 1999; CABI 2019). According to dendrochronological analyses, Huckaby and Moir (1995) reported the oldest tree of 325 years. However, Mason (1915) reported an age of about even 450 years from the Beaverhead National Forest in Montana in the Rocky Mountains.

Pine tree species are better known by their mycorrhizal interactions with several species of fungi (Sen 2001; Kozdrój et al. 2007; Kitagami, Matsuda 2020). They are closely related especially with the fungal genera *Rhizopogon, Suillus, Thelephora,* and *Pisolithus* (Tedersoo et al. 2007; Nuñez et al. 2009). Dickie et al. (2010) studied ectomycorrhizal fungal communities associated with the invasive *Pinus contorta* in New Zealand and found 14 ectomycorrhizal species, of which 93% were non-native ectomycorrhizal species and 7% were cosmopolitan fungal species. The study was conducted in an effort to increase the survival rate of plantings in newly established stands.

HABITAT AND ECOLOGY

Pinus contorta grows under a wide variety of climatic and soil conditions, which allows it to survive in extremely harsh environments (Satterlund 1975; Juntunen 2010). This ubiquitous tree species grows well not only on shallow slopes and in basins but also in a rugged rocky terrain and on steep (moist) slopes and mountains, including exposed gravel. It is more common in habitats of northern and eastern exposure (Musil, Hamerník 2007). Inland, and partly in the Rocky Mountains and northern Yellowstone National Park, USA, it has formed dense, pure stands following the extensive fires of 1988, which preclude the dominance of slower-growing spruce and fir (Anderson, Romme 1991).

Pinus contorta prefers temperate and boreal climates (Krajina 1969). This tree species is relatively resistant to frost damage and often survives in frost-prone areas. The species has an altitudinal habitat tolerance from sea level to 3 900 m a.s.l., and its populations adapt to coastal, continental, and subalpine conditions. The coastal form (var. *bolanderi*) grows mainly between sea level and 610 m a.s.l., while the inland form (subsp. *latifolia*) occurs from 490 m a.s.l. to 3 660 m a.s.l. (Little 1979; Lotan, Critchfield 1990). In the natural range *Pinus contorta* tolerates a very high temperature range. The minimum temperatures in the coldest month range between –57 ˚C and 7 °C and maximum temperatures in the hottest month between 27 °C and 38 °C; mean annual temperatures are in the range of –3 °C and 18 °C. Annual precipitation ranges between 250 mm and 5 000 mm (Lotan, Critchfield 1990).

Pinus contorta thrives in a wide range of topographic situations, both edaphic and geomorphological conditions. It grows well on gentle slopes and in hollows, but productive forest stands can also be found in an uneven and rocky terrain, and on steep slopes and ridges, including bare gravel. It grows on soils that vary widely, including dry and wet soils. However, drought is a major factor in the mortality of *Pinus contorta* seedlings during dry summers. Growth is best where the parent rocks are soils of granite, shale, and coarse-grained lava. Although fertile soils with high nitrogen content support its growth, *Pinus contorta* can also grow on infertile soil types (Despain 2001; Elfving et al. 2001; CABI 2019).

Within the *Pinus contorta* spectrum, we can find populations with a climax character growing in mixtures with other species, as well as very distinct pioneer populations that do not tolerate competition. In other cases, and especially in later successional stages, it is associated with several western conifers. In the coastal North Pacific, it is mixed with *Thuja plicata* D. Don, *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii* subsp. *menziesii* (Mirbel) Franco, *Chamaecyparis lawsoniana* (A. Murray) Parl., and *Sequoia sempervirens* (D. Don) Endl. In the northern part of its range, it also often grows with *Picea glauca* (Moench) Voss along the coast, *Tsuga mertensiana* (Bongard) Carriére, or alternatively, with deciduous trees (*Betula papyrifera* Marshall, *Populus tremula* L.), at higher elevations with *Tsuga mertensiana* (Bong.) Carr., *Picea engelmannii* Parry ex Engelm., *Abies lasiocarpa* (Hook.) Nutt., *Abies magnifica* A. Murr., *Pinus jeffreyi* Grev. & Balf., *Pinus flexilis* James, and *Pinus aristata* Engelm., at mid altitudes in the inland part, it grows along with *Pseudotsuga menziesii* subsp. *glauca* (Mayr) A. E. Murray, *Larix occidentalis* Nutt., *Abies grandis* (Douglas ex D. Don) Lindl., and *Picea pungens* Engelm., and at lower altitudes of the mountains, with *Pinus ponderosa* P. & C. Lawson (Preston, Braham 2002; Musil, Hamerník 2007; Farjon, Filer 2013; Farjon 2017). On drier slopes and plateaus, it often grows with *Pinus monticola* Dougl. ex D. Don and *Abies magnifica* A. Murr. At forest edges, it is accompanied by *Pinus albicaulis* Engelm. and *Pinus balfouriana* Grev. & Balf. (Pilát 1964). Stand diversity increases southward; in California, it is part of mixed coniferous and subalpine coniferous forests and meadows along with many other species. Because soils in these areas are much richer and fires are much less frequent, *Pinus contorta* is not dominant there (Preston, Braham 2002; Farjon, Filer 2013; Farjon 2017). Compared to these tree species, *Pinus contorta* is less competitive (Pfister, Daubenmire 1975; Amman 1977; Alexander 1986).

Fires play a substantial role in the succession of this pine because it becomes a dominant tree species on burned out sites. Some of the cones are serotinous and open only in response to an external stimulus, i.e. increased temperature during fire. Young seedlings do not have to face competition from other understory vegetation on the burned soil and spread rapidly (Agee 1994; Antos, Parish 2002). In areas of frequent fires, it can form so-called inhibited succession, where it dominates due to its ability to regenerate as one of the few dominant tree species (Agee 1994; Antos, Parish 2002).

Because of its invasiveness, *Pinus contorta* is also considered a research model for understanding the invasion process and impacts of pines in forest stands (Rejmánek, Richardson 1996; Richardson, Rejmánek 2004; Simberloff et al. 2010).

SILVICULTURE AND PRODUCTION

Pinus contorta has been purposely planted throughout Europe, South America, and New Zealand (Simberloff et al. 2010), but also, for example, in Iran (Nezhadgholam-Zardroodi et al. 2022). It was introduced into Europe as early as in 1852 (Svoboda 1976). The first plantation records come from Scandinavia, Great Britain, and New Zealand between 1880 and 1920, when several trial plantations were established (Skrøppa et al. 1980; Clements 1910; Muir 1984; Juntunen 2010). Other plantations were established in New Zealand for commercial purposes or erosion control (Richardson 1998). In Northern Europe, *Pinus contorta* was widely planted because it showed a higher yield per ha and faster growth than the native *Pinus sylvestris* (Karlman 1981; CABI 2019).

In stands in its natural range, *Pinus contorta* generally regenerates naturally after clear-cutting, group cutting, and heavy thinning (Alexander 1974; Lotan, Perry 1983; Schmidt, Alexander 1985; Koch 1996; Klinka et al. 1999). Substantially more seedlings are produced in stands when post-harvest residues are burned than when they are scattered across the site (Alexander 1966; Benson 1982). Natural regeneration can be enhanced by the mechanical soil preparation (Perry, Lotan 1977).

The method of harvesting and stand regeneration is determined by management objectives, habitat and stand conditions, susceptibility to diseases and insects, and potential fire occurrence (Alexander 1974; Koch 1996). When thinning on wind-exposed sites, the canopy must be reduced carefully to avoid windthrows, which often occur with severe thinning (Hatch 1967; Alexander 1986; Koch 1996). The susceptibility to windthrow is related to the strength and intensity of tending interventions, soil depth and water influence, stand density and health, and topographic exposure (Alexander 1974).

Stand tending improves growth, production quality, and survival of the remaining trees (Johnstone 1981, 1985; Stuart et al. 1989; Lotan, Critchfield 1990; Murphy et al. 1999). Thinning in the Rocky Mountain pine stands resulted in increased growth of the stand basal area, yet it is important to perform tending interventions early, especially in dense stands (Bella, De Franceschi 1977). Trees exhibiting good growth prior to release have the greatest release potential and should be treated as target trees (Murphy et al. 1999). Soil compaction during harvest and skidding can adversely affect the growth of regenerating pines, resulting in slowed growth and impaired natural regeneration succession (Clayton et al. 1987). After thinning, regenerating forests provide more food for deer and moose due to increased ground vegetation production (Austin, Urness 1982; Urness 1985). Management systems for *Pinus contorta* have been described by Alexander and Edminster (1981), Schmidt and Alexander (1985), Alexander (1986), and Koch (1996). Alternative management options for these stands were described by Benson (1982). Chemical tending interventions in stands were discussed by Johnstone (1985), while Sidhu and Chakravarty (1990) found that these interventions reduced seedling growth and mycorrhizal development. In the context of climate change, tending interventions in *Pinus contorta* play a significant and positive role in tree growth and water consumption in the short term, with more intensive thinning being more effective in mitigating the negative effects of drought in young overstocked forests in terms of water consumption (Wang et al. 2019).

In terms of production, the maximum stand stock in the Rocky Mountains in stands with a density of 1 980 trees$\cdot$ha^{-1} is reported to be 280 m$^3\cdot$ha^{-1} and only 21 m$^3\cdot$ha^{-1} for 4 450 trees$\cdot$ha^{-1}. In the extreme case, in stands of 70 years of age with 247 000 trees$\cdot$ha^{-1}, with an average height of only 1.2 m and $DBH < 2.5$ cm, a typical stand stock reached 168–224 m$^3\cdot$ha^{-1}. Stands reaching 336 m$^3\cdot$ha^{-1} have also been reported (Klinka 2002; Lotan, Critchfield 1990). Data are available from the states of Idaho and Montana on average stand characteristics at 80 years and 140 years of age. In the former case, at a density of 1 030 trees$\cdot$ha^{-1}, the height was 18 m, *DBH* was 20.6 cm, and the stock was 286 m$^3\cdot$ha^{-1}.

In the latter case, at a density of 680 trees·ha^{-1}, an average height of 25.3 m, and DBH of 26.7 cm, the stock was 449 m^3·ha^{-1}. In the Czech Republic, the stand stock of *Pinus contorta* reached 201 m^3·ha^{-1} at the age of 35 years. In this study comparing several pine species, the lower production potential was observed in *Pinus strobus* L. and *Pinus peuce* Griseb. (112–169 m^3·ha^{-1}), while higher production was found in other four pine species with a maximum in *Pinus ponderosa* (430 m^3·ha^{-1}; Podrázský et al. 2020). In 48-year-old stands on coal reclamation sites, a stock of 124 m^3·ha^{-1} was documented, with an average stock of 165 m^3·ha^{-1} for the studied introduced tree species (Vacek et al. 2021).

On plantations in the UK, at ca. 80 years of age, an annual increment was 4–14 m^3·ha^{-1} (Klinka 2002). Average annual production is 6–10 m^3·ha^{-1} (maximum 14 m^3·ha^{-1}·yr^{-1}), while up to 18 m^3·ha^{-1}·yr^{-1} is common in Ireland (Savill 2016). Research from the Czech Republic reported an overall average increment rate of 3–6 m^3·ha^{-1}·yr^{-1} (Podrázský et al. 2020; Vacek et al. 2021). In terms of climate change, cooler regions are experiencing higher increments due to increasing temperatures (McLane et al. 2011).

IMPORTANCE, APPLICATION, AND TIMBER QUALITY

Pinus contorta has a wide range of uses; historically it was used as medicine to treat various diseases or glue, through the construction of log cabins to the production of various posts, fences, but also as firewood (Arno, Ramona 2020). From an economic viewpoint, this pine is an outstanding species in its natural region (Farjon 2017). Especially in western North America, it is a leading production species, providing high-quality timber and having higher volume production than many other species from the same region (Klinka 2002; Farjon 2010; Praciak 2013). Its timber is suitable for the production of construction material (poles, sleepers, etc.) and carpentry (Pilát 1964; Tilki, Ugurlu 2008). Native Americans used to make poles for building their tents (tee-pees) from this pine, hence its American name lodgepole pine (Clements 1910; Mason 1915).

The wood is easy to plane, bend, stain, drill, and carve (Klinka 2002). The sapwood is highly permeable to preservatives, but impregnating the heartwood is more difficult (Klinka 2002; Savill 2016). Unimpregnated wood decays quickly (Pilát 1964). It is used for the production of sawlogs and lower-quality lumber: for building structures, frames, panelling, posts, poles, columns, mine timbers, railroad sleepers, flooring, fences, gates, crates, pallets, furniture, particleboard, plywood, etc. (Lotan, Critchfield 1990; Preston, Braham 2002). Its use in the pulp industry and in the production of composite materials is increasing (Farjon 2010), primarily due to its plantation cultivation (Klinka 2002), which is preferred for its rapid growth at an early age (Lotan, Critchfield 1990).

The wood of this species is soft, light to medium-heavy, with a density of 380–465 kg·m^{-3} (Praciak et al. 2013) or 470 kg·m^{-3} at 15% moisture content (Savill 2016). This species has a good wood texture and thin white to yellowish sapwood that is not distinctly separated from the yellow-brown heartwood (Klinka 2002; Preston, Braham 2002). It has straight wood fibres, low warping during drying, and a relatively homogeneous texture. The wood is similar to that of Scots pine, although it has a higher proportion of heartwood. *Pinus contorta* wood is not resistant to decay in contact with the ground, and decay occurs within less than 1 year (Savill 2016). It is also susceptible to wood-boring insect attacks (Klinka 2002). In addition, this pine is currently the subject of biomass research as a promising type of forest plantation for energy production (Álvarez-Álvarez et al. 2018).

Outside its natural range, *Pinus contorta* is a significant forest species, especially in Europe. In Northern Europe, it is more productive than the native *Pinus sylvestris* (Karlman 1981). In Sweden and Latvia, plantations of *Pinus contorta* were planted primarily for timber production, pulpwood and biomass for biorefineries (Elfving et al. 2001; Backlund, Bergsten 2012; Jansons et al. 2013). In Estonia, plantations have been established for the reclamation of oil shale extraction areas, abandoned agricultural lands, and for reforestation in forest stands (Kuznetzova et al. 2009). In New Zealand, Chile, and Denmark, *Pinus contorta* is used for soil protection and dune stabilization to minimize the soil erosion (Brockerhoff, Kay 1998; Peña et al. 2008). Because of its rapid growth and tolerance of poor soils, *Pinus contorta* is often used for reforestation of abandoned and disturbed areas, and for soil improvement (Dimitrovský, Vesecký 1979). In terms of forestry reclamation, it is one of the most beneficial tree species (Dimitrovský 1999, 2000; Vacek et al. 2021).

In the Czech Republic, it was widely used as a replacement tree species during the air pollution disasters in the 1960s to 1980s in the reforestation of vast air pollution openings in the Orlické hory Mts., Jizerské hory Mts. and Krušné hory Mts.(Vacek et al. 2003, 2021; Slodičák et al. 2005; Balcar et al. 2015; Čáp et al. 2018). It is also employed as an ornamental tree species in urban environments, especially in parks (Poleno 1985). In Iceland, it is used for Christmas trees (Juntunen 2010).

RISKS, PREDATORS AND DISEASES

Pine tree species show similar invasion processes all over the world involving two stages: (1) immigration and establishment, and (2) population expansion (Richardson et al. 1994). Several invasive impacts have been reported also for *Pinus contorta*, including effects on ecosystem processes and ecosystem services, such as reduced stream flow and modification of the nutrient cycle (van Wilgen et al. 2002; Simberloff et al. 2010). *Pinus contorta* has negative invasive effects on open forest stands in Chile (Peña et al. 2008; Langdon et al. 2010; Urrutia et al. 2013; Cóbar-Carranza et al. 2014). In this country, the invasion of *Pinus contorta* negatively affects the native low-density of Antarctic beech [*Nothofagus antarctica* (Forster) Oerst.] and Chilean pine [*Araucaria araucana* (Molina) K. Koch] protected forests (Urrutia et al. 2013; Cóbar-Carranza et al. 2014). These negative impacts include changes in vegetation structure through the addition of new structural elements to forest ecosystems, an increase in vegetation biomass, changes in distribution, and an increase in vegetation flammability (Cóbar-Carranza et al. 2014; CABI 2019).

Pinus contorta, in addition to the structural parameters of the stands, also affects native herbs and shrubs, reducing their richness, abundance, and diversity (Urrutia et al. 2013). Similar results in vegetation biodiversity have been found in New Zealand, where the species richness of grasses, herbs, shrubs, trees, ferns, mosses, and lichens in the *Pinus contorta* invaded areas has declined from 26 to 7 species over 30 years of invasion, including the loss of all native species (Ledgard, Paul 2008).

In New Zealand, Chile, and Argentina, *Pinus contorta* is considered an invasive species (Simberloff et al. 2010). In New Zealand, its natural regeneration has caused it to spread over large areas, leading the government to declare it a noxious weed (Ledgard 2001). Therefore, a major effort has been made to eradicate *Pinus contorta* in New Zealand and to prevent its spread, as well as to raise social awareness of the problem (Ledgard 2001; Gous et al. 2014). Other precautionary strategies include removing the existing and potential sources of spread, not planting *Pinus contorta*, and in particular, encouraging the growth of surrounding vegetation and sheep grazing (Ledgard 2001). Brockerhoff and Kay (1998) suggested the use of biological control in New Zealand using a species of insect that feeds on *Pinus contorta* cones. Based on host species, structural specificity, and their effect on seed production, *Conophthorus ponderosae* (*Scolytidae*), *Eucosma rescissoriana* (*Tortricidae*), and *Pissodes validirostris* (*Curculionidae*) are the most promising candidates for biological control (CABI 2019).

Physical elimination of *Pinus contorta* is the primary control measure in Australia, sometimes accompanied by the application of arboricides. In the state of New South Wales, the complete removal of not only *Pinus contorta* plantations, but also other pine tree species (*Pinus nigra* and *Pinus ponderosa*) was considered necessary to reduce seed sources of potential invasions (Richardson et al. 1994).

In terms of predators, squirrels are the most important seed eliminators (Lottan, Perry 1983). In North America, the most notable predator of *Pinus contorta* seeds is the American red squirrel (*Tamiasciurus hudsonicus*). Estimates of consumption rates range from 20% to 80% of annual production (Despain 2001). The Douglas squirrel (*Tamiasciurus douglasii*) is common in North America, where non-serotinous trees predominate, while *Tamiasciurus hudsonicus* occurs where serotinous trees predominate (Lotan, Perry 1983). Other predators also include rodents such as *Peromyscus*, *Microtus*, *Clethrionomys*, and *Eutamais*, they gather the dispersed seeds and cache some for future consumption. Small mammals with density higher than 5 animals·ha^{-1} are able to harvest more than 85% of the *Pinus contorta* seeds for 3 weeks (Sullivan, Sullivan 1982). Also cone-eating insects can pose a threat to *Pinus contorta*. Three insect species (*Diorvetria abietella, Eucosma recissoriana*, and *Laspeyresia* sp.) attack cones, but the seed yield does not appear to be significantly reduced by these insects (Lotan, Perry 1983; Despain 2001). Finally, birds also scavenge dispersed seeds from the forest floor (Eastman 1960). For comparison, 54% of study sites were predated by mice (maximum seed loss 100%) and 15% by birds (maximum seed loss 50%) in New Zealand (Ledgard 2001).

Dense stands of *Pinus contorta* are also susceptible to insect damage (Spellenberg et al. 2014). The most common pest is *Dendroctonus ponderosae* Hopkins, which attacks pines in July and August and spreads the fungus *Grosmannia clavigera* (Rob.-Jeffr. & R.W. Davidson) Zipfel, Z.W. de Beer & M. J. Wingf. For example, over 18 million ha of *Pinus contorta* forest stands were affected by a mountain pine beetle outbreak in western Canada (Bockstette et al. 2021). Pine beauty moth (*Panolis flammea* Denis & Schüffermiller) is another pest and a considerable defoliator in Northern Britain (Klinka 2002). European pine sawfly (*Neodiprion sertifer* Geoffroy in Fourcroy), bordered white (*Bupalus piniarius* Linnaeus), and common pine shoot beetle (*Tomicus piniperda* Linnaeus) also cause serious damage in Britain (Savill 2016). In America, the parasitic *Pinus contorta* dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) is also a significant pest, infecting up to 50% of stands in some areas.

In areas of its introduction, mortality of *Pinus contorta* has been reported in plantations by biotic pests, especially voles, and parasitic fungi, some of which also occur in its natural range. Of the parasitic fungi, snow mould (*Phacidium infestans*), *Scleroderris canker*, and *Gremmeniella abietina* are the most common in Scandinavia (Hansson, Karlman 1997; Karlman 2001). In the areas affected by the air pollution stress of the Jizerské hory Mts. and the Krkonoše Mts. in the Czech Republic, forest stands are often decimated by the browsing and bark stripping of deer game and subsequently destroyed by the attack of the honey fungus [*Armillaria mellea* (Vahl) P.Kumm.] (Vacek et al. 2012). In Scotland, *Pinus contorta* plantations have been affected by the pine beauty moth (*Panolis flammea*) (Watt, Hicks 2000). In Sweden, vertebrate pests of *Pinus contorta* include voles, moose, and western capercaillie (*Tetrao urogallus*). Voles eat the bark of seedlings and saplings, moose feed on the twigs, shoots, and bark of young trees, and capercaillie mainly on the needles of old trees (Engelmark et al. 2001).

Economic losses caused by biotic and abiotic factors in *Pinus contorta* forest stands are quite high in Europe. For example, in Sweden, these include infections by sweet fern blister rust (*Cronartium comptoniae*) and *Gremmeniella abietina* fungus (Karlman 2001; Stenlid et al. 2011).

Due to its shallow roots, *Pinus contorta* is susceptible to wind disasters (Lotan, Critchfield 1990). Strong winds, heavy snow, and frost can break or bend trees, particularly in excessively dense stands (Praciak et al. 2013). *Pinus contorta* suffers from crown breaks and wet snow much less than Scots pine (Pokorný 1963). On the eastern slopes of the Rocky Mountains in Alberta, it is occasionally damaged by winter desiccation (Bella, Navrátil 1987).

Finally, climate change – in particular heatwaves, long-term droughts, extreme events, secondary pests – are significant threats to forest production and stability (Rößiger et al. 2019; Vacek et al. 2019, 2020; Šimůnek et al. 2020; Hájek et al. 2021; D'Andrea et al. 2022). *Pinus contorta* is susceptible to the synergism of extreme temperatures combined with high precipitation variability or low precipitation during the vegetation season, primarily during May–July (Lo et al. 2010; Vacek et al. 2021). However, *Pinus contorta* is a highly resistant tree species to the influence of climatic factors. Of the 12 conifer species studied, the growth of *Pinus contorta*, along with *Pinus sylvestris*, was least affected by precipitation and temperature and, for example, they achieved lower radial increment variability compared to native tree species (Vacek et al. 2021). Moreover, researches showed that *Pinus contorta* × *Pinus banksiana* hybrids are more drought-resistant than monospecific *Pinus contorta* stands in relation to climate change (Bockstette et al. 2021). In general, the consequences of climate change are negative for *Pinus contorta* stands growing in lowland areas, where warmer temperatures and extreme droughts lead to a decline in growth (McLane et al. 2011). For these reasons, the species such as *Robinia pseudoacacia* (Ábri et al. 2021; Ábri, Rédei 2022), *Paulownia* (Pástor et al. 2022), *Pinus nigra* (Ayan et al. 2021) or *Pinus ponderosa* (Podrázský et al. 2020; Zhang et al. 2020) deserve increased attention in forestry research.

CONCLUSION

Lodgepole pine is a very interesting tree species for forestry use in Central Europe, primarily due to its resistance to biotic and abiotic factors, especially drought, minimum requirements for the soil environment, air quality, and also due to its considerable ability to colonize sites heavily disturbed by anthropogenic activity. This advantage has been reinforced in recent years by the ongoing climate change. Its great potential is also in forestry reclamation, where *Pinus contorta* is a well-adapted introduced species that appropriately performs the production and particularly, the non-production functions of the forest. Similarly, this is the case in areas heavily affected by air pollution and in urban green spaces where conditions are unfavourable for the cultivation of native forest tree species. However, proper tending operations are crucial because appropriate silvicultural interventions can significantly influence the production potential and increase resistance to the negative impacts of climate change.

Acknowledgement: Acknowledgement belongs to Jitka Šišáková, an expert in the field, and Richard Lee Manore, a native speaker, for checking English.

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Received: August 5, 2022
Accepted: September 12, 2022