



Black locust—Successful invader of a wide range of soil conditions



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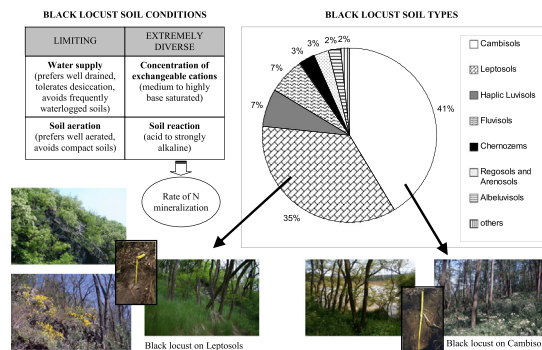
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HIGHLIGHTS

- We provided an overall assessment of black locust soil conditions.
- Black locust tolerates extremely diverse soil physical–chemical properties.
- Black locust seems to be limited by water supply and soil aeration.
- The most common are young soils (Cambisols, Leptosols and Arenosols).
- Species composition in BL stands was mostly affected by soil reaction.

GRAPHICAL ABSTRACT



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ABSTRACT

Black locust (*Robinia pseudoacacia*, BL), a species native to North America, has successfully invaded many types of habitats over the world. This study provides an overall assessment of BL soil conditions to determine the range of physical–chemical soil properties it can tolerate. 511 BL stands (for the soil types) and 33 permanent plots (for the soil chemistry) were studied in the Czech Republic. Relationships among different environmental variables (physical–chemical soil properties, vegetation characteristics and habitat conditions) were investigated and variables with the highest effect on species composition were detected. The results were compared with data in the literature for other parts of the secondary and native distributions of this species. This assessment showed that BL is able to tolerate extremely diverse soil physical–chemical conditions, from extremely acid to strongly alkaline, and from medium to highly base saturated soils with a gradient of different subsurface stoniness. Soil nitrate, N mineralization and nitrification rates also varied considerably and the concentrations of exchangeable phosphorus and ammonium were consistently low. N mineralization rate, incubated inorganic nitrogen and nitrates were positively correlated with base saturation and cation exchange capacity. The most common soil types were young soils (Cambisols, Leptosols, Arenosols, and coarsely textured Fluvisols). BL seems to be limited by water supply and soil aeration and prefers well aerated and drained soils, and tolerates desiccation but avoids compact soils and areas where the soils are frequently waterlogged. On steep slopes, BL was less vigorous, stunted and less competitive. By contrast, the tallest BL trees were found on sandy soils in a flat landscape. Number and share of nitrophytes in the herb layer were positively related to basic bedrock, soil reaction and N–NO₃/N ratio. Soil reaction was determined as the most important environmental characteristic explaining the variability in BL species composition in the Czech Republic.

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Abbreviations: Ass, association; BL, black locust; BS, base saturation; C, total carbon; CCA, canonical correspondence analysis; CEC, cation exchange capacity; C_{org}, organic carbon; PCA, principal component analysis; P_{ex}, exchangeable phosphorus; r_s, Spearman's nonparametric correlation coefficient.

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1. Introduction

Black locust (*Robinia pseudoacacia*), a nitrogen fixing tree belonging to the family *Fabaceae*, was introduced from its native range in North America (Fowells, 1965; Huntley, 1990) to other continents and currently is naturalized in Europe, temperate Asia, Australia, New Zealand, northern and southern Africa and temperate South America (Weber, 2003). In its native range, BL is listed as a component of mixed mesophytic forests and also readily colonizes open sites created by fire, floods, logging or storms (Boring and Swank, 1984a). The degree of invasion of different habitats in Europe differs (Chytrý et al., 2008). Chytrý et al. (2005) state that *R. pseudoacacia* is one of the top 10 neophytes with the broadest habitat range. It spreads mostly vegetatively by means of its aggressive root and trunk coppice shoots, whereas the seedlings are successful only on bare soil. The most invaded natural habitats include thermophilous grasslands (Kleinbauer et al., 2010; Vítková and Kolbek, 2010), sandy soils, shrubby and azonal forests, such as thermophilous oak, dry acidophilous oak, dry pine (Vítková and Kolbek, 2010), maple-lime (Kleinbauer et al., 2010), chestnut and riparian forests (Brus, 2006; Motta et al., 2009; Benesperi et al., 2012; González-Muñoz et al., 2013), urban-industrial wastelands, fallow lands, disturbed traffic corridors and at burnt sites (e.g. Dzwonko and Loster, 1997; Kim and Lee, 2005; Řehouňková and Prach, 2008; Yükses, 2012; Kowarik et al., 2013). Both climate change (Kleinbauer et al., 2010) and planting for forestry or landscaping (Kowarik, 2003) are likely to increase its distribution and possibly also enlarge the range of habitats it is able to colonize, including Central European zonal forests (Essl et al., 2011).

BL causes homogenization of the tree layer and creates specific stands, highly different from autochthonous plant communities (e.g. Wendelberger, 1954; Montagnini et al., 1991; Peloquin and Hiebert, 1999; Von Holle et al., 2006; Taniguchi et al., 2007; Kolbek and Jarolímek, 2008; Vítková and Kolbek, 2010; Benesperi et al., 2012; Sitzia et al., 2012). The strong effect of BL on native vegetation is probably caused by increased nutrient availability associated with the nitrogen fixing ability of the symbiotic *Rhizobium* bacteria (37 strains) occurring in BL root nodules (Batzli et al., 1992; Ferrari and Wall, 2007). Symbiotic fixation is an important input for the nitrogen cycle in BL stands, more important than litter mineralization or other sources (e.g. Liu and Deng, 1991; Tian et al., 2003; Williard et al., 2005). In its native range (southern Appalachian forests) it can fix 33 to 75 kg N ha⁻¹ year⁻¹, with a particularly high capacity for N₂ fixation in early to intermediate stages of secondary succession (Boring and Swank, 1984b). Symbiotic fixation recorded in its secondary range is even greater, 110 kg N ha⁻¹ year⁻¹ by four-year-old trees in Austria (Danso et al., 1995) and 112.3 kg N ha⁻¹ year⁻¹ by 25-year-old south-facing stands in Central Korea (Noh et al., 2010). According to Liu and Deng (1991), the main factors determining nitrogen fixation are soil acidity and available phosphorus.

Occurrence of nitrogen fixing trees in forest ecosystems results in subsequent increase in the soil nitrogen pool, nitrification and net N-mineralization rates and higher availability of mineral forms of nitrogen (ammonium, NH₄⁺ and nitrate, NO₃⁻) in both soil and solution (e.g. Binkley et al., 1982; Van Miegroet and Cole, 1984; Montagnini et al., 1991; Montagnini and Sancho, 1994). Enriched level of soil nitrogen is not only a result of release from decaying N-rich BL leaves and roots, but also from root exudates, which contain 1–2% of recently fixed N (Uselman et al., 1999; Tatenno et al., 2007). High rates of soil nitrification can result in a decrease in pH values of litter and topsoil and potentially a greater leaching of Ca, Mg, K, Na and PO₄-P ions from the soil (Van Miegroet and Cole, 1984). However, some authors, e.g. Montagnini and Sancho (1994) or Rice et al. (2004), have not confirmed the supposed acidification effect of nitrification. The allelopathic potential of BL has only been recorded in the laboratory (Nasir et al., 2005; Csiszár, 2009).

The first recorded BL plantation in the Czech Republic was in 1785 (Nožička, 1957). It was planted mainly in former pastures on steep eroded hillsides along rivers (especially Vltava—Fig. 1, Berounka, Sázava and Dyje) in order to stabilize sandy soils, aeolian sands and coarse fluvial deposits (Elbe lowland, Fig. 2, and parts of South Moravia) and ameliorate poor soils, and around transport corridors (Kolbek et al., 2004). Currently, it covers approximately 12,000 ha, i.e. 0.46% of the total forested area in the Czech Republic and occurs in most areas of the country below 500 m a.s.l. The largest stands are concentrated in the warmest part of the country, preferring south-facing slopes of 30–40° (Vítková et al., 2004). As a source of fast growing and valuable wood ameliorating poor soils it is widely used in forest plantings, resulting in rapid spread to natural systems (covering 0.2% of Czech Republic “NATURA 2000” sites). From phytosociological point of view, there are four types of *Robinia* stands with different soil conditions: (1) **species-rich nitrophilous stands** growing on alkaline to acid bedrocks (ass. *Chelidonio majoris-Robiniatum pseudoacaciae*) (Sádlo et al., 2014; Fig. 3); (2) **species-poor grassy stands**—tall BL forests with straight trunks (ass. *Arrhenathero elatioris-Robiniatum pseudoacaciae*) on strongly acid quaternary deposits (Sádlo et al., 2014; Fig. 2); (3) **open and mesic stands** with the herb layer dominated particularly by *Poa nemoralis* (ass. *Poa nemoralis-Robiniatum pseudoacaciae*) on upper and middle slopes on siliceous bedrock in deep river valleys (Sádlo et al., 2014); and (4) **dwarf and shrubby stands** on thermophilous rocky slopes (ass. *Melico transsilvanicae-R. pseudoacaciae*; Sádlo et al., 2014; Fig. 1).

The adaptability of BL to different habitat conditions and an absence of serious natural enemies in its secondary range makes it an economically attractive tree species, especially for short-rotation energy plantations (e.g. Grünewald et al., 2009; Rédei et al., 2010) and soil reclamation (e.g. Kim and Lee, 2005; Qiu et al., 2010; Yükses, 2012). However, regular silvicultural treatment is needed to maintain the short-rotation plantation productivity because of relatively low production of litter and periodic removal of organic matter (Vasilopoulos et al., 2007). Some of the economic benefits of BL, such as its vitality, excellent sprouting ability, abundant production of seed and improvement of soil conditions by nitrogen fixation, become a problem after the plantation is abandoned. Stumps of harvested trees resprout rapidly (e.g. Krízík and Körmöcz, 2000) and eradication with the aim of restoring original plant communities is very difficult, costly and time-consuming (e.g. Hruška, 1991; Peloquin and Hiebert, 1999; Halassy and Török, 2004; Böcker and Dirk, 2004, 2007; Malcolm et al., 2008; Yong-Chan et al., 2009; Vítková, 2011; Ivajnsič et al., 2012; Skowronek et al., 2014). Natural succession of abandoned BL plantations towards the natural communities is slow; Vasilopoulos et al. (2007) did not record any succession towards the nearby natural riparian forests even after 14 years. This is in marked contrast to the BL native range, where after 15–30 years BL is replaced by more competitive tree species (Boring and Swank, 1984a).

Although BL is the second most widely planted woody species in the world (Keresztesi, 1988), comprehensive information on its soil conditions is missing. From its native range, the data are rare and do not cover the range of environmental variability, coming solely from the Coweeta LTER site (southern part of the native range; Boring and Swank, 1984a,b; Montagnini et al., 1986; White et al., 1988; Montagnini et al., 1989; Montagnini et al., 1991). Although there are more data available from BL secondary range (e.g. Dzwonko and Loster, 1997; Šimonovič et al., 2001; Noh et al., 2010; Yanna et al., 2013), they usually come from isolated unevenly distributed sites only. Our specific objectives were to (1) assess the overall environmental variability of soil types invaded by *R. pseudoacacia* in the traditional Central European landscape (Czech Republic); (2) determine the range of physical-chemical soil characteristics tolerated by BL in the Czech Republic; (3) evaluate the most important characteristics influencing species composition and amount of nitrophytes in BL stands and (4) compare our findings with the literature data from the native

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