Ecological valence of expanding European ash (*Fraxinus excelsior* L.) in the Bohemian Karst (Czech Republic)

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ABSTRACT: In 2002 a study focused on the evaluation of height and density of expanding natural regeneration of *Fraxinus excelsior* L. (FE) was carried out on Velká hora Hill, a locality in the Bohemian Karst (Český kras). The examined area is located in Karlštejn National Nature Reserve and takes up around 31 ha. The parent rock is limestone. The expansion depends on soil and exposition conditions and relates to the water balance gradient. FE reached the highest densities (up to 6,000 individuals/400 m^2) on Velká hora's peak plateau on medium-deep, heavy-textured decarbonized soils. The lowest expansion (508 individuals/400 m^2) was found on slopes fully exposed to south (S) with water retention capacity lower than 20 mm. In total, the average density was 1,190 individuals/400 m^2. FE natural regeneration reached the highest average heights (around 210 cm) on *Fageto-Quercetum illimerosum mesotrophicum*, the smallest heights on *Carpineto-Aceretum saxatile*. Average height in the locality was 47 cm. No relation was found between FE natural regeneration height or density and the distance of a fertile specimen. The distance exceeded 70 m only in 3.4%. FE seeds could be detected almost everywhere at the area. FE is capable to establish itself on any location of the studied locality except ecologically extreme parts of rock steppe without forest and *Fagus sylvatica* L. stands occupying S slopes. On less favourable sites it is capable to use the protection of other tree species and as a low growing tree it can eventually dominate the site. In more favourable conditions it expands on the whole area, where it can dominate the undergrowth already at 1-m height. If the forest sites are left to natural development, a distinctive change in the tree species composition could take place in a short time period. Such a change could have an essential impact on light conditions, energy flux and species composition of plant and animal communities.

Keywords: Bohemian Karst; European ash; expansion; oak; forest ecosystem classification

Fraxinus excelsior L. (FE) is native to Europe, where it reaches 63° northern latitude, in the west it is limited by Ireland and Spain, in the east by the Volga River. It is absent in Greece, Italy and S Spain. Abundance in Asia Minor is unreliable (Koblížek 1997). The postglacial spread in Europe was investigated by Heuertz et al. (2004) on the basis of genetic information of various populations. Genetic variability of FE populations isolated due to unfavourable site conditions was described e.g. by Höltken et al. (2003). Older dendrological materials (Dengler 1930; Svoboda 1955) also reported FE expanding capability and its wide ecological plasticity. Currently there are differentiated alluvial, mountain and lime ecotypes (Chmelař, Úradníček 1996). In the Czech Republic (CR) FE is abundant from alluvial level of the planar grade to talus level of the mountain grade (in the Krkonoše Mts. up to 980 m above sea level – Koblížek 1997). It reaches 1,300 m a.s.l. in the Alps (Aas, Riedmiller 1997). It fulfils some characteristics of pioneer tree species, and is also often classified as such (Emborg et al. 2000; Prach, Pyšek 1997).

The expansion of *Fraxinus excelsior* L. has not appeared in the Czech Republic just in the last few years. It did not receive much publicity, but it has been noticed since the end of the 19th century (Pyšek, Tichý 2001). Driving out "original" tree species and changes in the whole forest phytocoenosis were described by Swedish and Danish scientists

(Malmer et al. 1978; Diekmann, Lawesson 1999; Emborg et al. 1996, 2000). Similar behaviour of the tree species is also quite common in Slovakia, Germany and other European countries. Hofmeister et al. (2004) described the expansion of FE in the Czech Republic, Slovakia and Sweden partly in relation with NOx deposition. It was not considered as the primary cause of expansion there. The whole process was evaluated as natural.

In vegetation evaluation (Zürich-Montpellier classification – Braun-Blanquet 1921) in CR (Chytrý, Tichý 2003), FE represents a diagnostic species for the class *Querco-Fagetea*, alliance *Alnion incanae*, *Tilio-Acerion*, suballiance *Alnenion glutinose-incanae*. According to units the species is also classified as constant and dominating species (except the alliance *Tilio-Acerion*).

The goals of this study were: 1) to record the present stage of FE expansion on Velká hora Hill – density and height of advance regeneration, so that the investigation could be repeated a few years later, including dynamics evaluation, 2) to record the localization of fertile specimens of *Fraxinus excelsior* L. in the studied area, 3) to find a proper research method and to evaluate FE advance regeneration according to a distance from fertile FE specimens and according to the locality conditions, 4) to outline possible phytocoenosis development.

The study did not try to find the reasons for expansive behaviour of FE on Velká hora Hill.

MATERIAL AND METHODS

According to a climatic-zone description, the Bohemian Karst (Fig. 1) belongs to the semi-humid area. Growing season lasts 150–170 days. SW and S winds prevail (Stárka 1984). Precipitation amount varies around 550 mm with maximum in the summer period. Average annual temperature is approximately 8.5°C, the warmest is July (18.0–18.5°C) and the coldest is January (around –1.5°C) (Anonymus 1960; Syrový 1958; actual data of Czech Hydrometeorological Institute). Besides precipitation, temperature and evaporation just above the semi-arid point, terrain relief and forest stands are the other most important factors (Mařan 1947).

The Bohemian Karst belongs to the geomorphological unit Hořovice Downs (Anonymus 1996). Šimunek (2002) reported that total N deposition was annually approximately 40 kg/ha in conifer forests and about 30 kg/ha in broadleaved forests. Intensive forest management near the Karlštejn castle was described already in the 14th century. Forests were important income sources even at that time (Černý 1949). Livestock grazing and intensive stump wood management were common there till the 19th and the first half of the 20th century.

The Protected Landscape Area (PLA) Bohemian Karst was established on an area of 12,838 ha on 12th April 1972. Velká hora Hill (around 4 km away from the town of Karlštejn, 49°56´24´´N lat., 14°10´52´´E long.) is the heart area of the National Nature Reserve (NNR) which received the status Protected Area in 1932. Forest ecosystems are nearly natural (sensu Vrška, Hort 2003). From geological aspects the locality belongs to America anticline of Barrandian Paleozoic with Devonian Limestones (Havlíček 1987). The area is highly valuable in entomologic and geobotanic terms. In this area Klika described for the first time an endemic association

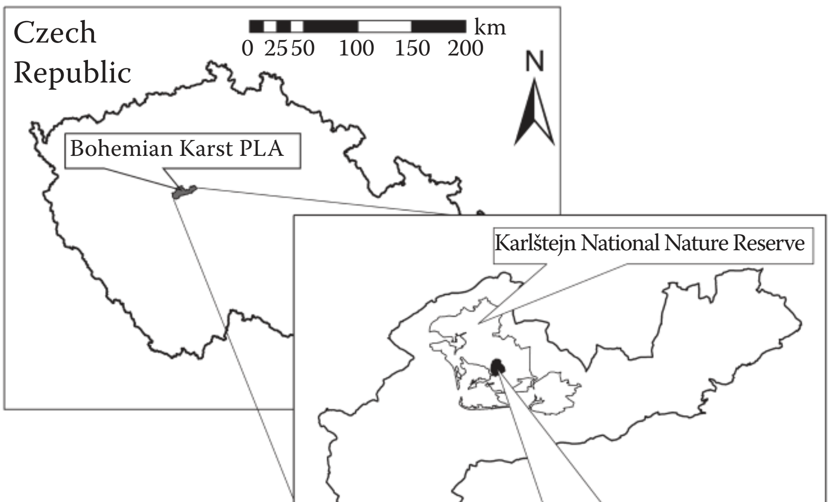

Fig. 1. Location of the studied area

of the Bohemian Thermophyticum – *Lathyro versicoloris-Quercetum pubescentis* (Klika 1928). Forest communities mostly belong to the alliance *Carpinion* Issler 1931, *Quercion pubescenti-petraea* Br.-Bl. 1932 nom. mut. propos., *Quercion petraea* Zólyomi and Jakucs ex Jakucs 1960, *Fagion* Luquet 1926. Unstocked forest lands are sharply distinct, mainly belonging to the order *Festucetalia valesiacae* Br.-Bl. et Tüxen ex Br.-Bl. 1949.

The study was carried out on the whole upland plain of Velká hora Hill and its surroundings including slopes of all expositions down to slope deluvia. Altitude varied between 280 and 422 m a.s.l. The studied locality covered approximately 31 ha. Terrain research was conducted in 2002. The Velká hora locality was divided into a grid of squares (20 × 20 m) that were the basic evaluation units and were considered internally homogeneous. The placing of the grid in the terrain was based on forest maps, altimetry, orthophotograph map and measuring equipment. Each segment was evaluated individually and described by the average height and density of FE natural regeneration. A modified method of data collection developed by Vrška (1999, 2002) was used. 7 categories for height and 6 categories for density were established. Yearlings (saplings with primary leaves) were not included.

Fructiferous (and potentially fructiferous) FE specimens were systematically recorded, as well as standing dead specimens according to nature conservation management arrangements. Each segment of the grid was evaluated. During statistical interpretation those two numbers were often summed together as the clearance of FE specimens was done 1–2 years earlier than terrain investigations. According to the used research methods (not including FE yearlings) it is obvious that earlier cleared specimens influenced the studied natural regeneration even in the research period.

Data evaluation was done in Canoco for Windows 4.5 (ter Braak, Šmilauer 2002), including the statistical testing of significance of environmental characteristics (also in Statistica 6.1 program) (STATSOFT 2003). Methodical approaches of Lepš and Šmilauer (2000, 2003) and Herben and Münzbergová (2001) were used and one-way analysis of variance ANOVA as well as GIS analyses were applied for data processing (ArcMap™8.3 program – Minami et al. 2000). The central points of squares substituted square units in calculations and were attributed characteristics describing the whole segments. Results were related to the units of CR forest ecosystem classification (Anonymus 1971/1976; Viewegh et al. 2003) and to environmental condi-

Table 1. Units of Czech forest ecosystem classification in Velká hora Hill (Viewegh et al. 2003; Trnčík et al. 2000; Podhorník 2000)

Forest site type complex (FSTC)		Forest site type (FST)	
0X	*Pinetum dealpinum (xerothermicum)*	0X2	Dealpine Pine with *Sesleria caerulea* (L.) Adr. on rock formations
1X	*Corneto-Quercetum (xerothermicum)*	1X2	Cornelian Cherry-Oak on rendzinas on exposed slopes
		1X8	Cornelian Cherry-Oak – steppe-forest
1C	*Carpineto-Quercetum subxerothermicum*	1C8	Water-deficient Hornbeam-Oak on limestones with *Brachypodium pinnatum* (L.) P.B.
1W	*(Fagi-) Carpineto-Quercetum calcarium*	1W2	Limestone Hornbeam (-Beech)-Oak on gentle slopes
		1W9	Limestone Hornbeam (-Beech)-Oak on steep slopes
1J	*Carpineto-Aceretum saxatile*	1J6	Hornbeam-Maple on limestones on warm gentle slopes
1A	*Aceri-Carpineto-Quercetum lapidosum*	1A9	Stony-colluvial Maple-Hornbeam-Oak on limestones on upper part slopes and on ridges
2W	*Fageto-Quercetum calcarium*	2W1	Limestone Beech-Oak with *Mercurialis perennis* L. on gentle slopes
		2W2	Limestone Beech-Oak with grasses
		2W9	Limestone Beech-Oak on steep slopes
2H	*Fageto-Quercetum illimerosum mesotrophicum*	2H5	Loamy Beech-Oak with *Luzula luzuloides* (Lamk.) Dandy et Wilmott and *Carex montana* L. on pitched flats
2D	*Fageto-Quercetum acerosum deluvium*	2D7	Enriched-colluvial Beech-Oak on limestones on deluvium
2A	*Aceri-Fageto-Quercetum lapidosum*	2A9	Stony-colluvial Maple-Beech-Oak on limestones on steep slopes
3J	*Tilieto-Aceretum saxatile*	3J6	Lime-Maple on limestones on steep slopes
3D	*Querceto-Fagetum acerosum deluvium*	3D1	Enriched-colluvial Oak-Beech on limestones on shaded deluvium
3W	*Querceto-Fagetum calcarium*	3W9	Limestone Oak-Beech on steep slopes

Table 2. Units of Czech forest ecosystem classification in the most important ecological gradients

	Increase of humus content in (surface) soil horizon				
Increase of water balance	0X2	–	–	–	–
	1X8	–	–	–	–
	1X2	–	–	–	–
	1C8	–	–	–	–
	–	1W9	–	1A9 ≈ 1J6	
	1W2	–	–	–	–
	–	2W9	–	–	–
	2W2	–	–	–	–
	2W1	–	–	–	–
	2H5	–	2D7	2A9 ≈ 3J6	
	–	3W9	–	–	–
	–	–	3D1	–	–

tions. The basic unit of the classification – Forest Site Type (FST) – was defined according to Zlatník (1956). Detailed stand characteristics of FSTs elaborated by Šamonil (2005) and Šamonil and Viewegh (2005) was also used.

Soil profile (from 2001) was classified according to FAO-ISSS-ISRIC (1998). Humus form was evaluated according to Green et al. (1993). Profile description and sampling were related to Valla et al. (2002) and Rejšek (1999). Research methods of laboratory analyses agreed with Anonymus (2003).

RESULTS

The map describing the units (FST) of Czech forest ecosystem classification corresponds with Podhorník (2000) and is enclosed in Fig. 2. An attached graph shows individual FSTs found at the locality. Headings of individual units are listed in Table 1.

Table 2 describes the main ecological gradients in FSTs. The vertical axis shows a water balance gradient, the horizontal axis a humus amount gradient. In FST 0X2 potential direct solar irradiation (PDSI) reached 4.5×10^6 kJ/m^2 during six months, in FST 3D1 it was only 3.2×10^6 kJ/m^2 during the same period (sensu Jeník, Rejmánek 1969). Water-retention capacity of soil, the second most important water balance factor in the Bohemian Karst, varies around 90 mm in FST 3D1, 2H5 and 3W9, while in FST 0X2 it usually drops below 10 mm. Lateral water movement is strongly reduced and could be neglected.

Forest site types listed on the right side of the table represent humus-enriched stands. In FST 1J6 and 1J3 the surface organo-mineral horizon can reach up to 50 cm while containing 5.5% of oxidizable carbon. The organo-mineral horizon of stands on the left side does not usually exceed 10 cm and oxidizable carbon amounts to 3.5%.

The main output of FE expansion evaluation is represented by the maps describing the density and

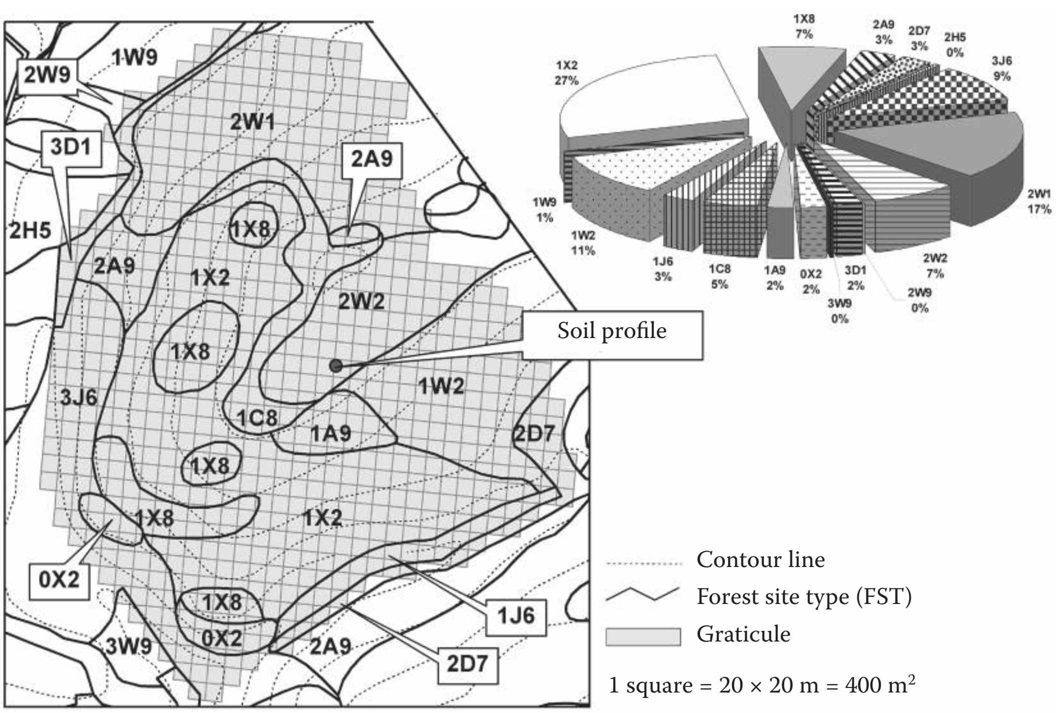

Fig. 2. Czech forest ecosystem classification map with contour lines and location of the studied area and a graph of FST representation in the locality

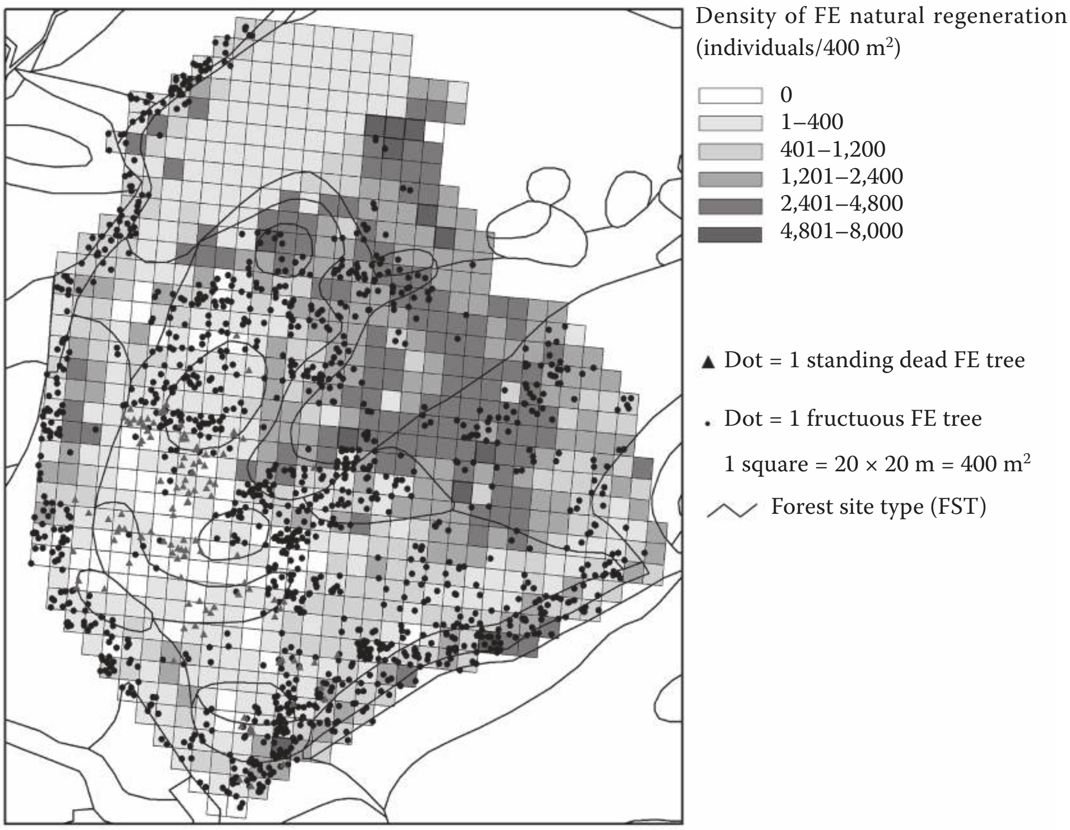

Fig. 3. Map of the density of FE natural regeneration with positions of fertile FE specimens

height of FE natural regeneration with recorded localities of fertile and earlier cleared FE specimens on Velká hora Hill (Figs. 3 and 4). Fig. 4 shows distances from the centre of each evaluated square to the nearest fertile FE specimen (or to the centre of the square containing such a specimen).

The one-way analysis of variance shows statistically significant differences ($p < 0.01$) between

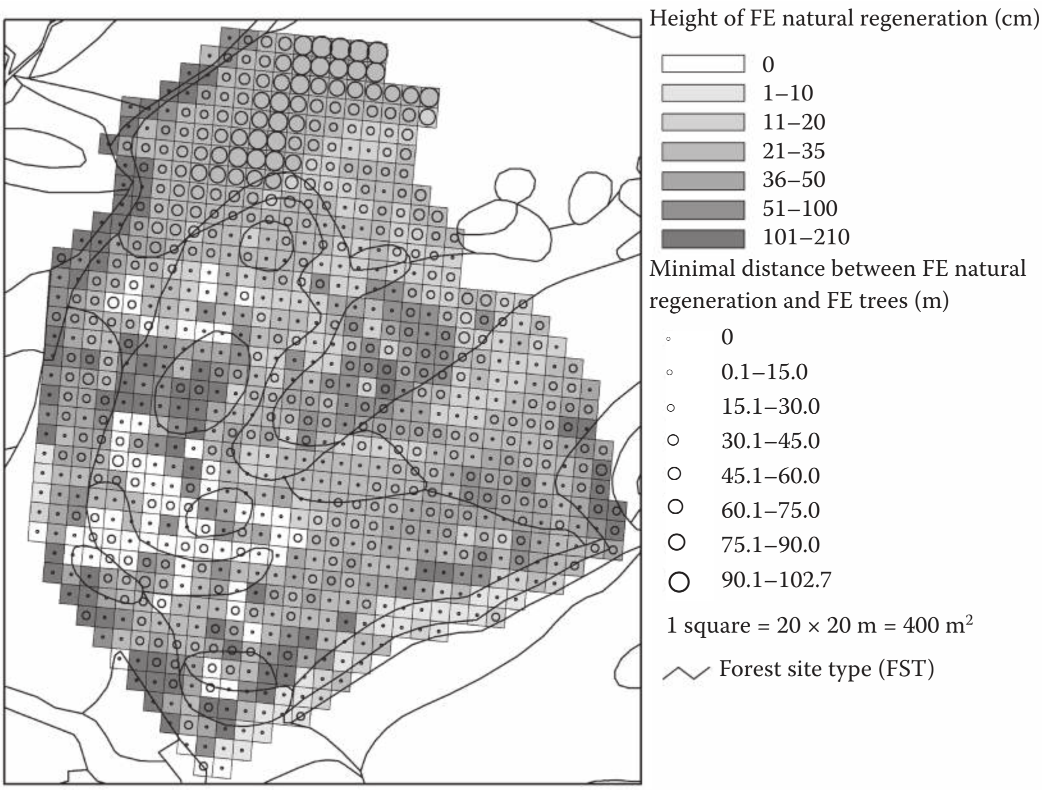

Fig. 4. Map of height of FE natural regeneration and minimal distance between natural regeneration and fertile trees

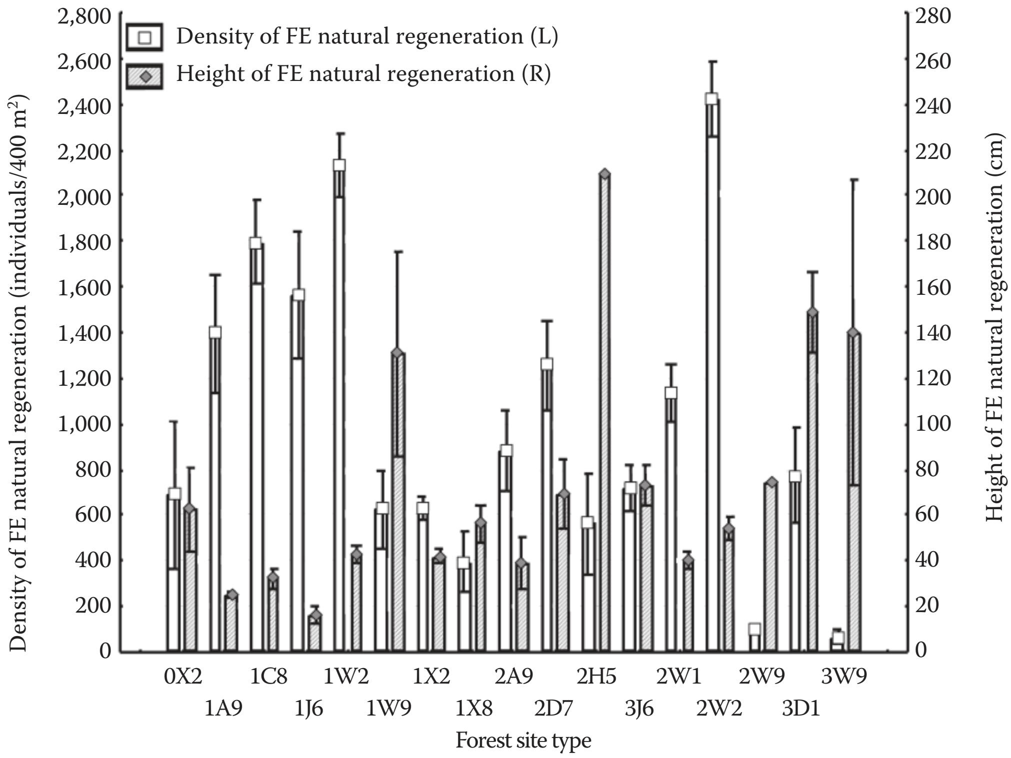

Fig. 5. Density and height of FE natural regeneration in units of Czech forest ecosystem classification (cf. Table 1). Means and standard errors (0.95) are shown

individual FSTs in the height and density of FE natural regeneration. The outputs of RDA analyses – Monte Carlo permutation test also confirm the same results. Obvious is the development of FE natural regeneration height and density along the water balance gradient. The output describing the

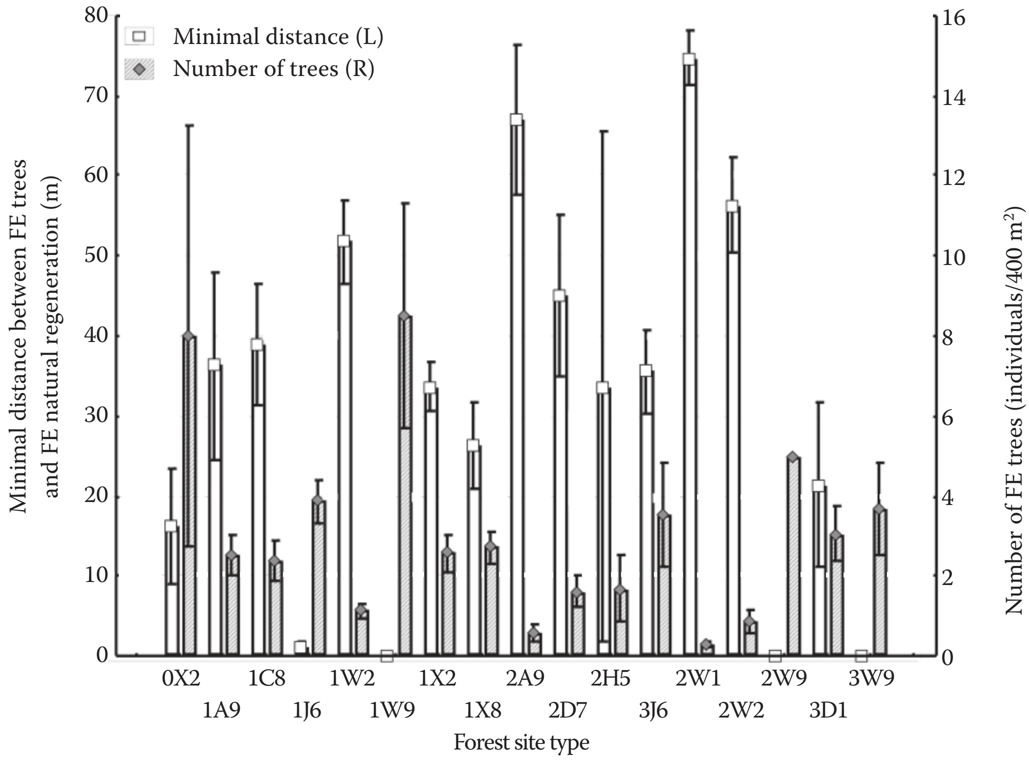

Fig. 6. Minimal distance between fertile FE trees and FE natural regeneration in units of Czech forest ecosystem classification. "The tree" means each stem. Means and standard errors (0.95) are shown

Table 3. Description of the soil profile on Velká hora Hill

Calcaric Cambisol (Endoskeletic, Chromic and Hypereutric)

Mark of horizon	Forest floor	Ln, Fa, Hh – Vermimul
A	**Mollic horizon**	0–6 cm, high content of roots, colour 7.5 YR 5/3, poor content of grit – limestone, loamy, medium-polyhedral, crumbly aggregates, loose, slightly moist, without HCl reaction, transition – sharp, linguiform
E	**Albic horizon**	6–28 cm, humus aggregates at several places, poor content of roots and stones – limestone, colour 7.5 YR 6/4, loamy to clay loam, medium-polyhedral, not very hard aggregates, weakly compact, dry, without HCl reaction, transition – gradual, warped
B	**Cambic horizon**	28–72 cm, humus aggregates at several places, sporadic roots, colour – non-homogeneous 5 YR 5/8, medium content of grit, frequent stones – limestone, clayey, coarsely polyhedral, hard aggregates, compact, poor content of argillans, slightly moist, weak HCl reaction, transition – diffusional, warped
$C_1 + C_2$	**Disintegration of parent material**	72–130 cm, nearly without roots, colour – non-homogeneous 5 YR 4/8, high content of stones – limestone, clayey, without structure, compact, slightly moist, stormy HCl reaction
	Parent material	+ 130 cm, limestone – Devonian, Lochkov

gradient of organic matter content in soil is not clear.

Average FE heights and densities in each FST are shown in Fig. 5, which also describes distances of FE regeneration from the seed source. FE reached the highest densities in the peak area of Velká hora Hill in FST 2W2: 2,534 individuals/400 m^2, followed by FST 1W2 with 2,260 individuals/400 m^2, and 1C8 with 1,814 individuals/m^2. The exposed southern slopes are the least affected by FE expansion (average values are: FST 1X8 – 508, 1X2 – 677, 1W9 – 655 individuals/400 m^2). Average density in the whole studied location was 1,190 individuals/400 m^2, which equals almost 30,000 individuals/ha.

FE reached the highest average heights in FST 2H5 – 210 cm and 3D1 – 149 cm. It is a good quality site with deeper soil profiles, higher water-retention capacity (WRC = approx. 80–100 mm) and lower sum of potential solar radiation. The lowest average height was measured in FST 1J6 – 17 cm, 1A9 and 1C8 – 26 cm. Average height of the whole locality was 47 cm, if only non-zero values were calculated, the average height was 52 cm.

In the examined locality 1,020 FE specimens (potentially fructiferous trees) with 1,278 trunks and 116 earlier cleared trees were found in total (Fig. 3). Almost 2 adult specimens (with 2 trunks) are at the average in one square (20 × 20 m). The highest aver-

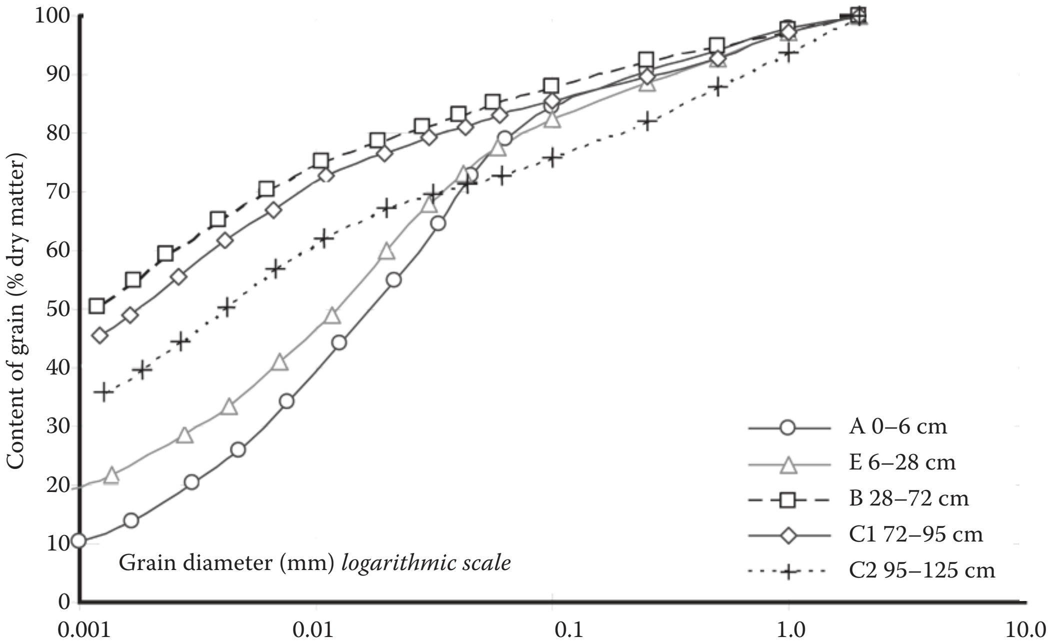

Fig. 7. Cumulative curves of particle size distribution of soil profile

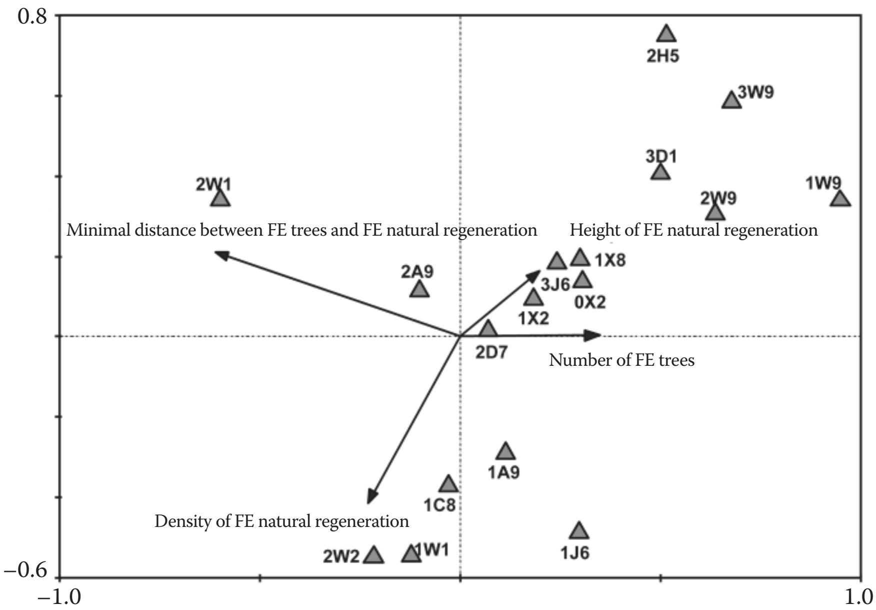

Fig. 8. Graph of RDA analysis

age number of fertile trees (including trees cleared earlier) occurred in rather rarely present FST 1W9 (8 individuals/400 m^2) and 2W9 (5 individuals per 400 m^2), further in 3W9, 3D1 and 1J6 (3–4 individuals/400 m^2). These were localities on steep slopes, mostly with humus-enriched soil. Nature

Table 4. Soil analyses on Velká hora Hill

Horizon, depth (cm)		A 0–6 cm	E 6–28 cm	B 28–72 cm
Dry matter 105°C (%)		97.46	98.30	95.88
Ashing loss 550°C (%)		10.35	4.69	7.85
Carbonate (%)		< 0.01	0.02	0.45
pH_{H_2O}		5.96	4.71	5.08
pH_{CaCl_2}		5.83	4.10	4.69
Oxidizable carbon C_{ox} (%)		3.36	0.86	0.44
Total nitrogen N_{Kjel} (%)		0.289	0.084	0.074
Available P spectrophotometer (mg/kg)		188.8	130.2	1,136.8
Extraction with 0.1 mol/l $BaCl_2$	Ca (mg/kg)	3,943.25	822.83	4,039.36
	K (mg/kg)	146.53	31.21	82.48
	Mg (mg/kg)	202.24	46.35	108.68
	Na (mg/kg)	11.32	8.77	22.01
	Al + H (mval/kg)	1.180	36.787	11.556
CEC-(Al + H) (mval/kg)		217.6	46.0	213.6
Cation exchange capacity (CEC) (mval/kg)		218.8	82.8	225.1
Extraction with Aqua regia (3:1, $HCl + HNO_3$)	Al (mg/kg)	16,785	19,161	51,273
	Ca (mg/kg)	5,398	1,636	12,317
	Fe (mg/kg)	32,616	32,891	46,789
	K (mg/kg)	1,575	1,221	5,188
	Mg (mg/kg)	1,463	1,459	3,340
	Na (mg/kg)	48.30	45.05	141.53
Particle-size distribution	0.1–2 mm (%)	15.6	17.6	12.0
	0.05–0.1 mm (%)	10.0	7.0	3.6
	0.01–0.05 mm (%)	34.8	28.6	10.0
	< 0.01 mm (%)	39.6	46.8	74.5

conservation management arrangements used to concentrate on the botanically and entomologically most valued parts of rocky steppes. Most of the cleared trees were found in FST 1X2 and 1X8 (99 individuals in total). The evaluation did not prove a significant relation between the height or density of FE natural regeneration and the distance of fertile (adult) FE specimens. On approx. 31 ha the estimated average distance was 15.3 m. This value exceeded 50 m only in 50 cases (6.3%) and 70 m just in 27 cases (3.4%). A maximal distance was 102.7 m. No correlation was found between the fertile tree location and the amount of natural regeneration at the locality. The fertile trees affect across the board and FE regeneration depends on individual site conditions to a larger extent. Average distances of individual FST vary (Fig. 6) as also confirmed by the analysis of variance.

Only a loose dependence was stated between FE regeneration height and density. The number of 6,000 individuals/400 m^2 found in lower height classes subsequently decreases – due to the influence of competition, etc. – and at 210 cm height it is usually around 220 individuals/400 m^2. At this height the regeneration can also easily reach up to 1,800 individuals/400 m^2.

Fraxinus excelsior L. flourishes well on the undulating peak plateau of Velká hora Hill (FST 2W2), where the soil was classified as Calcaric Cambisol (Endoskeletic, Chromic and Hypereutric) with lithologically conditioned albic horizon (Šamonil 2005). The description of soil profile, its chemical characteristics and grain size distribution are shown in Tables 3 and 4, and in Fig. 7. The soil is of relict character with rubification signs. A distinctive feature is that the upper layers of soil profile contain a higher amount of eolian material (around 30%). Cambic horizon is very heavy (75% fraction < 0.01 mm), decarbonated, non-aerated, with weak argillans. Water-retention capacity of the profile physiological depth is 81.7 mm. Soil conditions rapidly change across the studied locality. "The internal relief" (cf. Šály 1986) does not correspond to present surface. Poorly developed Leptosols are found on S exposition and on slopes with gradient > 20° (mostly in FST 1X8, 1X2, 1C8, 1J6, 2A9).

Fig. 8 shows the graphical output of RDA analysis, where FE natural regeneration characteristics were related to individual squares and the units of Czech forest ecosystem classification. The graph represents the above listed conclusions describing FE natural regeneration heights and densities in individual FST. The relation between the above-mentioned characteristics of advance regeneration is clearly visible. The increasing height is obviously related with a decreased number of regeneration individuals, indeed with no correlation to the source distance. The source distance is significant only in FST 2W1.

DISCUSSION

The presented research well corresponds with conclusions of similar research completed in other European countries focused on the expansive character of mesophilic woody species in forest sites dominated by *Quercus* spp. and *Carpinus betulus* L. (Malmer et al. 1978; Diekmann, Lawesson 1999; Emborg et al. 1996, 2000). Some of those localities also underwent the history of intensive management, while they are currently left to natural development. Such contrast could be one of the main reasons explaining the expansive behaviour of researched mesophytes, because the described development of FE natural regeneration could be definitely characterized as an expansion. FE behaviour resembles the manner of expanding woody species in the above listed cases and so recalls the statement of Sádlo and Pokorný (2004a): "The present expansion of European ash is not a consequence of today's unusual management measures, but of abnormal non-disturbance at forest sites" and further (Sádlo, Pokorný 2004b): "Expansion and invasions are not diseases of modern countryside, but the engine of landscape vegetation development. Within the changing environment, expansions are not an alternative to the stage without expansions, but to invasions."

The characteristics of FE regeneration researched on Velká hora Hill correspond with regional evaluation of Buriánek (1999). His highest densities were 1,250 individuals/are. The author stated that FE at the age 12–15 years and height 160 cm fully governed the shrub layer, which could lead to future elimination of light demanding woody species in forests. It is concluded on the basis of presented research that FE can govern the shrub layer in suitable sites even earlier, ca. at 1 m height. Buriánek (1999) reported a significant influence of fertile trees on natural regeneration density up to 70 m. Such conclusion cannot be verified, as the found average distance was 15.3 m.

It is not possible to agree with Nekolová (2002), who stated that ash demanded deeper, permeable soils rich in nutrients with a sufficient amount of calcium. This study shows its wide ecological adaptability. In the studied area it grows best on very heavy, partly decalcified soils (cf. Ellenberg et al.

1992; Diekmann 1996; Chmelař, Úradníček 1996; Smith et al. 2001). The above cited authors all agree with higher demands of FE for light, although it deals well with shade in the early growth stage. Our results also confirm the findings of Marigo et al. (2000), who described FE as capable to resist a high water deficit. FE survives even in locations exposed to high solar radiation with water-retention capacity below 20 mm. Höltken et al. (2003) described low competing abilities of FE when compared to oak (*Quercus* spp.) or beech (*Fagus sylvatica* L.). In the present conditions of the Bohemian Karst, FE can successfully compete with oak at least.

CONCLUSIONS

The presented study offers a discussion regarding the expansion behaviour (cf. Sádlo, Pokorný 2004a) of *Fraxinus excelsior* L. within the Bohemian Karst. Site conditions – mainly soil conditions and exposition – have a strong influence on FE expansion; obvious is also its dependence on the water balance gradient. The gradient of organic matter content in soils does not provide unambiguous results. FE grows very well on deeper, heavy, partly decalcified soils of less exposed localities. The most massive expansion is visible in these FST: Limestone Beech-Oak with grasses, Limestone Hornbeam (-Beech)-Oak on gentle slopes and Water-deficient Hornbeam-Oak on limestones with *Brachypodium pinnatum* (L.) P.B. Expansion in the above-mentioned sites has a sheet-like character, and FE natural regeneration is capable to govern the undergrowth and quickly shoot up (proliferate) already at 1 m height. The highest natural regeneration of FE – around 210 cm – takes place in good quality sites of FST Loamy Beech-Oak with *Luzula luzuloides* (Lamk.) Dandy et Wilmott and *Carex montana* L. on pitched flats. In extreme ecological sites such as FST: Cornelian cherry-Oak on rendzinas on exposed slopes, Cornelian cherry-Oak – steppe forest the expansion runs differently. The ash does not come up in sheet-like natural regeneration and its mortality is very high although some specimens at more favourable microclimatic places survive, mostly protected in the shade of individually growing oak specimens (*Quercus pubescens* L.). In time they grow through their protection, fruit and spread further. So the species can grow at rather unfavourable places. Only on a fully forest-free area such as FST Cornelian cherry-Oak – steppe forest the ecological conditions are so extreme that FE mortality is almost certain. In sites with dominating *Fagus sylvatica* L. the light conditions and strong beech natural regeneration cause rather weak FE regeneration at some places. In other cases FE proves to be very aggressive and when left to natural development, soon significant changes in the stand composition will occur with possible impacts on light conditions, energy fluxes and species composition of plant and animal communities.

An average distance between FE natural regeneration and the nearest fertile specimen was 15.3 m. Just in 27 out of 789 cases it exceeded 70 m. Maximal distance was 102.7 m. The studied locality does not show any differences in the distance of fertile trees from natural regeneration, as their impact is sheet-like and the species governs sites with favourable conditions.

Nature protection requires a clear definition of protected object and a decision whether to protect natural development of sites – may it have any possible results – or to preserve highly valued plant and animal communities which used to be influenced by human activities in the past. So far applied management approach in the locality suits neither one of the possibilities.

The study laid out good bases for repeated research and evaluation of FE natural regeneration dynamics that could be done in the whole location or in individual forest site types.

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Ekologická valence expandujícího jasanu ztepilého (*Fraxinus excelsior* L.) v Českém krasu (Česká republika)

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ABSTRAKT: Na Velké hoře v Českém krasu byla v roce 2002 na asi 31 ha hodnocena hustota a výška expandujícího přirozeného zmlazení *Fraxinus excelsior* L. (FE). Lokalita je součástí Národní přírodní rezervace Karlštejn. Geologickým podložím je vápenec. Zásadní vliv na vývoj expanze mají půdní a expoziční poměry, zřejmý je vývoj podél gradientu vodní bilance. Nejvyšších hustot (až 6 000 ks/400 m^2) dosáhl FE ve vrcholové plošině Velké hory na středně hlubokých, těžkých, odvápněných půdách. Nejméně expanduje na silně exponovaných jižních svazích (508 ks/400 m^2) s méně než 20 mm retenční vodní kapacity. Průměrná hustota byla celkově 1 190 ks/400 m^2. Nejvyšších průměrných výšek (210 cm) dosahovalo zmlazení FE na stanovištích *Fageto-Quercetum illimerosum mesotrophicum*, nejmenších na *Carpineto-Aceretum saxatile*. Průměrná výška pro lokalitu byla 47 cm. Nebyla zjištěna závislost mezi výškou či hustotou přirozeného zmlazení FE a vzdáleností k plodným jedincům. Ta byla pro celou lokalitu 15,3 m a jen ve 3,4 % případů překročila 70 m. Semena FE jsou v lokalitě téměř všudypřítomná. Mimo prakticky bezlesé, ekologicky extrémní partie skalních stepí a kromě porostů s konkurenčně schopným *Fagus sylvatica* L. na severních svazích má FE značný potenciál se prosadit. Na ekologicky exponovaných stanovištích prorůstá ochranu ostatních dřevin a jako nízký strom individuálně ovládne stanoviště. V příznivějších podmínkách je expanze naopak plošná – již od výšky 1 m může ovládnout podrost. Při ponechání porostů samovolnému vývoji dojde v blízké budoucnosti k výrazné změně dřevinné skladby s možnými dopady na světelné poměry, energetické toky a druhové složení rostlinných i živočišných společenstev.

Klíčová slova: Český kras; jasan ztepilý; expanze; dub; lesnická typologie

Na základě provedeného šetření lze hovořit o expanzním chování (Sádlo, Pokorný 2004a) *Fraxinus excelsior* L. v Českém krasu. Zásadní vliv na průběh expanze mají půdní a expoziční poměry, zřejmý je vývoj podél gradientu vodní bilance stanovišť a porostů. Gradient obsahu organické hmoty v půdě se ve výstupech neprojevuje jednoznačně. FE silně prosperuje na hlubších, těžkých a částečně odvápněných půdách méně exponovaných lokalit. Nejmasivnější je expanze FE na lesních typech (LT) 2W2 – vápencová buková doubrava sušší s travami, 1W2 – vápencová habrová doubrava (s bukem) na mírných svazích, 1C8 – suchá habrová doubrava na vápenci s *Brachypodium pinnatum* (L.) P.B. Zde je expanze plošná. Již od výšky asi 1 m je přirozené zmlazení FE schopné ovládnout podrost a rychle odrůstat. Největších výšek – okolo 210 cm – dosahuje na kvalitních stanovištích LT 2H5 – hlinitá buková doubrava s *Luzula luzuloides* (Lamk.) Dandy et Wilmott a *Carex montana* L. na plošinách. Na ekologicky extrémních stanovištích LT 1X2 – dřínová doubrava na rendzinách na exponovaných svazích a 1X8 – dřínová doubrava – drnová lesostep je průběh expanze odlišný. Jasan se zde nezmlazuje plošně a mortalita je značně vysoká. Jedinci FE však na místech mikroklimaticky příznivějších individuálně přežívají, nejčastěji v částečném zástinu jednotlivě rozmístěných *Quercus pubescens* L. Časem prorůstají svou ochranou, plodí a dále se rozšiřují. I zde má dřevina potenciál se prosadit. Pouze na zcela bezlesých partiích LT 1X8 – dřínová doubrava – drnová lesostep jsou ekologické podmínky natolik extrémní, že mortalita FE je prakticky stoprocentní. V porostech s dominancí *Fagus sylvatica* L. naopak světelné podmínky i silná obnova buku a jeho konkurenceschopnost způsobují, že je zde FE v přirozeném zmlazení touto dřevinou potlačován. V ostatních případech se FE prosazuje velmi agresivně a při ponechání porostů samovolnému vývoji dojde v blízké budoucnosti k výrazné změně dřevinné skladby porostů s možnými dopady na světelné poměry, energetické toky a druhové složení rostlinných i živočišných společenstev.

Průměrná vzdálenost mezi přirozeným zmlazením FE a nejbližším plodným jedincem je 15,3 m, pouze ve 27 případech ze 789 překročila 70 m. Maximální vzdálenost činila 102,7 m. Na lokalitě se neprojevují rozdíly v postavení plodných stromů vůči přirozenému zmlazení, neboť jejich působení je plošné a zejména na stanovišti záleží, zda se dřevina prosadí.

Z pohledu ochrany přírody je nezbytné pevně definovat předmět ochrany a rozhodnout, zda bude chráněn samovolný vývoj – ať je jakýkoli – nebo současná, neobyčejně cenná, ale zároveň lidskou činností v minulosti modelovaná rostlinná a živočišná společenstva. Dosud prováděné managementové zásahy na lokalitě nevyhovují žádné z obou možností.

Studie položila dobrý základ pro opakované šetření a zhodnocení dynamiky FE zmlazení. Vývoj bude možné studovat nejen pro celou lokalitu, ale také diferencovaně podle stanovištních podmínek.

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