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REVIEW PAPER

Importance and potential of Scots pine (*Pinus sylvestris* L.) in 21st century

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Abstract

We are currently witnessing significant global changes in climate conditions. We cannot change the natural conditions, but with regard to sustainable landscape management, we can increase our knowledge of tree species and adapt forest management to them. Surprisingly, one of the most affected tree species in Central Europe today is Scots pine (*Pinus sylvestris* L.). The following literature review summarizes over 200 studies from 1952–2022 regarding Scots pine across its entire range while addressing various topics in the ecology and management of this taxon. It is a tree species with a large natural range, nearly covering the entire Eurasian area. In the Czech Republic, it is the second most important tree species in terms of industrial wood production. Scots pine is characterized not only by a significant genetic variability of its populations but also by its wide ecological plasticity. Typically, it grows on sandy soils, poor habitats, and stony scree–but also in peat bogs. The wide habitat valence justifies the economic significance of this species, both in terms of its high production potential (mean annual increment of up to 10.8 m^3 ha^{-1} yr^{-1}) but also its wide range of use. However, in the light of climate variations, the practices of Scots pine silviculture are also gradually transforming from the traditional reforestation by clear-cutting to a more natural system–shelterwood felling. In view of climate change, its range of distribution is changing, as with other species, but Scots pine remains a very resistant tree species, depending on the habitat.

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

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1. Introduction

Scots pine (*Pinus sylvestris* L.) is one of the most ecologically and economically important tree species in Europe (Krakau et al. 2013; O'Reilly-Wapstra et al. 2014; Sevik & Topacoglu 2015; Wójkiewicz et al. 2016). It is a taxon with a wide climatic and edaphic range (Kelly & Connolly 2000; Úradníček et al. 2001; Durrant et al. 2016; Vacek et al. 2016). Due to the fact that it does not tolerate considerable shading–among other things–it tends to be displaced from rich habitats by competing tree species (Průša 2001; Mikeska et al. 2008). However, extensive forest stands of Scots pine are typically found on dry and poor sandy soils, in areas with sandstone subsoils, and on extreme sites with limited soil depth, as well as on peatland (Kučera 1999; Vacek et al. 2017, 2021a; Șofletea et al. 2020).

In Europe, Scots pine occurs at elevations ranging from lowlands to mountains, and in different ecotypes (Bílek et al. 2016; Hebda et al. 2017; Łabiszak et al. 2017; Vacek et al. 2022). Different ecotypes of Scots pine are based on populations that have survived from the Late Glacial period in the form of isolated refugia in Central Europe (Jankovská & Pokorný 2008; Mikeska et al. 2008; Tóth et al. 2017). Presumably, some of the refugia of autochthonous Scots pine may have provided the basis for the developmental lineages of the different ecotypes occurring in Central Europe. The oldest pine forests in the Czech Republic grow on rock outcrops, in rock formations, on serpentinite, and mineral-poor and dry sands. Regarding development, pine forests on peat bogs are younger (Plíva 1971; Mikeska et al. 2008; Poleno et al. 2009). The natural habitat for Scots pine ranged from the oligotrophic to herb-rich pine forests (Øyen et al. 2006; Mikeska et al. 2008; Vacek et al. 2022).

Historically, the oldest acrofossil evidence and sedimentary records showed the presence of Scots pine

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between 70,000 BP in Carpathian Basin to 20,000 BP in Hungarian plain (Magyari 2011; Tóth et al. 2017). However, current autochthonous pine and pine-oak forests were formed by the evolution of vegetation mostly during the 10,000 years of the Postglacial era. Scots pine and silver birch (*Betula pendula* Roth.) were the most abundant tree taxa in the Early Postglacial. The present occurrence of Scots pine can, therefore, be considered as a remnant of its original range and a relic of the Early Postglacial phases, especially on such ecotopes that were not suitable for other tree species due to edaphic reasons (Staszkiewicz 1968; Jankovská & Pokorný 2008). Although these azonal communities have gradually evolved since the Preboreal, they have only been preserved in extreme habitats with limited competition from other tree species. The first stands of pine and birch appeared in Central Europe in the older Holocene–in the Preboreal (Husová 1999; Mikeska et al. 2008). In the Boreal period, light pine forests with an admixture of common hazel (*Corylus avellana* L.) appeared in the mentioned area. In the Atlantic period of climatic optimum, mixed deciduous forests predominated by oak (*Quercus* spp.) developed, but at the same time, in colder and more humid areas, Norway spruce (*Picea abies* [L.] Karst.) also spread rapidly. Approximately 6200 to 4000 years ago, European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) began to spread, especially in the mid-elevations (Bolte et al. 2007; Mikeska et al. 2008). All of these tree species then gradually forced pine into habitats where they could not compete with it in terms of autoecology. In the Epi-atlantic, a natural zonation of climax vegetation was established, and pine thus retreated to habitats of an extreme and azonal nature (poor sands, rocks, peat bogs). In extreme habitats that were unapproachable to human intervention, communities similar to the current ones eventually formed (Husová 1999; Poleno et al. 2007; Mikeska et al. 2008).

However, what is the role of Scots pine in the 21st century, when climate change is altering the range of forest tree species and their growth optimum (Falk & Hempelmann 2013; Dyderski et al. 2018; Klopčič et al. 2022)? This literature review, based on over 200 studies, aims to assess the dynamics, opportunities, and risks of Scots pine from the perspective of climate change in European forests with a focus on the Czech Republic. Specifically, the review focuses on (i) morphological description of the species, (ii) taxonomic classification, (iii) natural range and distribution, (iv) habitat and ecological preferences, (v) silviculture and production, (vi) importance and uses, and (vii) threats and diseases, all within the context of climate change.

2. Morphological description of the species

Scots pine is characterized by a highly variable habitus, growing to an average height of 26 m but reaching up to 40 m in optimum conditions, while in extreme habitats, we find dwarf pines or shrubby pines (Mikeska et al. 2008; Praciak et al. 2013). Scots pine can live up to 300 years (exceptionally, up to 750 years) (Pokorný 1963; Koblížek 2006; Musil & Hamerník 2007; Wallenius et al. 2010). Many different ecotypes of Scots pine can be distinguished, including different characteristics of tree size or crown shape (Svoboda 1953; Businský 1999).

The root system of the pine is massive, consisting, in most cases, of a taproot with richly branched lateral roots (Poleno et al. 2009). Pine roots are very plastic with respect to habitat conditions, but they also react to, for example, the tilting of the tree (Čermák et al. 2008). It is the significant plasticity and resistance of the pine root system that makes the pine a valuable stabilizing tree in some habitats (Kacálek et al. 2017). In the northern and

Fig. 1. Habitus of the tree, branch, needle, cone, and seed of Scots pine (*Pinus sylvestris* L.).

northeastern parts of the European range, the Scots pine crown is slender with fine branching, whereas arched to umbrella-shaped crowns and thick branches are typical for pines in Central and Southern Europe. The trunk of the tree is most often straight, but on extreme sites, it is often crooked and twisted (Pokorný 1963; Koblížek 2006; Musil & Hamerník 2007; Praciak et al. 2013). At the base of the trunk, the pine is covered with a thick, cracked, grey-brown bark. In the upper parts of the tree, the bark turns orange or rusty red, and it peels off in scaly patches (Úradníček et al. 2001; Musil & Hamerník 2007). Scots pine has greenish-brown and glabrous annuals, and older twigs tend to be grey-brown (Fig. 1). The needles of Scots pine are stiff and pointed, with a slight longitudinal twist, 1–8 cm long, up to 2 mm wide, dark green or bluish grey-green in color, and generally growing in pairs on brachyblasts, with a life span of 2–3 years. The buds at the ends of the annuals are elongated-ovate, pointed, without resin, or weakly resinous, and covered with rusty-colored, membranous scales (Pokorný 1963; Úradníček et al. 2001; Koblížek 2006; Praciak et al. 2013; Krakau et al. 2013).

Scots pine is a monoecious tree species; male and female strobili differ in Scots pine. While male strobili are ovoid, 4–8 mm long, usually yellow (rarely red), female strobili are 5–6 mm long, usually pink. The male strobili grow at the base of the elongating shoot instead of needles, most often in the lower part of the crown, while the female strobili grow at the end of the last year's branches in the upper part of the crown (Úradníček et al. 2001; Musil & Hamerník 2007). The cones are usually single or in groups of 2–3, pedunculate or nearly sessile, ovoid-conical, rounded at the base, often asymmetrical, nonglossy, grey-brown, 2.5–7 × 2–3.5 cm. Seed scale shields are rhombic, more developed on the illuminated side, and flat to pyramidal. The cone umbo is small, flat, or short-tipped, light brown, shiny, and without black edging. Seeds are ovoid, 3–4 mm long, whitish, brown or grey to black, with 3–4 times longer brownish to reddish brown wings, and pincer-like at the base (Koblížek 2006; Musil & Hamerník 2007; Praciak et al. 2013).

Pines flower in spring and early summer (April–June) for the first time, at around the age of 15 years. In a closed stand, they do not flower until the age of 30–40 (Úradníček et al. 2001; Musil & Hamerník 2007). The flower primordia of male and female strobili are formed in the summer of the previous year (Johnson & More 2006). More than 12 months after pollination, the germinating pollen resumes its growth and fertilizes the egg. Shortly after, in June (year 2), the entire formation rapidly enlarges and reaches the final cone size in the summer. In early October, the cones ripen. In favorable weather, a small number of seeds emerge during October–December, but the main period of cone opening is in the spring of year 3. The empty cones fall off during the summer of the 3rd year after pollination. A seed year in pine occurs on average every 3rd to 6th year (Pokorný 1963; Úradníček et al. 2001; Koblížek 2006; Musil & Hamerník 2007; Poleno et al. 2009; Praciak et al. 2013). The number of pure seeds in 1 kg is 74–245 thousand. The average weight of 1,000 seeds is 6.3 g. Well-stored seeds can remain viable for up to 15 years (Musil & Hamerník 2007; Poleno et al. 2009).

3. Taxonomic classification

According to Řepka & Koblížek (2007), Scots pine (*Pinus sylvestris* L.) is classified into the following taxonomic categories: Domain: *Eukarya*; Kingdom: *Plantae*; Subkingdom: *Viridiplantinae*; Developmental lineage: *Streptophytae*; Developmental branch: *Cormophytae*; Developmental stage: *Gymnospermae*; Division: *Pynophyta*; Family: *Pinaceae*; Genus: *Pinus*; Species: *Pinus sylvestris*, however, splits into numerous lower taxa. Given the vast Eurasian range of Scots pine, an intraspecific taxonomic system is very difficult to set (Kindel 1995). Nevertheless, Scots pine can be divided into the following four varieties: *Pinus sylvestris* var. *sylvestris*; *Pinus sylvestris* var. *lapponica* Hartm., 1849; *Pinus sylvestris* var. *mongolica* Litvinov, 1905, and *Pinus sylvestris* var. *hamata* Steven, 1838.

The variation within the taxon *Pinus sylvestris* is indeed extremely large. Over 140 subspecies, varieties, and forms have been studied. In terms of distribution, approximately 22 geographical varieties are categorized. Svoboda (1953) divides the species into three basic climatypes: northern, steppe, and mountain pine. Łabiszak et al. (2017) demonstrated the distinct character of following groups: mountain, lowland and coastal populations. Businský (1999) divides Scots pine into varieties according to geography and morphological features: *P. sylvestris* var. *sylvestris* (including the former var. *sibirica*), *lapponica*, *hamata*, and *mongolica*. In addition to the subdivisions mentioned above, a number of forms have also been detailed in terms of their economic utility–according to the quality of the timber and habitus of the pine (in the Czech Republic, "Třeboň pine" or "Týniště pine"). Other forms are based on the variability of needles, bark, and cones (according to the shape of the shield, f. *plana*, f. *gibba*, f. *reflexa*, and according to size, f. *macrocarpa*, f. *microcarpa*). In nature, Scots pine forms spontaneous hybrids with *Pinus mugo*, *Pinus uncinata* and *Pinus uncinata* subsp. *uliginosa* (Businský 1999; Musil & Hamerník 2007; Poleno et al. 2009; Sobierajska et al. 2020).

4. Natural range and distribution

Scots pine has the largest range of all described pines. The distribution range of Scots pine mainly includes the temperate and cooler belts of much of Europe and Asia (this area is otherwise known as Eurasia), and in Europe from northern Portugal and Scotland to the Far East between 37°–70.5° N latitude. The center of its range is Siberia. In Europe, Scots pine is rarely found in the Mediterranean. The northernmost occurrence in Europe is in Lapland (Fig. 2; Úradníček et al. 2001; Musil & Hamerník 2007; Durrant et al. 2016).

Pinus sylvestris var. *sylvestris* (Syn. *P. sylvestris* subsp. *sibirica* [Ledebour] Businsky) is typical in Europe (north to ca. 62° N), its range extending to the Far East (to ca. 142° E). *Pinus sylvestris* var. *lapponica* (Hartman) occurs from northern Scandinavia to NW Siberia, approximately north of 62° N latitude. *Pinus sylvestris* var. *hamata* (Steven) (Syn. *Pinus armena* K. Koch; *P. kochiana* Klotzsch ex K. Koch) is found in the Caucasus region and Transcaucasia south to S Armenia, W Azerbaijan, and Turkey. *Pinus sylvestris* var. *mongolica* (Litvinov) (Syn. *Pinus sylvestris* subsp. *kulundensis* Sukaczev) occurs in Northern Mongolia, NE China, and SE Siberia (Businský 2008).

The Scots pine does not occur naturally on the steppes of southern Ukraine, southern Russia, or in the oceanic lowlands of the British Isles and Denmark. Outside its core Eurasian range, however, Scots pine has also secondarily spread in North America, where it is mainly cultivated on plantations (Poleno 1990; Úradníček et al. 2001; Musil & Hamerník 2007; Schildler et al. 2010).

In Central Europe, deciduous forests are the dominant communities (Leuschner & Ellenberg 2017), while pine forests are restricted to poor habitats (Ahti & Oksanen 1990). In the Czech Republic, Germany, and Poland, native Scots pine currently grows only in islands in extreme relict habitats (Heinken 2007; Chytrý 2013). In Poland, Scots pine is the main economic tree species, covering 58% of the forest area (DGLP 2021). In the Czech Republic, Scots pine occupies 16.1% of the forest area (MZe 2021), with its lowest frequency in the Polabí sandy terraces of poor loamy sands, on the serpentinite rocks of the Slavkov Forest and the Bohemian-Moravian Highlands, and on the boulder slopes and scree of the Šumava Mountains (the highest occurrence of Scots pine in the Czech Republic is on the scree near Plešné Lake at an altitude of 1,070 m). Scots pine is also found on sands and peaty soils, the edges of peat bogs in the Třeboň region, on sandstone cliffs and rock formations in Northern and Northeastern Bohemia, and on rocky and steep slopes of river valleys. It also grows on the outcrops of the Drahanská vrchovina (Drahany Uplands), on the scree of the Hrubý Jeseník Mountains, and on limestone rocks of Southern Moravia. Typically, however, Scots pine is also cultivated in many places outside of its natural range, which is only 3.4% out of the current total of 16.1% in the forests of the Czech Republic (Musil & Hamerník 2007; Mikeska et al. 2008; Poleno et al. 2009; MZe 2021).

The frequency of pine forests in the Czech Republic is shown in Fig. 3. In natural forest areas (NFA), the highest abundance of pines can be seen in the North Bohemian Sandstone Plateau and the Bohemian Paradise – NFA 18 (36.6%), in the South Bohemian Basin – NFA 15 (19.7%), the West Bohemian Upland – NFA 6 (17.14%), and the Lusatian Sandstone Upland – NFA 19 (11.78%). In other natural forest areas of the Czech Republic, the representation of pine is significantly lower.

Pine forests have a unique position in the development and zonation of vegetation. Regarding the coexistence of Scots pine with other tree species, its colonization of most of the landscape in the Postglacial times was a critical moment. Later, Scots pine spread to soils and habitats where other tree species could not adapt (Horsák & Chytrý 2010). Naturally preserved, Scots pine retained its dominant position only on sandstone bedrock and sandy sediments in general, primarily on Cretaceous sandstones and sands, serpentinite, and, in extreme conditions, also on limestone, peats, and on rocky outcrops of various acid rocks (relict). In particular, fires were more frequent on dry sands, an essential natural factor in the colonization of the landscape by pine. The majority of the sites mentioned above are located approximately in the climate range of forest vegetation zones 3–4, i.e.,

Fig. 2. Scots pine distribution in Eurasia; native range; introduced and naturalised (synanthropic) area (Caudullo et al. 2017).

300–700 m above sea level. Contrarily, some inversion sites with spruce, or higher, precipitation-deficient areas on sediments can be assessed as climatically "higher" (Mikeska et al. 2008; Vacek et al. 2022).

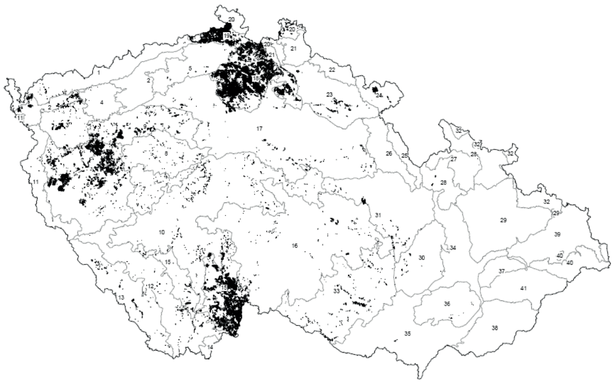

Fig. 3. Representation of natural pine forests (forest altitudinal zone 0 – pine forest) in the Czech Republic (GIS-ÚHÚL Brandýs n. L., modified according to Mikeska et al. 2008).

5. Habitat and ecological preferences

Scots pine is a typical pioneer tree species (Linder et al. 1997; Durrant et al. 2016). It is a distinctly light-demanding tree species that barely tolerates shading but can adapt to a wide range of conditions in terms of soil and climate requirements (Plíva 1971; Mikeska et al. 2008; Poleno et al. 2009). The soils of pine forests on which pine appears are predominantly sandy to gravelly, permeable, arid, and acidic types of arenaceous podzol or arenaceous cambisol. On extreme geological substrates, it is lithic leptosol, podzolic ranker, and arenaceous regosol. On sites influenced by water, it is mainly stagnic cambisol, stagnic podzol, and gleyic podzol. On transitional peatlands with groundwater, fibric histosol, occasionally gleyic histosol and gleyic podzol occur. Only in sporadically occurring basophilous pine forests do we find haplic rendzic leptosol, cambic r. l., detrital r. l., or modal leptosol (Vacek et al. 2022).

Scots pine adapts to a wide climatic range, with a vegetation period of 90–200 days, an annual precipitation of 200–1,780 mm, and a common mean annual temperature of 5–9 °C. It tolerates frost and the occasional lack of precipitation, as well as poor soil of extreme – rocky, sandy, and peaty – habitats, where it is unrivaled in monocultures (Richardson 1998; Mikeska et al. 2008). Its deep root system and thick bark make Scots pine resistant to fires and able to regenerate on the mineral soil of burn sites. Its ecological optimum is far from the physiological one. Scots pine does not occur naturally in nutrient-rich habitats but is often cultivated there locally (Úradníček et al. 2001; Musil & Hamerník 2007; Koblížek 2006; Poleno et al. 2009).

Three groups of relict pine forests can be characterized in Central Europe:

- Continental Eastern European to South Siberian pine forests growing in contact with sub-xerophilous oak forests on gravelly terraces of larger rivers (class *Pulsatillo-Pinetea sylvestris*, alliance *Pulsatillo-Pinion*), their marginal distribution in the Alps is linked to the rain shadow of the inner Alpine valleys.
- Basophilous (flowery) pines on marl, limestone, and dolomite rocks and on serpentinites (class *Erico-Pinetea*, alliance *Erico-Pinion*), whose distribution extends from the Balkans through the limestone foothills of the Alps to Central Europe.
- Oligotrophic pine forests belonging to the boreal coniferous forests (class *Vaccinio-Piceetea*), within which they form a group including primary relict pine forests of siliceous rocks, sandy soils, and peat bog pine forests (alliance *Dicrano-Pinion*). While the first two groups are only marginally found in the Czech Republic, oligotrophic pine forests are relatively common in the Czech Republic (Kučera 1999; Mikeska et al. 2008).

Within the European Forest Types (EFT) (Marchetti 2007), all pine forests are designated by the units: 1.2 Pine and pine-birch boreal forest; 2.2 Sub-boreal Scots pine forest; 2.4 Sub-boreal black pine forest; 2.5 Mixed pine-birch forest (Scots pine); 2.6 Mixed pine-oak forest (pine-oak forest – Scots pine and common oak); 3.1 Subalpine larch-Swiss pine-dwarf pine forest (European larch, Swiss pine, and dwarf pine); 3.3 Alpine pine forest (Scots pine and black pine); 10.1 Thermophilous Mediterranean pine forest; 10.2 Black pine forest of the Mediterranean and Anatolia region; 10.3 Canary Island pine forest; 10.4 Scots pine forest of the Mediterranean and Anatolia region; 10.5 Mountain Mediterranean pine forest; 11.1 Coniferous and mixed peat forest; 11.3 Birch peat forest.

In Europe, in the poorest habitats, Scots pine forms monocultures. In slightly richer habitats or boggy and upland areas, it grows together with oaks (*Quercus petraea*, *Quercus robur*), European beech (Fagus sylvatica), silver birch (*Betula pendula*), Norway spruce (*Picea abies*), European larch (*Larix decidua*), silver fir (*Abies alba*), and other pines (primarily *Pinus nigra*, *Pinus uncinata*) (Mason & Alìa 2000; Kelly & Connolly 2000; Úradníček et al. 2001; Musil & Hamerník 2007).

In the Czech Republic, Scots pine is found mainly in alliance associations *Erico-Pinion*, *Dicrano-Pinion*, and *Vaccinion*, in rock alliance associations *Alysso-Festucion pallentis*, *Asplenion serpentini*, *Seslerio-Festucion glaucae* (Chytrý et al. 2001). The accompanying tree species of lowland and wooded-hill variants of Scots pine are mainly *Quercus petraea*, *Tilia cordata*, *Carpinus betulus*, *Acer campestre*, and *Betula pendula*. Within the upland variant, Scots pine grows with *Picea abies*, *Abies alba*, *Fagus sylvatica*, *Larix decidua*, and *Betula pendula* (Mikeska et al. 2008; Poleno et al. 2009).

In terms of habitat, three basic variants of Scots pine can be identified:

- Lowland – pioneer: grows primarily on sandy soils, in monocultures with a minimal or no admixture of other tree species, regenerates on mineral soil in clearings and open areas. It grows quickly when young, bears fruit early and does not tolerate competition from other species;
- Wooded-hill – pioneer: grows mainly on sandy soils, rocky ecotopes, and peat soils, mostly in monocultures with little admixture of other tree species, regenerates on mineral soil in clear-cuts and open areas;
- Montane – climax: grows mostly in mixtures (with spruce, fir, and beech) at higher altitudes (700–1,000 m) but also descends to lower altitudes. It regenerates under the canopy and does not tolerate open habitats (clear-cuts). It sometimes dominates its competitors in height and has a large wood production (Mikeska et al. 2008; Poleno et al. 2009).

Under conditions of global climate change, Scots pine is increasing its range at higher altitudes and in northern locations, and, conversely, declining due to dieback in the southern part of its European range (Benito Garzón et al. 2008; Reich & Oleksyn 2008; Matìas & Jump 2012).

6. Silviculture and production

In silviculture and production, forest structure is a crucial element, quantified primarily by stand density, canopy, vertical canopy structure, stand basal area, horizontal tree distribution, heterogeneity in the spatial arrangement of trees, the volume of deadwood, or categorization of individuals into tree classes (Pommering 2002; Puettmann et al. 2008; Silver et al. 2013). Stand structure noticeably influences most variables in the forest ecosystem, but in the context of forest regeneration and the silviculture of different tree species, it also influences the existence and establishment of natural regeneration, especially for shade-tolerant tree species (Jaworski 2000; Poleno et al. 2009). The aforementioned forest structure issue is crucial for Scots pine silviculture, which requires a high intensity of light for its successful growth in juvenile stages (Vacek et al. 2016); Oleskog & Sahlén (2000) reported about 30% of free space light. Numerous studies, e.g., Urbieta et al. (2011), Carnicer et al. (2014), and Martin-Alcón et al. (2015) show that as light availability decreases, the quantity and quality of natural regeneration decreases in pine stands with higher canopy density. In contrast, Pardos (2017), Schönfelder et al. (2017, 2018), and Lundqvist et el. (2019) report that lower light intensity compared to clear-cuts can lead to higher quality in natural regeneration in Scots pine. Brichta et al. (2020) also mention in their study that partial cover of the parent stand in turn may have a positive effect on the abundance of natural regeneration. Of course, light conditions of natural regeneration can also be impaired by competition from herbaceous vegetation (Lucas-Borja et al. 2011; Mirschel et al. 2011; Prévosto et al. 2012; Hyppönen et al. 2013). If we proceed with the clear-cut, the use of seed trees is recommended, not only as part of supporting natural regeneration, but also to increase the radial growth of the remaining mature individuals (Brichta et al. 2019).

However, one of the most important factors for the success of natural regeneration of Scots pine is the weather conditions, i.e., temperature and precipitation in close relation to light during seed germination and initial seedling growth (Oleskog & Sahlén 2000b; Puhlick et al. 2012). Pine seeds are able to germinate at 6 °C, however, the optimum temperature is up to 20–25 °C with a seed moisture content of approximately 35% (Oleskog & Sahlén 2000). Another factor limiting seed germination can be a thick layer of surface humus, which prevents roots from penetrating the mineral soil layer (Hille & den Ouden 2004; Oleskog & Sahlén 2000a). Scots pine germinates optimally only on mineral soil, and therefore soil scarification is usually used in pine regeneration (Örlander et al. 1996; Remeš et al. 2015; Aleksandrowicz-Trzcińska et al. 2017; Saursaunet et al. 2018; Ilintsev et al. 2021). The germination of Scots pine seeds can also be supported artificially - by cold stratification (Houšková et al. 2021) or low-intensive coherent seed irradiation (Novikov et al. 2021). Some sources describe wood ash fertilization for improving the soil environment (Remeš et al. 2016; Petrovský et al. 2018). On dry sites, soil preparation also improves the water supply in the root zone because transpiring herbaceous vegetation is removed by these interventions (Fleming et al. 1994). Moreover, bare mineral soil has less variability in water availability than a humus layer (Oleskog & Sahlén 2000a). Soil preparation increases soil temperature (Nilsson & Örlander 1999; Bedford & Sutton 2000), accelerates humus decomposition, and increases mineral availability (Lunmark-Thelin & Johansson 1997; Nilsson, Örlander 1999; Nilsson et al. 2006), thus increasing the probability and rate of seedling growth (Karlsson & Örlander 2000; Mattsson & Bergsten 2003; Nordborg & Nilsson 2003) and reducing soil bulk density (MacKenzie et al. 2005).

Scots pine produces seeds annually, but moderate to heavy seed years typically occur every 3–6 years (Poleno et al. 2009; Przybylski et al. 2021). Pine seeds are dispersed primarily by wind, with effective seed dispersal occurring up to a maximum distance of 30–100 m from the parent tree (Farmer 1997; Adams 1992; Mikeska et al. 2008). However, sufficient soil moisture is required for seed germination and seedling establishment (MacKenzie et al. 2005). Seedling numbers in Scots pine stands have been reported to range from 0.5–2.3 pcs m^{-2} (Nilsson et al. 2002; Karlsson & Nilsson 2005; Erefur et al. 2008; Marcos et al. 2007; Marozas et al. 2007; Beghin et al. 2010; Mirschel et al. 2011; Jäärats et al. 2012) with a maximum of 10 pcs m^{-2} (Mirschel et al. 2011). Understory recovery typically starts at 10% relative radiation (Ulbrichová et al. 2018).

In the first years of seedling development, due to unfavorable abiotic and biotic factors, seedlings undergo considerable self-thinning. (Aleksandrowicz-Trzcińska et al. 2018). The ecotone effect also influences seedling growth, with a higher density of seedlings tending to occur at the edge of the stand compared to the interior (Vacek et al. 2017b). A risk for newly established pine stands can be, for example, grubbing by the pine weevil (*Hylobius abietis* L.) (Kovalchuk et al. 2015; Lundborg et al. 2016) or the formation of proleptic shoots, which, however, are removed in sparse cultures and growths by cutting or simple selection regeneration individuals (Slodičák & Novák 2007). Although the natural regeneration of Scots pine is generally dominated by small-scale clear-cuts and border cutting areas, shelterwood methods of natural regeneration are increasingly used in the context of global climate change (Bílek et al. 2016; Brichta et al. 2020). Shelterwood natural regeneration methods are now common, for example, in Scandinavia (Hyppönen et al. 2013; Lundqvist et al. 2019), Germany (Spathelf et al. 2015; Drössler et al. 2017), Poland (Bielak et al. 2014; Aleksandrowicz-Trzcińska et al. 2017, 2018), and also in some areas in the Czech Republic (Bílek et al. 2017, 2018; Brichta et al. 2020). This way of natural regeneration is more favorable with respect to the nature of microhabitats under advancing global climate change (Montero et al. 2001; Matías & Jump 2012; Aleksandrowicz-Trzcińska et al. 2014, 2017, 2018; Vítámvás et al. 2019; Brichta et al. 2020).

Thus, within the diverse conditions of pine management, natural regeneration can be achieved by a clear-cutting system with different sizes and orientations of cutting. These also include border cutting, patch cutting, large- and small-area shelterwood cutting, transitioning to group or individual selections (Poleno et al. 2009). Within ecologically oriented management, two basic silvicultural approaches can be implemented. The first is to aim for the areal initiation of natural regeneration under the parent stand; the second is small-area group regeneration with a transition to selection principles. In both cases, the start of regeneration must be preceded by the determination of a suitable time frame for the silvicultural development of the stand. Determining the minimum stand age for the start of regeneration depends on the specific conditions of the stand, taking into account its age, quality, expected production, the presence of spontaneous regeneration, habitat conditions, and the nature of the vegetation. The parent stand must not incur production losses by premature harvesting, especially of the best quality trees (Poleno et al. 2009; Bílek et al. 2016, 2018; Vacek et al. 2022).

The first cleaning and thinning from above are carried out by negative selection, i.e., by removing dominant, malformed, or damaged individuals at the crown and dominant level. Thinning from below is not desirable, but self-thinning is a natural process in pine stands. On the other hand, higher numbers of individuals ha^{-1} are recommended in the age of up to about 10 years of growth in order to achieve a better morphological quality of the trees (Houšková & Mauer 2014). Even before reaching a height of 5 m, however, it is necessary to thin out the stand in order to increase its stability against the action of wet snow (Novák et al. 2013). The height to diameter ratio is then most affected by thinning in young pine stands, as the stand's age increases, the growth response to thinning also decreases (Dušek et al. 2011). But it is also possible to maximize production or reduce silviculture costs by thinning the stand (Sloup & Lehnerová 2016). In most habitats, the healthy development of pine stands requires an understory of shade or semi-shade tree species. These are usually self-seeding trees, which are intentionally left in the stand during the process of pine stand tending. Later, at about 50 years of age, a combined thinning is carried out to encourage the development of as many quality individuals as possible depending on the production capacity of the site (about 150–300 target trees). In addition to trees suppressing the crowns of the target trees, we remove damaged, diseased, and severely malformed trees through stand-improving tending operations. We encourage the presence of soil-improving and admixed tree species to increase the species diversity of pine stands (Poleno et al. 2009; Vacek et al. 2022). Considering the mostly very poor pine habitats, it is recommended to leave the residual biomass after thinning in the stand (Novák et al. 2017), and this despite the consideration of soil pH deterioration (Peřina & Vintrová 1958).

Pine stands are generally restored by border cutting and small- and large-area clear-cutting, but shelterwood cutting is becoming a common practice too. However, the yield from pine stands during regeneration cannot be precisely totaled. Considering the significant genetic variability of Scots pine (Kosinska et al. 2007; Businský 2008) but also its wide ecological amplitude and habitat range (Plíva 1971; Mikeska et al. 2008; Poleno et al. 2009), the production indices of Scots pine stands vary widely (Table 1). Depending on the parameters mentioned above, as well as on the type and intensity of management, we can conclude that Scots pine stand stock volumes in Europe are indeed quite variable. While the studies by Starr et al. (2005) or Makkonen & Helmisaari (1999) describe roughly 140-year-old pine stands with a stand volume up to 100 m^3 ha^{-1} from the lowlands of Finland, the work by Gallo et al. (2020) reports stand volume up to 441 m^3 ha^{-1} in montane pine stands in Spain. Substantially high stocks are in the lowland areas in Poland, where the stock of Scots pine stands over 130 years reaches up to 740 m^3 ha^{-1} (Bielak et al. 2014). Particularly in Poland, Scots pine is a common tree species and is even considered the primary economic tree species (DGLP 2021). The highest mean annual increment (MAI) in the Czech Republic is reported by Vacek et al. (2021a) – 10.87 m^3 ha^{-1} yr^{-1}. The high production

Table 1. Overview of available publications related to Scots pine (*Pinus sylvestris* L.) production parameters.

Study	Country	Altitude [m a.s.l.]	Age [year]	DBH [cm]	Height [m]	Basal area [$m^2\,ha^{-1}$]	Volume [$m^3\,ha^{-1}$]	MAI [$m^3\,ha^{-1}\,yr^{-1}$]	Density [trees ha^{-1}]
Vacek et al. (2016)	Czech Republic	245–267	70–130	26–31	21–24	33–40	320–434	3.08–5.50	508–660
Bílek et al. (2016)	Czech Republic	270–600	129–191	25–42	14–25	25–47	177–456	0.93–2.39	476–1,072
Bílek et al. (2016)	Poland	470	191	42	19	19	159	0.83	200
Vacek et al. (2017)	Czech Republic	575–630	123–130	24–36	15–23	12–33	91–267	0.70–2.05	172–512
Gallo et al. (2020)	Czech Republic	600–590	142–145	25–27	16–19	27–28	240–245	1.69	488–552
Gallo et al. (2020)	Spain	1710	140	21–46	9–20	33–46	231–441	1.65–3.15	276–996
Vacek et al. (2021a)	Czech Republic	250–495	40–46	15–22	17–23	38–47	318–500	7.07–10.87	1,355–2,822
Vacek et al. (2021c)	Czech Republic	430	48	19	17.5	45	364	7.92	1,700
Starr et al. (2005)	Finland	35–280	35–200	12–38	10–25	11–29	48–315	1.37–1.58	374–2,660
Montero et al. (2001)	Spain	1700	41–66	17–31	15–21	49	364–478	7.24–8.89	635–2,104
Makkonen & Helmisaari (1999)	Finland	144	37	8	8	15	70	1.89	2,660
Van Oijen et al. (2013)	Austria	495	60	27	18	—	—	—	790
Van Oijen et al. (2013)	Belgium	50	66	28	20	—	—	—	380
Van Oijen et al. (2013)	Estonia	40	73	26	26	32	374	5.12	—
Vanninen & Mäkelä (2000)	Finland	150	16–71	4–23	4–22	19–23	—	—	595–18,727
Pretzsch et al. (2015)	Europe	20–1,290	69	28	22	41	413	11.3	970
Bielak et al. (2014)	Poland	79–151	124–132	39–47	30–36	—	319–740	2.57–5.60	177–324
del Río et al. (2008)	Spain	1,200–1,750	41–50	14–20	7–13	35–49	159–321	3.89–6.42	1,415–5,495
Beker et al. (2021)	Poland	100	25–95	13–31	15–28	27–40	256–396	4.17–10.24	402–2,590

Notes: DBH – diameter at breast height, MAI – mean annual increment

potential is also illustrated by the work of Vacek et al. (2021c), where Scots pine achieved the highest increment and stand volume of all 12 coniferous tree species studied on reclamation dumps following coal mining. On the other hand, Lovynska et al. (2019) describes that, for example, in the conditions of the Northern Steppe of Ukraine, Scots pine shows a lower volume production than the acacia tree (*Robinia pseudoacacia* L.).

7. Importance and use

Scots pine is one of the most important economic tree species not only in Central Europe but also in Eurasia (Praciak et al. 2013; Sevik & Topacoglu 2015; Lundqvist et al. 2019). Due to its dynamic ecological plasticity and ability to occupy hostile habitats, pine plays a crucial role in both forestry and, subsequently, in the timber industry. Pinewood has an orange-brown heartwood and a broader yellow sapwood. The annual rings are very distinctive, hence, there is a considerable difference in density and hardness between spring and summer wood (Pokorný 1963). The density of the wood substance reaches values between 0.412 and 0.541 g cm^{-3} (Table 2). It should be added, however, that wood density values for pine have a wide variance; this is due not only to the transition between spring and summer woods but also to the extreme genetic variability of the species. The differences in wood density of Scots pine individuals may also be due to its silviculture and different degrees of stand canopy. While individuals with a well-lit crown exhibit lower wood density, trees sheltered by the parent stand possess higher wood density (Schönfelder et al. 2017). Compared to the wood density of spruce, which is approximately 0.410 g·cm^{-3} (Repola 2006; Saranpää 2003), the wood density of pine can be up to 0.100 g·cm^{-3} higher.

The distinctly differentiated summer rings on pine wood are also complemented by its natural luster; in the case of pine, it is due to its high resin content, which makes the wood very durable, especially in water and humid environments, which is why it is mainly used for water structures, pumps, mine timber, sleepers, masts, poles, and fencing; the wood might require impregnation for increased durability (Milner 1992; Reynolds & Bates 2009; Farjon 2010; McLean 2019). Pine timber is also used to manufacture of timber structures, particularly composite timber, in timber construction, lumber, furniture, and paneling (Davies et al. 2002; Kuklík 2005; Hairstans 2018), as it has similar durability to larch timber (British Standards Institute 1994). Lower-quality wood is used for fiber and fuel (McLean 2019).

The distillation of the wood was used to prepare tar and, subsequently, black pitch, lamp oil, and essential oils. Burning the heavily resinous wood of stumps and roots yielded soot, which was utilized to make domestic ink and printing ink. By scarring the trunks or peeling the bark, the resin was extracted (Neumann 2015). In many countries, including the Czech Republic, the traditional methods of slitting and debarking live Scots pine trees and capturing the resin that oozes out (so-called pitching) are no longer allowed. Resin was widely used for sealing and impregnating ships but also as a medicine or natural glue. It is also a source of natural turpentine, which, together with its distillation residue (colophony), is the starting material for several other products such as varnishes, paint thinning solvents, insecticides, rubbers, printing inks, etc. (Schreiner et al. 2018; Praciak et al.

Table 2. Overview of the available publications related to Scots pine (*Pinus sylvestris* L.) wood density.

Study	Schönfelder et al. (2017)	Wagenführ (2002)	Novák (1970)	Lexa et al. (1952)	Repola (2006)	Saranpää (2003)	Auty et al. (2014)	Fundova et al. (2018)
Density [g cm^{-3}]	0.488–0.541	0.510	0.470	0.510	0.412	0.460	0.423	0.430

2013; Gardner 2013; McLean 2019). Black pine wood impregnated with resin was also used to make torches in the Balkans (Musil & Hamerník 2007).

Pine essential oil contains a variety of terpenes. These substances contained in essential oils and other products are known for their pleasant aroma, which helps to calm the nervous system, relieve stress, release anxiety and tension, and refresh the mind. They are also a component of perfumes, aromatic soaps, massage oils, air fresheners, and similar products (Podlech 2002; Schreiner et al. 2018). Pine bark contains antioxidants, flavonoids, tannins, and a variety of vitamins and has been consumed by, for example, Native Americans for centuries. It was used as a remedy against scurvy by Russian Cossacks in Siberia and the Far East (Aleksandrov 1969). Traditionally, the inner bark of Scots pine was used by the Sámi as a source of food and packaging material in Lapland until the late 19th century (Zackrisson et al. 2000). Commercially, the shredded bark of Scots pine is considered a valuable by-product in horticulture (Moore 2011). The bark is also used to make insulation products for buildings (Pásztory & Ronyecz 2013).

In the past, the maceration of fresh needles was used to prepare a tissue called sosnovka or "forest wool", which was used to make carpets, blankets, or as a stuffing material. The essential oil contained in pine has medicinal uses. Extracted from the resin, needles, and buds, it has antiseptic properties. It is used to relieve respiratory and lung diseases, and rheumatic disorders, as a sedative, and also in aromatherapy (Ciesla 1998).

In extreme habitats, Scots pine acts as an anti-erosion and reclamation tree species (Vacek et al. 2021a, c). However, besides the soil-protective function, pine also performs other ecological functions; several fungal species form mycorrhizal, parasitic, and saproparasitic associations with pine trees. About 120 fungal species have been observed in ecto- and endotrophic symbiosis with pine roots. For consumption, boletes, Bay boletes, brittlegills, and blewits are collected (Klán 1989; Carlile & Watkinson eds.1994; Gryndler et al. 2004; Antl 2014). The collection of bilberries and cranberries, as well as other forest fruits are also abundant in pine forests (Šišák 2006).

8. Threats and diseases

Currently, the most discussed threat to Scots pine stands is undoubtedly drought and the associated decline in groundwater levels due to climate change (Vacek et al. 2016; Gao et al. 2017; Buras et al. 2018). It is climatic stress periods that negatively affect the photosynthetic activity of Scots pine (Flexas & Medrano 2002; Reddy et al. 2004). Increasing air temperatures, along with low water availability, are responsible for a range of other diseases, as well as reduced tree defense capacity against insect pests (Allet et al. 2015; Haberstroh et al. 2022). Although Scots pine is considered a resistant tree species to precipitation deficiency, pine stands across Europe have still been enormously damaged by recurrent drought in recent years (Merlin et al. 2015; Vacek et al. 2017; Buras et al. 2018), when, in particular, precipitation is the main factor affecting pine growth processes (Vacek et al. 2019). It can be argued that Scots pine is now one of the most threatened tree species in Europe (Gao et al. 2017; Buras et al. 2018; Etzold et al. 2019). As a rule, stands with a homogeneous structure or stands with an unsuitable pine ecotype are the most affected (Bottero & Vacchiano 2015; van Halder et al. 2019). Paradoxically, the cause of pine dieback may be its taproot system (Lokvenc et al. 1985), which does not adapt to absorb available precipitation from surface soil layers as the water table recedes. Not only is the amount of available water gradually becoming depleted, but its nutrients (S, P) are currently lacking in pine stands as well (Prietzel et al. 2020). The solution to the decline appears to be the silviculture of structurally differentiated pine stands (del Río Gaztelurrutia et al. 2017; Brichta et al. 2020), as well as mixed pine stands (Czerepko 2004; Pretzsch et al. 2013; Zeller et al. 2017; Vacek et al. 2019). In some places, pine is already spontaneously shifting its range into communities of deciduous trees (Haberstroh et al. 2022). However, it is still a relatively resistant tree species to the effects of climate change, considering the habitat. For example, Vacek et al. (2021c) reported that Scots pine was the most resistant of the 12 tree species studied concerning the effects of climate extremes in the Czech Republic.

Common insect pests of pine trees include the nun moth, pine tree lappet, common pine shoot beetle, bark beetles (genus *Dendroctonus*), or tortrix. Trees can also be attacked by plant parasites and semi-parasites such as mistletoe and related species (Mutlu et al. 2016). Trees weakened by pests or by various abiotic stresses (e.g., drought) are susceptible to damage by fungal pathogens, the spread of which may be enhanced in monospecific commercial plantations. For example, *Sphaeropsis sapinea* and *Cenangium ferruginosum* cause withering and dieback of pine trees, while *Mycosphaerella pini*, *Lophodermium seditiosum*, and related species cause needle cast. Various species of rust and cenangium are also damaging. *Cronartium asclepiadeum* infests primarily Scots pine. Pine twisting rust (*Melampsora pinitorqua*) is a dioecious rust that causes typical twisting of shoots, especially in Scots pine (Fjellborg 2009). Naemacyclus needle cast, which causes browning and needle dieback, is caused by the fungus *Cyclaneusma minus*. Among the wood-destroying fungi are fire sponge, *Onnia triquetra*, crisped sparassis, honey fungus, or velvet-top fungus (Businský & Velebil 2011; Pešková & Čížková 2015). The sawfly species *Diprion pini* and *Neodiprion sertifer* can cause severe defoliation, making the tree susceptible to attack by other pests (Virtanen et al. 1996; Langström et al. 2001). Scots pine is also attacked by *Ips acuminatus*, *Pityogenes chalcographus*, *Tomicus piniperda*, *Tomicus minor*, *Phaenops cyanea*, and *Ips typographus*, which can also be a vector of various fungal pathogens, such as *Armillaria ostoyae* (Kirschner et al. 2001; Jankowiak & Hilszczański 2011; Giordano et al. 2013; de Rigo et al. 2016). The most important pest of pine seedlings cannot be neglected, namely the pine weevil (*Hylobius abietis* L.) (Modlinger 2015; Kovalchuk et al. 2015; Lundborg et al. 2016). New seedlings and individuals of natural regeneration can also be attacked by *Armillaria mellea* (Nárovcová 2010). For these reasons, fungal pathogens and nnot only bark insects in pine stands need to be given increased attention, and remediation measures should be implemented quickly in case of their occurrence (Zahradník & Zahraníková 2014).

Dieback of pine seedlings and saplings is also caused by biotic factors, especially fungi of the genera *Fusarium* and *Alternaria* (Petersson & Örlander 2003; Hódar & Zamora 2004; Dobbertin et al. 2007; Wermelinger et al. 2008; Nowakowska & Oszak 2008; Rigling et al. 2010; Zweifel et al. 2012; Mutlu et al. 2016), and abiotic factors, primarily drought (Oleksyn et al. 1994; Prus-Głowacki & Godzik 1995; Baquedano & Castillo 2006; Sudachkova et al. 2009). The seeds of pine trees can be eaten by birds (crossbills, woodpeckers), rodents (squirrels, voles, various mice), and, as a dietary supplement, by some carnivores (marten, mink, sable). Young pine needles are consumed by game, birds (capercaillie), and caterpillars of many insect species, which can cause considerable damage (Musil & Hamerník 2007). Cloven-hoofed game also inflicts damage on Scots pine by browsing and bark-stripping, yet it is a very resistant tree species compared to spruce or fir (Cukor et al. 2022).

9. Conclusion

Scots pine is a tree species resistant to many environmental factors; it is a fast-growing Eurasian pine that is one of the most economically significant coniferous tree species in the Czech Republic and Europe. In suitable habitats, it has a high production potential and can provide high-quality, easily workable timber for various construction purposes and furniture. This is of considerable importance in terms of carbon sequestration and adaptation to ongoing climate change. Scots pine, due to its pioneering strategy, is also an outstanding reclamation tree. Until recently, it was also considered to be a drought-tolerant species because of its deep taproot, although this is now proving to be a disadvantage due to the fact that the water table is dropping. Nevertheless, it is still a relatively resistant species to climatic extremes compared to other tree species. In the future, however, it is crucial to focus on a detailed and comprehensive study of European Scots pine provenances in the context of silviculture under climate change. Yet, in light of the increasing needs of society, a study of the non-productive functions of pine stands is also essential.

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