

REVIEW PAPER

Challenges and risks of Serbian spruce (*Picea omorika* [Pančić] Purk.) in the time of climate change – a literature review

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Abstract

Serbian spruce (*Picea omorika* [Pančić] Purk.) is a Balkan endemic coniferous species, the expansion of which is restricted by limited knowledge. This literature review paper compiles findings from 176 scientific papers and presents a summary of research results that pertain to the Serbian spruce potential in general, with a specific focus on European forests from 1951 to 2022. It summarizes the importance of its taxonomy, biological and ecological characteristics, site demands, production and silviculture, risks and pests, as well as the potential of this tree species in relation to global climate change. Serbian spruce is very resistant to the negative effect of air pollution and extreme heat waves compared to other spruce species, especially the most economically important spruce species in Europe—Norway spruce (*Picea abies* [L.] Karst.). Moreover, its radial growth shows highly balanced annual increments, and the density and technical parameters of the wood are comparable with Norway spruce. On the other hand, the highest weakness may be the limited genetic variability. Despite its rather limited natural range, Serbian spruce can be considered one of the most adaptable spruces to anthropogenic factors and climate change, and a valuable tree species for urban landscapes. Its production potential of wood on acidic, dry and extreme sites makes it attractive for forestry, through its introduction.

Key words: silviculture; ecology; threats; wood production; European forests

Editor: Bohdan Konôpka

1. Introduction

Currently, forest ecosystems are exposed to numerous disturbances due to climate change (Seidl et al. 2017; Jactel et al. 2019; Vacek et al. 2020). Disturbances such as extreme drought, wildfires, invasions by insect pests and fungal pathogens, and increased occurrence of windstorms and floods affect forest function, dynamics, structure, and species composition, including the spread of non-native species (Bolte et al. 2009; Abdullah et al. 2019; Venäläinen et al. 2020). Climate change significantly affects the susceptibility of forests to calamities, but also the intensity, frequency, duration, and timing of the disturbances (Stanturf et al. 2014). In Central Europe, rising air temperatures, coupled with uneven distribution of precipitation, more frequent and longer-lasting droughts are an increasing risk to the growth, ecological stability, and vitality of forest stands during climate change (Brázdil et al. 2009; Kolström et al. 2011; Vacek et al. 2019). The subsequent secondary bark beetle calamity (primarily, *Ips typographus*) and other

biotic pests caused large-scale forest dieback, resulting in loss of ecosystem functions and economic disruption (Šimůnek et al. 2021; Maitah et al. 2022). Meanwhile, introduced tree species can contribute to mitigation and adaptation of forest ecosystems (Gossner et al. 2016; Podrázský et al. 2016; Mondek & Baláš 2019; Remeš et al. 2020; Ayan et al. 2021; Vacek et al. 2022). As a feasible potential replacement for the currently declining Norway spruce (*Picea abies* [L.] Karst.) under conditions of global climate change (Toth et al. 2020; Bosela et al. 2021) one of several options could be Serbian spruce (*Picea omorika* [Panč.] Purk.) overlooked by silvicultural practice so far.

The Serbian botanist Josif Pančić first described the Serbian spruce in 1875 in the Tara Mountains near the village of Zaovine (Fukarek 1956). It was only after comparative studies with similar spruce species (*Picea obovata*, *P. orientalis*, *P. ajanensis*) that this spruce was recognized as a new coniferous species (Pančić 1876; Purkyně 1877). Of the approximately 35 *Picea* species recognized by recent classifications (Schmidt, 1998), only the Serbian and Norway spruce occur naturally in Europe.

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While Norway spruce is widely distributed throughout Europe, Serbian spruce is restricted to a very small area in Western Serbia and Eastern Bosnia and Herzegovina, where it is a Tertiary relict and endemic species (Ballian et al. 2006; Aleksić & Geburek 2014). In general, the spectrum of endemic and relict plant species present in the Northern Balkans and the area of the former Yugoslavia is extremely rich (Šilić 1990). Due to such a small natural range, Serbian spruce has been legally protected in the territory of the former Yugoslavia since 1964 and was included in the IUCN Red List in 1998 (Čolić 1951; Conifer Specialist Group 1998; Aleksić et al. 2017).

Outside of its natural range, Serbian spruce was introduced in the late 19th century (Meyer 1960; Mitchel 1975). It is of great value as an ornamental tree in large gardens and parks, valued especially in Europe and North America, for its attractive columnar crown shape, blue color, and resistance to air pollution (Dallimore & Jackson 1961; Schmidt 1998; Mihaljević & Jelaska 2005). Moreover, it can grow well in a wide range of climatic and soil conditions, including rock promontories and scree slopes, where it naturally forms mixed forests (Wardle 1956; Ballian et al. 2016). Its potential for wood production and carbon sequestration is also not negligible (Vacek et al. 2021). However, its poor natural regeneration, destructive fires, and strong competition from other tree species have severely limited the growth and spread of Serbian spruce in the past (Čolić 1987; Ivetić & Aleksić 2016). However, the question is what global climate change will bring for this unique tree species in the future.

This literature review of 176 references aims to survey the opportunities, challenges, and risks of endemic Serbian spruce stands in European forests with a focus on the ongoing climate change. The specific objectives were to assess (i) the Serbian spruce description and morphol-

ogy, (ii) the species taxonomy, (iii) area of distribution, (iv) habitat and ecology, (v) silviculture and production, (vi) importance and use of wood, and (vii) threats and risks of this tree species.

2. Species description and morphology

The Serbian spruce is a tree with a very slender, conical crown, at most 3.5 m wide, reaching a height of 18–30 m, occasionally up to 50 m, and a diameter at breast height (dbh) of up to 100 cm (Vidaković 1993, Fig. 1). Height growth is relatively rapid, reaching 3–4 m, 5–6 m, 7–8 m, and about 12 m at 10, 15, 20, and 30 years of age, respectively (Pokorný 1981). Other authors report that its height ranges from 1.5–2 m and 8–10 m at the age of 10 and 20 years (Král 2002). The highest growth rate is recorded between 20 and 30 years of age. For comparing, Serbian spruce grows slightly faster than Norway spruce in acidic habitats in Central Europe (Pilát 1964). The same is true in acidic habitats in mountain immission areas in the Czech Republic (Vacek et al. 1994).

Unlike Norway spruce, Serbian spruce does not tolerate complete shading, especially by deciduous trees on nutrient-rich sites. In such habitats, it does not grow and lags—initially, only in diameter, and later, in height growth. In general, it requires a looser canopy cover habitat than Norway spruce. In the Czech Republic (CR), the largest specimen of Serbian spruce at the University Forest Enterprise (Masaryk Forest Křtiny) reached a dbh of 49.3 cm and a height of 30 m at 66 years of age (Král 2002). Vacek et al. (2021) reported an average height of 13.6 m and a dbh of 20.7 cm on a reclaimed spoil heap in the Sokolov region (stand age of 48 years).

The bark is brown and thin and flakes off in sheets. The annual shoots are grey-brown, with dense, fine hair



Fig. 1. Tree habitus, branch with cones, back and face of needle and scales with seed of Serbian spruce (*Picea omorika* [Pančić] Purk.).

(Pokorný 1981). The branches are downward-sloping and short. The terminal branches are slightly ascending, and the buds are reddish brown, without resin (Farjon 2010, 2018). In the stand, the trunks are cleared of branches only up to half the height (Svoboda 1953). Needles are 8–18 mm long, 1.1–1.8 mm wide, flat, dark green on the face, shiny, and without stomata (Radonović et al. 2014, Fig. 1). Two white stripes are distinct on the reverse. The needles are keeled on both sides. They densely girdle the twig on the upper side and are arranged in two rows on the lower side (Vidaković 1991).

Flowering begins at a relatively early age and appears from April to June, depending on the habitat. Both pollen and seeds are dispersed by wind. Pollen is about 75 to 87 μm long and about 52 to 60 μm wide (Jovančević 1962). Although the pollen is smaller than that of Norway spruce, its rate of sedimentation (ca. 5.2 cm s^{-1}) is nearly identical (Eisenhut 1961). Male strobili are ca. 1 cm long, light red, and located at the tips of the lower branches. Female strobili are ca. 3–4 cm long, reddish-purple, confined to the upper branches at the very top of the crown. They usually occur at the end of small twigs or grow directly from the stem within the first 10 m of the crown apex (Jevtić 1960).

Fertility in loose stands begins at 12–15 years of age, and in closed stands, at 40 years (Svoboda 1953). Strong seed years tend to occur at two-year intervals, yet relatively abundant fructification can occur annually (Jevtić 1960). Oscillations in fructification are reported by Čolić (1966) and Gajić (1994), depending primarily on the habitat, age, and coenotic position of the tree within the population. In artificially established single-species stands, Král (2002) reports that co-dominant and dominant trees fructify almost annually. Trees older than 100 years produce 4–8 kg of cones (Gajić 1994).

The cones of this spruce are elongated, ovoid, about 3–6 cm long, 2–5 cones on a twig; young cones are purple in color, and later, they are brown, cinnamon in color, with broad, rounded, finely toothed seed scales at the end. These scales have indistinct longitudinal stripes on the outside. The number of fertile scales per cone is 66–90. The cones ripen in October and November and remain on the tree for two years (Aleksić 2008). The seeds are black-brown, 1.7–3.8 mm long, and winged. The wings are 5–8 mm long and 4–6 mm wide (Jevtić 1960). According to Krstić (1950), the absolute weight of seeds with wings (1,000 seeds) ranges from 1.50 to 4.95 g and without wings from 1.10 to 4.10 g. A cone weighs 1.24–9.21 g, and 1 kg of cones contain an average of 248 cones. One kg of larger cones (5–6 cm) yields 23.6 g of seeds with wings. Pintarić (1970) found very high germination values for seeds immediately after shelling (96%), for seeds up to three years old, the germination rate was 78%, and for seeds after 6.5 years of storage, it was only 4%. Individual reproductive success of Serbian spruce was uneven among tree individuals, with 25% of local adults siring 70% of the sampled juveniles (Aleksić et al. 2022).

Serbian spruce reproduces mainly by generative reproduction, but vegetative reproduction has also been observed (Čolić 1966; Vidaković 1991). Seedlings from natural generative regeneration usually have 5–6 cotyledons of 10–12 mm in length. The growth of Serbian spruce is relatively slow at a young age, with the greatest increment in height between the 20th and 30th year when it matches that of Norway spruce (Úradníček & Chmelář 1995).

Serbian spruce is a self-pollinating and hybridizing species (Kuitinen & Savolainen 1992; Aleksić & Geburek 2014; Ivetić & Aleksić 2016). Other factors influencing the levels and spatial distribution of genetic diversity include the geographical range of the species, as endemic species tend to depauperate (Hamrick & Godt 1996). Novák (1927), Langner (1959), and Stern & Roche (1974) reported that the Serbian spruce is morphologically uniform. Langner (1959), however, found variations in phenology. Geburek & Krusche (1985) found that populations of Serbian spruce were less variable in growth characteristics than Sitka spruce (*Picea sitchensis* [Bong.] Carr.) or their hybrids. However, variability in several morphological traits has been reported, for example in needle thickness and width, volume and number of the intercellular spaces or dimensions of resin ducts (Gajić 1994; Ivetić & Aleksić 2016).

Serbian spruce can hybridize with other species of the genus *Picea*, such as Sitka spruce (Langner 1959; Vidaković 1963; Roulund 1971), white spruce (*Picea glauca* [Moench] Voss) – (Roulund 1971; Mikkola 1972; Nienstaedt 1977; David & Keathley 1996), and black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.) – (Nienstaedt 1977) and can produce interspecific hybrids. Backcrosses of *Picea sitchensis* \times *Picea omorika* with Sitka spruce show better frost resistance and juvenile-stage vigor on poor soils in Denmark (Nielsen & Roulund 1992).

In artificial plantations, genetic diversity may be reduced in newly established stands (Ivetić & Aleksić 2016), but this may not always be the case. Kuitinen et al. (1991) described a good example of an artificially established population of Serbian spruce used as a seed source in Finland, which was established from seeds from a natural population from Bosnia and Herzegovina. The expected heterozygosity, as assessed by allozymes, in the population cultivated for two generations in Finland ($H_e = 0.15$) was similar to that of the natural population ($H_e = 0.13$) in Bosnia and Herzegovina (Kuitinen et al. 1991).

3. Taxonomy

Historically, close fossil relatives of Serbian spruce, *Picea omorikoides* and *P. paleomorika*, were still growing in Central Europe in the Second Interglacial, i.e., in the period called Mindel/Riss (500,000–340,000 years ago); therefore, the Serbian spruce is sometimes considered

a Tertiary relict (Pilát 1964; Vidaković 1991; Ravazzi 2002). The closest living relatives of the Serbian spruce are Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and Brewer spruce (*P. breweriana* S. Watson) in North America, and Japanese bush spruce (*P. maximoviczii* Regel ex Mast.), Meyer spruce (*P. meyeri* Rehder & E. H. Wilson), Korean spruce (*P. koraiensis* Nakai), Koyamae spruce (*P. koyamae* Shiras.), and Siberian spruce (*P. obovata* Ledeb.) in East Asia (Pilát 1964; Vidaković 1991; Aleksić 2008). Schwerin (1929 in Vidaković 1991) described two varieties of *Picea omorika*: the variety *serbica* Schwer., with short branches and a narrow pyramidal crown growing in its native range, and the cultivated variety *P. omorika borealis*, with a broader crown occurring outside the range of its original distribution. Isajev (1987) and Milovanović (2007) described these and four other varieties of *Picea omorika*. Vidaković (1991) considers these varieties, except the *serbica* variety, as horticultural forms or cultivars. The most commonly found is *Picea omorika Pendula*, which is a columnar cultivar with an even narrower habitus than the original *Picea omorika* species, and strictly weeping branches (Hieke 1984, 1994).

4. Area of distribution

Serbian spruce is restricted to a small area along the Drina River on the border of Serbia and Bosnia and Herzegovina, with a total area of only 4 km² (Fukarek 1951a, 1975; Pintarić 1999; Ballian et al. 2006, Fig. 2).

In these both countries, reserves with natural populations of Serbian spruce reaches 31 km² (Ivetić & Aleksić 2016). Aleksić & Geburek (2014) declare that the total natural range of the Serbian spruce in the Central Balkans covers ca. 10,000 km². Most of the autochthonous stands protected by law grow in the Tara National Park, located in the mountain range of the same name in Western Serbia. Isolated populations are also found in the Mileseva River canyon. In contrast to Serbia, entire biotopes of Serbian spruce are protected in Bosnia and Herzegovina (Tošić 1983). Other isolated stands of several hundred individuals grow between Višegrad, Rogatica, and Srebrenica. Further south, there are two isolated populations called Čajniće and Foča (Tošić 1983; Ballian et al. 2006; Mataruga et al. 2011). However, the reduced area of all the original populations is evidently small and probably does not exceed 60 ha (Burschel 1965).

In total, more than 30 natural populations consisting of several hundred to several thousand trees are situated in the core area, and only three populations are located south of this region (Ballian et al. 2006; Ivetić & Aleksić 2016). However, some authors report a much lower number of natural populations and of trees as well (Nasry et al. 2007). On the other hand, Čolić (1966) lists 102 locations with either large populations, clusters of trees, or solitary trees of Serbian spruce. Some of these tree clusters and single trees are thought to represent remnants from previously widely distributed populations, while others are believed to have originated from wind-dispersed seeds of neighboring populations (Čolić 1966; Gajić 1994).

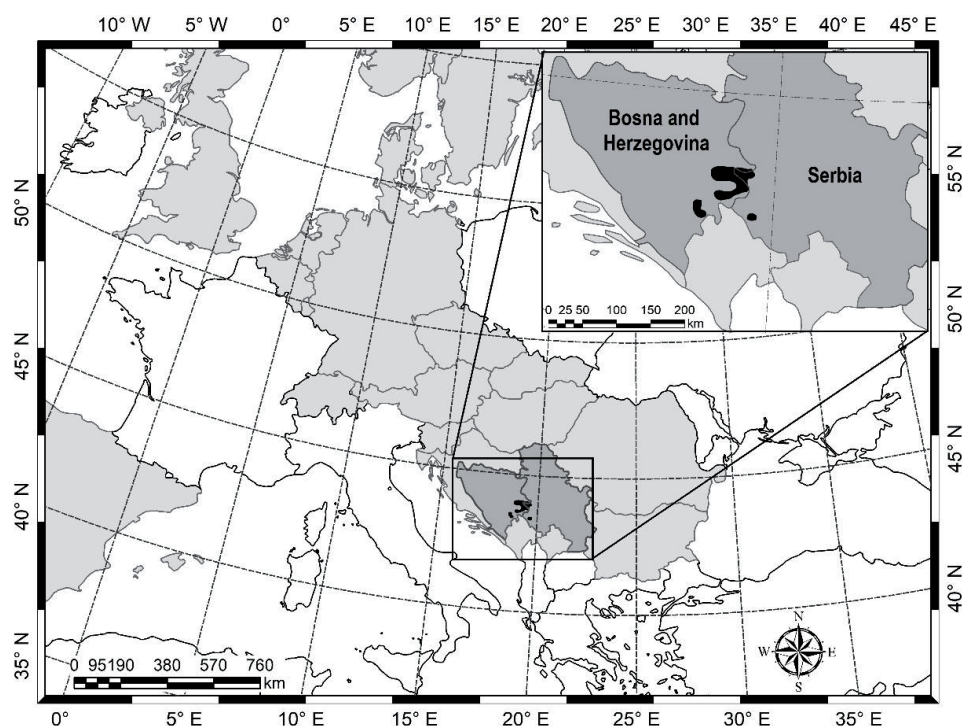


Fig. 2. Area of distribution of Serbian spruce (*Picea omorika* [Pančić] Purk.); light gray color = countries with introduced plantations, dark gray color = countries with native distribution, black color = area of native distribution (made in ArcGIS software, edited according to Ballian et al. 2006; Stevanović et al. 2014).

Paleobotanical records indicate that this endemic species is the result of a general reduction from a wide range of areas covering most of Central Europe during the interstadial period at the beginning of the last glaciation about 100,000 years ago (Ravazzi 2002). The survival of the Serbian spruce in the Dinaric Alps is due to its current genetic structure, which retains ancient imprints (Aleksić 2008; Aleksić & Geburek 2010).

In addition to its initial use as an ornamental tree species in parks, the forestry use of Serbian spruce has a long tradition (Ivetić & Aleksić 2016). Planting outside its natural range began in the late 19th and early 20th centuries in Switzerland (1881–Meyer 1960), Great Britain (1889–Mitchel 1975), Estonia (1890–Kasesalu 2002), Denmark (before 1940–Møller 2013), Finland (1932, second generation plantation–Kuittinen & Savolainen 1992), and the CR (1934–Král 2002). For most of these translocations, the origin of the seedlings is not traceable (Ivetić & Aleksić 2016).

The Serbian spruce is found as an ornamental tree in numerous castle and city parks not only in Europe but also in Asia, North and South America, and Africa (Schmidt 1998). The Serbian spruce is a very popular ornamental tree in Germany, for example, and has been planted in parks much more frequently than other rare species on the IUCN Red List (Schmidt & Tegeler 2014). It is also one of the most frequently introduced tree species in the Netherlands (Buitemveld 2012) as well as in the CR (Svoboda 1953; Pilát 1964; Hieke 1978, 1984, 1994). In the CR, they are found in castle parks such as Dačice, Hluboká nad Vltavou, Chlum u Třeboně, Kamenice nad Lipou, Konopiště, Kopidlno, Kozel, Manětín, Mělník, Sychrov, Slatiňany, Třeboň, Vrchotovy Janovice, in the botanical gardens of Troja and Na Slupi in Prague, in the dendrological garden in Průhonice, and in the Křtiny arboretum (Hieke 1984).

Serbian spruce has been widely introduced into areas with industrial air pollution (Dallimore & Jackson 1967; Vacek et al. 2003, 2021). In the CR, they are especially in the air-polluted areas of the Krušné hory Mountains, Jizerské hory Mts., Krkonoše Mts. and Trutnov area (Vacek et al. 2003; Slodičák et al. 2005, 2008; Dimitrovský et al. 2008; Vacek et al. 2021).

5. Habitat and ecology

The current habitats of the Serbian spruce are mainly found on steep eastern, northern, and western exposures of rocky slopes, predominately on limestone, but also on serpentines (Zmajevački Potok population) and marginally on waterlogged soil (Mitrovac population) at altitudes between 750 and 1,600 m a.s.l. (Pilát 1964; Janoković 1985; Vidaković 1991; Aleksić & Geburek 2014). Despite its shallow roots, it barely tolerates insufficiently aerated peaty soil (Crawford 1989). This behavior is reminiscent of its early Pleistocene ancestors,

growing on peatlands in ancient times and recorded by in situ macrofossils (Bůžek et al. 1985; Ivetić & Aleksić 2016). Typical Serbian spruce habitats are characterized by high humidity, evenly distributed annual precipitation, heavy snow cover, and low winter temperatures (Ostojić 2005). The mesoclimate is typical of mountainous, oceanic regions with cold winters and dry summers with an average annual temperature of 5–7 °C and precipitation of around 1,000 mm (Stefanović et al. 1983, 1995; Janković 1984; Ivetić & Aleksić 2016). Burschel (1965) indicates that this species adapts well to habitat conditions due to its short branches and slender crown.

Serbian spruce is tolerant of cold in relation to its root system (Bigras et al. 2001), early and late frosts (Meyer 1960; Nymoen 1978; Vidaković 1991), air pollution (Dallimore & Jackson 1967; Kasesalu 2002; Vacek et al. 2003), and extremely harsh environmental conditions (Kuittinen et al. 1991). Its tolerance to shading is rather low (Svoboda 1953; Tucić & Stojković 2001; Tusić et al. 2005; Ostojić & Dinić 2012).

Its natural regeneration strongly depends on available, favorable habitat conditions and competition from other ligneous species (Čolić 1957; Ostojić 2005). Recently, it has been regenerating well in Serbia at the Crvene Stene location. Ostojić (2005) states that in dense forests where Serbian spruce is the main stand-forming species, it is advisable to improve its natural regeneration by local removal of its main competitors such as Norway spruce, silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.). In contrast, on sites with loose canopy closure where Serbian spruce is not a major stand-forming species, partial removal of its competitors actually enhanced their natural regeneration rather than that of Serbian spruce.

Burschel (1965) reports that only extreme steep slopes and limestone cliffs are successfully recolonized, as they suffer from competition from deciduous trees on edaphically favorable sites. Stands in which Serbian spruce makes up 50–70% are rare (*Piceetum omoricae* Trenq.). In better habitats, it is being displaced by silver fir and Norway spruce because Serbian spruce is less resistant to shading (Novák 1927; Gajić et al. 1994). Only on steep rocky and windswept sites can it withstand competition from these trees (Fukarek 1951a; Svoboda 1953).

As a pioneer species, Serbian spruce quickly occupies gaps after various calamities such as fires, etc. (Čolić 1966, 1987). However, when mixed with more competitive species such as Norway spruce, it retreats to gullies and other extreme sites less covered by its competitors (Gajić et al. 1994). It forms both pure and mixed stands. It is often dominant in the stand together with Norway spruce and black pine (*Pinus nigra* J. F. Arnold) at higher elevations or with European beech, silver fir, Scots pine (*Pinus sylvestris* L.), European hop-hornbeam (*Ostrya carpinifolia* Scop.), black alder (*Alnus glutinosa* [L.] Gaertn.), and European aspen (*Populus tremula* L.) at lower elevations (Pilát 1964; Vidaković 1991; Jovanović

2000; Ivetić & Aleksić 2016). In mixtures, it is found mainly on poor soils, as it is not very competitive on richer soils (Kralović 1951; Wardle 1956).

6. Silviculture and production

At present, Serbian spruce is cultivated far beyond its natural range, including on non-calcareous soils, podzolic sands, in central taiga, in the mixed forest zone, and in the forest-steppe up to the Volga and the Urals (Vidaković 1983; Farjon 2010; Farjon & Filer 2013; Möller 2013; Farjon 2017). Since its discovery by Pančić in 1872, it has spread everywhere in Europe and has done remarkably well as far as Sweden, Finland, and Moscow (Tucić & Stojković 2001). Sometimes, it can get slightly damaged

by frost at the highest altitudes. It also grows very well on dry soils, where even Scots pine does not thrive (Svoboda 1953). It is, therefore, a coniferous species with minimal habitat requirements, whereas all other conifers fail and become stunted, while Serbian spruce grows vigorously and upright (Svoboda 1953).

The natural regeneration of Serbian spruce is restricted to relatively open habitats (Čolić 1957). After seed dispersal, germination is relatively low, and most seedlings in dense canopies die within the first year (Ostojić & Dinić 2009) due to the species' low tolerance to shading (Tucić & Stojković 2001). Natural regeneration is absent on sites with dense herbaceous cover, while contrarily, it is most successful in habitats where it is mixed with pine, as such sites are characterized by sufficient light at ground level (Ostojić & Dinić 2012).

Table 1. Overview of available publications related to Serbian spruce (*Picea omorika* [Pančić] Purk.) production parameters.

Study	Country	Altitude [m a.s.l.]	Slope [°]	Age [yr]	Diameter [cm]	Height [m]	Basal area [m ² ha ⁻¹]	Volume [m ³ ha ⁻¹]	Density [trees ha ⁻¹]
Ivetić & Aleksić 2016	Bosna and Herzegovina	300		40	22.0	15.0			
Ivetić & Aleksić 2016	Bosna and Herzegovina	650		25	15.0	10.0			
Ivetić & Aleksić 2016	Serbia	1260–1290	5–10	40	16.0	14.9			
Ivetić & Aleksić 2016	Serbia	420–460	5–10	27	12.0	8.0			
Ivetić & Aleksić 2016	Serbia	1050–1080	15–20	40	13.0	11.0			
Ivetić & Aleksić 2016	Serbia	715–720	5	50	17.0	13.0			
Ivetić & Aleksić 2016	Serbia	250	5–10	35	17.0	12.0			
Ivetić & Aleksić 2016	Serbia	13–160	10–15	30	16.0	16.0			
Král 2002	Czechia	330–350	0–5	35	16.7				653
Král 2002	Czechia	330–350	0–5	39	18.0	14.3			645
Král 2002	Czechia	330–350	0–5	49	22.2	17.9			497
Král 2002	Czechia	330–350	0–5	60	29.8	22.0			165
Král 2002	Czechia	330–350	0–5	67	28.9	22.5			408
Krstić et al. 2012	Serbia	990	5–10	51	20.3	18.9			1336
Parzych et al. 2018	Slovakia	220–370	5	51	15.8	84.0			
Petrović et al. 2021	Serbia	1130			29.1	22.2			
Petrović et al. 2021	Serbia	1200			30.0	28.4			
Petrović et al. 2021	Serbia	960			31.0	25.8			
Popović et al. 2021	Bosna and Herzegovina	1330	30–40		26.0	29.2	52.9	649	995
Popović et al. 2021	Bosna and Herzegovina	1300	30–40		24.7	29.0	58.7	716	1225
Popović et al. 2021	Bosna and Herzegovina	1360	30–40		29.9	30.7	57.1	755	810
Popović et al. 2021	Bosna and Herzegovina	1310	30–40		25.4	30.2	65.1	794	1285
Špulák et al. 2019	Czechia	970		20	11.4	6.15			
Vacek et al. 2021	Czechia	430	0–5	48	20.7	13.6	29.9	169	933

Table 2. Production and dendrochronological characteristics of Serbian spruce (*Picea omorika* [Pančić] Purk.) forest stands compared to other tree species in the western part of the Czechia (coal reclamation site; stand age 48 years, altitude 402–444 m; Vacek et al. 2021 and unpublished data).

Species	Diameter [cm]	Height [m]	Stem volume [m ³]	Basal area [m ² ha ⁻¹]	Stand volume [m ³ ha ⁻¹]	MAI [m ³ ha ⁻¹ y ⁻¹]	SDI	NPY	Temperature [°C]	Precipitation [mm]
<i>Picea omorika</i>	20.7	13.6	0.191	29.9	169	3.67	0.51	—	2×	5×
Coniferous tree species										
<i>Larix decidua</i>	14.8	16.1	0.114	31.6	200	4.38	0.81	—	1×	3×
<i>Picea abies</i>	14.3	13.7	0.114	29.3	191	4.17	0.62	2×	5×	7×
<i>Picea mariana</i>	10.4	10.8	0.040	16.8	80	1.74	0.40	2×	4×	6×
<i>Picea pungens</i>	14.5	10.8	0.083	23.9	118	2.56	0.49	2×	7×	6×
<i>Pinus concorta</i>	20.1	13.3	0.200	19.4	124	2.69	0.44	2×	2×	1×
<i>Pinus nigra</i>	15.4	15.1	0.125	41.9	277	6.01	1.04	1×	2×	2×
<i>Pinus ponderosa</i>	15.1	10.6	0.092	35.6	183	3.98	0.90	2×	7×	6×
<i>Pinus rotundata</i>	9.7	10.9	0.027	32.2	117	2.54	0.97	3×	4×	5×
<i>Pinus sylvestris</i>	18.5	17.5	0.221	45.1	364	7.92	1.05	—	1×	4×
<i>Pinus strobus</i>	14.7	10.8	0.091	14.1	71	1.54	0.40	3×	5×	4×
<i>Pseud. menziesii</i>	20.8	16.3	0.275	40.6	343	7.47	0.80	2×	2×	2×
Deciduous tree species										
<i>Acer platanoides</i>	9.2	9.2	0.035	20.7	86	1.86	0.61	6×	5×	6×
<i>Alnus glutinosa</i>	8.9	7.3	0.016	8.2	20	0.44	0.24	6×	5×	3×
<i>Betula pendula</i>	11.7	13.4	0.051	15.8	77	1.67	0.42	4×	6×	2×
<i>Quercus petraea</i>	10.1	8.9	0.037	17.2	64	1.38	0.53	1×	4×	6×
<i>Tilia cordata</i>	10.0	8.5	0.029	22.3	82	1.79	0.62	—	2×	3×

Notes: MAI – mean annual increment, SDI – stand density index, NPY – negative pointer year (year with extremely low radial growth), Temperature – radial growth sensitivity to air temperature and Precipitation – sensitivity to precipitation (both number of significant months from April of previous year to September of current year).

As a pioneer species, it dominates in loose stands, where—during succession—it can be suppressed later by shade-tolerant species (Ivetić & Aleksić 2016).

Another possibility for the conservation or spread of this species in suitable habitats is artificial cultivation with planting material of suitable provenance (Ivetić & Aleksić 2016). Serbian spruce should be planted in groups to replicate the natural appearance of these stands (Ostojić & Dinić 2009). In hard-to-reach places, an alternative to planting may be sowing seeds. In recent years, seeding has been recommended as an appropriate strategy for reintroducing endangered species (Laborde & Corrales-Ferrayola 2012; Atondo-Bueno et al. 2016), either by seeding in open habitats or as a complement to sparse planting in secondary forests.

The success of establishing a forest by directly planting depends on the ability of the population to adapt to the new environment (Ivetić et al. 2016). Intentional relocation of genotypes must meet certain prerequisites and is defined by several factors (Dumroese et al. 2015). The actual movement of Serbian spruce reproductive material for planting can be characterized as a transfer regardless of geographical scales (Koskela et al. 2014). Seed orchards (Tucović & Isajev 1988) are used to ensure a sufficient amount of reproductive material, providing a continuous supply of seeds of controlled origin for planting stands (Ivetić & Aleksić 2016).

Artificially established stands have to be intentionally tended to maintain a looser canopy (Svoboda 1952; Král 2002). In particular, selective removal of individual trees is recommended in stands with a dense canopy to reduce the main competitors of Serbian spruce (Ostojić & Dinić 2012; Aleksić & Geburek 2014; Popović et al. 2021). At the same time, Fukarek (1956) states that felling trees near Serbian spruce trees may disturb the ecological conditions of the site. However, removing individual trees of competing species can be beneficial even in older stands, as they can create gaps with favorable light conditions, which enhance the start of natural regeneration of Serbian spruce (Ivetić & Aleksić 2016).

Silvicultural practices in Serbian spruce stands are similar to those of Norway spruce, except that a slightly looser canopy must be maintained for successful growth, as it does not tolerate shading. It grows to about the same height as the Norway spruce, but the diameter growth is weaker (Svoboda 1953).

In terms of production potential, overview of available publications related to Serbian spruce in European countries are showed in Table 1. Generally, acidic and dry habitats are the most suitable for Serbian spruce, where it is usually more productive than the native Norway spruce (Svoboda 1953). The results obtained at the Masaryk Forest Křtiny (CR) show that within the largest groups of forest habitat types, 3H (*Querceto-Fagetum illimerosum trophicum*), 4A (*Tilieta-Fagetum acerosum lapidosum*), and 4K (*Fagetum acidophilum*), the fastest growing is the Serbian spruce growing on 4K—per the Czech forest

ecosystem classification (Viewegh et al. 2003). On 4K, the growth rate of Serbian spruce is equal to the yieldable values of Norway spruce. On dry sites (4A), Serbian spruce can outgrow and replace most of the native tree species, including Norway spruce (Král 2002).

The maximum documented stand volume of Serbian spruce forests reaches $794 \text{ m}^3 \text{ ha}^{-1}$ in Bosna and Herzegovina (Popović et al. 2021). Král (2002) reports the largest tree volume at 66 years of age— 2.26 m^3 in South Moravia. On coal reclamation sites in western Bohemia, Serbian spruce averaged 0.19 m^3 and a stand volume of $169 \text{ m}^3 \text{ ha}^{-1}$ at age 48 (Table 2). In comparison, Norway spruce reached similar production parameters (0.11 m^3 , $191 \text{ m}^3 \text{ ha}^{-1}$). The highest production potential of the introduced tree species was shown by Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco— 0.28 m^3 , $343 \text{ m}^3 \text{ ha}^{-1}$), while the bog pine (*Pinus rotundata* Link— 0.03 m^3 , $113 \text{ m}^3 \text{ ha}^{-1}$) and white pine (*Pinus strobus* L.— 0.09 m^3 , $75 \text{ m}^3 \text{ ha}^{-1}$) were the least suitable for production. At the same age, the Serbian spruce stands achieved an average carbon sequestration of 68.5 t ha^{-1} with a total biomass of 131 t ha^{-1} (Vacek et al. 2021). However, the volume yield of Serbian spruce can often be reduced due to an open canopy (Holubčík 1968).

7. Importance and application of wood

Wood density of Serbian spruce is similar to Norway spruce (Kommert 1990). It is characterized by small and densely packed tracheids, while compression wood is found typically in heavy form (Timell 1986; Nedzved et al. 2018). Moreover, this tree species can resist mechanical stress well. Serbian spruce trees subjected to static bending show a strong response of the wood to static bending and compression (Mitrović et al. 2015; Nedzved et al. 2018). Wood is also characterized by very low amount of volumetric shrinkage compared to other tree species (Farsi & Kiaei 2014). Serbian spruce wood is highly valued because of its good quality and technical parameters. As a building material, it is generally used for roof structures or, in the past, for cheese ripening vessels (Krüssmann 1985; Vidakovic 1993). Steady annual radial growth is also substantial for the quality of the wood. Vacek et al. (2021) reported that Serbian spruce achieved the steadiest diameter increment of all 12 coniferous species studied. Mean wood density reaches $508\text{--}534 \text{ kg ha}^{-1}$ with the proportion of late wood about 15.2% (Petrović et al. 2021). Compared to other tree species, wood density of Serbian spruce is higher than Norway spruce or silver fir and comparable to pine tree species (Table 3). In its native range the timber from this tree species is used for pulping in the paper industry and as construction material (Ramsay & Macdonald 2013).

Table 3. Wood density (standard moisture content – 12%) of Serbian spruce (*Picea omorika* [Pančić] Purk.) compared to other tree species.

Tree species	Wood density [kg m ⁻³]	Study
<i>Picea omorika</i>	508–534	Petrović et al. 2021
Coniferous tree species		
<i>Abies alba</i>	310–450	Hoadley 1990; Mihai & Mirancea 2016; Mihai et al. 2021
<i>Larix decidua</i>	511–583	Cukor et al. 2020; Zeidler et al. 2022
<i>Picea abies</i>	341–463	Zeidler et al. 2017; Cukor et al. 2020; Zeidler et al. 2022
<i>Pinus nigra</i>	531–643	Oliva et al. 2006; Zeidler 2007
<i>Pinus sylvestris</i>	488–541	Schönfelder et al. 2017; Zeidler et al. 2017
<i>Pseud. menziesii</i>	488–568	Remes & Zeidler 2014; Zeidler et al. 2017
Deciduous tree species		
<i>Alnus glutinosa</i>	391–540	Claessens et al. 2010; Kiaei 2013
<i>Betula pendula</i>	623–650	Borůvka et al. 2018; Dobrowolska et al. 2020
<i>Fagus sylvatica</i>	653–807	Borůvka et al. 2018; Gryc et al. 2008a, b; Piętko et al. 2019
<i>Quercus robur</i>	538–748	Humar et al. 2008; Zeidler & Borůvka 2016; Alfaro-Sánchez et al. 2020
<i>Tilia cordata</i>	374–480	Hoadley 1990; Čihák et al. 2014

Its aesthetic qualities and tolerance to urban and air-pollution environments, insect pests, and climate change are highly valued (Dallimore & Jackson 1961; Vacek et al. 2003, 2021). Compared with Norway spruce, Serbian spruce reached greater resistance to snow, ice, frost, and bark scaling by deer (Meyer 1960). This is why it is used more than other conifers in cities with high levels of pollution. It is also a suitable tree species for afforestation of degraded and reclaimed areas, such as coal mine disposal sites (Vacek et al. 2021). The Serbian spruce deserves a more prominent place in commercial and residential landscapes (Poleno 1985). It can be used in group plantings, as a solitary tree, or even as an evergreen street tree, either in pure or in mixed populations in some very successful combinations with other species (Vujkovic et al. 1993). Its narrow habitus and blueish color make it a distinguished urban landscape tree. It is a satisfactory alternative to the widespread Norway spruce and blue spruce (*Picea pungens* Engelm.). There are currently several cultivars of Serbian spruce produced in ornamental-plant nurseries (Krüssmann 1972, 1985). Serbian spruce is one of the most commonly cultivated spruce species in European parks and gardens (Schmidt 1998; Pushka 2022), and the large extent of cultivation and its ecological amplitude reflects the ability of this species to adapt to different habitat conditions. Serbian spruce is also often used as a Christmas trees (Duck et al. 2003, 2004).

8. Threats, diseases, and pests

The current decline in the population of Serbian spruce is related to its low ability to compete with other forest species (Mataruga et al. 2011). The small range of this endemic spruce is composed of isolated populations, and their abundance and fertility affect the genetic structure, which is specific to each population due to genetic shifts

(Geburek 1986; Kuittinen & Savolainen 1992; Ballian et al. 2006). However, other results show a relatively high genetic variation that is characteristic of conifers (Kuittinen et al. 1991). A substantial problem is the small number of seed trees and their low natural regeneration, which may be exacerbated by climate change (Ballian et al. 2006). For this reason, the Serbian spruce now has an endangered species status (Mataruga et al. 2011). Currently, there are only limited data on insect and disease damage to the Serbian spruce. The most serious pests include the pine weevil (*Hylobius abietis* L.) which is affecting young coniferous stands in Europe (Barredo et al. 2015; CABI 2015). Serbian spruce partially coexists with the natural occurrence of this pest (Barredo et al. 2015). Serbian spruce is susceptible to the European spruce bark beetle (*Ips typographus*) and great spruce bark beetle (*Dendroctonus micans*) – (Doom 1974; Vujičić & Budimir 1995; de Rigo et al. 2016). It can be at risk from attacks by the gregarious spruce sawfly (*Pristiphora abietina*) – (Doom 1974; Rigo et al. 2016). The Sitka spruce weevil (*Pissodes strobi*) also has the potential to seriously affect the growth of the Serbian spruce (Vidakovic 1993). In recent years, as a result of climate change (extreme temperatures, long-term droughts), the double-spined bark beetle (*Ips duplicatus*) is a new threat to Serbian spruce, especially in urban habitats in Central Europe (Vakula et al. 2021).

In terms of fungal pathogens, it is vulnerable to the fungus *Gremmeniella abietina*, which causes annual shoot dieback (Thomsen 2009; de Rigo et al. 2016). Also, due to changing environmental conditions, there is an increasing number of Serbian spruce trees infected with the dark honey fungus (*Armillaria ostoyae*), with a timeline from infection to tree death of approximately three years (Keča 2010; Jezdimirović 2016).

The most serious problem for the Serbian spruce is fires, which have significantly reduced its spread during the 20th century (Kralović 1951; Fukarek 1951a, 1956; Čolić 1966; Tošić 1983; Mataruga et al. 2011). Historically, fires have affected approximately 40% of the Serbian spruce populations, especially in the western part of its range (Fukarek 1951b; Čolić 1987). Although some populations have been completely destroyed multiple times, many have successfully recovered after sites have been burned (Čolić 1987). The recovery of Serbian spruce following disturbances such as forest fires has also been common in terms of the Holocene history of this species (Finsinger et al. 2017). This evidence would suggest that forest fires may play a consequential role not only in the natural recovery of the species but also in modeling the genetic structure of its populations (Mataruga et al. 2020).

In terms of climate change, weather extremes, in particular, heat waves (Sippel & Otto 2014) and a decrease in precipitation (Ivetic & Aleksić 2019), have also had an impact on the damage to Serbian spruce stands in the last two decades. Vacek et al. (2021) also documented a rela-

tively higher sensitivity of Serbian spruce to suboptimal precipitation distribution (however, lower compared to spruce), and at the same time, its high resistance to temperature fluctuations. This work also indicates that, in terms of negative pointer years (years with extremely low radial increment), it is – together with Scots pine and European larch (*Larix decidua* Mill.) – the most persistent tree species in the context of negative climate change and extreme effects.

9. Conclusion

The Serbian spruce is a very undemanding tree species in terms of soil and climatic environments. In the most extreme soil conditions, it is unrivaled by other conifers. Moreover, it is resistant to climatic extremes, weather fluctuations, and heat waves. This makes it a very promising tree species to replace the declining Norway spruce during global climate change, particularly in Central Europe. Compared to Norway spruce, it has a similar wood quality and can achieve a higher volume yield in acidic and dry habitats. It has considerable potential, especially in anthropogenically damaged areas, and is a suitable tree species for urban greenery because of its resistance to air pollution and high temperature. However, due to its limited distribution range and lack of exact information, it is important to focus on comprehensive and detailed long-term research on the introducing of Serbian spruce into suitable habitats and its possible use not only in ornamental horticulture but also in forestry to increase diversity in the future. The problem lies in the fact that this rare European conifer is highly restricted and endangered not only from a demographic and biogeographic but also from a genetic perspective due to its endemism reducing genetic diversity. For protection of native Serbian spruce stands and its introduction to other areas it is necessary to concentrate on research connected with genetic and ecotype variation and establishing of seed orchards from trees of mixed origin.

Acknowledgement

This study was 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). Acknowledgement goes to Jitka Šišáková, an expert in the field, and Richard Lee Manore, a native speaker, for checking English. We also thank to Josef Macek for graphic design of figures and to anonymous reviewers for their constructive comments.

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