https://doi.org/10.17221/96/2020-JFS

Effect of structure and dynamics of forests on the occurrence of *Erythronium dens-canis*

Stanislav Vacek[1], Rostislav Linda[1], Ivo Králíček[2], Karel Vančura[1], Anna Prokůpková[1], Romana Prausová[2]*

[1]*Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Prague, Czech Republic*

[2]*University of Hradec Králové, Faculty of Science, Hradec Králové, Czech Republic*

**Corresponding author: vacekstanislav@fld.czu.cz*

Citation: Vacek S., Linda R., Králíček I., Vančura K., Prokůpková A., Prausová R. (2020): Effect of structure and dynamics of forests on occurrence of *Erythronium dens-canis*. J. For. Sci., 66: 349–360.

Abstract: The paper presents the results of a study on the impact of forest stand structure and development in 1998 to 2018 on the occurrence of dog's tooth violets (*Erythronium dens-canis* L.) in the Medník National Nature Monument, Czech Republic. The research was carried out in mixed European hornbeam and sessile oak stands, herb-rich European beech stands and the Sázava-river Norway spruce ecotype stands. The site and stand characteristics of the following three forest stand types were compared: 1) oak-hornbeam forests, 2) herb-rich beech forests and 3) secondary spruce forests. The results showed that the ratio of sterile and fertile plants was 2.9 to 1. The occurrence of *E. dens-canis* was higher in older stands with differentiated structure. On the contrary, stands characterized by a higher number of trees and basal area negatively affected the population size of *E. dens-canis*. Significantly, the density of *E. dens-canis* decreased with increasing stand density index (*SDI*) and increased with increasing diameter differentiation index in relation to tree neighbours (TM_d). During the period of 20 years, the *E. dens-canis* population increased by 40.4% on permanent research plots, while the highest changes were observed on spruce plots (+92.1%) and the lowest increase was in oak-hornbeam forests (+18.0%). The highest numbers of *E. dens-canis* plants were found in herb-rich beech forests (1 774 plants·ha^{-1}), lower numbers occurred in oak-hornbeam forests (784 plants·ha^{-1}) and minimal in secondary spruce forests (51 plants·ha^{-1}).

Keywords: dog's tooth violets; stand structure; oak-hornbeam stand; herb-rich beech stand, secondary spruce stand; Medník National Nature Monument

It is a long-term goal of forest management to leave significant parts of specially protected areas to spontaneous development (Götmark 2009; Šimůnek et al. 2019, 2020; Prokůpková et al. 2020), allowing for establishment of more diversified, i.e. more resistant stands (Vacek et al. 2014; Seidl et al. 2016; Bílek et al. 2016; Hájek et al. 2020) that can provide a wide range of ecosystem services (Gamfeldt et al. 2013; Mina et al. 2018). In most areas of protection, specific management focusing on the main nature conservation theme is applied (DeFries et al. 2007), which is – in this case – maintaining and improving the northernmost population of dog's tooth violets (*E. dens-canis* L.; *Liliaceae*) in Europe.

This single European species of the genus *Erythronium* is widely distributed in Southern Europe, while the population in Central Europe is critically endangered (Bartha et al. 2015; Nagy et al. 2019). *E. dens-canis* occurs mainly in mesic mixed deciduous forests (e.g. *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1967) and mesic meadows, especially in the lowlands with sporadic distribution range to mountain areas

Supported by the Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences.

https://doi.org/10.17221/96/2020-JFS

(Guitián et al. 2002; Mondoni et al. 2012; Pupillo, Astuti 2017). At present, lowland populations have become rare due to anthropogenic effects, for example extensive replacement of natural forest areas with agricultural fields (Mondoni et al. 2012).

Perhaps no species of the Czech flora has attracted such attention as *E. dens-canis* on the Medník Hill downstream the Sázava River (Hendrych 2004). Since 1870, more than 100 newspaper articles and about 25 academic essays have been devoted to the issue (Pivničková, Pecina 1980; Hendrych 2004; Sádlo 2009). Above all, these works discuss the autochthony or allochthony of the *E. dens-canis* in the Czech flora and the conditions of its existence and abundance in the Medník National Nature Monument (NNM).

In the Czech Republic, *E. dens-canis* is protected by law, but excluded from the Red List in 2012 as an allochthonous species (Grulich 2012). However, its autochthony or allochthony in this country is still a matter of dispute. For example, Sádlo (2009) presented three possible explanations of its occurrence:

– it is autochthonous, and it originated from the relict survival of a former areal expansion,
– it is autochthonous, and it spread by local introduction, enabled by natural mechanisms of long-distance spreading,
– it is allochthonous, and it spread by local introduction through human activity.

At Medník, *E. dens-canis* grows in several microsites that were repeatedly affected by gold mining, coppice management, forest grazing and timber rafting in the past (Ložek et al. 2005), which rather supports the theory of introduction. On the other hand, there are other plant species very rare in the area, such as the hirsute sedge (*Carex pilosa* Scop.) from the Carpathians, growing at Medník as well (Malíček 2005).

This paper deals with the effect of three types of forest stands on the occurrence of *E. dens-canis* at the Medník NNM between 1998 and 2018. The objective was to determine: (*i*) production parameters, structure and diversity of tree layer in oak-hornbeam stands, herb-rich beech stands and secondary spruce stands; (*ii*) density and dynamics of fertile and sterile individuals of *E. dens-canis* during 20 years (1998, 2008 and 2018) in each forest type and (*iii*) interaction between the structure and diversity of forest stands and the occurrence of *E. dens-canis.*

MATERIAL AND METHODS

Study area. The Medník NNM at an altitude of 220–416 m a.s.l. is located in the territory of the Hradištko town (the Prague-West district), on the left bank of the Sázava Canyon (Figure 1). The motive for the protection of this area since 1930 has

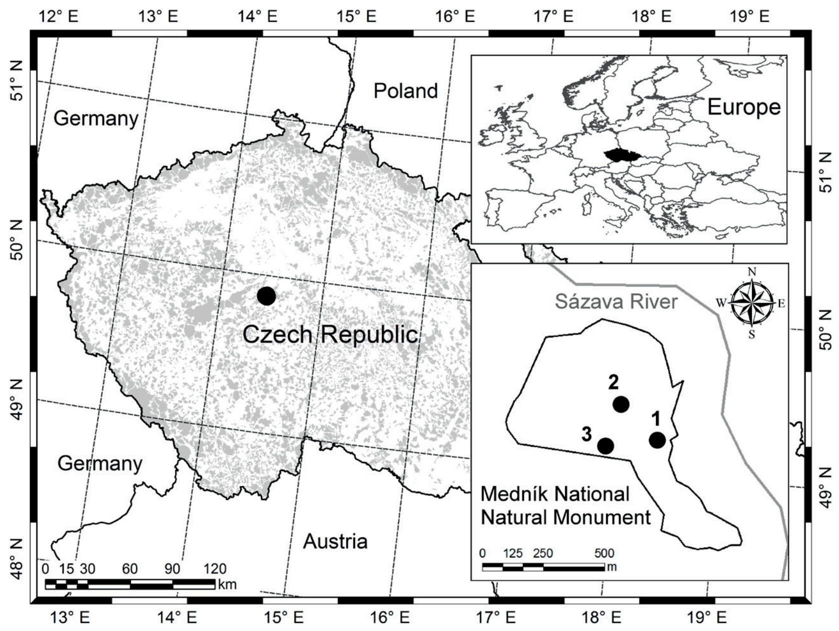

Figure 1. Localization of permanent research areas in the Medník National Nature Monument (Map data source: ©ArcČR, ARCDATA PRAHA, ZÚ, ČSÚ, 2016)

https://doi.org/10.17221/96/2020-JFS

Figure 2. *Erythronium dens-canis* (fertile – upper left and sterile – upper right) in a beech stand – below in the Medník National Nature Monument (photo: S. Vacek)

been to maintain and support the population of *E. dens-canis* (Figure 2), a species critically endangered in the Czech Republic (Holub, Procházka 2000) in its isolated northernmost European locality, and also to maintain natural slope forests with a number of protected and endangered species of flora and fauna on an area of 31.10 ha (43.67 ha in total, including the NNM protection zone). The average annual air temperature of the locality is 8–9 °C and the annual precipitation is 550–600 mm (Tolasz et al. 2007). The bedrock consists mainly of metabasites and partly of granodiorites. The prevailing soil types are mesotrophic Cambisols and Ranker Cambisols.

In the NNM, linden oak-hornbeam stands dominate with a 63% share. It is a coppice forest with dominant European hornbeam (*Carpinus betulus* L.) and admixed small-leaved linden (*Tilia cordata* Mill.), large-leaved linden (*Tilia platyphyllos* Scop.) and sessile oak (*Quercus petraea* /Matt./ Liebl.) and interspersed individuals of sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), field maple (*Acer campestre* L.), European beech (*Fagus sylvatica* L.), Scots elm (*Ulmus glabra* Huds.) and wild service tree (*Sorbus torminalis* /L./ Crantz). These are plant communities of the alliance *Carpinion* Issler 1931 and rich-base plant associations *Melampyro nemorosi-Carpinetum* Passarge 1962 and *Stellario-Tilietum* Moravec 1964. Quite abundant (30%) are herb-rich beech stands with dominant *Fagus sylvatica* and admixed *Carpinus betulus* as dominant tree species. Sparsely interspersed is *Quercus petraea* and silver birch (*Betula pendula* Roth). These are plant communities of the suballiance *Eu-Fagenion* Oberdorfer 1957 em. Tx. 1960 and the association *Dentario enneaphylli-Fagetum* Oberdorfer ex W. et A. Matuszkiewicz 1960. The share of relict spruce stands of the Sázava-river Norway spruce ecotype (the alliance *Piceion abietis* Pawłowski et al. 1928) with interspersed *Betula pendula* is 6% and the share of seral stand with dominating *Betula pendula* is 1%. Adolescent and adult stands dominate significantly.

The local forests lost their natural character not later than in the late prehistoric times (La Tene period, 400–100 B.C.), when they were constantly influenced by forest grazing, timber harvesting and gold mining (Barvířová 1935; Waldhauser 1988, 1995).

https://doi.org/10.17221/96/2020-JFS

Table 1. Basic stand and site characteristics of permanent research plots

PRP	GPS	Altitude (m)	Aspect	Slope (°)	Alliances of association	Species	Mean age (year)	Mean diameter (cm)	Mean height (m)	Mean volume ($m^3 \cdot ha^{-1}$)
1A, 1B	49.870472N 14.452042E	300	NE	28	*Carpinion*	Cb, Tp, Qp, Ap, Apl, Ac, Fs, Ug	76	19	16	246
2A, 2B, 2C, 2D	49.871371N 14.450304E	330	N	5	*Fagion*	Fs, Cb, Qp, Bp	117	45	30	346
3A, 3B	49.870320N 14.449531E	380	NNE	8	*Piceion abietis*	Pa, Bp	99	38	32	458

Cb – *Carpinus betulus,* Tp – *Tilia platyphyllos, Tilia cordata,* Qp – *Quercus petraea,* Ap – *Acer pseudoplatanus,* Apl – *Acer platanoides,* Ac – *Acer campestre,* Fs – *Fagus sylvatica,* Ug – *Ulmus scabra,* Bp – *Betula pendula*, Pa – *Picea abies*

The study was conducted on 3 permanent research areas with 8 permanent research plots (PRP). Two PRP (1A, 1B) were covered by oak-hornbeam stands, four PRP (2A, 2B, 2C, 2D) by herb-rich beech stands and the last two PRP (3A, 3B) by secondary spruce stands (Table 1).

Data collection. To determine the structure of the tree layer of forest stands, a theodolite was used in the establishment of 8 PRP of 50 × 50 m in size (0.25 ha) in 1998, and Field-Map technology (IFER) in 2008 and 2018. The position of all trees of breast height diameter (DBH) ≥ 4 cm was localized. Crown projection was measured at least in 4 directions, perpendicular to one another. Tree height and height of the live crown base were measured with a Vertex laser hypsometer (to the nearest 0.1 m) and DBH was measured with a metal calliper (to the nearest 1 mm).

Flowering and sterile individuals of *E. dens-canis* were counted separately on each of 8 PRP (1A–3B) in spring (from mid-March to mid-April) 1998, 2008 and 2018.

Data analysis. The stand volume was calculated by volume equations published by Petráš, Pajtík (1991). The density of the tree layer was determined according to stand density index (*SDI*), crown closure (*CC*) and crown projection area (*CPA*). Species diversity was analysed in the framework of species heterogeneity (Shannon 1948) and species evenness (Pielou 1975). The structural diversity assessment included the calculations of diameter and height differentiation index (Füldner 1995), species profile index in relation to vertical structure (Pretzsch 2009) and stand diversity index (Jaehne, Dohrenbusch 1997). The spatial distribution (horizontal structure) was determined according to the aggregation index (Clark, Evans 1954). Diversity was evaluated using the SIBYLA software (Fabrika, Ďurský 2005) – (Table 2).

At first, the relation between fertile and sterile individuals on selected PRPs in the years of evaluation was tested by chi-squared test. For graphical visualization of the relations between measured or computed parameters of the structure, production

Table 2. Overview of indices describing the biodiversity and their common interpretation

Criterion	Quantifiers	Label	Evaluation
Horizontal structure	Aggregation index	*R* (C&Ei)	mean value $R = 1$; aggregation $R < 1$; regularity $R > 1$
Vertical diversity	Species profile index	*A* (Pi)	range 0–1; balanced vertical structure $A < 0.3$; selection forest $A > 0.9$
Structure differentiation	Diameter dif.	TM_d (Fi)	range 0–1; low $TM < 0.3$; very high differentiation $TM > 0.7$
	Height dif.	TM_h (Fi)	
Species diversity	Heterogeneity	*H´* (Si)	minimum $H´ = 0$, higher $H´$ = higher values
	Evenness	*E* (Pi)	range 0—1; minimum, $E = 0$, maximum $E = 1$
Complex diversity	Stand diversity	*B* (J&Di)	monotonous structure $B < 4$; uneven structure $B = 6–8$; very diverse structure $B > 9$

https://doi.org/10.17221/96/2020-JFS

Table 3. Stand structure and production characteristics in various forest types in 1998, 2008 and 2018

PRP	Year	Age (y)	*DBH* (cm)	*h* (m)	*N* (trees·ha^{-1})	*BA* (m·ha^{-1})	*V* (m^3·ha^{-1})	*CPA* (ha)	*CC* (%)	*SDI*
	1998	64	15.9	14.0	1390	27.6	175	4.92	99.3	0.64
1A-1B	2008	74	17.1	15.1	1336	30.8	219	5.03	99.3	0.70
	2018	84	18.3	15.9	1262	33.2	256	5.05	99.4	0.74
	1998	105	47.2	28.6	162	28.1	467	1.76	82.7	0.41
2A-2D	2008	115	49.3	29.4	157	29.6	506	1.76	82.7	0.43
	2018	125	51.6	30.4	146	30.1	528	1.71	81.8	0.43
	1998	88	33.3	29.3	480	41.9	533	1.20	69.9	0.64
3A-3B	2008	98	36.4	30.3	471	49.3	637	1.34	73.6	0.72
	2018	108	39.5	31.1	458	56.1	733	4.92	77.3	0.80

Age – average stand age, *DBH* – mean quadratic breast height diameter, *h* – mean height, *N* – number of trees per hectare, *BA* – basal area, *V* – stand volume, *CPA* – crown projection area, *CC* – canopy closure, *SDI* – stand density index

and diversity of tree layer, the redundancy analysis (*RDA*) was performed using CANOCO 5 (Lepš, Šmilauer 2003). The parameter symbols are explained in Table 3 and 4.

Linear regression was used to assess the effects of parameters, which showed the highest correlation with the abundance of *E. dens-canis* on selected PRPs. R software (R Core Team 2018) was used for all computations related to linear regression analyses.

RESULTS

Structure of the tree layer

Close-to-nature oak-hornbeam stands

The number of live trees ranged from 1268 to 1512 trees·ha^{-1} in 2008 (Table 3). In 20 years, the total numbers decreased by 8.4–9.5%. *SDI* ranged between 0.60 and 0.68 in 1998; and it increased by 13–16% in the same period, while *CPA* increased only very slightly (by 2–3%). The average basal area was 26.1–29.0 m^2·ha^{-1} in 1998, increasing by 19–22% in 20 years. The stand volume of coppice-with-standards ranged between 171 and 178 m^3·ha^{-1} in 1998, when hornbeam accounted for 50–61%, linden for 18–20% and oak for 17–31%. In the 20 years' period, the stand volume increased by 43–51%: 51–58% in hornbeam, 32–59% in linden and 20–29% in oak. On PRP 1A and 1B, the highest number of trees with the lowest stand volume was observed from all PRP (Table 3).

Close-to-nature herb-rich beech stands

The number of live trees ranged from 144 to 172 trees·ha^{-1} in 2008 (Table 3). In 20 years, the total numbers decreased by 2.4–11.7%. *SDI* ranged between 0.39 and 0.44 in 1998, slightly increasing on PRP 2B–2D in 20 years' time (by 2–15%) and

Table 4. Diversity of tree layer in various forest types in 1998, 2008 and 2018

PRP	Year	*R* (C&Ei)	*A* (Pri)	*B* (J&Di)	TM_d (Fi)	TM_h (Fi)	*H´* (Si)	*E* (Pii)
	1998	1.436	0.502	8.630	0.316	0.194	0.444	0.508
1A-1B	2008	1.427	0.509	8.561	0.329	0.195	0.446	0.510
	2018	1.396	0.509	8.551	0.341	0.209	0.443	0.506
	1998	1.141	0.377	6.058	0.388	0.282	0.201	0.400
2A-2E	2008	1.151	0.343	5.810	0.386	0.259	0.212	0.421
	2018	1.119	0.359	5.737	0.398	0.258	0.227	0.452
	1998	1.187	0.359	5.953	0.242	0.139	0.189	0.256
3A-3B	2008	1.183	0.369	5.248	0.254	0.133	0.175	0.250
	2018	1.168	0.363	4.878	0.263	0.126	0.170	0.243

R – Clark-Evans index of aggregation, *A* – species profile index, *B* – stand diversity index, TM_d – diameter differentiation index, TM_h – height differentiation index, *H´* – index of species heterogeneity, *E* – index of species evenness

https://doi.org/10.17221/96/2020-JFS

slightly decreasing on PRP 2A (by 5%). In the same period, *CPA* on PRP 2A, 2B and 2D decreased (by 5–10%) and increased (by 11%) on PRP 2C. The average basal area was 26.4–31.1 $m^2 \cdot ha^{-1}$ in 1998, increasing by 2–18% on PRP 2B–2D and decreasing by 1% on PRP 2A during the monitored 20 years. The stand volume ranged between 419 and 545 $m^3 \cdot ha^{-1}$ in 1998, when beech accounted for 79–97% and hornbeam for 3–15% in. In the 20 years' time period, the stand volume increased by 4–24%: 2–13% in beech and 0–74% in hornbeam. On PRP 2A, the lowest number of trees was recorded from all PRPs.

Secondary spruce stands

The number of live trees ranged between 476 and 484 trees$\cdot ha^{-1}$ in 2008 (Table 3). In 20 years, the total numbers decreased by 2.6–6.6%. *SDI* ranged between 0.61 and 0.66 in 1998, increasing by 23–28% in the 20 years' time period. In the same period, *CPA* increased by 21–26%. The average basal area was 39.1–44.6 $m^2 \cdot ha^{-1}$ in 1998, increasing by 31 to 38% in 20 years. The stand volume ranged between 494 and 571 m^3 ha^{-1} in 1998, when spruce accounted for 83–97%. In the 20 years' time period, the volume increased by 34–41%; 35–44% in spruce. Overall, the largest stand volume (767 m^3 ha^{-1}) was recorded on PRP 3A in 2018 from all PRPs.

Biodiversity of the tree layer

Close-to-nature oak-hornbeam stands

Horizontal structure (*R* index) of the tree layer in hornbeam-oak stands was random to regular in the investigated period (Table 4). The diameter and height differentiation of the structure (TM_d and TM_h) was medium. Vertical structure (*A*) shows high diversity. Overall stand diversity by *B* index indicates a diverse structure throughout the study period. Species diversity was medium according to the entropy *H´* and species evenness *E*. Compared to other forest types, the highest stand diversity, vertical diversity and species diversity were observed in oak-hornbeam stands.

Close-to-nature herb-rich beech stands

The horizontal structure of tree layer in the herb-rich beech stands shows a random spatial pattern during the 20 years study (Table 4). Species profile index *A* shows the balanced vertical structure on PRP 2A–2B and moderately diversified structure on PRP 2C–2D. The diameter differentiation TM_d was low on PRP 2A and 2D and moderate on PRP 2B and 2C. The height differentiation TM_h of the structure was low on PRP 2A, 2C and 2D, and moderate on PRP 2B. Overall stand diversity *B* indicates an even structure on PRP 2A, 2B and 2D, and an uneven structure on PRP 2C during the investigated period. In terms of species diversity according to entropy *H´*, PRP 2A, 2B show very low diversity, PRP 2D low diversity and PRP 2C shows medium diversity. In terms of species evenness *E*, PRP 2A, 2C and 2D show predominantly medium diversity and low biodiversity is on PRP 2B.

Secondary spruce stands

The horizontal structure of trees in the secondary spruce stands shows random aggregation according to *R* index during the study period (Table 4). Vertical structure shows medium diversity according to *A* index. The diameter differentiation TM_d was low. The height differentiation TM_h of the structure was very low on PRP 3A and low on PRP 3B. Stand diversity index *B* indicates an even to monotone structure on PRP 3A and an uneven structure on PRP 3B during the investigated period. In terms of species diversity according to entropy *H´* and species evenness *E*, PRP 3A shows very low diversity and PRP 3B low biodiversity. Generally, the lowest diversity from all compared forest types was determined in these spruce PRPs.

The occurrence of *Erythronium dens-canis* in various stand types

The occurrence of *E. dens-canis* in various stand types (oak-hornbeam, herb-rich beech and secondary spruce stands) on the studied PRP is presented in Table 5. The maximum occurrence of *E. dens-canis* during the monitored period was recorded in herb-rich beech stands (1 774 plants$\cdot ha^{-1}$), considerably lower in oak-hornbeam stands (784 plants$\cdot ha^{-1}$) and minimal in secondary spruce stands (51 plants$\cdot ha^{-1}$). Specifically, the highest density of 2552 plants$\cdot ha^{-1}$was observed on beech PRP 2A in 2018. In the years 1998–2008 there was a slight decrease, stagnation or only a very small increase in the population of *E. dens-canis* while in the years 2008–2018 it increased noticeably. During the period of 20 years, the population of *E. dens-canis* increased by 40.4% on all PRP, while the highest change was observed in spruce stands (+92.1%), while the lowest increase was in oak-

https://doi.org/10.17221/96/2020-JFS

Table 5. *Erythronium dens-canis* occurrence in various forest types in 1998, 2008 and 2018

Density (plants·ha^{-1})	1A-1B (*Carpinion*)			2A-2D (*Fagion*)			3A-3B (*Piceion abietis*)		
	1998	2008	2018	1998	2008	2018	1998	2008	2018
Sterile	500 ± 70	588 ± 75	634 ± 94	1 170 ± 314	1 212 ± 317	1 398 ± 301	32 ± 22	38 ± 27	50 ± 26
Fertile	172 ± 34	198 ± 18	262 ± 43	505 ± 135	458 ± 141	578 ± 137	6 ± 6	10 ± 7	18 ± 7
Total	672 ± 97	786 ± 75	896 ± 124	1 675 ± 447	1 670 ± 454	1 976 ± 435	38 ± 27	48 ± 34	68 ± 32

hornbeam stands (+18.0%). The ratio of sterile to fertile plants was 2.9:1 in total. The highest occurrence of *E. dens-canis* was recorded in stand openings where the ratio of sterile to fertile individuals was significantly lower (1.7:1).

Relationship between *Erythronium dens-canis* and forest structure and diversity

The chi-squared test of independence in the counts table (Table 5) showed insignificant results (chi-squared = 13.52, df = 23, *P*-value = 0.94). This result is consistent with the results of RDA, where no difference in the abundance of fertile and sterile individuals in relation to stand parameters was observed, see Figure 3.

Generally, the occurrence of *E. dens-canis* is higher in older, differentiated stands (positive correlation with *TMd*, *TMh*, *dbh* and *h* was observed). Contrary to that, the high stand density, which is naturally connected with higher basal area and number of trees on PRP, negatively affects the population size of *E. dens-canis*. Linear regression (the relation of *E. dens-canis* abundance on PRPs to the most significant parameters revealed by RDA – *SDI* and *TMd*) confirmed effects of parameters which showed the highest correlation with the number of *E. dens-canis* plants (Figure 4). Both parameters appeared to be significant indicators of *E. dens-canis* occurrence – the number decreased with increasing values of stand density index (*SDI*) and increased with increasing diameter differentiation (*TMd*).

DISCUSSION

Structure of the tree layer

In Europe, attention has recently been paid to mixed oak and beech stands as important timber production species (del Río et al. 2014; Vacek et al. 2018, 2019a). In oak-hornbeam stands, the number of trees ranging between 1 268 and 1 512 individuals per ha in 1998 indicates very variable medium-aged stands and a significant influence of the original way of pasture management. In former coppices, the canopy has improved significantly, as documented in similar cases at other sites (Paillet

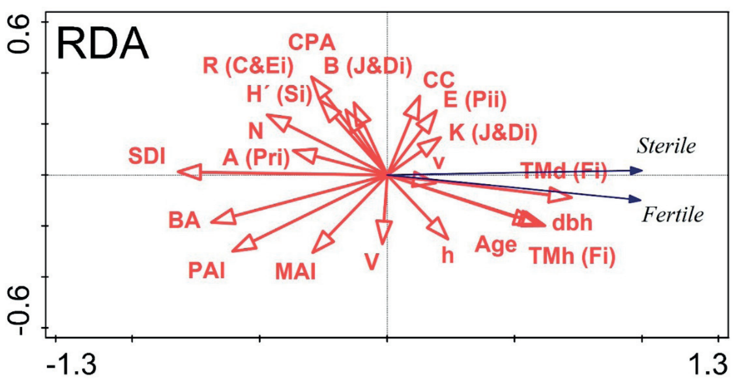

Figure 3. Ordination diagram for the redundancy analysis. A permutation test showed significant results on all axes (pseudo-F = 232, p = 0.004). The first two axes explained 99.9% of variability;

R – Clark-Evans index of aggregation, A – species profile index, B – stand diversity index, TM_d – diameter differentiation index, TM_h – height differentiation index, H' – index of species heterogeneity, E – index of species evenness, DBH – mean quadratic breast height diameter, h – mean height, N – number of trees per hectare, BA – basal area, V – stand volume, CPA – crown projection area, CC – canopy closure, SDI – stand density index

https://doi.org/10.17221/96/2020-JFS

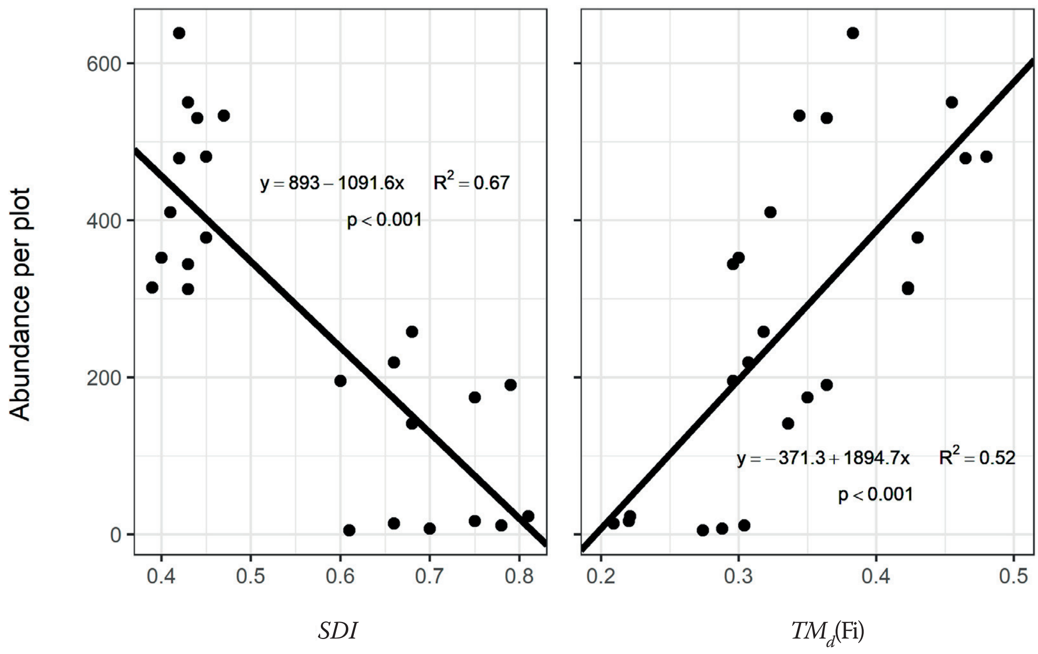

Figure 4. The relationship between the abundance of *Erythronium dens-canis* per plot and the most significant parameters affecting its abundance identified by redundancy analysis (Figure 3); *SDI* – stand density index, TM_d (Fi) – diameter differentiation index

et al. 2010; Müllerová et al. 2015). At the same time, *SDI* has increased by 13–16% in the period under review, which may gradually lead to a change in the species composition (Petritan et al. 2012) like in our case (increase of the share of fast-growing tree species compared to oak). Some authors suggest the original form of management might influence the stand even 100 years later (Paillet et al. 2010; Müllerová et al. 2015).

In herb-rich beech stands the number of trees (144–178 trees per ha in 1998) is reduced due to specifics of the locality to improve conditions for the *E. dens-canis* populations in its isolated northernmost European distribution area (Hendrych 2004; Sádlo 2009). *E. dens-canis* needs sufficient light for successful growth (Guitián et al. 2002). Beech is the strongest competitor in this locality, which corresponds to its ecological characteristics (del Río et al. 2014; Bošela et al. 2016), and therefore it maintains its dominant position. Similar results from comparable stand and habitat conditions from the Orlické hory Mts. (478–601 $m^3 \cdot ha^{-1}$) were reported by Vacek et al. (2014, 2017). Expansion of beech natural regeneration was confirmed also in the Jizerské hory Mts. (Slanař et al. 2017) and Broumov region (Vacek et al. 2015).

In the secondary spruce stands, the original number of trees ranging from 476 to 484 tress$\cdot ha^{-1}$ decreased slightly during the monitored period. Spruce stands throughout Europe are currently at great risk from ongoing climate change, especially rising temperatures and summer drought (Zang et al. 2014; Cukor et al. 2019; Vacek et al. 2019b, 2020) that lead to bark beetle outbreaks (Krejčí et al. 2013; Putalová et al. 2019; Toth et al. 2020). In addition, the stand volume increased by 41% in 20 years. The results show that despite all climate change threats, the spruce stands in monitored localities have not been significantly affected, probably due to the specific microclimate and sufficient water resources.

Biodiversity of the tree layer

The spatial arrangement of the studied oak-hornbeam stands is relatively variable from slightly regular through mostly clustered to random. Slightly different results were given by Rozas (2003), who presented a clustered structure for old-growth beech-oak lowland stands, mainly due to gaps in the canopy that arise after the death of dominant trees. Vacek et al. (2018) also presented relatively heterogeneous results for oak stands, where the high forest showed predominantly random distribution while the low forest was characteristically clustered. In spruce and herb-rich beech stands, spatial distribution of trees was random with tendency to regular

https://doi.org/10.17221/96/2020-JFS

distribution. Similarly, Bulušek et al. (2016) documented prevailing regular to random horizontal structure for beech forests in sites of lower altitudes. A mostly random to moderately regular spatial pattern was also observed for beech and spruce forests in the Krkonoše Mts. (Zahradník et al. 2010).

The overall diversity of stands, which is strongly influenced by habitat conditions (Vacek et al. 2015; Čater, Diaci 2017; Králíček et al. 2017), was markedly differentiated: the oak-hornbeam stands had a diversified structure, the herb-rich beech stands had an even to uneven structure and the secondary spruce stand structure ranged from monotone to uneven. The results show a broad diversity of vegetation, whether caused by microhabitat conditions, species composition, age or forest management in the past. In relation to age, it has been documented that the younger developmental stages tend to be more diverse than the older ones (Spitzer et al. 2008) although our results do not prove that.

Erythronium dens-canis occurrence in various stand types

The highest occurrence of *E. dens-canis* during the monitored period was recorded in herb-rich beech stands, while it was considerably lower in oak-hornbeam stands and minimal in secondary spruce stands. Higher numbers of *E. dens-canis* plants were confirmed in older and more differentiated stands. Contrarily, the high *SDI*, naturally associated with higher basal area and number of trees, negatively affects the *E. dens-canis* population.

The numbers of *E. dens-canis* plants in the protected area vary considerably from tens to thousands of flowering individuals (e.g. Růžička 1927; Vorel 1990; Hendrych 2004). These works suggest that the abundance of *Erythronium dens-canis* decreased over the years. The estimation of the *E. dens-canis* numbers is probably influenced by the fact that, in a thick layer of raw humus, sterile specimens are particularly hard to notice when compared to the flowering ones, since they are partially covered by leaves. In addition, the area of the protected territory has been decreasing over the years (Hendrych 2004). This locality is exceptionally convenient for *E. dens-canis*. It is a typical oak-hornbeam habitat, even comparable to the natural *E. dens-canis* sub-Mediterranean oak forests of the alliance *Erythronio-Carpinion* (Sádlo 2009). For example, *Carex pilosa*, *Hierochloë australis* and *Melica uniflora* grow here, supporting the idea of *E. dens-canis* autochthony. *E. dens-canis* has quite a wide range of distribution from humus-richer types of thermophilic oak stands through oak-hornbeam stands to herb-rich beech stands (Hendrych 2004). *E. dens-canis* at Medník could be a relic of the warm pre-Holocene epoch (Hendrych 2004; Ložek 2007). It is now apparent that some thermophilic species of the oceanic climate have survived the cold and continental fluctuations of the Pleistocene in our conditions until now (Stewart, Lister 2001). However, it is difficult to explain why, after such a long time, the *E. dens-canis* would remain in a single location in the Czech Republic, at Medník (Sádlo 2009). Similarly to Medník, the occurrence of *E. dens-canis* in the Brzotínské skaly National Nature Reserve in the Slovak Karst is discussed, where *E. dens-canis* is accompanied by another relict species *Carex brevicollis* (Kochjarová et al. 2004).

A significant geophyte, the *E. dens-canis* is quite easy to grow wild. Hendrych (2004) mentioned planting and subsequent growing wild at nearby Štěchovice, at the South Bohemian town of Milevsko and at several localities in Austria and Switzerland. Indeed, it is not rare for the alliance *Erythronio-Carpinion* to grow wild in our conditions. Numerous examples were presented by Pyšek et al. (2002).

Pyšek et al. (2002) considered *E. dens-canis* to be an introduced species and listed it in the Catalogue of Alien Species. Sádlo (2009), however, stated that neither natural nor anthropogenic origin of *E. dens-canis* at the Medník locality could be confirmed or rejected without direct evidence. However, it is necessary to continue to protect *E. dens-canis* at its location in Medník.

CONCLUSION

Since 1930, the stands of oak-hornbeam, herb-rich beech and secondary spruce in the Medník locality have been specifically managed to maintain and expand the population of *Erythronium dens-canis*, i.e. legally protected species in the Czech Republic. The largest population of *E. dens-canis* was found in herb-rich beech forests. In terms of supporting management practices, the oak-hornbeam stands have long been managed as coppices while the herb-rich beech and secondary spruce stands were undergoing very strong tending interventions carried out to reduce the canopy and eliminate the lower layer. Generally, a decrease in stand density has a positive effect on the *E. dens-canis* population. Moreover, natural regen-

https://doi.org/10.17221/96/2020-JFS

eration is almost absent in the studied stands due to damage caused by ungulates. This is an almost optimum condition for the *E. dens-canis* population, but in view of the continuing disintegration of beech and spruce stands, it will become a serious issue.

REFERENCES

Bartha L., Sramkó G., Volkova P.A., Surina B., Ivanov A.L., Banciu H.L. (2015): Patterns of plastid DNA differentiation in Erythronium (Liliaceae) are consistent with allopatric lineage divergence in Europe across longitude and latitude. Plant Systematics and Evolution, 301: 1747–1758.

Barvířová, O. (1935): Památek v okolí Jílového II. Z Doby vlády keltských Bójů. Vltavské proudy, 14: 7–8.

Bošela M., Štefančík I., Petráš R., Vacek S. (2016): The effects of climate warming on the growth of European beech forests depend critically on thinning strategy and site productivity. Agricultural and Forest Meteorology, 222: 21–31.

Bílek L., Vacek S., Vacek Z., Remeš J., Král J., Bulušek D., Gallo J. (2016): How close to nature is close-to-nature pine silviculture? Journal of Forest Science, 62: 24–34.

Bulušek D., Vacek Z., Vacek S., Král J., Bílek L., Králíček I. (2016): Spatial pattern of relict beech (*Fagus sylvatica* L.) forests in the Sudetes of the Czech Republic and Poland. Journal of Forest Science, 62: 293–305.

Clark P.J., Evans F.C. (1954): Distance to nearest neighbour as a measure of spatial relationship in populations. Ecology, 35: 445–453.

Cukor J., Vacek Z., Linda R., Vacek S., Marada P., Šimůnek V., Havránek F. (2019): Effects of bark stripping on timber production and structure of Norway spruce forests in relation to climatic factors. Forests, 10: 320.

Čater M., Diaci J. (2017): Divergent response of European beech, silver fir and Norway spruce advance regeneration to increased light levels following natural disturbance. Forest Ecology and Management, 399: 206–212.

DeFries R., Hansen A., Turner B.L., Reid R., Liu J. (2007): Land use change around protected areas: management to balance human needs and ecological function. Ecological Applications, 17: 1031–1038.

del Río M., Condés S., Pretzsch H. (2014): Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. Forest Ecology and Management, 325: 90–98.

Fabrika M., Ďurský J. (2005): Algorithms and software solution of thinning models for SIBYLA growth simulator. Journal of Forest Science, 51: 431–445.

Füldner K. (1995): Strukturbeschreibung von Buchen-Edellaubholz-Mischwäldern. Göttingen, Dissertation Forstliche Fakultät Göttingen, Cuvillier Verlag: 146.

Gamfeldt L., Snäll T., Bagchi R., Jonsson M., Gustafsson L., Kjellander P., Ruiz-Jaen M.C., Fröberg M., Stendahl J., Philipson C.D., Mikusiński G., Andersson E., Westerlund B., Andrén H., Moberg F., Moen J., Bengtsson J. (2013): Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications, 4: 1340.

Götmark F. (2009): Experiments for alternative management of forest reserves: effects of partial cutting on stem growth and mortality of large oaks. Canadian Journal of Forest Research, 39: 1322–1330.

Grulich V. (2012): Red List of vascular plants of the Czech Republic: 3rd edition. Preslia, 84: 631–645.

Guitián P., Medrano M., Guitián J. (2002): Seed dispersal in *Erythronium dens-canis* L. (Liliaceae): variation among habitats in a myrmecochorous plant. Plant Ecology, 169: 171–177.

Hendrych R. (2004): *Erythronium dens-canis* a jeho historie v Čechách. Zprávy České botanické společnosti, 39: 185–216.

Hájek V., Vacek Z., Vacek S., Bílek L., Prausová R., Linda R., Bulušek D., Králíček I. (2020): Changes in diversity of protected scree and herb-rich beech forest ecosystems over 55 years. Central European Forestry Journal, 66: in press.

Holub J., Procházka F. (2000): Red list of vascular plants of the Czech Republic – 2000. Preslia, 72: 187–230.

Jaehne S.C., Dohrenbusch A. (1997): Ein Verfahren zur Beurteilung der Bestandesdiversität. Forstwissenschaftliches Centralblatt, 116: 333–345.

Kochjarová J., Turis P., Blanár D., Hrivnák R., Kliment J. & Vlčko J. (2004): Cievnaté rastliny Muránskej planiny. Reussia, Suppl., 1: 83–182.

Králíček I., Vacek Z., Vacek S., Remeš J., Bulušek D., Král J. Štefančík I., Putalová T. (2017): Dynamics and structure of mountain autochthonous spruce-beech forests: impact of hilltop phenomenon, air pollutants and climate. Dendrobiology, 77: 119–137.

Krejčí F., Vacek S., Bílek L., Mikeska M., Hejcmanová P., Vacek Z. (2013): The effects of climatic conditions and forest site types on disintegration rates in Picea abies occurring at the Modrava Peat Bogs in the Šumava National Park. Dendrobiology, 70: 35–44.

Lepš J., Šmilauer P. (2003): Multivariate Analysis of Ecological Data using CANOCO. Cambridge, Cambridge University Press: 269.

Ložek V., Kubíková J., Špryňar P. (2005): Střední Čechy. In: Mackovčin P., Sedláček M. (eds): Chráněná území ČR, svazek XIII., Brno, Praha, AOPK ČR a EkoCentrum: 902.

Ložek V. (2007): Zrcadlo minulosti. Česká a slovenská krajina v kvartéru. Praha, Dokořán: 216.

Malíček J. (2005): Lichens of Medník National Nature Monument in the Sázava River valley (Central Bohemia). Bryonora, 55: 46–55.

https://doi.org/10.17221/96/2020-JFS

Mina M., del Río M., Huber M.O., Thürig E., Rohner B. (2018): The symmetry of competitive interactions in mixed Norway spruce, silver fir and European beech forests. Journal of Vegetation Science, 29: 775–787.

Mondoni A., Rossi G., Probert R. (2012): Temperature controls seed germination and dormancy in the European woodland herbaceous perennial *Erythronium dens-canis* (Liliaceae). Plant Biology, 14: 475-480.

Müllerova J., Hédl R., Szabó P. (2015): Coppice abandonment and its implications for species diversity in forest vegetation. Forest Ecology and Management, 343: 88–100.

Nagy T., Pfliegler W.P., Takács A., Tökölyi J., Molnár A. (2019): Distribution, infection rates and DNA barcoding of *Uromyces erythronii* (Pucciniaceae), a parasite of Erythronium (Liliaceae) in Europe. Willdenowia, 49: 13–20.

Paillet Y., Bergès L., Hjältén J., Ódor, P., Avon, C., Bernhardt-Römermann M., Bijlsma R.J., De Bruyn L., Fuhr M., Grandin U., Kanka R., Lundin L., Luque S., Magura T., Matesanz S., Mészáros I., Segastiá M.T., Schmidt W., Standovár T., Tothmérész B., Uotila A., Valladares F., Vellak K., Viranen R. (2010): Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation Biology, 24: 101–112.

Petráš R., Pajtík J. (1991): Sústava česko-slovenských objemových tabuliek drevín. Lesnický časopis, 37: 49–56.

Petritan A.M., Biris I.A., Merce O., Turcu D.O. Petritan I.C. (2012): Structure and diversity of a natural temperate sessile oak (*Quercus petraea* L.) – European Beech (*Fagus sylvatica* L.) forest. Forest Ekology and Management, 280: 140–149.

Pielou E.C. (1975): Ecological Diversity. New York, Wiley: 165.

Pivničková M., Pecina P. (1980): Příspěvek k autekologii kandíku psího zubu (*Erythronium dens-canis* L.) ve státní přírodní rezervaci Medník. Ochrana přírody, 1: 207–229.

Pretzsch H. (2009): Forest dynamics, growth and yield. Berlin, Heidelberg, Springer: 223–290.

Prokůpková A., Vacek Z., Vacek S., Blažejová J., Schwarz O., Bulušek D. (2020): Dynamics of natural regeneration of mountain forests after wind disturbance: Model study for the krkonose mts. (Czech Republic). Zprávy lesnického výzkumu, 65: 72–81.

Pupillo P., Astuti, G. (2017): Population structure of *Erythronium dens-canis* L. (*Liliaceae*) in the northern Apennines (Italy). Italian Botanist, 4: 1–14.

Putalová T., Vacek Z., Vacek S., Štefančík I., Bulušek D., Král J. (2019): Tree-ring widths as an indicator of air pollution stress and chmate conditions in different Norway spruce forest stands in the Krkonoše Mts. Central European Forestry Journal, 65: 21–33.

Pyšek P., Sádlo J., Mandák B. (2002): Catalogue of alien plants of the Czech Republic. Preslia, 74: 37–186.

R Core Team (2018): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/.

Rozas V. (2003): Regeneration patterns, dendroecology, and forest-use history in an old-growth beech–oak lowland forest in Northern Spain. Forest Ekology and Management, 182: 175–194.

Růžička J. (1927): Kandík – *Erythronium dens-canis*. – Lesnická práce, 6: 232–233.

Sádlo J. (2009): *Erythronium dens-canis* in Bohemia: can we accept its native origin? Zprávy České botanické společnosti, 44: 1–10.

Seidl R., Spies T.A., Peterson, D.L., Stephens S.L., Hicke J.A. (2016): Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. Journal of Applied Ecology, 53: 120–129.

Shannon C.E. (1948): A mathematical theory of communications. Bell System Technical Journal, 27: 379–423.

Slanař J., Vacek Z., Vacek S., Bulušek D., Cukor J., Štefančík I., Bílek L., Král J. (2017): Long-term transformation of submontane spruce-beech forests in the Jizerské hory Mts.: dynamics of natural regeneration. Central European Forestry Journal, 63: 213–225.

Spitzer L., Konvička M., Beneš J., Tropek R., Tuf I.H., Tufová J. (2008): Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. Biological Conservation, 141: 827–837.

Stewart J.R., Lister A.M. (2001): Cryptic northern refugia and the origins of modern biota. Trends in Ecology & Evolution, 16: 608–613.

Šimůnek V., Vacek Z., Vacek S., Králíček I., Vančura K. (2019): Growth variability of European beech (*Fagus sylvatica* L.) natural forests : Dendroclimatic study from Krkonoše National Park. Central European Forestry Journal, 65: 3–11.

Šimůnek V., Sharma R.P., Vacek Z., Vacek S., Hůnová I. (2020): Sunspot area as unexplored trend inside radial growth of European beech in Krkonoše Mountains: a forest science from different perspective. European Journal of Forest Research, 1–15.

Tolasz R., Míková T., Valeriánová T., Voženílek V. (eds.) (2007): Climate atlas of Czechia. Olomouc, Czech Hydrometeorological Institute and Palacký University, 256.

Toth D., Maitah M., Maitah K., Jarolínová V. (2020): The Impacts of Calamity Logging on the Development of Spruce Wood Prices in Czech Forestry. Forests, 11: 283.

Vacek S., Vacek Z., Podrázský V., Bílek L., Bulušek D., Štefančík I., Remeš J., Štícha V., Ambrož R. (2014): Structural Diversity of Autochthonous Beech Forests in Brou-

https://doi.org/10.17221/96/2020-JFS

movske Steny Austrian Journal of Forest Science. Austrian Journal of Forest Science, 131: 191–214.

Vacek S., Vacek Z., Bulušek D., Bílek L., Schwarz O., Simon J., Šticha V. (2015): The role of shelterwood cutting and protection against game browsing for the regeneration of silver fir. Austrian Journal of Forest Science, 132: 81–102.

Vacek S., Vacek Z., Ulbrichová I., Bulušek D., Prokůpková A., Král J., Vančura, K. (2019a): Biodiversity dynamics of differently managed lowland forests left to spontaneous development in Central Europe. Austrian Journal of Forest Science, 136: 249–282.

Vacek Z. (2017): Structure and dynamics of spruce-beech-fir forests in Nature Reserves of the Orlické hory Mts. in relation to ungulate game. Central European Forestry Journal, 63: 23–34.

Vacek Z., Vacek S., Bílek L., Král J., Remeš J., Bulušek D., Králíček I. (2014): Ungulate Impact on Natural Regeneration in Spruce-Beech-Fir Stands in Černý důl Nature Reserve in the Orlické Hory Mountains, Case Study from Central Sudetes. Forests, 5: 2929–2946.

Vacek Z., Vacek S., Podrázský V., Bílek L., Štefančík I., Moser W.K., Bulušek D., Král J., Remeš J., Králíček I. (2015): Effect of tree layer and microsite on the variability of natural regeneration in autochthonous beech forests. Polish Journal of Ecology, 63: 233–246.

Vacek Z., Vacek S., Bílek L., Král J., Ulbrichová I., Simon J., Bulušek D. (2018): Impact of applied silvicultural systems on spatial pattern of hornbeam-oak forests. Central European Forestry Journal, 64: 33–45.

Vacek Z., Vacek S., Slanař J., Bílek L., Bulušek D., Štefančík I., Králíček I., Vančura K. (2019b): Adaption of Norway spruce and European beech forests under climate change: from resistance to close-to-nature silviculture. Central European Forestry Journal, 65: 129–144.

Vacek Z., Prokůpková A., Vacek S., Cukor J., Bílek L., Gallo J., Bulušek D. (2020): Silviculture as a tool to support stability and diversity of forests under climate change: study from Krkonoše Mountains. Central European Forestry Journal, 66: 116–129.

Vorel O. (1990a): Kandík psí zub. Zpravodaj ochrany přírody okresu Praha-západ, 11: 6.

Vorel O. (1990b): Evidence kandíku v SPR Medník. Zpravodaj ochrany přírody okresu Praha-západ, 11: 85–86.

Waldhauser J. (1988): Keltské rýžování zlata na Jílovsku – mýtus, nebo realita? Rozpravy Národního technického muzea v Praze 20: 7–30.

Waldhauser, J. (1995): Celtic gold in Bohemia. In Prehistoric Gold in Europe. Dordrecht, Springer: 577–596.

Zahradník D., Vacek S., Bílek L., Nosková I., Vacek Z. (2010): Horizontal structure of forest stands on permanent research plots in the Krkonoše Mts. and its development. Journal of Forest Science, 56: 531–540.

Zang C., Hartl-Meier C., Dittmar C., Rothe A., Menzel A. (2014): Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Global Change Biology, 20: 3767–3779.

Received: June 25, 2020
Accepted: August 24, 2020