A REVIEW ON NATURAL STAND DYNAMICS IN BEECHWOODS OF EAST CENTRAL EUROPE

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Abstract. This paper aims to present a review on the natural stand dynamics as recorded in 'virgin' and other untreated beech forest reserves in East Central Europe. This information can contribute to defining the reference point for nature-based management of beech forests. Topics covered include: distribution of beech, major beech forest types, growth characteristics, seed production and survival, germination and establishment, growth and mortality patterns during development, regeneration cycles, dead wood and herbaceous vegetation dynamics. Based on the analyses of scientific traditions, strengths and weaknesses of available information, recommendations for future research activities are also formulated.
Keywords. *Fagus sylvatica, forest dynamics, virgin forest*

Introduction

This paper is aimed at reviewing information on natural stand dynamics in beechwoods of East Central Europe. The motivation for such review comes from the strong belief that in our region the extremely high biological values of beech forests have become threatened as a result of fast changes in ownership structure and economic forces in this region. The only way to provide long-term solution to this problem is to resolve the challenge of sustainable forest management, which has to be based on natural processes. This means that the knowledge base on natural processes is of utmost relevance for improving beech management, for assisting the multifunctional utilization of these forests.

The area covered includes the Czech Republic, Slovakia, Southern Poland, Ukraine, Romania and Hungary, and covers the Carpathian and Pannonic biogeographic provinces and the southern tip of the Central European province [Meusel 1965/1984 in 28].

This review bears the sign of two important peculiarities:

(1) Limited accessibility of information;
(2) Strong scientific traditions in describing forest stand structures and distinguishing of forest units (e.g. Braun-Blanquet type associations, forest types, site types, ecosystem types).

This latter also means that far less emphasis has been put on studying processes than in countries with different scientific traditions [c.f. 66, 72, 113, 114, 115, 116].

As far as it was possible, information on natural stand structure and dynamics in beechwoods is based on observations and research in unmanaged, near-natural stands.

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Most of them are protected as Forest Reserves or National Parks. Besides, several observations and research results from managed beech forests are also used.

The review is based on material we got know about (many publications are not referenced) and we got access to (many are in periodicals not easily available or inaccessible). The papers used were published in Czech, Slovakian, Polish, Russian, Romanian, German, English, French and Hungarian languages.

Early works on the virgin forests of the Carpathians were published from the second half of the 19th century. Some of them are just nice descriptions of the experience of seeing them [15, 46, 63], others contain some basic information on the structure and possible utilization of these forests [17, 18, 20, 21, 22, 23, 62]. Works of Zlatnik [119, 120, 121] and the major books by Prusa [79] and Korpel [43] contain the most substantial information on the structure and composition of virgin forest remnants in the Czech Republic and the Slovakian and Ukrainian Carpathians. In Hungary Czájlik [7, unpublished works] started to conduct systematic forest reserve studies. *Table 1* contains basic information of the unmanaged near-natural reference sites that were used for this review.

Beech in East Central Europe

Status of beechwoods in East Central Europe

Beech is an important tree species in the Carpathian Mts. and also in the Carpathian basin. This area is the easternmost part of its range in Central Europe (*Fig. 1*).

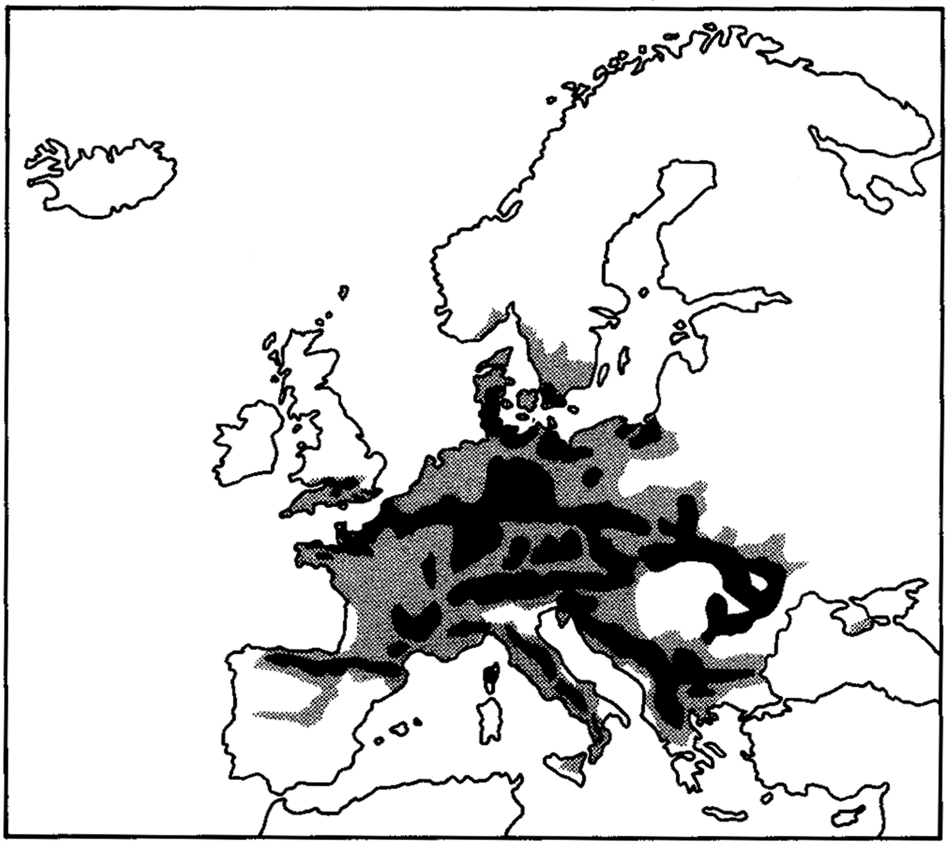

Figure 1. *Natural range of beech (Fagus sylvatica) and major areas of Beech woodland (dark). Source:* [74].

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Table 1. *Sites with near-natural beech woodland in which permanent plots have been established to monitor long-term vegetation changes. For tree species: B - Beech; Sp - Spruce; F - Fir; Sy - Sycamore; E - Elm; A - Ash; H - Hornbeam; L - Lime; O - Sessile oak; W - Wild service tree; Bi – Birch. Information is collected from* [79, 80, 105, 106, 107, 108, 109, 110, 111, 112] *for Czech Republic,* [43, 45] *for Slovakia,* [31, 32, 33, 34] *for Poland,* [103] *for Ukraine,* [25] *for Romania, Czájlik (pers. comm.),* [67, 93] *for Hungary.*

Site name	**Major tree species**	**Site characteristics** **S**ize, **N**utrient status; **E**levation; **M**ean **A**nnual **T**emp; **P**recipitation (annual/in growing season); **S**now cover; **L**ength of **G**rowing **S**eason (days warmer 5/10°C)	**Year of recording**
Czech Republic			
Polom	Sp, B, F	**S**: 19.4 ha; **N**: Mesotrophic; **E**: 545-625 m a.s.l; **MAT**: 6°C; **P**: 786 mm/465 mm **LGS**: 210/140 days	1973, 1995
Razula	F, B, Sp	**S**: 23.2 ha; **N**: Mesotrophic; **E**: 600-812 m a.s.l; **MAT**: 6.2°C; 150 freezing days **P**: 1088 mm/613 mm; **LGS**: 205/125 days	1972, 1995
Salajka	B, F, Sp	**N**: Eumesotrophic; **E**: 715-820 m a.s.l; **MAT**: 5.4°C; **P**: 1144 mm **LGS**: 190/133 days	1974, 1994
Zakova hora	B, Sp	**S**: 17.1 ha; **N**: Mesotrophic; **E**: 725-800 m a.s.l; **MAT**: 5°C; **S**: 40 cm; **P**: 916 mm **LGS**: 110-120 days	1888, 1939, 1968, 1974, 1995
Stozec	B, Sp, F	**S**: 16.17 ha; **N**: Mesotrophic; **E**: 750-900 m a.s.l; **MAT**: 5°C;**P**: 793 mm **LGS**: 240/120 days	1974
Zofin	B, Sp, F	**S**: 97.72 ha; **N**: Eumesotrophic; **E**: 735-825 m a.s.l; **MAT**: 4.3°C; **S**: 0.5-1 m; **P**: 915 mm/615 mm; **LGS**: 180/120 days	1974-75
Boubin	B, Sp, F	**S**: 46.66 ha; **N**: Mesotrophic; **E**: 900-1100 m a.s.l; **MAT**: 4.2°C; **S**: 100-140 days; **P**: 867 mm; **LGS**: 115 days	(1847), 1954; 1959; 1964; 1969, 1972, 1984-89, 1996
Milesice	Sp, B, F	**S**: 9.63 ha; **N**: Mesotrophic; **E**: 1070-1125 m a.s.l; **MAT**: 3.7°C; **P**: 757-867 mm	1972, 1996
Mionsí	B, Sy, F	**S**: 5.92 ha; **E**: 620-950 m a.s.l; **MAT**: 6.6°C; **P**: 1228-1370 mm	
Diana	B, Sp, Sy	**S**: 21.9 ha; **E**: 500-532 m a.s.l; **MAT**: 7.5°C; **P**: 723 mm	1991-94
Slovakia			
Boky	O, B, H	**S**: 176.49 ha; **N**: Oligomesotrophic; **E**: 280-590 m a.s.l; **MAT**: 7.5°C; **P**: 720 mm	1974; 1979; 1984
Bujanov	O, B, H	**S**: 88.2 ha; **N**: Mesotrophic; **E**: 420-760 m a.s.l; **MAT**: 7°C; **P**: 675 mm	1966; 1976; 1981; 1992
Sitno	B, O, Sy	**S**: 92.68 ha; **N**: Mesotrophic; **E**: 750-1011 m a.s.l; **MAT**: 6°C; **P**: 850 mm	1977; 1987
Kasivárová and Lesná	O, B, H	**S**: 28.55 ha; **N**: Mesotrophic; **E**: 475-600 m a.s.l; **MAT**: 8°C; **P**: 750 mm	1966/1969; 1972; 1983; 1992
Vihorlat (Kyjov)	B, A, Sy	**S**: 53.4 ha; **N**: Mesotrophic; **E**: 700-820 m a.s.l; **MAT**: 6°C; **P**: 750-800 mm **LGS**: 190-200 days	1963; 1973; 1983
Rozok	B, Sy	**S**: 67.1 ha; **N**: Mesotrophic; **E**: 520-796 m a.s.l; **MAT**: 7°C; **P**: 780 mm; **LGS**: 190 days	1970/1979; 1979; 1989
Havesová	B, Sy	**S**: 171.32 ha; **N**: Mesotrophic; **E**: 500-650 m a.s.l; **MAT**: 7°C; **P**: 700-800 mm	1979; 1989
Stuzica	B, Sy, F	**S**: 659.4 ha; **N**: Mesotrophic; **E**: 650-1220 m a.s.l; **MAT**: 5-6°C; **P**:850-1000 mm	1971; 1981(transsect 4–6); 1991

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Table 1. *(continued)*

Site name	Major tree species	**Site characteristics** **S**ize, **N**utrient status; **E**levation; **M**ean **A**nnual **T**emp; **P**recipitation (annual/in growing season); **S**now cover; **L**ength of **G**rowing **S**eason (days warmer 5/10°C)	Year of recording
Badin	F, B, Sy	**S**: 30.7 ha; **N**: Mesotrophic; **E**: 710-770 m a.s.l; **MAT**: 5.5-6°C; **P**: 850-900 mm	1957/1970; 1970; 1977; 1983/1987
Dobroc	F, Sp, B	**S**: 101.82 ha; **N**: Oligotrophic, acid; **E**: 720-1000 m a.s.l; **MAT**: 4.5-5°C; **P**: 800-960 mm	1958/1968; 1974; (1988)
Hroncokoy grun	B, A, Sy, F, Sp	**S**: 54 ha; **N**: Oligomesotrophic; **E**: 600-950 m a.s.l; **MAT**: 5°C; **P**: 800-850 mm	1962; 1972; 1982; 1992
Pol'ana	Sp, F, B, Sy	**S**: 685.8 ha; **N**: Mesotrophic; **E**: 560-1458 m a.s.l; **MAT**: 4-4.5°C; **P**: 900-1000 mm	1974; 1984
Komárnik	B, F, E	**S**: 733 ha; **N**: Eumesotrophic; **E**: 360-580 m a.s.l; **MAT**: 6.4-8.8°C; **P**: 600-1200 mm	1957-1968
Romania			
Runcu, Zarand	O, B	**S**: 262.6 ha; **N**: Eumesotrophic; **E**: 340-660 m a.s.l; **MAT**: 7.6-9.4°C; **P**: 750-925 mm	
d'Izvoarele Nerei, Banat	B, Sy, E, A, H	**S**: 4816 ha; **N**: Acid mull-moder; **E**: 700-1400 m a.s.l; **MAT**: 3.5-7.3°C; **P**: 1030-1340 mm	
d'Iauna-Craiova, Cerna	B, (F)	**S**: 1545.1 ha; **N**: Acid moder; **E**: 700-1733 m a.s.l; **MAT**: 4.7-7.3°C; **P**: 1000-1250 mm/700-787 mm	
Retezat I.	B (Sp)	**S**: 6630 ha (whole reserve); **N**: Acid, moder; **E**: 940-950 m a.s.l; **MAT**: 4.7-6.8°C; **P**: 950-1280 mm	
Retezat II.	Sp, F, Bi, B	**N**: Acid moder, Oligotrophic; **E**: 1126-1195 m a.s.l; **MAT**: 4.7-6.8°C; **P**: 950-1280 mm	
Hungary			
Kékes	B, Sy-A-L	**S**: 54.8 ha; **N**: Mesotrophic; **E**: 750-950 m a.s.l; **MAT**: 5.7°C; **P**: 840 mm/480 mm; **S**: 113 days	1992, 2002
Őserdő	B, Sy, A	**S**: 59.3 ha; **N**: Eumesotrophic; **E**: 800-900 m a.s.l; **MAT**: 6-7°C; **P**: 800-900 mm	
Alsóhegy	B-H, O, W, L	**S**: 112.8 ha; **N**: Eutrophic; **E**: 300-400 m a.s.l; **MAT**: 8°C; **P**: 700 mm	1994, 2002
Poland			
Babia Gora	Sp, B, F		1976, 1986
Gorce	Sp, F, B		1981, 1991
Bieszczady	B, Sy		
Ukraine			
Ugolsky	B	**N**: Eutrophic; **E**: 710 m a.s.l; **MAT**: 7.1°C; **P**: 1390 mm; **LGS**: 150-160 days	1975
Sirokoluzansky		**E**: 740 m a.s.l; **MAT**: 7.1°C; **P**: 1390 mm; **LGS**: 150-160 days	1975

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Beech is one of the most important forest species in the countries covered by this review. *Table 2* shows potential and current share of beech in the forest vegetation of the respective countries.

Table 2. *The importance of beech forests in Central European countries. Source:* [26] *for CZ;* [87] *for SL;* [117] *for PL;* [94] *for UR;* [25] *for RO;* [6] *and* [29] *for H.*

Country	**Forest area (% territory)**	**Potential beech area** (% forest area)	**Actual beech area** (% forest area)
Czech Republic	2 632 000 ha (33.4%)	37.9	5.8
Slovakia	1 920 000 ha (40%)	46.3	30.4
Poland	8 700 000 ha (28.1%)		4
Ukraine			556 800 ha in the Carpathians
Romania	6 370 000 ha (26.7%)	18	30.7
Hungary	1 678 600 ha (18%)	19.5	6.3

Beech forests are associated with the submontane and montane zones of the Carpathians, with beech increasing in frequency above the thermophilous foothill oak forests. Although beech once occupied almost all the montane zone from 600 to 1200 m, apart from in the warmer parts of the Carpathians they have been gradually replaced at higher elevations by coniferous forests of *Abies alba* and *Picea abies*. In general, the limit of beech distribution increases in the inner mountains, for example rising from 550–1100 m at Babia Gora to 800–1200 m at Vysoke Tatry. The analysis of historic data showed that it occurred at many locations even in the Great Hungarian Plain [37]. Details on the altitudinal limits of beech distribution are given in *Table 3*.

Table 3. *Altitudinal limits of beech in the Carpathian and Pannonic floristic provinces. Source:* [19].

Region (as shown in [19])	**Lower limit of trees**	**Lower limit of beech forest**	**Upper limit of beech forest**	**Upper limit of individual trees**
NW Carpathians	339	378	1133	1181 (1220)
N-Central Carpathians	329	330	1246	1258 (1352)
NE Carpathians	254	354	1245	1284 (1335)
E Carpathians			1307	1335 (1396)
S Carpathians			1319	1381 (1441)
Krassó-Szörény Mts.	182	197	1418	1403 (1444)
Transdanubian and Northern Mid-Mts	263	281		
Bihar Mts.	241	360	1301	1351 (1497)
Mecsek Mts.	210	210		
Outer Somogy	200	200		
Sopron-Kőszeg-Szentgotthárd	312	394		
Transsylvanian lowlands (Mezőség)	390	411		
Great Hungarian Plains	82			

Beech forests develop on all types of rocks over a wide area characterized by different climates, so there is no uniformity in the characteristics of beech forest soils [11]. Typical beech forests have slightly acid to alkaline soils, while degraded beech forests have strongly acid soils. The higher the acidity is, the less typical the undergrowth becomes, until finally, forest floor vegetation takes a spruce forest character. As Zlatnik [118] observed, soil acidity rises with increasing humidity of the

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climate, i.e. with altitude and in deep shaded valley bottoms. In this region podzolization frequently corresponds to the degradation of beech forest soils, i.e. the effects of forest utilization [10].

Climatic and other factors limiting beech in East Central Europe

The climate of Central Europe is largely dominated by the high-pressure system of East Europe. For this reason the climate is generally less humid, colder in winter, and warmer in summer than in the Atlantic region. The degree of continentality increases with the distance from the Atlantic. In the southwestern part of Hungary Submediterranean effect is also considerable. Mountain ranges have considerable effect on the local climates. In the mountains snow cover can last up to five months. *Table 4* shows data on mean monthly temperature and precipitation of selected sites in East Central Europe.

Several indices of „climate goodness" were introduced. Not reviewing those it can be claimed safely, that the length of growing season – though definitions are not straightforward – varies greatly within the area covered. According to data of Mayer [50] it is 170 days in the south Carpathians at 600 m a.s.l., whereas only 115 at 1450 m a.s.l. (see also *Table 1*).

In this part of the world the distribution of beech is limited either by summer drought or winter frost. It is reported in several papers that late spring frost can harm young beech trees. Extreme cold winters like in 1928–1929, when temperature fell to -42 °C, beech forests can be seriously damaged. In 1928–1929 more than 10 000 ha of beech forests were damaged in then Polish, nowadays Ukrainian Carpathians [30, 38, 44, 47]. The upper beech range is often affected by damage caused by wind, snow and ice [1, 24, 39, 40, 86].

For characterizing the lower limit of beech growth, Ellenberg [14] developed an index, the so-called Ellenberg quotient (*Q*) for Central Europe:

$$Q = \frac{Mean\ July\ \ temperature\ \ (°C)}{Annual\ \ precipitation\ \ (mm)} \times 1000$$

Values below 20 indicate pure beech climate, between 20 and 30 its competitive vigour decreases, and above 30 oak becomes more competitive than beech.

Main beech forest types

It is not a simple task to give a short account of beech forest types of the region, since Braun-Blanquet-type phytosociology has developed along partly different paths in the respective countries. Even worse, forest scientists have developed their forest type/forest site type systems rather independently from vegetation scientists, though the level of separation is different in the respective countries (*Table 5*).

To give a short account of the major beech forest types, it is reasonable to consider different substrates (eutrophic, mesotrophic, oligotrophic), altitudinal zones (colline, submontane, montane) and biogeographic provinces (Central European, Carpathian, Pannonian, *Fig. 2*).

In its optimum, beech forms almost pure stands with only scattered associate species. At lower elevations oaks *(Quercus petraea, Q. robur)* and hornbeam *(Carpinus betulus)* are important associates, however, this forest type is not well represented among natural

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Table 4. *Mean monthly temperature and precipitation data for selected sites. Source:* [79, 105, 106, 107, 108, 109, 110, 111, 112] *World Climate Database.*

Mean temperature (°C)	**(m a.s.l)**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Year**	**IV-IX**
Polom	590 m	-3.0	-2.0	2.0	6.0	11.0	14.0	16.0	15.0	12.0	7.0	2.0	-2.0	6.0	12.3
Razula	730 m	-4.3	-3.2	1.0	5.2	10.6	13.4	15.7	14.8	11.3	6.4	1.1	-2.2	6.2	11.5
Salajka	722 m	-4.7	-3.5	-0.1	4.8	10.5	13.3	15.3	14.2	11.0	6.2	0.9	-2.7	5.4	14.4
Zakova hora	760 m	-4.7	-3.9	-0.1	4.4	10.2	13.0	14.8	13.9	10.5	5.5	0.1	-3.1	5.0	11.1
Stozec	766 m	-4.0	-3.0	0.0	4.0	10.0	12.0	14.0	13.0	10.0	5.0	0.0	-3.0	5.0	10.5
Zofin	780 m	-4.3	-4.5	-0.4	3.4	8.9	11.8	13.6	12.6	9.3	4.5	-0.3	-3.1	4.3	11.8
Boubin	1003 m	-5.0	-4.0	-1.0	2.0	8.0	12.0	13.0	12.0	9.0	4.0	0.0	-3.0	4.0	9.3
Milesice	1058 m	-5.3	-4.5	-1.3	2.7	8.2	11.1	12.9	12.2	8.7	4.4	-0.5	-3.7	3.7	9.3
Mionsi	530 m	-3.2	-2.3	1.2	6.0	11.5	14.5	16.2	15.3	11.9	7.2	2.4	-1.1	6.6	12.6
Diana	451 m	-2.4	-1.3	2.6	7.1	12.6	15.7	17.6	16.7	12.9	7.6	2.3	-1.1	7.5	13.8
Stuzica		-2.7	-0.6	4.4	10.5	15.6	18.6	20.1	19.6	15.5	9.7	4.8	0.1	9.7	16.6
Kékes	1010 m	-3.9	-3.7	0.6	5.7	11.0	13.1	15.7	15.5	12.2	7.2	0.5	-2.0	6.1	12.2
Alsóhegy	233 m	-2.9	-0.5	4.2	10.2	15.2	18.4	20.1	19.3	15.2	9.4	3.7	-0.5	9.3	16.4

Average rainfall (mm)		**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Year**	**IV-IX**
Polom	590 m	54.0	45.0	46.0	56.0	75.0	82.0	99.0	90.0	63.0	63.0	56.0	57.0	786.0	465.0
Razula	730 m	70.0	73.0	76.0	70.0	88.0	125.0	128.0	120.0	82.0	88.0	88.0	80.0	1088.0	559.0
Salajka	722 m	83.0	76.0	82.0	82.0	92.0	121.0	134.0	127.0	89.0	90.0	89.0	79.0	1144.0	645.0
Zakova hora	760 m	71.0	61.0	58.0	65.0	79.0	88.0	107.0	96.0	76.0	75.0	67.0	72.0	916.0	511.0
Stozec	766 m	55.0	50.0	43.0	57.0	75.0	89.0	100.0	87.0	65.0	60.0	53.0	59.0	793.0	473.0
Zofin	780 m	47.0	48.0	45.0	71.0	94.0	113.0	142.0	116.0	79.0	61.0	47.0	52.0	915.0	615.0
Boubin	1003 m	58.0	61.0	49.0	63.0	88.0	98.0	112.0	96.0	69.0	61.0	51.0	61.0	867.0	526.0
Milesice	790 m	49.0	47.0	41.0	54.0	74.0	84.0	102.0	83.0	61.0	57.0	50.0	55.0	757.0	458.0
Mionsi	730 m	94.0	91.0	89.0	90.0	113.0	139.0	159.0	163.0	111.0	101.0	91.0	89.0	1330.0	775.0
Mionsi	600 m	81.0	73.0	86.0	80.0	117.0	120.0	158.0	156.0	112.0	85.0	82.0	78.0	1228.0	743.0
Mionsi	530 m	78.0	74.0	84.0	100.0	133.0	160.0	179.0	174.0	118.0	106.0	87.0	77.0	1370.0	865.0
Diana	575 m	54.0	45.0	43.0	57.0	60.0	73.0	89.0	76.0	58.0	57.0	53.0	58.0	723.0	413.0
Stuzica		59.0	48.0	47.7	50.8	65.6	92.4	81.3	79.2	61.9	60.4	60.4	66.2	773.9	431.2
Kékes	1010 m	46.0	47.7	48.8	61.4	144.5	101.4	42.2	73.2	55.2	44.4	61.5	44.4	759.4	477.9
Alsóhegy	233 m	29.2	29.7	30.3	40.9	65.0	87.5	66.3	67.6	40.7	35.0	44.8	38.5	576.3	368.0

forest remnants. In the main beech zone sycamore *(Acer pseudoplatanus)*, witch elm *(Ulmus glabra),* mountain ash (*Fraxinus excelsior*), rowan *(Sorbus aucuparia)*, small-leafed lime *(Tilia cordata)* and Norway maple *(Acer platanoides)* are the main associates. At higher elevations silver fir (*Abies alba*) and Norway spruce (*Picea abies*) become important tree species.

Table 5. *Major references for national forest type classifications based on phytosociological and forest/site/ecosystem type approaches of forest vegetation.*

Country	Major phytosociological accounts	Major forest/ site/ ecosystem type systems
Czech Republic	Domin [11] Neuhäusl [64] Neuhäuslova et al. [65]	Zlatnik [122] Pista and Prusa [73] Randuska [81]
Slovakia	Domin [11] Michalko et al. [58]	Zlatnik [122] Randuska [81]
Poland	Szafer [95] Szafer [96]	
Ukraine	Domin [11]	
Romania	Sanda et al. [84]	Pauca-Comanescu [70] Donita et al. [12]
Hungary	Soó [92] Bartha et al. [3] Borhidi [5]	Májer [52]

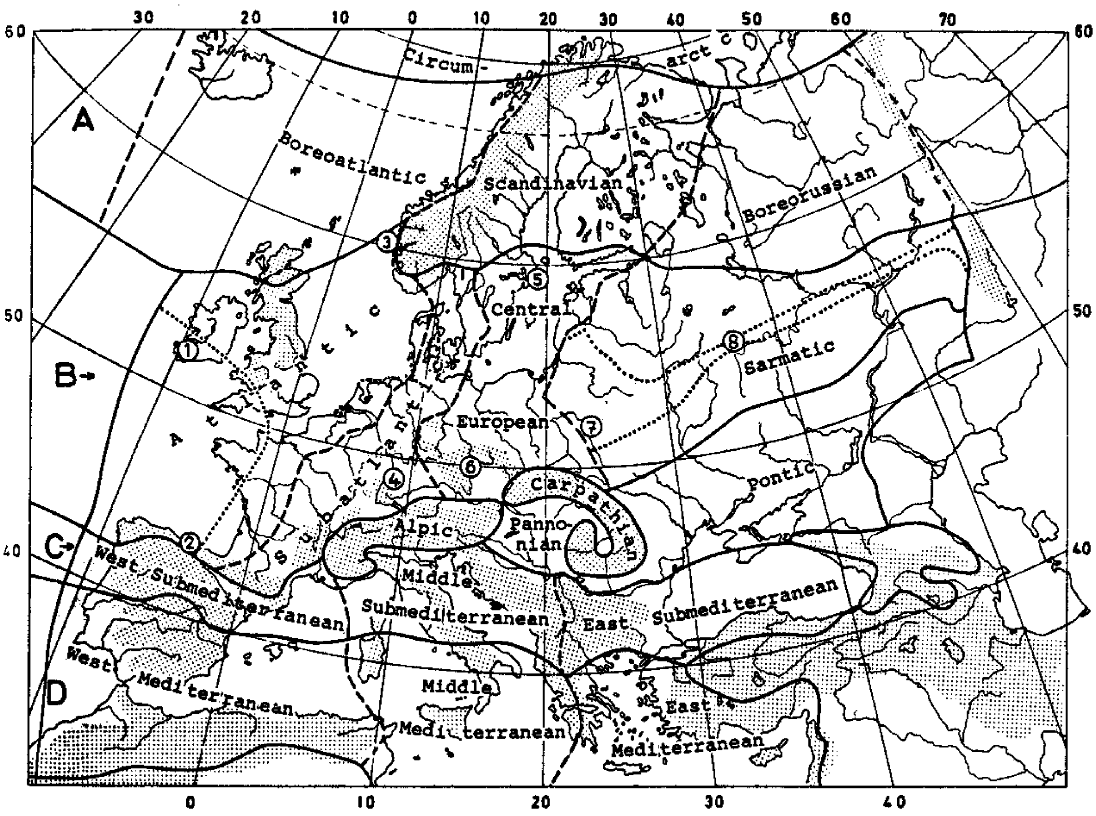

Figure 2. *Biogeographic Provinces of Europe. Source: after Meusel in* [28].

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Carpathian Province

The largest tracks of beech forests belong to the Carpathian Province. Vegetation scientists distinguished many associations for this area. A simplified picture is given in Michalko et al. [58] where beech forests are grouped into 7 units for mapping the potential natural vegetation of Slovakia.

For the same country Zlatnik distinguished 46 major forest type groups, with many more subgroups, intergroups and geographic variants. Of these, 22 contain beech as a major component [81, 122].

In Romania Pauca-Comanescu [70] and Donita et al. [12] published detailed accounts of major beech forest ecosystem types. The 15 beech ecosystem types in Donita et al. [12] are distinguished on the bases of phytosociological associations, forest types, soil types and climatic characteristics. These main groups also cover beech forests of the Polish and Ukrainian Carpathians. East of the Carpathians beech reaches the limit of distribution to the east. Szafer [95] and Stojko [94] described forest types of this region.

Central European Province

Only a small part of the area covered by this review belongs to this province, namely the middle and western part of the Czech Republic. In addition to the Carpathian beech forest types this area is characterised by the acidophilous Hercynian beech forests belonging to the *Luzulo-Fagion* alliance, and the beech-fir woods characteristic in the montane belt of the Sudeten and the Sumava Mts (*Dentario enneaphylli-Fagetum*).

Pannonic Province

In the Pannonic Province beech forests grow in the low mountains of Transdanubia and northeastern Hungary, and at low altitudes in the westernmost part of Hungary. Beech wood in the northeastern part resemble to the submontane-beech woods of Slovakia, whereas those in Transdanubia (west of the river Danube) contain more atlanto-mediterranean species. Special beech forest associations (e.g. *Vicio-oroboidi-Fagetum* Borhidi, *Helleboro odor-Fagetum*) were described in the southern part of Hungary, where illyric (West-Mediterranean) floristic effects (e.g. *Knautia drymea, Lathyrus venetus, Asperula taurina, Tamus communis*) are strong.

Characteristics of beech and its associates

In this chapter main characteristics of beech are discussed, in some cases important associates are also included.

Growth performance

Depending on site conditions, beech trees can grow to a considerable size (40–45 m height, over 1 m dbh) and age (over 350 years). Standing volume can be as high as 1195 m^3/ha, and basal area can reach 67 m^2/ha (*Table 6*). Annual average productivity varies greatly according to site types, and variation among years is also considerable. Kosut [45] carried out a detailed study in the Komárnik region in East Slovakia. He showed, that the mixed stand produced 27.56 m^3 (beech – 20.30, silver fir – 6.12, sycamore – 0.94, ash – 0.18, hornbeam – 0.02) between 1958 and 1968 on the 0.5-hectare sample plot, so the average annual productivity was 5.6 m^3/ha. Tree ring analyses showed great variations among years, especially for silver fir.

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Table 6. *Density, basal area and volume of major tree species in selected Romanian natural forests. Species: S - Spruce; F - Fir; B - Beech. Source:* [9, 76].

Site name	**Tree number (N/ha)**				**Basal area (m²/ha)**				**Volume (m³/ha)**			
Species	**S**	**F**	**B**	**Sum**	**S**	**F**	**B**	**Sum**	**S**	**F**	**B**	**Sum**
E Carpathians												
Cosna	189	58	111	358	27	15	8	50	364	199	81	644
Cosna	194	64	93	351	24	13	7	44	324	176	71	571
Stulpicani	80	109	93	282	10	20	8	38	132	297	111	540
Ostra	105	102	98	305	13	18	7	38	151	242	75	468
Ostra	399	159	15	573	31	13	1	45	262	155	8	425
Tomnatec	350	150	170	670	42	22	3	67	649	350	28	1027
Rebra	146	—	244	390	34	—	19	53	564	—	314	878
SE Carpathians												
Viforata	68	242	118	428	9	37	14	60	125	533	222	880
S Carpathians												
Cheia	73	190	98	361	3	16	6	25	31	197	69	297
Cheia	—	457	365	822	—	31	15	46	—	363	164	527
Cheia	—	151	211	362	—	11	18	29	—	116	246	362
Cheia	—	56	265	321	—	2	27	29	—	21	360	381
Cheia	—	300	153	453	—	21	12	33	—	267	162	429
Cheia	—	134	140	274	—	14	12	26	—	180	158	338
Glodeasa	—	178	130	308	—	18	22	40	—	257	347	604
Piatra Arsa	—	190	82	272	—	37	16	53	—	538	263	801
Piatra Arsa	—	173	89	262	—	37	13	50	—	503	198	701
Piatra Arsa	5	131	110	246	—	32	11	43	3	485	166	654
Piatra Arsa	4	168	196	368	—	10	23	33	5	129	388	522
Piatra Arsa	3	147	130	280	—	13	20	33	3	192	353	548
Piatra Arsa	—	240	84	324	—	23	6	29	—	278	80	358
Piatra Arsa	4	183	164	351	1	17	11	29	6	206	131	343
Piatra Arsa	—	229	101	330	—	21	8	29	—	244	95	339
Zgarbura	—	258	128	386	—	17	3	20	—	—	—	—
Zgarbura	—	174	90	264	—	16	1	17	—	—	—	—
Curtea de Arges	—	203	237	440	—	22	21	43	—	302	301	603
Romani	—	38	282	320	—	3	35	38	—	35	498	533
Romani	618	—	9	627	38	—	1	39	385	—	11	396
Romani	—	108	163	271	—	17	23	40	—	232	346	578
Parang	—	—	—	660	—	—	—	—	—	—	—	1013
Ponor	220	—	262	482	13	—	31	44	143	—	460	603
Ponor	287	—	307	594	19	—	33	52	153	—	484	637
Nera	—	—	373	373	—	—	—	—	—	—	1195	1195

Popescu-Zeletin and Petrescu [75] found that diameter increment was ca. 1 cm in 6 years for the majority of trees, higher rates (4–6 cm) being confined to medium-sized trees.

Table 7 shows data on tree size and growth characteristics for selected reference sites.

In managed forests the correlation between age and size, and also between dbh and height is rather consistent, so growth tables for different site types were developed. However, in natural forests these relationships are strongly influenced by the history of individual trees. Abrupt height and radial growth can follow decades of suppression in shade tolerant species, like beech and silver fir, when they have been released from the shade of overstorey trees [43].

Productivity is highest on well-aerated and well-drained soils with slightly acidic to neutral chemistry. Sandy substrates and temporary water saturation can decrease growth potential and competitive vigour of beech (c.f. data in *Table 1*). Beech usually forms the upper canopy layer, though in certain forest types (e.g. mixed beech-fir on acid substrate, mixed beech-spruce on mesotrophic sites) silver fir or Norway spruce give the dominant layer and beech gives the secondary canopy layer [70].

Competition and disturbances can reduce growth or they can lead to mortality of trees. Competition is strongest in younger stages especially when dense regeneration develops over larger patches. However, this situation is rather rare in natural beech forests. In a Romanian virgin stand Popescu-Zeletin and Petrescu [75] showed that competition was strongest at the „pole stage" (dbh 3–10 cm), since 56–92% of conifers and 82–98% of beech trees died in the 6-year period of investigation. Beech is extremely flexible even at older ages, so canopy growth can follow and utilize resources opened up by the death of other trees.

Data on the strength, frequency and biological effects of disturbances are rather scarce, and in many cases incomplete to judge their importance in forest dynamics [16, 72]. This is especially true for natural forests of East Central Europe. Under prevailing climatic conditions wind, ice and snow are the major abiotic disturbance factors in the beech forests of the region.

Wind was reported for several „virgin forest" as important disturbance agent. Badin Virgin Forest in Slovakia suffered from serious wind damage in 1947, but recording of stand structure started only 10 years later [43, 86]. A heavy gale impacted the surroundings of the Boubin Virgin Forest in Czech Republic on 26 October 1870, which caused extensive - though not quantified - wind breakages [79, 112]. Popescu-Zeletin reported in a Romanian virgin forest site, that many trees (13–32% of conifers and 18–67% of beech) had been destroyed by windthrow between 1949 and 1955.

Table 7. *Exemplary data of dbh, tree height, standing volume and basal area for selected reference sites. Data are given by species indicated as B - beech, F - silver fir, S - Norway spruce, Sy - sycamore, Source:* [43, 79, 80, 110, 111, 112].

Site name	Age	Dbh	Height
Zofin F	425	176	45.3
Badin F	350-400	148	49.5
Badin B	210-230	108	45
Boubin S	440	162	57.6
Boubin F	450	145	51.8
Boubin B		91	45.5
Milesice S		105	45
Milesice F		87	40
Milesice B		68	37
Kyjov B	250	112	
Razula S		94	53.5
Razula F		148	41
Razula B		100	44.5
Dobroc S		134	54
Dobroc F	450	193	58
Dobroc B		118	

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In Slovakia Konopka [40] studied the volume of salvage cutting caused by wind, snow and ice between 1961 and 1995 in Slovakian forests. Salvage cutting caused by wind, snow and ice during 1985–95 was 800 000, 180 000, and 35 000 m^3, respectively. Norway spruce and silver fir were the species most frequently damaged by wind, Norway spruce and Scots pine by snow, and Scots pine and European beech by ice. However, these data mostly relate managed, often planted (e.g. spruce on beech sites) forests. The same limitation is valid for the study of the causes of wind and ice damage in the Börzsöny Mts, Hungary [1]. The authors studied a 70 km^2 area, where serious ice and wind damages occurred in 1996 and 1999, respectively. Unfortunately pre-disturbance measurements are missing, so only the area affected could be studied in detail. As *Table 8* shows, ice created more large gaps than wind.
Adult beech trees are usually not seriously affected by biotic disturbances. Fungi are the most important biotic agents causing damage to beech, since the anatomical and chemical makeup of tree trunks make it rather susceptible [27]. Mechanical wounds caused by abiotic factors or forestry operations can open places for successful infection. Species that might attack beech trees are shown in *Table 9*. Szontágh investigated 188 beech trees in a 1 ha plot in the Őserdő Reserve in Hungary. He found that in the mixed-aged (0-150 years) stand fungi attacked 49 trees (26%). Of the 553 m^3 volume 172 m^3 (31%) were affected [Szontágh in 27]. Leaf-miners (e.g. *Rhynchaenus fagi,*) can attack up to 20% of beech trees [98, 99].

Table 8. *Comparison of sizes of canopy gaps created by severe ice or wind-damage in beech forests near to Királyrét, Börzsöny Mountains, Hungary.*

	Gaps created by severe ice-damage in 1996 (n =)	**Gaps created by severe wind-damage in 1999 (n = 33)**
Size		
Maximum size (m^2)	80756	66579
Average size (m^2)	19162	15803
Minimum size (m^2)	627	663
Area	**N**	**n**
<5000 m^2	20	10
5000–<10000 m^2	6	8
10000–<15000 m^2	0	5
15000–<20000 m^2	2	2
20000–<50000 m^2	12	5
50000–<85000 m^2	5	3

Regeneration characteristics

Beech generally regenerates by seeds, which are produced periodically. Frequency of seed production and success of establishment is greatly affected by site characteristics and weather conditions. Density and spatial distribution of established seedlings is strongly affected by disturbance patterns in the overstorey. In natural beech forests regeneration is rather patchy, since canopy gaps are usually small.

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Table 9. *Fungi affecting the growth of adult beech trees. Source:* [27, 88].

Species name	Organ affected
Microsphaera alphitoides Griff. et Maubl.	leaf
Phyllactinia suffulta (Rebent.) Sacc.	leaf
Nummularia bulliardi Tul.	branch
Nectria galligena Bres.	trunk
Nectria ditissima Tul.	trunk
Fomitopsis pinicola (Sw. ex Fr.) Gill.	trunk
Fomes fomentarius (L. ex Fr.) Gill.	trunk
Inonotus radiatus (Sw. ex Fr.) Karst.	trunk
Laetiporus sulphureus (Bull.) Bond. ex Sinq.	trunk
Ganoderma applanatum (Pers.) Pat.	trunk
Inonotus obliquus (Pers.) Pil.	trunk
Daedalea quercina (L.) Fr.	trunk
Grifola gigantea (Pers.) Pilát	trunk
Oxyporus populinus (Fr.) Donk.	trunk
Pholiota squarrosa Huds. ex Fr.	trunk
Polyporellus squamosus Huds. ex Fr.	trunk
Pleurotus ostreatus (Jacq. ex Fr.) Kummer	trunk
Xanthochorus obliquus (Pers.) B. et G.	trunk
Xanthochorus cuticularis (Bull.) Pat.	trunk

Seed production and dispersal

Beech is characterized by periodic seed production starting when beech trees are 40–50 years old, but in closed dense stands they start producing fertile seeds only at the age of 60–80 years [4]. Periodicity of seed production is rather irregular. However, observations show that individual beech trees can produce seeds in consecutive years [56]. In general mast years are followed by lower seed production [8], and on optimal sites seed production is more frequent and more reliable (regular) than on suboptimal sites where certain environmental factors (precipitation, soil moisture content, etc.) can be limiting [56]. In the eastern part of its distribution beech flowers more often than in e.g. West Europe, but this phenomenon does not lead to more frequent seed production. For this reason detailed studies were carried out to investigate the factors affecting successful fructification. It was shown that both meteorological and biotic factors (pests) affect successful seed production. Best fructification occurred when temperature was between 15 and 25 °C, and relative humidity did not fall below 26–33% [56]. Phaenology of individual trees (early or late flowering) and social position within the stand (height class of Kraft) also affected seed production. In Hungary mast years occur every 6–8 years on the average, but even within such a small country, seed production is more frequent in the western part where climatic condition are more favourable [52, 83]. Májer [53] published the results of a historical study on beech seed crops in the Bakony Mts., Hungary, over the last 242 years. A heavy crop can be expected (on average) once every 14 years, an average crop every 7 years, and a poor crop every 3–4 years. However, heavy crops can occur at short intervals (1948, 1951). In the Ukraine several authors studied the amount and periodicity of beech seed production. They also showed that seed years are more frequent in the Carpathians (optimal sites) than at lower elevations east of the Carpathians [35]. In Opolia Tretjak [102] reported beech seed years of different intensity using a 5-scale system (1: 1–2 million seed/ha, 2: 2–3 million, 3: 3–4 million, 4: 4–5 million, 5: more than 5 million): 1916–5; 1922–4; 1936–3; 1931–5; 1934–1; 1936–4; 1941–2; 1943–4; 1945–4; 1947–5; 1951–5. Kaplunovszkij

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[36] reported four „better than average" seed years between 1960 and 1969, which means that 54–77% of mature trees produced seeds. In 1962 all trees with dbh >40 cm produced seeds. In Romania Papava [68] found that fructification is extremely variable, is strongly correlated with altitude, and mast years occur once in every 3–4 to 6–8 years. Badea et al. [2] published a comprehensive account of studies carried out in 1957-64 on seed production, effects of climatic factors and of methods of regeneration felling on the establishment and development of regeneration.

The number of seeds produced shows high spatial variability within a single stand. Márkus [54] studied the number of beech seeds in a 100 year old beech stand in the Bakony Mts, Hungary. He set up a grid with 25 m intervals, and sampled beech seeds at each grid points. Using the data collected in 91 sample plots he showed that at edges seed numbers per unit area were higher than within the stand. This effect could be traced as far as 1.5 tree height from the edge. Not only absolute numbers, but also the proportion of vital seeds decreased from the edge to the inner stand. He also observed that beech seeds were almost always found in groups of a few. Mendlik [57] compared seed numbers at the edges and in the centre of a stand where he found much lower numbers (5-10 nuts/m²), than at the edges (40-50 nuts/m²). In 1964 Márkus and Mátyás [55] carried out a country-wide survey of seed production in Hungary. They collected data from 611 forest ranges from all over the country representing all forest regions where beech occurs. They found large variation within each forest region, but the average differences in the amount of beech seeds produced in different forest regions could be explained by the climatic differences of previous year. In the western part of the country, where June and July of 1963 were cool and rainy, much less seeds were produced than in the northeastern part of the country.

Korpel [42] and Saniga [85] studied the dynamics of seed shedding and got similar results. Korpel found that on the average, of the 399 seeds shed on 1 m^2, 18.7% germinated. Saniga [85] found that the amount of seeds shed until September 25, October 20 and October 31 were 465.3, 321.3 and 274.5 kg/ha, respectively. Based on thousand-seed-weight data he estimated that on the average 399 seeds per m^2 were shed. Average proportion of fertile seeds was 53%, 71%, 65% for the three sampling period, so the average number of fertile seed per m^2 was 244.

Seed size also shows natural variation. Parpan et al. [69] collected seeds in 1982 from 45 locations within the natural range of beech in the Ukraine. The heaviest and most elongated seeds were from Podolia and the lightest and least elongated from the mountains of Transcarpathia. Results suggest a clinal variation from the [eastern] lowlands to the [western] mountains. Smelkova [90, 91] carried out biometric studies of 14 seed samples collected from beech stands aged 70–130 years in 11 localities throughout Slovakia at altitudes between 290–940 meters. Negative correlation was found between stand age, altitude and the dimensions and weight of seeds and embryos. Stand density and topographical aspect had no significant effect.

Beech is a species with poor dispersal. Large nuts fall beneath the mother trees, only topography can play a role in short distance dispersal. Certain bird species eat beechnuts. Turcek [104] studied the retrieval of beechnuts collected and hidden by jay *(Garrulus glandarius*) and nutcracker (*Nucifraga caryocatactes*) in Slovakia, including a brief discussion of the silvicultural importance of the seeds not retrieved.

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Seed predation and mortality of young seedlings

Mortality of beechnuts and seedlings is very high. Many animals, e.g. wild boar, roe deer, red deer, rodents and birds use beech seed for food. Mortality caused by rodents is less dramatic in years when seed production is low, because gradation of rodents can not arise [36, 101].

Exact studies are almost lacking on the dynamics and exact causes behind this dramatic mortality. One important factor is infection by fungi. Prochazkova [77, 78] studied infection of seeds for several tree species. Based on the analysis of 466 seed samples collected from Czechoslovakia, 44 species of fungi were found on beech seeds. Beechnuts were most frequently attacked by *Trichothecium roseum* (79%), *Penicillium* (76%), *Rhizopus stolonifer* (61%) and *Alternaria alternata* (51%). Pathologically important species, especially *Fusarium* spp. *(F. avenaceum, F. oxysporum, F. sporotrichoides* v. *sporotrichoides)* were determined in 12% of samples. 43% of seed samples originating from Slovakia were infected (up to 5% of seeds/sample) by *Fusarium* species. In addition to the *Fusarium* species, isolated pathogens included *Phytophthora cactorum, Rhizoctonia solani, Cyclindrocarpon magnussianum*. In Poland Skrzypczynska [89] studied the fate of 2100 seeds that had fallen under beech trees in the Ojcow National Park, Poland. Damaged seeds constituted 8.3% of the total, and the agent responsible was identified as *Cydia fagiglandana*; 40.6% of seeds were viable and 51.1% were empty. In Slovakia Saniga [85] found that 90% of first year's mortality was caused by mould and mice.

Germination and initial establishment

Beechnuts usually germinate in April or May depending on snow cover. Young seedlings are often infected by *Phytophora cactorum* (Leb. et Cohn.) Schroet [88]. In Hungary Mendlik [57] published data on the number of seedlings in the first year after seed production. In spring 1981 he found 110–170 thousand seedlings/ha. By autumn the numbers decreased to 30–70 thousand. Germination success and the number of surviving seedling were higher at forest edges. The main cause of seedling mortality was damage caused by aphids. Domin [11] made the interesting observation that partly decomposed litter impeded successful germination in nudum beech forests with thick litter layer. The few individuals that survive out of thousands help to weaken the litter layer, and then a new generation of young beech trees can establish themselves under these sparse groups.

Dead wood can provide appropriate establishment site for tree species in certain forest types. The importance of nursery logs is well known from boreal forests, where soil is covered by thick carpet of mosses that impedes successful establishment. In mixed or deciduous forest this role of logs has received less attention, although the presence of characteristic stilt roots have been observed in several Central European natural forests (Standovár personal observation). Szewczyk and Szwagrzyk [97] studied regeneration on soil and on decaying wood in a natural mixed stand in Babia Gora National Park, in the Western Carpathians, S. Poland. They found that logs covered around 6% of the forest floor. Regeneration was co-dominated by beech and fir seedlings, while spruce was less numerous. Average seedling density on the soil with herb layer (240/100 m^2) was higher than on the logs (even on the strongly decayed ones) at 177/100 m^2. However, the density of fir and spruce seedlings was higher on the rotten wood than on soil. Seedling survival of all species was better on the logs, especially for conifers. Because of the total dominance of beech among saplings, the

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presence of fir and spruce in the next generation of canopy trees depends strongly on their regeneration on decaying wood.

Development of seedling

Information from managed forests

Most of the studies dealing with growth and success of beech regeneration are carried out in managed beech stands, using experimental plots with different treatments. Standard silvicultural textbooks deal with the problems of how fast and intensively old stands should be opened to provide beech regeneration with appropriate environment and to avoid competition from herbaceous weeds and other tree species like ash. These works are not reported here.

However, the results of a detailed study that was carried out in semi-natural beech forests of the Carpathians are briefly summarized as an example. Saniga [85] made observations on beech natural regeneration over a 10-year (1981–1991) period in three plots (87%, 73%, 70% canopy closure) in a 85 years old beech stand. He found that seedling survival was the lowest in the most shaded plot for all time steps studied. But even in this most shaded plot the number of eleven-year old seedlings was 27 000 per hectare in 1991. The other two plots contained 43 700 and 53 200 seedlings, respectively. Height growth was not different in the first five years, but later the effect of light could be traced.

Besides light, soil water can also limit the success of regeneration. Coping with too much water is as problematic for young beech trees as surviving too dry periods. For this reason, silvicultural systems, like uniform shelterwood, can destroy regeneration by causing soil water saturation at moist sites, and by drying out less humid sites. In the first case competition of tall herbs (e.g. *Impatiens noli-tangere, Dryopteris filix-mas*) and appearance of mould can be detrimental. In the latter case competition from old trees and drought can impede successful regeneration. Special cutting protocols were developed to overcome these problems. In Hungary Török [100] published a method that was developed in the Bakony Mts. He applied uneven cutting regimes taking into account the direction of shade that old trees shed.

Game browsing is one of the major problems of nature-based forest management throughout Europe. In spite of its overwhelming importance there are hardly any exact study on the effects of browsing. Instead, foresters in many regions have set up demonstration exclosures. However, these plots are usually without measured controls and even within the exclosure young trees are not counted or measured.

Information from unmanaged natural forests

Permanent plot studies in unmanaged forest reserves usually record trees above certain dbh, usually above 7, 10 or 20 cm, hence missing the most dynamic part of the regeneration processes. However, there are studies, where regeneration was also recorded and followed in time. There is one study in which regeneration succession is followed after a serious wind disturbance. One of the permanent plots set out by Korpel in the Badin Forest Reserve was placed in that part of the reserve, which was felled by a serious wind. Korpel made recordings on the tree stand in a 0.5 ha plot every 10 years from 1957. All trees larger than 7 cm dbh were recorded. In 1986 and 1996 Saniga repeated the measurements, but he also measured young trees in 9 age and size classes. He showed that the number of large trees (>7 cm) was 2589 and 2410 per hectare in 1986 and 1996, respectively. The proportion of goat willow + aspen decreased from

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71.6% to 66.5%, whereas the proportion of beech increased from 26.1% to 31.1%. Among small trees the number of goat willow sprouts are very high (650/ha) because of strong deer browsing, which also affected silver fir [86].

Regeneration dynamics in small patches created by the death of individual old trees could be followed in those reserves where tree mapping is accompanied by more detailed (usually transect) sampling of crown projection, regeneration and herbaceous species [41]. This could provide the basis for studying the relationships among different vegetation layers. Understanding the dynamics of early phases of regeneration would also require more frequent than usual (once in every 10–20 years) sampling. Another approach was followed in the study of several Czech forest reserves. There they mapped the patches where regeneration was abundant, but trees did not reach 10 cm dbh [79, 105, 106, 107, 108, 109, 110, 111, 112]. In this way the total area and pattern of regeneration groups could be followed. This kind of information is available for the Polom, Razula, Zakova Hora, Boubin, Milesice, Mionsi and Diana Forest Reserves. The general message of these studies is that the success of regeneration is as much dependent on stand dynamics as on game pressure. In several reserves fencing was necessary to initiate the growth of advanced browsed regeneration and to make the establishment for new generations possible.

The effects of game species are usually assessed indirectly by the possibilities of natural regeneration without fencing, or by setting up demonstration exclosures. Miscicki and Zurek [59] presented an example of the rare quantitative studies. They studied damage to natural regeneration in the Gorce National Park in Poland, where killing of deer had been banned since the establishment of the park in 1981. Regeneration and browsing/stripping damage were assessed by species. Fir (*Abies alba*) was stripped most and heavily browsed, followed by sycamore (*Acer pseudoplatanus*) and rowan (*Sorbus aucuparia*). Beech (*Fagus sylvatica*) and spruce (*Picea abies*) were only slightly damaged. The proportion of fir and sycamore decreased in successively larger diameter classes. The level of browsing in the park was assessed as 280% of the admissible value, while damage to the stem surface (stripping and other) was assessed as 580% of the admissible value.

Regeneration cycles in natural forests

The aim of studying natural forest dynamics has been to describe and understand the nature and length of the developmental cycles of forests throughout Europe. Major scientists in the field recognized different stages of development, and saw these natural forests as mosaics of patches in different development stages [41, 42, 43, 48, 49, 51, 60, 79, 123]. However, there are several obstacles to drawing general conclusions from these results.

Major characteristics of existing researches

Naturalness of sites

It is important to bear in mind that the reference sites used in these studies differ greatly in their naturalness. Each site has their own management history from no management to grazing and non-intensive timber extraction (e.g. only dead wood). They also differ in their sizes. It is hard to compare an isolated reserve of up to 100 hectares in a cultural landscape with a vast near-natural forest area of several thousands hectares in a forested landscape of 100 000 hectares. These differences could affect the

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pattern of disturbance, propagule source, the presence of large predators and many other factors that influence forest development. As it was observed in several reference sites, the density of large herbivores had overwhelming effect on development, so differences in game pressure should be taken into consideration.

Scientific approaches

An interesting aspect of Central European forest dynamics research is that it developed in countries where the dominant view on biological communities was based on the equilibrium theory. Classic Braun-Blanquet-type phytosociology typically described characteristic patches of mature managed forests. Emphasis was put on distinguishing distinct vegetation units (associations).

Another important feature is that the major emphasis has been put on the tree component from mensurational viewpoint. Most results show dimensions, productivity, standing crop and their changes through the regeneration cycle. Effects of site quality have always been in the focus in these investigations.

These studies had to face the problems of the incompatibility between thinking in homogenous types (associations, site types, forest types) and experiencing heterogeneity, i.e., complex fine-grained mosaic structure in naturally dynamic forests. This problem was clearly seen by early phytosociologists [e.g. 11], but later got mostly forgotten.

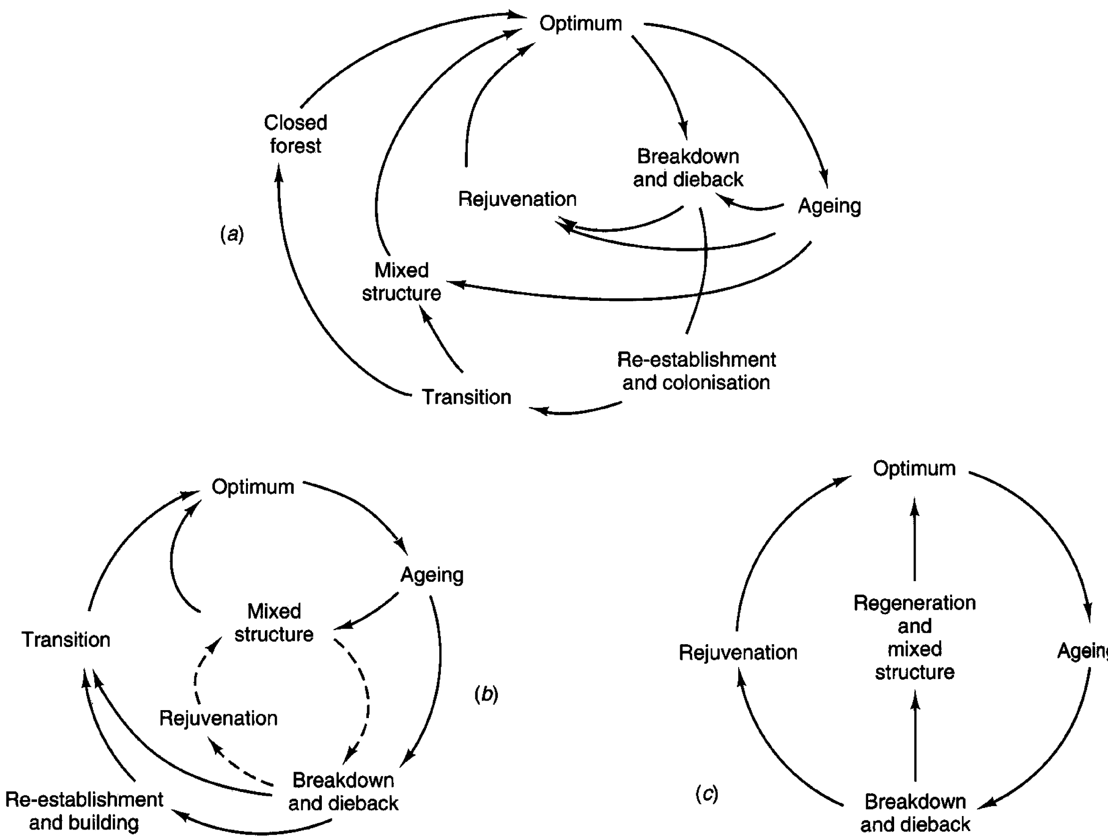

Figure 3. *Development phases of virgin forests **(a)** as recognised by Leibundgut* [48] *for Central Europe, with alternative versions by **(b)** Zukrigl et al.* [123] *and Mueller-Dombois* [61]. *Dashed lines in **(b)** indicate uncommon transitions. Source:* [71].

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A major tool in understanding forest dynamics was the concept of forest cycles described by forest development stages. The systems developed by different authors are not completely compatible (examples are shown in *Fig. 3*), the categories used are loosely defined, the mapping units of the mosaic might be of different size, so the perceived mosaic might have different spatial resolution (grain-size) according to the system used. Another consequence is that the recognition of stages and phases is observer-dependent, which might cause problems for long-term observations.

Important results

In this section examples are given for the most typical type of results that were published in the scientific literature.

Stand development

Most efforts have been put into studying changes of tree species composition, tree dimensions (height, dbh, basal area, distribution by size-classes) along the forest cycle. Models of the stages and length of the cycles were constructed and the equilibrium share of stages in the forest mosaic was defined (*Figs. 4–7*).

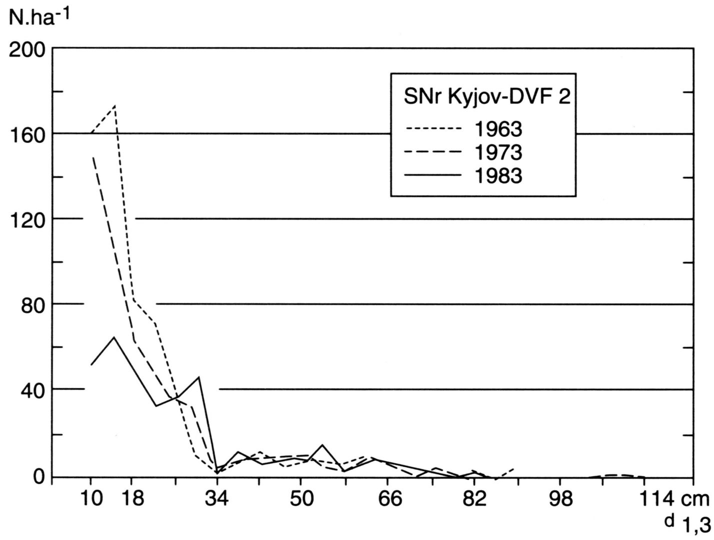

Figure 4. *Diameter distribution of trees in permanenet plot 2 in the Kyjov Forest Reserve in 1963, 1973, 1983. Source:* [43].

Patterns of natural mortality caused by competition and natural disturbance was compared in some cases. Dziewolski and Rutkowski [13] studied a 26.88 ha patch of the Wladiyslaw Orkan Forest Reserve in the Gorce Mts., southern Poland. Patterns of mortality were studied between 1969 and 1986 in 20 sampling plots, 0.05 hectare each. After the second measurement in July 1986, serious wind damage occurred on 12/13 August 1986. With the next measurement in September 1986 they could compare species and size distribution of dying trees. As *Fig. 8* shows, most of the 219 trees that died between 1969 and 1986 were small, whereas the wind in August 1986 killed more large trees.

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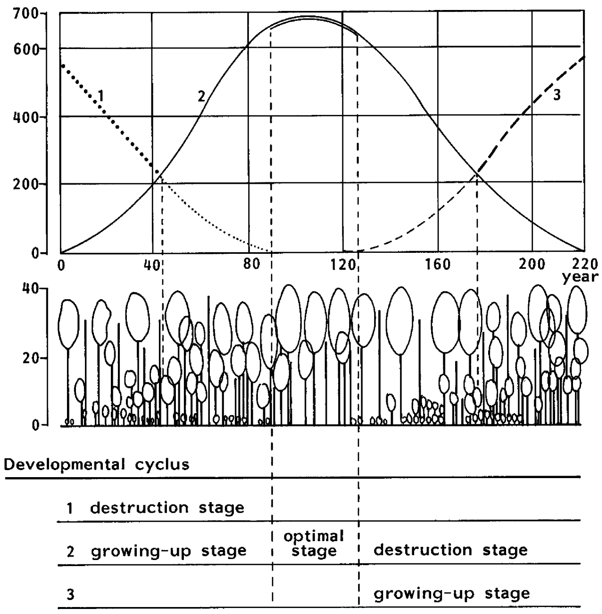

Figure 5*. Korpel's model of beech forest cycle, simplified by Koop* [41].

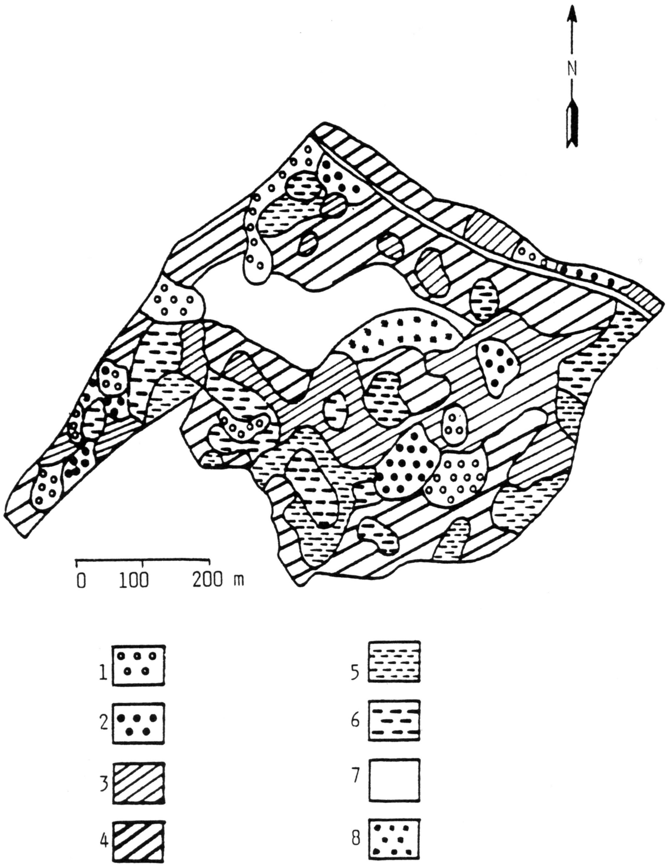

Figure. 6*. Mosaic of forest developmental phases in the Badin Forest Reserve. Source:* [43]. *1. Early growing-up phase; 2. Late growing-up phase; 3. Early collapsing phase; 4. Late collapsing phase; 5. Early optimal phase; 6. Late optimal phase; 7. Initial phase; 8. Transition phase.*

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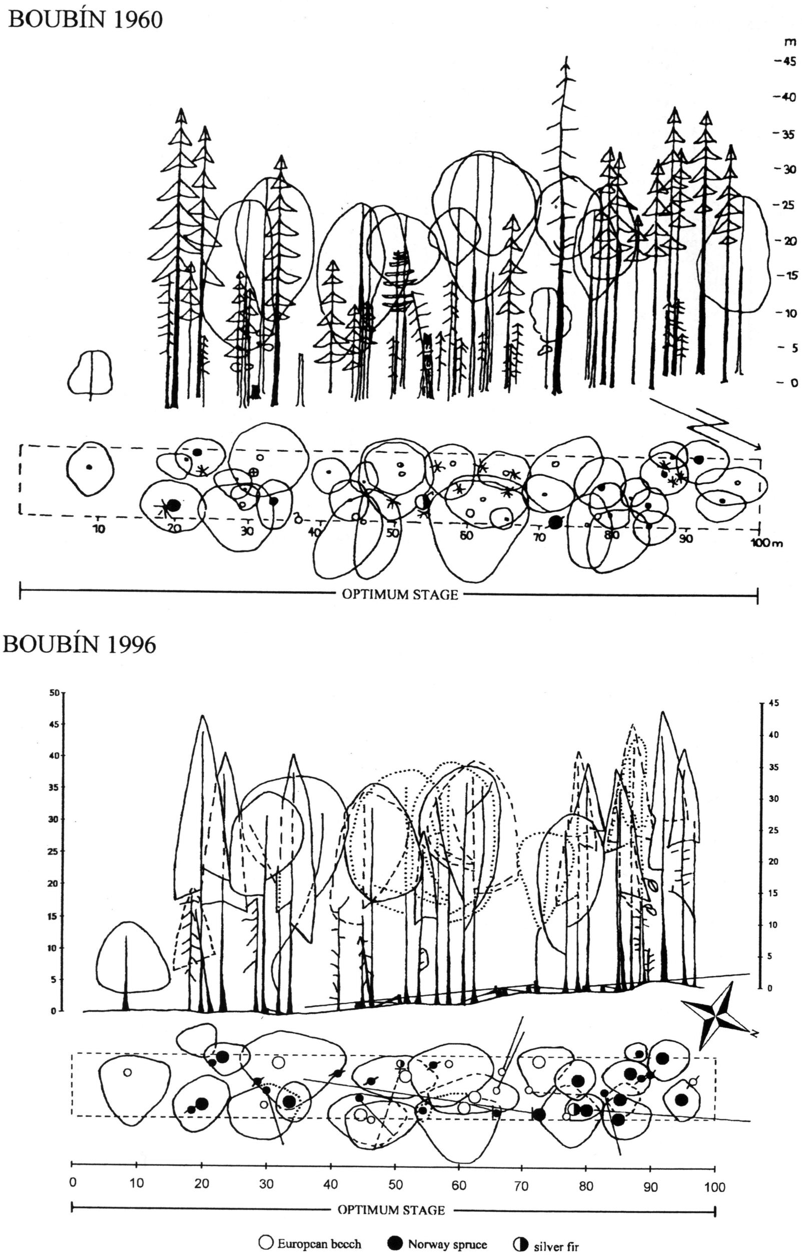

***Figure** 7. Changes of stand structure in the Boubin Forest Reserve illustrated by transect profiles drawn in 1960 and 1996 Source:* [112].

Dead wood

Dead woody material is an important component of natural forests, which is often missing from managed forests. So, several studies described the amount and very rarely also the decay stage of dead wood through the forest cycle. A typical example is shown for the Milesice Forest Reserve in the Czech Republic. The total volume of dead timber increased from 751 m^3 to 851 m^3, whereas the number of dead trees from 324 to 684 in the whole reserve from 1972 to 1996 [110]. The distribution among species is shown in *Table 10*. If dead trees are distributed among developmental stages and different types

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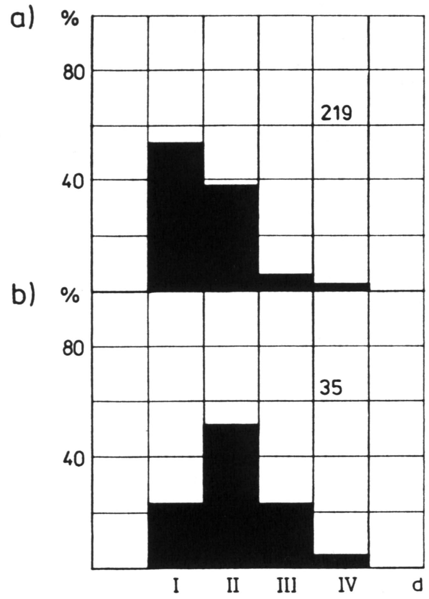

Figure 8. *Trees that died between 1969 and 1986 in the Wladiyslaw Orkan Forest Reserve* [13]. *Distribution of trees into diameter classes: I: 7–15 cm; II: 15–35 cm; 3: 35–55 cm; IV: 55–75 cm; a) natural loss 1969–1986 (21 trees); b) windfall in August 1986 (35 trees).*

of dead wood (standing dead tree, snag, log) then other aspect of dead wood dynamics can be traced. As *Table 11* shows, there are much more standing dead trees in the optimal stage than in the destruction stage, where fallen logs are more numerous.

The ecological role of dead wood is much less intensively studied in Central European beech forests than in the boreal zone [e.g. 67].

Table 10. *Distribution of the number and volume of dead trees among species in the Milesice Forest Reserve. Source:* [110].

	Number of trees		Timber volume (m^3)	
	1972	**1996**	**1972**	**1996**
Spruce	211	423	437.74	613.97
Fir	53	156	217.31	469.44
Beech	40	105	95.79	144.09

Table 11. *Distribution of the number of dead wood among developmental stages and dead wood types in the Milesice Forest Reserve. Source:* [110].

	Stage of growth		Optimum stage		Stage of disintegration	
	1972	**1996**	**1972**	**1996**	**1972**	**1996**
Standing	9	13	151	136	43	136
Snag		14		32		32
Log	14	23	20	117	87	117
Total	23	50	171	285	130	285

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Herbaceous vegetation

The composition of forest floor vegetation is widely used for recognizing forest types with different site quality. Forest floor vegetation can also be a serious competitor for young tree seedlings. For these reasons studying herbaceous vegetation in natural forests has always been an important task. Several authors studied the reaction of vegetation to changes in light conditions in forest reserves [e.g. 79, 93]. Resmerita [82] made a thorough analysis of herbaceous species occurring in Romanian beech forests. Of the 562 species known from beech sites 185 were grouped on the basis of their reaction to light. The system distinguishes 13 shade tolerant species, 25 shade-semishade species, 50 semishade species, 42 semishade species that tolerate light, 50 semishade-light species and 5 light species. Of the 5 light species *Chamerenion angustifolium* and *Rubus idaeus* are always present in clearings. Real shade species always disappear after large gaps have been created, whereas others can survive for several years: *Athyrium filix femina, Dryopteris filix-max, D. carthusiana, Geranium robertianum, Euonymus latifolia, Festuca drymea, Luzula luzuloides, L. sylvatica, Lysimachia nummularia, Polygonatum verticillatum.* Light tolerating semishade species can survive very long in large gaps: *Campanula persicifolia, Dactylis polygama, Melampyrum nemorosum, Poa nemoralis, Solidago virga-aurea, Thalictrum aquilegifolium, Vaccinium myrtyllus et vitis-idaea, Veronica officinalis.* The first species that recolonize gaps after canopy closure are: *Pulmonaria mollissima, P. officinalis, Symphytum tuberosum, Geum urbanum, Geranium robertianum, Polygonatum odoratum, Brachypodium sylvaticum, Dactylis polygama, Plathanthera bifolia, Epipactis helleborine, Athyrium filix-femina, Dryopteris filix-mas.*

Future tasks

To be able to get better ecological understanding of natural beech forests, this research area needs several improvements in our region. Among others:

- It is of utmost importance to clarify our definitions and sampling methods used for describing forest development stages so that different observers can collect comparable data.
- More specific analyses are needed to study relationships among different strata of forest vegetation. For this purpose spatially explicit individual-based approaches should also be used.
- Besides species and size distributions of trees, spatial structure of the stands should also be studied in more detail.
- The role of environmental heterogeneity in regeneration processes should be specifically addressed. Types, frequency and ecological role of microsites created by natural disturbances should be studied.
- Especially for conservation applications, it is essential to carry out specific studies on the relationships between certain forest-dwelling species and forest developmental stages or structural elements. This requires the inclusion of several animal groups into our studies.

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