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

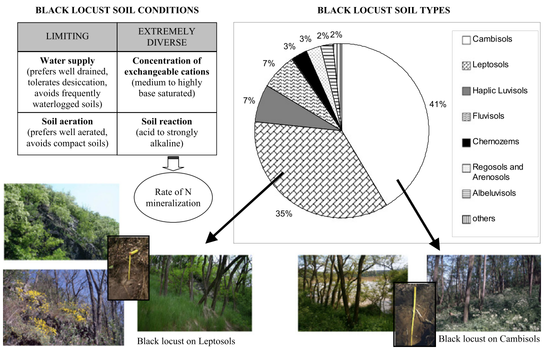
Michaela Vítková [a,*], Jaroslav Tonika [b], Jana Müllerová [a]

[a] Institute of Botany, Academy of Sciences of the Czech Republic, 25243 Průhonice, Czech Republic
[b] Faculty of Science, Charles University, Institute for Environmental Studies, Benátská 2, 12801 Praha 2, Czech Republic

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–NO_3/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.

[*] Corresponding author. Tel.: +420 271015241; fax: +420 271015105.
E-mail addresses: michaela.vitkova@ibot.cas.cz (M. Vítková), jaroslav.tonika@gmail.com (J. Tonika), jana.mullerova@ibot.cas.cz (J. Müllerová).

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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, shrubbery 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; Řehounková and Prach, 2008; Yüksek, 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 N_2 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, NH_4^+ and nitrate, NO_3^-) 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; Tateno 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 PO_4–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-Robinietum pseudoacaciae*) (Sádlo et al., 2014; Fig. 3); (2) **species-poor grassy stands—**tall BL forests with straight trunks (ass. *Arrhenathero elatioris-Robinietum 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. *Poo nemoralis-Robinietum 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; Yüksek, 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. Krízsik and Körmöczi, 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; Ivajnšič 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

Fig. 1. Rocky habitat invaded by *Robinia pseudoacacia* in the valley of the Vltava River (Vítková, May 2012).

and other parts of the secondary range to detect similarities in BL soils in different parts of the distribution range.

2. Methods

2.1. Study area

Due to its history and geomorphology, the Czech Republic can be considered as an example of traditional Central European landscape. In our study, 33 permanent plots each with an area of 250 m^2 were established in 1997–1999 (Fig. 4) in particular types of vegetation (based on a syntaxonomical approach; Vítková and Kolbek, 2010), covering the diversity of bedrocks, soil types and different habitats (Table 1). On each plot, phytosociological relevé using a seven-grade scale of abundance and dominance (Braun-Blanquet (1964) was recorded. Nitrophilous species were determined using Ellenberg nitrogen indicator value six or higher (Ellenberg et al., 1991).

The annual temperature ranged between 6.6 and 9.1 °C, annual precipitation 494–604 mm (moderate Atlantic-continental climate), altitude 150–380 m a.s.l. and slope 0–50° (Table 1). The plots were selected in unmanaged successionally mature (at least 40 years old) BL stands growing in open landscape or suburban areas. Most of the sites originated as spontaneous BL invasion into natural communities, with about 20% of the stands self-regeneration from plantations established at the end of the 19th to the middle of the 20th century. None of the forests studied were subjected to recent forest management.

2.2. Soil characteristics

At each of the 33 permanent plots a test pit was dug, soil profile was described and samples of bedrocks, soils and lumps of soil from A and B horizons were collected. Lumps of soil were impregnated with retin Epofix-Struers both before and after sectioning. The surface of each thin section was ground down using carborundum (600). Thin sections of soil were prepared by the Czech Geological Survey and used to

Fig. 2. Grassy black locust stand on Arenosol and aeolian sand bedrock (Vítková, June 2011).

Fig. 3. Nitrophilous black locust stand on Cambisol and granodiorite bedrock at the base of slope (Vítková, June 2013).

supplement knowledge on the petrological composition of rocks and physical–chemical properties of the soil.

Soil was sampled twice, at the end of the growing season (after a hot and dry summer when legumes mature, which occurred in the second half of September 1999) and at the beginning of the growing season (after a cold and wet spring, before black locust bud burst, which occurred in the second half of April 2000). Each 1 kg sample was collected separately for A and B horizons from five randomly located points. Fresh soil was immediately sifted in the field through a 2 mm sieve; fine earth was transported to the laboratory in a cooler and used to determine ammonium (NH_4^+) and nitrates (NO_3^-). Other soil analyses (pH, base saturation, exchangeable phosphorus, carbonate concentration, total carbon and nitrogen, and net N mineralization and nitrification rates) were carried out on air-dried fine earth, some only for one growing season (see Table 2). Unsifted fresh soil samples in the field were taken with the shovel into the plastic bags to assess the subsurface stoniness and into the closable aluminous desiccant dishes to determine gravimetric soil moisture and dry matter according to ISO 11465 (1993). Stoniness was calculated in percentage as the ratio of the weight of desiccated skeleton (inorganic particles larger than 2 mm) and total weight of dry soil sample. Gravimetric soil moisture was expressed also in percentage as the mass of water per unit mass of dry soil (105 °C). Dry matter is dry soil residue after drying at 105 °C, expressed as a percentage of soil dried in the air.

Active pH was measured according to McLean (1982). Methods of Moore and Chapman (1986) were used to determine base saturation

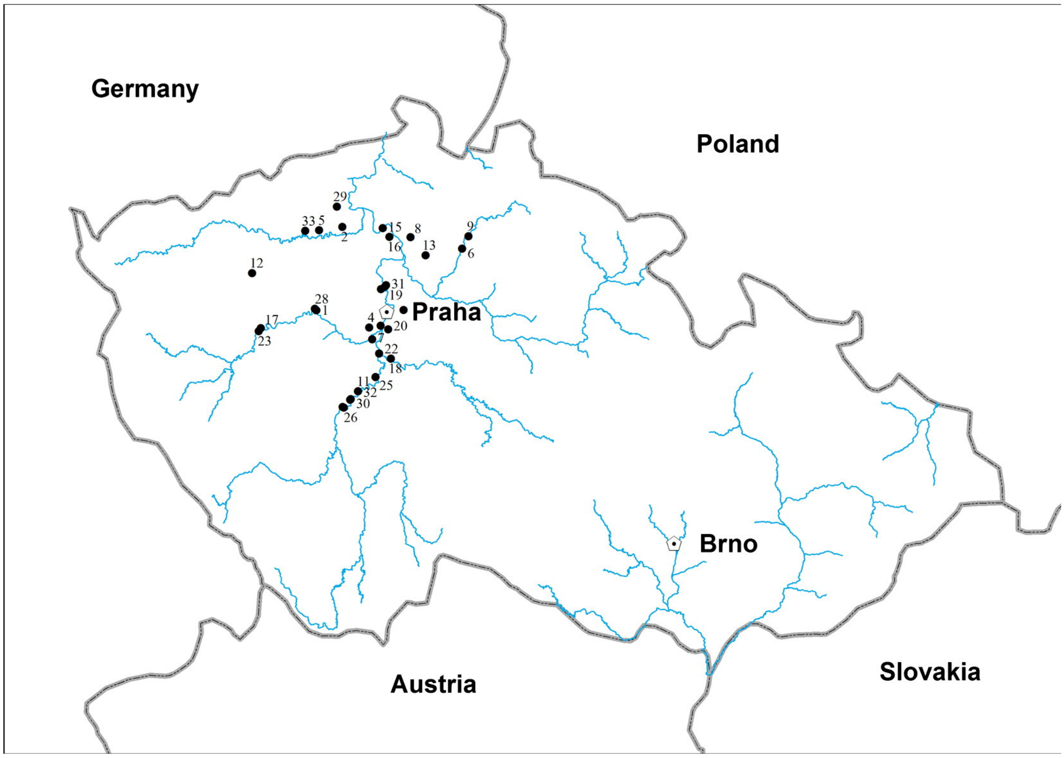

Fig. 4. Black locust stands studied in the Czech Republic.

Table 1
Habitat characteristics of black locust stands studied in the Czech Republic.

Number	Type	Syntaxon	Soil type	Bedrock	Altitude	Slope	Aspect	Annual precipitation	Annual temperature
1	Species-rich nitrophilous	*Chelidonio-Robinietum*	Eutric leptosol	Spilite	310	30	203	541	7.9
2	Species-rich nitrophilous	*Chelidonio-Robinietum*	Eutric leptosol	Basalt	360	35	158	539	7.5
3	Species-rich nitrophilous	*Chelidonio-Robinietum*	Rendzic leptosol	Diabase	285	30	158	495	9.0
4	Species-rich nitrophilous	*Chelidonio-Robinietum*	Rendzic leptosol	Limestone	315	30	180	511	8.4
5	Species-rich nitrophilous	*Chelidonio-Robinietum*	Rendzic leptosol	Olivine basalt	270	10	135	532	7.8
6	Species-rich nitrophilous	*Chelidonio-Robinietum*	Calcic leptosol	Calcareous sandstone	240	40	180	530	8.3
7	Species-rich nitrophilous	*Chelidonio-Robinietum*	Cambic leptosol	Paleozoic schist	220	35	158	496	9.1
8	Species-rich nitrophilous	*Chelidonio-Robinietum*	Arenosol	Quarzite sandstone	210	30	113	513	8.2
9	Species-rich nitrophilous	*Chelidonio-Robinietum*	Lithic cambisol	Calcareous sandstone	240	30	203	535	8.2
10	Species-rich nitrophilous	*Chelidonio-Robinietum*	Dystric cambisol	Quarcite	240	20	158	494	9.0
11	Species-rich nitrophilous	*Chelidonio-Robinietum*	Dystric cambisol	Quartz diorite	280	25	158	566	8.5
12	Species-rich nitrophilous	*Chelidonio-Robinietum*	Fluvisol	Carbon-Permian sandstone	330	30	225	577	7.6
13	Species-rich nitrophilous	*Chelidonio-Robinietum*	Fluvisol	Calcareous sandstone	230	20	180	508	8.4
14	Species-poor grassy	*Arrhenathero-Robinietum*	Arenosol	Eolian sands	150	0	–	498	8.6
15	Species-poor grassy	*Arrhenathero-Robinietum*	Arenosol	Eolian sands	150	0	–	498	8.6
16	Species-poor grassy	*Arrhenathero-Robinietum*	Arenosol	Eolian sands	190	0	–	507	8.3
17	Open and mesic	*Poo-Robinietum*	Typic leptosol	Proterozoic schist	290	45	113	573	8.0
18	Open and mesic	*Poo-Robinietum*	Typic leptosol	Amphibole schist	200	35	158	524	8.9
19	Open and mesic	*Poo-Robinietum*	Cambic leptosol	proterozoic schist	210	50	270	498	8.4
20	Open and mesic	*Poo-Robinietum*	Cambic leptosol	Proterozoic schist	280	35	270	511	8.8
21	Open and mesic	*Poo-Robinietum*	Cambic leptosol	Amphibolite	300	40	135	625	7.7
22	Open and mesic	*Poo-Robinietum*	Lithic cambisol	proterozoic Schist	240	45	338	520	8.8
23	Open and mesic	*Poo-Robinietum*	Lithic cambisol	Phylite	350	35	225	586	7.8
24	Open and mesic	*Poo-Robinietum*	Lithic cambisol	Syenodiorite	310	30	203	574	8.5
25	Open and mesic	*Poo-Robinietum*	Lithic cambisol	Amphibole schist	300	40	158	555	8.4
26	Open and mesic	*Poo-Robinietum*	Lithic cambisol	Amphibole schist	350	35	113	604	8.1
27	Open and mesic	*Poo-Robinietum*	Dystric cambisol	Lydite	250	30	113	482	8.9
28	Open and mesic	*Poo-Robinietum*	Arenic cambisol	Proterozoic schist	290	35	203	527	8.3
29	Open and mesic	*Poo-Robinietum*	Haplic luvisol	Basalt	380	20	203	580	6.6
30	Dwarf and shrubby	*Melico-Robinietum*	Lithic leptosol	granodiorite	330	45	90	574	8.5
31	Dwarf and shrubby	*Melico-Robinietum*	Lithic leptosol	Spilite	260	30	203	497	8.5
32	Dwarf and shrubby	*Melico-Robinietum*	Lithic cambisol	Quartz diorite	300	30	158	566	8.5
33	Dwarf and shrubby	*Melico-Robinietum*	Chernozem	Olivine nephelinite	260	25	203	557	7.5

by exchangeable cations (Ca^{2+}, Mg^{2+}, H^+, Al^{3+}) using titration and atomic absorption spectroscopy (AAS). Exchangeable phosphorus (P_{ex}) was measured photometrically using a UV–vis Spectrometer Unicam 400 (Olsen, 1982). Total carbon (C) and nitrogen (N) content were analyzed according to Monar (1972) with combustion of soil followed by determination of oxides. Carbonate concentration was determined by following ISO/DIS 10693 (1995). Organic carbon (C_{org}) was calculated as the difference between total carbon and carbonate carbon. Nitrogen mineralization and nitrification were measured by incubating in aerobic laboratory incubators for 28 days following ISO 14238 (1997), and after moistening (3 ml of water added to each 10 g of sample) and pre-incubation for one week at 28 °C. The results of soil analyses were converted to dry matter to eliminate the different water content among soil samples. Cation exchange capacity (CEC), base saturation (BS), and C_{org}/N, N/P_{ex}, $N–NO_3/N$ and $N–NH_4/N$ ratios were calculated from the results of the soil analyses according to Sparks et al. (1996). Nitrification tests were carried out in the Research Institute for Soil and Water Conservation (VÚMOP) and other laboratory analyses in the Analytic Laboratory of the Institute of Botany CAS.

2.3. Soil types

Assessment of the main soil types, where BL is naturalized, was based on the analysis of 511 different BL stands in the Czech Republic. 310 sites were field surveyed by the authors in 1998 to 2013, describing habitat characteristics including soil type, vegetation and recent management (unpubl.). The resting 201 stands were excerpted from literature (Svobodová, 1952; Blažková, 1961; Větvička, 1961; Sofron, 1964; Němec, 1981) and Czech National Phytosociological Database (Chytrý and Rafajová, 2003), and their soil types derived from soil maps at a scale of 1:50000 (Czech Geological Survey). The nomenclature of soil types follows IUSS (2006).

2.4. Data analysis

Data was evaluated using statistical packages NCSS 6.0 and Canoco 5 (Šmilauer and Lepš, 2014). Inter-correlations between two measured soil characteristics were determined by calculating Spearman's non-parametric correlation coefficient (r.s.). Changes of soil characteristics with the soil depth were tested using paired two-sample *t*-tests. An unconstrained ordination method was used to detect relationships among habitat conditions (altitude, slope, aspect, annual precipitation, annual temperature, soil type, bedrock), vegetation characteristics (syntaxonomical unit, tree height, cover of tree, shrub and herb layer, total number of species, number of nitrophytes, and share of nitrophytes cover to total cover of the herb layer) and physical–chemical soil properties (see Chapter 2.2) in multidimensional space. These 55 variables studied in 33 permanent plots were used as response data. Most of them were quantitative but soil type, bedrock, aspect and syntaxonomical unit were used as factors. Aspects between 135 and 225° (from SE to SW) were coded as “warm”, the others as “cold”. Ion concentrations with differences larger than one order of magnitude were log transformed before Canoco analysis. Because response data were not compositional, principal component analysis (PCA) with scaling and standardizing was performed. To decide which of the soil properties describe best the variability in species composition of BL stands, we used constrained ordination with phytosociological relevés as response data and soil properties as explanatory variables. Due to long gradient (4.5 SD units) canonical correspondence analysis (CCA) with forward selection was chosen. The Monte Carlo permutation test with 999 unrestricted permutations was used to test the significance of the constrained ordination model. Comparison of results between constrained and unconstrained ordination applied to the same response

Table 2
Physical–chemical characteristics of the soils in black locust stands growing in different parts of the world.

		Native range	Secondary range							Secondary range					
		USA[1,2]	Poland[3]	Slovakia[4]	Croatia[5]	Korea[6]	China[7,8]			Czech Republic					
	Depth (cm)	North Carolina March[1]/July[1]/Average[2]								Min		Max		Average (s.d.)	
			September	May	–	–	October[7]/July[8]			April	September	April	September	April	September
Number of plots		3	1	3	1	2	2	Min	Max	33					
Annual average temperature [°C]		13	7.7	9.5	10.1	12.2	15.4/8.8			7.5		9.1		8.2	
Annual precipitation [mm]		1810	686	600–650	950	1344	1106.5/505			482		625		542	
Altitude [m a.s.l.]		1000	242	140–230	110–135	100–120	447/1431			150		380		270	
Stoniness [%]	0–10	–	–	–	–	25–26	–	25	26	0	–	90	–	31 (23)	–
	11–25	–	–	–	–	–	–	–	–	0	–	80	–	#28 (15)	–
Soil moisture [%]	0–10	29.7[2]	3.0	–	–	27.8–29.3	25.9/–	3.0	29.3	7.0	2.1	133.1	86.1	30.8 (27.2)	15.0 (17.3)
	11–25	28.5[2]	–	–	–	–	–	–	–	4.8	1.2	118.4	20.3	24.0 (29.2)	7.3 (5.1)
pH (KCl)	0–10	–	–	3.6–5.2	4.2	–	–	3.6	5.2	2.8	3.0	7.6	7.2	4.7 (1.4)	4.5 (1.3)
	11–25	–	–	4.0–5.2	4.9	–	–	4.0	5.2	3.1	3.5	8.0	7.6	4.7 (1.6)	4.8 (1.6)
pH (H_2O)	0–10	–/5.8/5.6[2]	5.6	4.0–5.2	5.4	4.3–4.6	4.6/8.8	4.0	8.8	3.4	3.5	7.9	7.6	5.2 (1.3)	5.8 (1.3)
	11–25	5.7[2]	–	4.6–4.9	5.7	–	–	4.6	5.7	3.65	4.2	8.3	8.1	5.5 (1.4)	5.6 (1.5)
Ca^{2+} [mg/kg]	0–10	735/773	230	–	–	–	–	230	230	–	264	–	20,956	–	4840 (4888)
	11–25	307/322	–	–	–	–	–	–	–	–	112	–	15,828	–	3600 (4396)
Mg^{2+} [mg/kg]	0–10	149/151	8.8	–	–	–	–	8.8	8.8	–	13	–	1945	–	404 (413)
	11–25	86/82	–	–	–	–	–	–	–	–	29	–	2438	–	474 (664)
Al^{3+} [mg/kg]	0–10	–	–	–	–	–	–	–	–	–	0	–	2363	–	523 (648)
	11–25	–	–	–	–	–	–	–	–	–	0	–	1465	–	386 (455)
H^+ [mg/kg]	0–10	55.0/62.9	–	–	–	–	–	–	–	–	0	–	44.9	–	7.5 (8.8)
	11–25	52.4/62.6	–	–	–	–	–	–	–	–	0	–	15.1	–	5.6 (4.6)
CEC [meq/100 g]	0–10	10.7/11.7	1.2	–	–	11.0–15.1	–	1.2	15.1	–	5.7	–	113.3	–	34.1 (25.0)
	11–25	7.67/8.73	–	–	–	–	–			–	4.0	–	99.2	–	26.8 (25.0)
BS [%]	0–10	47/45	–	–	–	–	–	–	–	–	31	–	100	–	74 (24)
	11–25	21/27	–	–	–	–	–	–	–	–	18	–	100	–	69 (29)
NO_3–N [mg/kg]	0–10	4.5/3.3/11.7[2]	35.5	–	–	–	–	35.5	35.5	2.1	0.0	30.1	203.4	12.1 (9.2)	24.3 (34.4)
	11–25	1.6/0.9/3.3[2]	–	–	–	–	–	–	–	0.1	0.0	13.4	12.1	5.6 (4.3)	3.4 (3.2)
NO_3–N/N [%]	0–10	0.37/0.23/0.35[2]	–	–	–	–	–	–	–	0.02	0.00	0.71	0.81	0.18 (0.16)	0.34 (0.20)
	11–25	0.27/0.14/0.23[2]	–	–	–	–	–	–	–	0.00	0.00	0.93	0.65	0.27 (0.27)	0.16 (0.16)
NH_4–N [mg/kg]	0–10	3.9/2.6/4.9[2]	13.6	–	–	–	–	13.6	13.6	1.7	1.5	45.2	33.7	7.8 (8.0)	6.8 (6.2)
	11–25	3.31/2.18/1.68[2]	–	–	–	–	–	–	–	0.9	1.3	9.0	28.6	3.5 (1.9)	4.6 (6.3)

NH_4–N/N [%]	0–10	0.32/0.18/0.15[2]	–	–	–	–	–	–	–	0.03	0.02	0.28	0.23	0.10 (0.07)	0.10 (0.06)
	11–25	0.57/0.35/0.11[2]	–	–	–	–	–	–	–	0.02	0.03	0.77	1.61	0.17 (0.14)	0.26 (0.36)
N [%]	0–10	0.12/0.14/0.33[2]	0.10	0.06–0.30	0.25	0.08–0.24	0.47/0.70	0.06	0.70	0.18	0.18	2.61	2.55	0.89 (0.60)	0.71 (0.52)
	11–25	0.06/0.06/0.15[2]	–	0.04–0.13	–	–	–	0.04	0.13	0.06	0.09	2.14	0.39	0.33 (0.40)	0.21 (0.08)
C–CO_3^{2-} [%]	0–10	–	–	–	–	–	–	–	–	0.00	0.00	0.44	1.44	0.06 (0.10)	0.07 (0.25)
	11–25	–	–	–	–	–	–	–	–	0.00	0.00	1.02	2.92	0.14 (0.27)	0.21 (0.70)
C [%]	0–10	4.33[2]	1.05	–	3.50	–	5.75/–	1.05	5.75	2.16	1.96	27.64	31.31	10.97 (7.40)	8.84 (7.12)
	11–25	2.23[2]	–	–	0.40	–	–	0.40	0.40	0.68	1.18	19.55	5.07	3.72 (3.65)	2.57 (1.27)
C_{org} [%]	0–10	2.38/2.63	–	0.58–5.00	–	1.96–4.12	–/5.90	0.58	5.9	1.94	1.96	27.64	31.31	10.91 (7.43)	8.78 (7.12)
	11–25	1.15/1.26	–	0.05–0.16	–	–	–	0.05	0.16	0.55	1.18	19.07	5.07	3.58 (3.61)	2.35 (1.15)
C_{org}/N or *C*/*N*	0–10	19.7/18.3/13.6[2]	10.5	1.4–16.7	13.2	17.2–24.5	12.2/8.4	1.4	24.5	9.5	10.3	15.3	15.9	12.3 (1.6)	12.0 (1.4)
	11–25	20.3/21.2/15.2[2]	–	1.0–1.3	–	–	–	1.0	1.3	4.0	8.2	15.0	15.6	11.5 (2.4)	11.3 (1.7)
P_{ex} [mg/kg]	0–10	10.7/9.8	35.6	–	–	9.1–18.4	–/2.5	2.5	35.6	–	1.5	–	110.9	–	20.9 (20.9)
	11–25	5.7/3.9	–	–	–	–	–	–	–	–	0.2	–	45.2	–	11.4 (12.1)
N/P_{ex}	0–10	114/145	–	–	–	–	–	–	–	–	36	–	3259	–	691 (689)
	11–25	102/159	–	–	–	–	–	–	–	–	27	–	9556	–	941 (2248)
Nitrification [mg/kg/28 days]	0–10	34.5/34.3/36.0[2]	–	–	–	–	–	–	–	−14.2	–	299.6	–	81.2 (66.0)	–
	16–30	12.0/10.2	–	–	–	–	–	–	–	–	–	–	–	–	–
Ammonification [mg/kg/28 days]	0–10	−3.6[2]	–	–	–	–	–	–	–	−71.6	–	108.9	–	−24.4 (34.6)	–
N mineralization [mg/kg/28 days]	0–10	34.9/30.9/33.0[2]	–	–	–	–	–	–	–	−13.8	–	327.1	–	56.8 (67.1)	–
	16–30	12.2/7.4	–	–	–	–	–	–	–	–	–	–	–	–	–

[#] Blocks of rock or bedrock are not included in stoniness.

[1] Montagnini et al. (1986)—2 localities (Coweeta hydrologic laboratory), March/July 1982.

[2] Montagnini et al. (1989)—1 locality (Coweeta), average values of soil properties from April to October 1984.

[3] Dzwonko and Loster (1997)—1 locality (Kraków region).

[4] Šimonovič et al. (2001)—3 localities (Záhorie).

[5] Vrbek and Pilaš (2011)—1 locality (Đurđevački pijesci).

[6] Noh et al. (2010)—2 localities (Seoul).

[7] Yanna et al. (2013)—1 locality (Zijin Mountain).

[8] Wang et al. (2012)—1 locality (Zhifangghou, Loess Plateau).

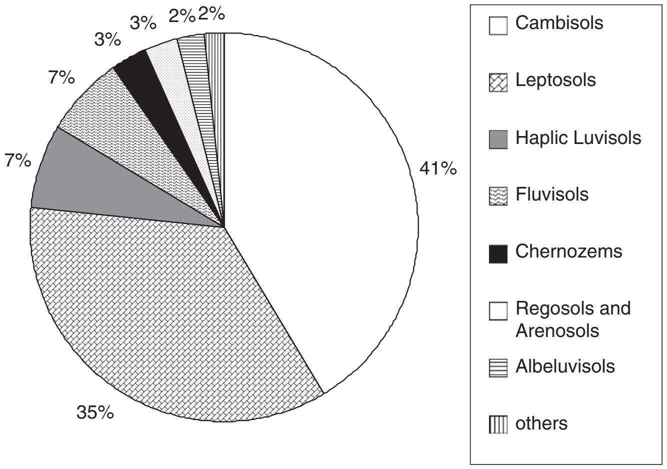

Fig. 5. The most common soil types under the black locust stands growing in the Czech Republic.

data (phytosociological relevés) allowed to evaluate percentage efficiency of constrained axis.

2.5. Literary comparison

All available data on BL physical–chemical soil characteristics published in international scientific journals or national journals in English or at least with an English abstract or summary were collected using Web of Science and Google Scholar. These were used for comparison of soil conditions in different parts of BL native and secondary range.

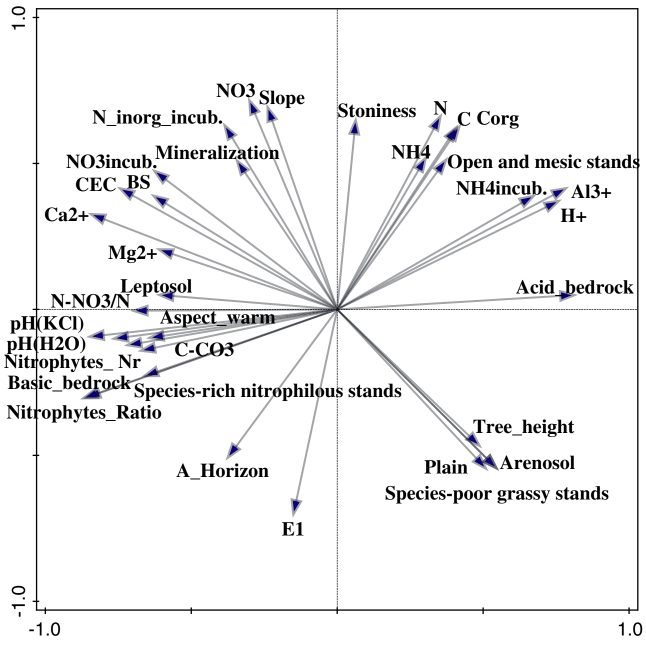

Fig. 6. PCA ordination diagram for 55 environmental variables—habitat conditions (altitude, slope, aspect, annual precipitation, annual temperature, soil type, bedrock), vegetation characteristics (syntaxonomical unit, tree height, cover of tree, shrub and herb layer, total number of species, number of nitrophytes, and percentage of nitrophytes in herb layer) and physical–chemical soil properties detected on 33 permanent plots. 35 best-fitting characteristics are shown. First two PCA axes explain 42% of the total variability. NH4incub. is concentration of N-NH_4 after incubation; NO3incub. and N_inorg_incub. have the same meaning for N-NO_3 and sum of N-NH_4 and N-NO_3.

3. Results and discussion

3.1. Soil types in Central European BL stands

In Central Europe, BL grows mostly on young soils in which horizon differentiation is beginning (86%; Fig. 5). Most frequent are Cambisols (41%; Fig. 5) with a weak, mainly brownish Cambic subsurface B horizon, which are the most common soils in the Czech Republic (45%). The second most abundant soils are azonal Leptosols (35%; Fig. 5) on river valley slopes in which the A horizon is either very shallow on hard (Lithic Leptosols) or highly calcareous material (Rendzic and Calcaric Leptosols), or deeper but extremely gravelly and/or stony soils. Their shallowness or stoniness implies low water holding capacity and serious limitation for vegetation cover. These conditions cause shrubby growth form of BL (up to 5 m tall) and decline its competitiveness in favour of drought-adapted native shrubs such as *Crataegus* sp., *Prunus spinosa* and *Rosa* sp. Erosion control was therefore the main reason for BL plantations (Fig. 1). At the bases of slopes, BL stands are usually found on azonal Fluvisols with a weak brown AC-profile (7%; Fig. 5). The last category of young soils under BL stands is Regosols and Arenosols on sandy soils (Fig. 2; 3% in Fig. 5). The later soil type proved to be the most suitable for BL growth (Fig. 6). Arenosols in the flat landscape of the Elbe River lowlands are often invaded by species-poor grassy BL forests with the BL tree height up to 30 m (Fig. 2).

All of the above mentioned soil type groups are well drained. The long-term filling of soil pores with stagnant groundwater is not usual. The deeper soils under BL stands are Haplic Luvisols (7%), Chernozems (3%) and Albeluvisols (3%; Fig. 5).

3.2. Physical–chemical properties in Central European BL stands

3.2.1. Stoniness

The range of subsurface stoniness varies from 0 to 90%, with less than 10% on eolian sand, sandstone and basaltoid bedrock. The most frequent are gravel and stony soils with more than 50% on Ordovician and Proterozoic schists, amphibolitic schists and spilites. Rocky outcrops are common.

3.2.2. Gravimetric soil moisture

In the Czech Republic, BL stands occur mostly on dry or drying out soils, with the two exceptions—a) Eutric Leptosols on spilite with biogenic aggregate formation caused by high edaphon activity and b) Dystric Cambisols at the base of lydite outcrops with a thick O_h-horizon, where the gravimetrically determined soil moisture content of fine earth was as high as 86.1% and 70.8% respectively even at the end of a hot and dry summer. After excluding these exceptions, the average soil moisture in A-horizon was 11%. The differences between localities were more marked after a wet spring when average soil moisture was up to 31%. The driest soils were recorded on weathered parent rocks with sandy eluvium (granodiorites, quartz diorites, syenodiorites) and eolian sands. After wet and cold springs, sands with dust particles between quartz grains were able to retain water. BL does not grow on wet soils in which the water has stagnated for a long period; however on such Arenosols in the Elbe River lowland, BL stands survived even a centennial flood. The only effect of this flood in 2003 was an increase in the cover of the nitrophilous species *Chelidonium majus* (probably due to nutrient enrichment).

3.2.3. Soil reaction, base saturation and soil carbonates

Soil reaction and degree of base saturation in BL stands varied greatly depending on parent rock. In the Czech Republic, BL grows in extremely acid soils over lying lydite ($pH(H_2O) = 3.4$), eolian sands (3.8) and Proterozoic schist (3.9), as well as in mildly alkaline soils on basalt (7.4), limestone (7.4), Ordovician schist (7.5), olivine nephelinite (7.6), Carbon-Permian sandstone (7.6) and moderately alkaline soil on calcareous sandstone (7.9). However, 69% of BL stands grow in extremely and very strongly acid soils.

Base saturation (BS) also varied greatly—from medium saturation (31–50%, e.g. Proterozoic schists, eolian sands, lydite or quartzite) to highly saturated (more than 75%; e.g. granodiorite, spilite, diabase, amphibolite or calcareous sandstone and limestone). Base saturation of A-horizon in BL stands was usually very good with an average value of 74% (Table 2). Low CEC values (less than 12 meq/100 g) were recorded for eolian sands and quarzite sandstone and very high values (more than 40 meq/100 g) for basic rocks (basalt, spilite, diabase or limestone). Calcium was the most important exchangeable cation with other elements playing only a marginal role. However, calcium content varied considerably depending on the type of bedrock (from 264 mg/kg on eolian sands up to 20956 mg/kg on spilite; Table 2). The highest concentration of Mg^{2+} was recorded for olivine nephelinite (1945 mg/kg), and the lowest for eolian sands (13 mg/kg). At nine localities with either extremely acid or very strongly acid soils on schist bedrock and clay minerals that served as a source of aluminum, BS was recorded in the Al cycle. Soils rich in carbonates were described on the following bedrocks: diabase, spilite, basanite, olivine nephelinite, limestone and calcareous and Carbon-Permian sandstones. On acid substrates, the carbonates were only present in the upper part of the A-horizon, which was rich in shells, especially those of the gastropod *Helix pomatia*.

Expected positive correlations between soil reaction and exchangeable calcium (r.s. = 0.782; $p < 0.001$), magnesium (r.s. = 0.604 and $p < 0.001$), CEC (r.s. = 0.547; $p = 0.001$) or BS (r.s. = 0.933; $p < 0.001$), and negative correlations between soil reaction and exchangeable aluminum (r.s. = −0.847; $p < 0.001$) or hydrogen (r.s. = −0.818; $p < 0.001$) arise from cation exchange processes (e.g. Sparks et al., 1996). Soil pH was significantly increasing with the soil depth ($p = 0.01$), whereas exchangeable cations showed statistically insignificant change.

Soil reaction was detected as the most important ($p = 0.0001$) from 55 studied environmental characteristics to drive the species composition and amount of nitrophytes in BL stands. Other environmental characteristics were not significant after the influence of pH was filtred out. Efficiency of constrained axis (pH) was 81% of the total variability explained by unconstrained axis.

3.2.4. Exchangeable phosphorus

In the stands studied, exchangeable soil phosphorus was present at a relatively low concentration. The average value of phosphorus was 20.9 mg/kg (Table 2). The minimum value (under 2 mg/kg) was recorded in grassy stands on slopes of river valleys. The maximum of 110.9 mg/kg measured in a nitrophilous BL stand dominated by *Anthriscus cerefolium* var. *longirostris* is considerably greater than other measures.

3.2.5. Total carbon, nitrogen and C_{org}/N ratio

Total nitrogen content was strongly positively associated with total carbon (r.s. = 0.983; $p < 0.001$), because most of both elements come mainly from organic matter. Carbonates occurred only rarely and in low concentrations; therefore strongly positive correlation between total and organic carbon was detected (r.s. = 0.999; $p < 0.001$). Consistent with the above mentioned findings, maximum values of total C and N were recorded at the same localities (Table 2)—on eutric Leptosol with a thick layer of litter from the shrub *Grossularia uva-crispa* and dystric Cambisol dominated by *Impatiens parviflora* (cf. Hofmeister et al., 2009). High contents of both these elements were recorded in stands with a low soil reaction, base saturation and mineralization in which the litter layer was formed by poorly decomposing biomass of grasses, such as *P. nemoralis* or *Avenella flexuosa*. Consistently, both elements were negatively and significantly associated with soil pH (C_{org}: r.s. = −0.599; $p < 0.001$; N: r.s. = −0.560; $p < 0.001$). The lowest values (Table 2) for both total carbon and nitrogen were recorded on basalt, and in spring also in nitrophilous stands (Fig. 3), probably due to rapid mineralization of organic matter. Both elements significantly decreased with depth in the soil profile ($p < 0.01$).

Maximum C_{org}/N (more than 15; Table 2) was measured in stands dominated by the grasses *Brachypodium sylvaticum*, *Poa angustifolia* and *P. nemoralis* growing on green schist and *Calamagrostis epigejos* dominated stands on eolian sands (Fig. 2). Minimum values of around 10 were recorded for stands dominated by nitrophytes growing on basic rocks (Fig. 3) and surprisingly also for dwarf and shrubby stands (Fig. 1). C_{org}/N ratio was significantly negatively correlated with pH (r.s. = −0.615; $p < 0.001$) and BS (r.s. = −0.561; $p = 0.008$). C_{org}/N ratio usually varied between 10 and 12; higher values were reached only where the pH(H_2O) was lower than 4.3. Low value of C_{org}/N indicates high quality of soil and rapid rates of decomposition (Killham, 1994; Manzoni et al., 2010). According to our observations, BL produces relatively small amounts of leaf litter and therefore only a thin layer of moder or mull-like moder humus develops in stands of this tree. Composition of the herb layer, especially cover of nitrophilous species with broad leaves or slope, can be an important factor, as lightweight BL leaves are drift easily and deposit on lower parts of the slope.

3.2.6. N mineralization, nitrification and ammonification

In the BL stands studied, the rate of N mineralization at the beginning of the growing season differed (Table 2). The maximum rate of N mineralization (327.1 mg $NH_4 + NO_3$–N/kg/28 days) and nitrification (299.6 mg NO_3–N/kg/28 days), and a high rate of ammonification (27.5 mg NH_4–N/kg/28 days) was recorded in a stand growing in moist Eutric Leptosol on spilite with high edaphon activity. Most of the mineralized nitrogen was formed by NO_3–N, except in BL stands at the base of lydite outcrops, where intense mineralization (113.3 mg/kg/28 days) was caused by high ammonification (108.9 mg/kg/28 days). The intensity of ammonification was negative or near zero except at three localities. This demonstrates that the majority of the NH_4-N input was nitrified during incubation. Immobilization of nitrogen (indicated by negative or very low intensity of N mineralization, ammonification and nitrification) was recorded at BL stands with dense grass cover (*Arrhenatherum elatius*, *Bromus erectus*, *P. nemoralis*, *Festuca ovina* or *A. flexuosa*) on totally different bedrocks (aeolian sand, Proterozoic schist and olivine nefelinite).

From all studied environmental variables including soil properties (see Chapter 2.4), N mineralization rate, incubated inorganic nitrogen and nitrates were the best positively correlated with the base saturation and CEC (Fig. 6). Intensity of N mineralization was significantly positively correlated with the concentration of NO_3-N before incubation (r.s. = 0.453; $p = 0.008$), and NO_3-N (r.s. = 0.688; $p < 0.001$) and inorganic nitrogen (r.s. = 0.820; $p < 0.001$) produced during incubation. Nitrification rate followed closely N mineralization (r.s. = 0.720; $p < 0.001$); therefore the quantity of nitrates and inorganic nitrogen after incubation was also positively correlated with nitrification (r.s. = 0.800 and 0.677, respectively; both $p < 0.001$). High initial concentrations of ammonium were associated significantly with low ammonification rates (r.s. = −0.709; $p < 0.001$). Intensity of ammonification decreased significantly with the increase in the rate of nitrification (r.s. = −0.612; $p = 0.03$). The majority of NH_4–N was consumed; hence these ions were usually not accumulated in the soil profile of BL stands.

No correlation was detected between number/share of nitrophytes and nitrification or N mineralization (Fig. 6). Surprisingly, high rates of both characteristics were detected in nitrophilous as well as dwarf and shrubby stands on granodiorite outcrops. Unlike laboratory conditions (i.e. sufficient soil moisture—60% of maximum capillary capacity, and high temperature—28 °C), in natural conditions low soil moisture (8%) probably prevented the development of nitrophilous species.

3.2.7. Inorganic forms of nitrogen

Concentrations of all forms of nitrogen decreased significantly with the soil depth ($p < 0.01$). The volume of nitrates reached very different values, especially in September 1999, when samples were collected after a long dry period. Nitrate concentration was significantly positively correlated with CEC (r.s. $= 0.569$; $p = 0.004$) and soil moisture (r.s. $= 0.635$; $p < 0.001$). We detected no nitrates in eolian sands containing little moisture with low N mineralization rate, and maximum NO_3–N (203.4 mg/kg; Table 2) in spilite debris with the highest soil moisture content and N mineralization rate. Between September and April, the concentration decreased at most localities (from 24.3 mg/kg to 12.1 mg/kg on average; Table 2), probably due to intake of spring species of plants and leaching from the A horizon. At most localities, the contribution of nitrates to the total nitrogen was higher than that of ammonium ions, especially in BL stands in which the herb and shrub layers were dominated by nitrophytes (Figs. 3 and 6). High number and ratio of nitrophytes were typical for nitrophilous BL forests on alkaline soils (Fig. 6).

The ammonium concentrations varied less compared to nitrates and were markedly low in most BL stands. High values were usually associated with the clay mineral content in bedrock. The quantity of NH_4–N increased significantly from September 1999 to April 2000 (6.8 to 7.8 mg/kg on average; minimum in autumn on granodiorite rock steppe—1.5 mg/kg; maximum in spring on Proterozoic schists 45.2 mg/kg; Table 2), probably due to decomposition and mineralization of dead organic matter and weathering of bedrock caused by large fluctuations in temperature. Concentration of ammonium in the A-horizon was correlated significantly positively with soil moisture (r.s. $= 0.597$; $p < 0.001$), total nitrogen (r.s. $= 0.667$; $p < 0.001$) and both total (r.s. $= 0.703$; $p < 0.001$) and organic (r.s. $= 0.692$; $p < 0.001$) carbon, and negatively with soil reaction (r.s. $= -0.458$; $p = 0.007$). The relationships described above are confirmed by Fig. 6, from which it is evident that NH_4–N was accumulated in skeletal acid soils rich in organic matter with a high content of organic carbon and total nitrogen. Such soils are preferred by open and mesic BL stands where poorly decomposing biomass of grasses *A. flexuosa* and *P. nemoralis* dominate and nitrophilous species are rare (see Fig. 6).

3.3. Comparison of BL soil types from different parts of its distribution range

The variability of soil types in BL stands corresponds to the diversity of habitats which BL is able to invade. Tree vegetation and soils in BL stands in the northern Appalachian Mountains (part of its native range) and in its secondary range in Central Europe are very similar (Hagner, 1999; IUSS, 2006). The most common soil type in both is Cambisol with incipient soil formation. Cambisols dominate both in temperate and boreal regions but are less common in the tropics and subtropics (IUSS, 2006). Outside Europe, BL is common in temperate Asia, Australia, New Zealand, northern and southern Africa and temperate South America (Weber, 2003), but there is no information on the soils on which they grow in these areas. In the sub-tropical zone in China, BL occurs on Cambisols (Yanna et al., 2013).

The humid climate in the southern Appalachians (North Carolina; Boring and Swank, 1984a; Montagnini et al., 1989; Huntley, 1990) differs from the conditions prevailing in the Czech Republic. In the southern Appalachians BL stands dominate on Luvisols and Acrisols whereas in the Czech Republic with moderate climate, these are rare (Haplic Luvisols cover 7% and Albeluvisols 2%; Fig. 5). In Central Spain with a Mediterranean climate, BL occurs mainly in riparian forests and forest plantations on Calcic Luvisols and Fluvisols (Calcaric and Eutric; Castro-Díez et al., 2009). In north-eastern Slovenia, Ivajnšič et al. (2012) report that the most frequently invaded soils are Stagnosols (38%), followed by Fluvisols (21%) and Eutric Cambisols (17%). In the Czech Republic, Fluvisols (7% of the localities studied; Fig. 5) occur in BL stands growing at the bases of slopes, mostly in river and stream valleys. Both in its native range (Huntley, 1990) and the Czech Republic, BL rarely grows on poorly drained, compact plastic or waterlogged soils. The reason could be that nitrogen fixation is inhibited in such environments. Aleksandrova et al. (1994) report that nodule formation, nitrogenase activity and ureide transport in BL organs are inhibited and the total biomass per plant is lower when growing in alluvial-meadows than in sandy soils.

In continental Europe, BL stands usually thrive on Arenosols developing in sand dunes (Keresztesi, 1988; Šimonovič et al., 2001; Vrbek and Pilaš, 2011) or on river terraces formed from loamy sand or coarser fragments of up to 35 percent by volume, as in the Elbe lowlands (Czech Republic, our study; Fig. 2). In accordance with Samarakoon et al. (2013) we found that BL is able to tolerate the temporary filling of pores in sandy soil with water and is to some degree resistant to scouring (i.e. removal of substrate from the root-anchoring zone and the exposure of its roots).

Although Fowells (1965) and Huntley (1990) state that very dry sites and soils less than 24 in deep (aprox. 60 cm) are unsuitable for BL in its native range, in the Czech Republic it often invades such habitats (Fig. 1). Leptosols were present in 35% of the stands studied (Fig. 5), of which the most frequent were lithic and typic Leptosols with a dry and narrow A horizon. BL also occasionally grows in rocky soils (foothill of the Southern Alps; Cierjacks et al., 2013) and in the Vesuvius National Park (Southern Italy) it occurs on shallow Andosols with weak profile differentiation (De Marco et al., 2013). To conclude, in its secondary range BL often grows in soils that are drier and shallower than those in its native range (Huntley, 1990).

3.4. Comparison of BL physical–chemical soil properties in different parts of its distribution range

Even though BL can markedly change the soil environment, the physical-chemical properties of soils in areas where BL occurs have never been discussed comprehensively. Some authors deal with particular aspects, such as nitrogen fixation (e.g. Boring and Swank, 1984b; Danso et al., 1995; Noh et al., 2010), soil nitrogen and its transformation (e.g. Guofan and Tingxiu, 1991; Moon, 1999; Rice et al., 2004; Malcolm et al., 2008; Castro-Díez et al., 2009), carbon dynamics (e.g. Harris and Riha, 1991), litter decomposition (e.g. White et al., 1988; Harris and Safford, 1996; Yanna et al., 2013) and microbial analysis (e.g. Eaton and Farrell, 2004; Landgraf et al., 2005; Wang et al., 2012). There are several comparisons of BL invaded and non-invaded sites (e.g. Montagnini et al., 1986, 1991; Dzwonko and Loster, 1997; Rice et al., 2004; Landgraf et al., 2005; Von Holle et al., 2006; Malcolm et al., 2008; Castro-Díez et al., 2012; De Marco et al., 2013; González-Muñoz et al., 2013; Zhou et al., 2013; Cools et al., 2014) or BL stands and native grasslands (Qiu et al., 2010).

Soil characteristics of BL stands in its native range were investigated in detail only in its southern part (western North Carolina, the Coweeta LTER, 2 sites) with humid continental climate (e.g. Boring and Swank, 1984a,b; Montagnini et al., 1986, 1989, 1991; White et al., 1988) and are missing from the northern part of native range that would be comparable to the Central Europe regarding the climate, tree vegetation and soil types. The data available from the secondary range also do not cover the whole variability of BL soil conditions and describe situation at isolated sites only. Additionally, different analytical methods were used between the current and previous studies, further preventing such statistical analysis. This makes the statistical comparison of our results to published data and comparison of primary and secondary range soil conditions problematic. The biggest barrier is the application of various extraction agents, simple and composite, with diverse chemical composition (neutral electrolytes, chelate solutions, acids and their salts, oxidation reagents), which show different extraction impact (cf. Sparks et al., 1996; Ure, 1996; Zbíral, 1999; Kulhánek et al., 2009; Zbíral and Němec, 2009). Moreover, the nutrient availability in forest floor varies depending on many factors such as climatic conditions, stand age or vegetation season (e.g. Nadelhoffer et al., 1984; Pastor and Post, 1986; Brais et al., 1995). Considering the above mentioned, our results could be compared with published data from primary and secondary range on a qualitative basis only.

3.4.1. Soil moisture

Variability in soil moisture influences mineralization of organic matter and release of mineral nitrogen into the soil solution (e.g. Cassman and Munns, 1980; Stark and Firestone, 1995), as well as nutrient leaching due to the weathering of the bedrock. Under BL stands, the soil can quickly dry out because of the later and less dense foliation; however a large root system enables BL to obtain water, even in dry stands (e.g. Göhre, 1952). Větvička (1965) found a greater uptake of water by roots in the upper soil layer (5 cm) in BL compared to both oak and mixed BL-oak forests.

3.4.2. Soil reaction and base saturation

Black locust is able to grow in a variety of soil conditions (Table 2). In its native range, soil reaction ranges from extremely acid (4.0) to moderately alkaline (8.2; Fowells, 1965; Vogel, 1981) with no apparent effect on growth (Huntley, 1990), whereas in its secondary range it is 3.2 (extremely acid soil reported by Kowarik, 1992 for Germany) to 7.9 in Europe (moderately alkaline by Castro-Díez et al., 2009 for Central Spain and the Czech Republic) and 8.8 in the world (strongly alkaline soils in China according to Yanna et al., 2013; Table 2). Using fertilizer experiments, Fowells (1965) observed decrease in the growth of BL in pH above 6.9, however in the Czech Republic BL stands grew well in soils ranging from 3.4 to 7.9. Medium saturated soils (Table 2; Montagnini et al., 1986) were recorded for Coweeta LTER (BL in its native range), while in the Czech Republic base saturation reached up to 100%, i.e. highly saturated alkaline soils.

3.4.3. Phosphorus and nitrogen

Forest soils are usually poor in terms of NH_4–N and NO_3–N; symbiotic N_2 fixation by BL increases the amount of available nitrogen for plants (Boring and Swank, 1984b). Deficiency of phosphorus in BL stands decelerates and finally inhibits symbiotic fixation of atmospheric nitrogen (Liu and Deng, 1991), even before causing tree growth to cease (Úlehlová, 1989). On basic soils, phosphorus can be a limiting element. The low measured concentration of phosphorus in our research could be a consequence of a low amount of apatite in the bedrock, higher leaching of PO_4-P ions (cf. Van Miegroet and Cole, 1984; Montagnini et al., 1989), or its intensive uptake by BL roots and accumulation in leaves (cf. Montagnini et al., 1989). In the case of a shortage of phosphorus high nitrogen availability does not lead to higher vitality of an ecosystem (Van Oorschot et al., 1997).

The content of NO_3–N was higher in BL soils than in the native forests at Coweeta LTER (BL native range), whereas there were no differences in the NH_4-N concentrations, total nitrogen and C/N in these soils (Montagnini et al., 1989). Nitrate concentrations and nitrification potentials in BL stands growing on slopes of various aspects were similar (Montagnini et al., 1986). The values cited from the native range by Montagnini et al. (1986) –4.45 mg/kg in March and 3.25 mg/kg in July were much lower compare to our measured average NO_3–N concentrations (12.13 mg/kg in April and 24.34 mg/kg in September), and Dzwonko and Loster (1997) values from Poland (35.5 mg/kg in September; Table 2). Nevertheless, comparison with other studies is difficult because the concentration of soil NO_3–N depends on many factors such as climatic conditions and stand age, and varies greatly both spatially and temporally even at the same locality (e.g. Boring and Swank, 1984a; Nadelhoffer et al., 1984; Cambardella et al., 1994; Montagnini et al., 1991; Brais et al., 1995; our unpublished data). Montagnini et al. (1991) state that the seasonal pattern is caused by interactions between nitrification, plant and microbial uptake, denitrification and leaching, with the lowest nitrate concentrations reached during winter due to limited nitrifying activity, and in July due to greater plant uptake. Also dry conditions minimize the loss of nitrates through leaching and reduce the rate of mineralization of organic matter (e.g. Montagnini and Sancho, 1994). Peaks in October and November are caused by high production of NO_3–N and decreased uptake by plants (Montagnini et al., 1991). According to these findings, our measurements were higher in September (end of the growing season) than in April (beginning of the growing season, following a long and cold winter). Montagnini et al. (1989) in accordance with our research recorded decrease of NO_3–N, NH_4–N, total nitrogen and carbon with soil depth.

3.4.4. Nitrification and its acidifying effect

Consistent with Montagnini et al. (1986), net N mineralization was very closely correlated with nitrification rate. In both the native range and our study area, all the NH_4–N was consumed during incubation and the rate of ammonification decreased significantly with increasing nitrification. Montagnini et al. (1989) conclude that the availability of ammonium in BL soils is the main factor controlling nitrification, ammonification is more important than exchangeable Ca^{2+} or pH (Montagnini et al., 1986). In comparable periods, the value of total nitrogen detected in the native range (Boring and Swank, 1984a; Montagnini et al., 1986) reached the minimum measured in our study (Table 2). Equally, the nitrification and mineralization rates were near the lower limit (Table 2), which may be due to the different ages of the BL stands—12 years in Coweeta (Montagnini et al., 1986) and more than 40 years in our study. Consistent with Castro-Díez et al. (2009), immobilization of nitrogen was detected in dense grassy BL stands with a large input of carbon-rich plant material. Harris and Riha (1991) report an inverse relationship between C and N mineralization, which eventually resulted in N immobilization.

Van Miegroet and Cole (1984) showed that acidification of the top 10 cm of soil under red alder (*Alnus rubra*, a nitrogen fixing tree) coincided with intense nitrification, which provided a major source of H^+ from the dissociation of the strong HNO_3 acid produced by this microbial oxidation reaction. In the BL stands Montagnini et al. (1986) detected the highest nitrification activity in the top 15 cm of the soil. Nitrification was found to be a greater source of acidification than deposition of atmospheric H^+, even in areas markedly affected by acid precipitation (Van Miegroet and Cole, 1984). Simultaneously, NO_3^- leaching could result in an increase in the concentration of N in the groundwater. For the foothills of the Cascade Mts. (near Seattle, WA), Van Miegroet and Cole (1984) reported that the presence of large amounts of mobile NO_3^- in solution triggered accelerated cation leaching and caused selective redistribution of exchangeable Ca^{2+} from A to B horizon. While this acidifying effect of nitrification was not detected in the BL stands in its native range (Montagnini et al., 1991), the soil reaction in the Czech Republic (this study) significantly increased with the depth of the soil profile, whereas redistribution of exchangeable cations was not recorded. In forests composed of nitrogen non-fixing tree species, Augusto et al. (2002) mentioned other possible sources of acidification in topsoil as litter decomposition, deposition and root exudates. The tree layer species composition is very important, because leaf litterfall rich in Ca^{2+} and Mg^{2+} (e.g. ash, lime or maple) can reduce acidifying effect and increase the nutrient availability in topsoils (Guckland et al., 2009; Langenbruch et al., 2012). Although BL leaves have similarly high cation content (Montagnini et al., 1989; Rice et al., 2004), in our study there were no signs of acidifying effect being reduced in the topsoil. The cause of a BL acidifying effect has not been explained yet.

4. Conclusions

In its secondary range, BL grows in a wide range of soils. The most common soil types are shallow young soils, such as Cambisols, Leptosols, Arenosols and Fluvisols with incipient soil formation. Thriving BL stands were also recorded growing in deep and rich Chernozems (in continental Europe), and Acrisols and Luvisols with an Argic illuviation horizon (in sub-humid and wet subtropical climates). The best conditions for the growth of BL appear to be sandy soils like Arenosols.

BL is also able to tolerate diverse soil chemistry. Soil reaction varied from extremely acid (pH(H_2O) 3.2 in the secondary and 4.0 in the native range) to moderately and strongly alkaline (8.2 in the native and 8.8 in the secondary range). Also the base saturation varied greatly—from medium (30–50%) to highly saturated soils up to 100%. Although Fowells (1965) mentions that limestone soils are the best for BL growth, in the Czech Republic BL produces similar high-quality stands on basaltoids and aeolian sands. Water supply and soil aeration seem to limit colonization by BL more than the soil chemistry. In both its native and secondary range, BL prefers well aerated and drained soils. It can survive the drying out of the soil profile and avoids compact soils and those that are waterlogged for long periods of time, probably because this inhibits nitrogen fixation. Low soil moisture on slopes has considerable effect on the vigor of BL and causes scrubbiness and a decline in competitiveness in favor of drought-adapted native shrubs such as *Crataegus* sp., *P. spinosa* and *Rosa* sp.

High flexibility of BL makes it favorable species for forest planting; however it poses serious problems in nature conservation, lowering biodiversity, spreading spontaneously into the surroundings, and preventing the natural ecosystem restoration.

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