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LEAF MORPHOLOGY AND THE DYNAMICS OF FROST-HARDINESS OF SHOOTS IN TWO PHENOLOGICAL FORMS OF EUROPEAN BEECH (FAGUS SYLVATICA L.) FROM SOUTHERN POLAND

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ABSTRACT

Dynamics of shoot development, leaf morphology and changes in frost-hardiness of leaves from spring to autumn was studied in two phenological forms of European beech (Fagus sylvatica L.) in years 1996-2000. The investigations were conducted in southern Poland, in research plots situated at elevations ranging from 250 to 1050 m. It was found, that trees classified as an early flushing form had longer and wider leaves and longer petioles (on average 11-15%) as compared with trees belonging to the late form. Leaf dimensions declined with increasing elevation of the research plots, especially in the early growth form (r ranging from –0.8953 to –0.9811). Determining frost-hardiness of young shoots with the Dexter's method (on the basis of the index of

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damage according to Pearce), conducted by freezing tree shoots in a refrigerator at various times indicated, that in autumn both phenological forms did not differ in the degree of frost-hardiness. However, in the early spring, several weeks before budbreak, the early flushing form showed a significant decline in frost-hardiness of shoots, as indicated by larger frost damages than in the late form. In spring the differences in frost hardiness among both phenological forms increased. The results of the investigations suggested, that the early form of European beech is not only more susceptible to late frosts, but also the buds are more vulnerable to the frost damage in the early spring, in the time before any signs of budbreak are visible.

Key words: Fagus sylvatica, phenological forms, frost-hardiness, leaf morphology

INTRODUCTION

The European beech (Fagus sylvatica L.) shows large variability in morphological and physiological traits [31, 32]. On the basis of those traits different ecotypes, geographical races and forms have been described [9, 36]. Even trees growing close to one another can show substantial differences in time of budbreak in spring etc. [4, 18, 21, 33]. At the end of the XIXth century Danckelman (cited after [10]) suggested, that time of budbreak in beech is determined genetically. That opinion was supported by the findings of several authors [10, 28, 39]. However, the differences in times of development between the early and late growth forms in European beech are influenced by environmental factors, among the others by temperatures [3, 8, 15, 38].

European beech (Fagus sylvatica L.), as a species typical for a maritime type of climate, belongs to the group of tree species characterised by the lowest level of frost-hardiness among the native trees of Poland. It is frequently damaged by late frosts [21]. After the severe winter of 1928/29 a large-scale decline of beech stands was observed in Poland, Rumania, Austria, Germany and even in Denmark [12, 13, 14].

Also after winters characterised by weak but persistent frosts, or after winters with large temperature differences, a dieback of young shoots, damage to the bark and occurrence of frost injuries on tree stems was observed [12, 15, 18].

Because of the large vulnerability to low temperatures in young leaves and shoots of European beech the early growth form is subjected to a greater risk of damage by late frosts than the late growth form [1, 15, 16, 19, 20, 26, 27, 37]. For example, the late frost (ranging from –6 to –13 °C) which occurred in the Tatra Mountains on May 20, 1952, caused a total loss of leaves and young shoots in the already developed early growth form; however, the late growth form was damaged to a lesser extent [19]. Myczkowski [20, 21, 23] and Różański and Mączka [30] suggested, that in the Tatra Mountains and in Beskidy occurred two distinct ecotypes of European beech, growing close to one another in tree stands. The one ecotype is a late-flushing one, relatively frost-resistant and characterized by a single-stem tree form. The other one is early-flushing, vulnerable to late frosts. In breeding programs for European beech, especially in mountain regions, a selection for late flushing in widely applied [10, 11, 19, 20, 27, 37].

Until now there is no information about the dynamics of temporal changes (from spring to autumn) in frost-hardiness of shoots in early and late forms of European beech. The aim of the investigations presented here was to analyze the dynamics of frost-hardiness. Apart from that, the phenological phases of trees and leaf morphology in early and late form of European beech were also studied.

MATERIALS AND METHODS

The investigations were conducted in southern Poland in years 1996-2000. In the year 1996 in two forest districts (Buda Stalowska in the Kolbuszowa upland and Limanowa in the Beskid Wyspowy mountains) seven study plots, ranging in elevation from 250 to 1050 m, were chosen. Tree stands selected for the study ranged in age from 15 to 85 years (Table 1). In spring 1996 30 trees flushing early and 30 flushing late were chosen and permanently marked in each study plot. In the next year the field observations were repeated for the study site 1a; in addition for the entire study no 1 the time of budbreak was determined based on observations of twigs collected in early spring (March 14) and kept in water in the laboratory. At the turn of July and August 1996 for each permanently marked tree 30 leaves were collected (from an exactly defined part of the crown). In total 900 leaves from trees flushing early and 900 leaves from trees flushing late were collected. Leaf sizes (leaf length, leaf width, length of the petiole) were measured for each collected leaf. In addition, in the experiment site 1a the dynamics of shoot development as well as leaf discoloration and leaf fall was observed. In the experiment 1b the percentage of trees developing lammas shoots was estimated at the end of July, and phenological phases in autumn were ascertained at three distinct times, and their entire dynamics was estimated on the basis on interpolation. In the beginning of winter of 1996 and in early spring and full spring of 1997 one-year old twigs were collected and kept in refrigerators. The diffusion of electrolytes from their tissues was determined using the method of Dexter et al. [5], and indices of damage due to freezing were evaluated employing the formula by Pearce [25]. A detailed description of these methods was given in earlier publications [6, 7].

Table 1. Characteristics of experimental plots

No. of plot	Altitude [m]	Exposition	Type of soil	Site	Stand composition	Age of beech trees	Height of beech trees [m]
Exper. 1a 1996/97 Forest district Buda Stalowska, VI Małopolska							
1	250	–	lessive soil	LSw	Mo-Bk-Db	15	
2	250	–	podzol soil	LSw	Db-So-Mo-Bk	85	
Exper. 1b 1996/97 Forest district Limanowa, VIII Karpacky Gebirge, Beskid Wyspowy							
3	650	N-E	acid brown soil	LG	Bk-Jo	60	21
4	675	S		LG	Bk-Jo	45	15
5	900	S-E		LG	Bk	20	3
6	910	S		LG	Bk	30	5
7	1050	N		LGM	Bk	15	2
Exper. 2 1997/98 Experimental Station Krynica Górska, VIII Karpaty Gebirge, Beskid Sądecki							
8	700	N-W		LMG	afforested farmland	4	0.7
Exper. 3 1999/2000 Forest district Myślenice, VIII Karpaty Gebirge, Beskid Makowski							
9	550	N	brown soil	LGM	Bk-Jo	10	2

LSw - fresh forest   Mo – larch
LG - mountain fortile forest   Jo - fir
LGM - mixed mountain forest   Bk - beech

To check the validity of the results, a next experiment was carried out. In spring 1997 in a 4-year old plantation of European beech representing 8 provenances (growing in a strictly designed experiment site in the open near Krynica – experiment number 2) groups of trees flushing early and flushing late were identified. Because a late frost on May 28, 1997 caused strong damages to young leaves and shoots, measuring the leaf dimensions was pointless. Thus the field work was limited to determining phenological phases and estimating the frost damages to shoots, as a fraction of last-year shoots that turned dead before mid-August. Results for trees flushing early and flushing late were given in table 5 as mean values for all 8 provenances altogether. In the years 1999 and 2000 in an experiment plot located in the Myślenice forest district (Beskid Makowski range) the study was repeated (experiment no 3) employing the same methods as in study no 1. The results were statistically analyzed.

RESULTS

Phenological phases

In all 9 sample plots substantial differences were ascertained among trees in respect to time at which they attain certain phenological phases (Table 2).

In the year 1996 (experiment 1) the earliest budbreak occurred in sample plots 1 and 2, which are situated at lowest elevation of about 250 m. In these plots the differences in the time of budbreak (7 – 10 days) between trees flushing early and flushing late were also larger than elsewhere. With increasing elevation time of budbreak was delayed – approximately by 2 – 2.5 days per each 100 m elevation gain. In the experiment no 1 the accuracy of classification of individual beech trees into classes flushing early and flushing late was supported both by the results of field observations and by the results of observations conducted on twigs cut in the late winter and kept in laboratory conditions. These observations supported also the finding that trees from upper elevations start the budbreak with a substantial delay. Also in the experiment no 2 (in all eight provenances under study) and in experiment no 3 substantial differences in times of occurrence of various phenological phases (ranging from 4 to 6 days) were found between the beeches flushing early and flushing late (Table 2).

Table 2. Phenological phases of early and late form of beech

Number		Year	Date in field condition								The shoots transferred to laboratory on March 14th	
			bud swelling		flushing		discoloration		leaf fall		bud swelling	
exp.	plot		W	P	W	P	W	P	W	P	W	P
1a	1	1996	23.04	30.04	02.05	07.05	01.10	14.10	13.10	23.10		
		1997	20.04	30.04	01.05	06.05					24.03[a]	29.03[b]
	2	1996	18.04	24.04	26.04	02.05	18.09	28.09	03.10	10.10		
		1997	17.04	26.04	29.04	03.05					29.03[b]	7.04[c]
1b	3	1996	26.04	01.05	07.05	11.05	22.09	29.09	01.10	06.10		
		1997									08.04[c]	15.04[d]
	4	1996	28.04	02.05	07.05	12.05	18.09	29.09	01.10	05.10		
		1997									07.04[c]	12.04[d]
	5	1996	04.05	08.05	11.05	16.05	16.09	28.09	29.09	04.10		
		1997									15.04[d]	26.04[f]

	6	1996	04.05	08.05	11.05	16.05	16.09	28.09	29.09	01.10		
		1997									20.04[e]	24.04[f]
	7	1996	07.05	11.05	14.05	18.05	16.09	23.09	27.09	30.09		
		1997									15.04[d]	24.04[f]
2	8[x]	1997	08.05	13.05	13.05	18.05	29.09	01.10	08.10	18.10		
3	9	1999	20.04	04.05	08.05	14.05	23.09	29.09				

W - early form of beech P - late form of beech x - mean for 8 provenances

In the experiment no 1a it was ascertained, that in early flushing beeches growing in the upland region the process of development of the lammas shoots started more than ten days earlier and occurred in larger number of trees than in beeches flushing late (Table 3). In mountain areas (experiment 1b) development of lammas shoots occurred very seldom, and in sample plots no 3 and 4 in the year 1996 it was not found at all. In autumn the degree of lignification of shoots was similar in all trees; only in several beeches belonging to the early form a tendency for earlier lignification was observed.

In all experiments the early flushing beeches displayed also earlier discoloration of leaves in autumn and earlier leaf fall. In the experiment 1 a, in which the dynamics of phenological phases in autumn was observed on every second day, a significant positive correlation was found between the time of bud swelling in spring on the one hand, and time of leaf discoloration in autumn (r = 0.980), time of beginning of leaf fall (r = 0.972), and time of the intensive leaf fall (r = 0.993) on the other.

Table 3. Dynamics of lammas shoots developing (Experiment 1)

Number of plot	Form	Percent of trees developing lammas shoots							
		date of determining, july 1996							
		1	4	8	12	16	20	24	28
1	W	0	24	24	36	36	36	44	44
	P	0	0	0	0	12	20	20	20
2	W	0	0	25	25	25	31	31	31
	P	0	0	0	0	0	20	20	20
3	W								0
	P								0
4	W								0
	P								0
5	W								20
	P								13
6	W								17
	P								13
7	W								10
	P								10

W - early form of beech P - late form of beech

Leaf features

In seven of eight plots under study (experiments 1 and 3), irrespectively of the elevation, topography and tree age, leaves of beeches flushing early were longer and wider (on average 11%) and had longer petioles (on average 15%) than beeches flushing late (Table 4). Leaf dimensions decreased with the increasing elevation of study plot (from 250 m to 900-1050 m) (experiment 1), in a more uniform way in the early-flushing trees than in the late flushing ones, which is indicated by the correlation coefficients (from –0.8953 to –0.9811 and from –0.6452 to –0.9213, respectively) (Table 6). Per each 100 m elevation gain the leaf length decreased on average by 3.6 mm (i. e. 4.4%), leaf width decreased by 2.1 mm (4.1%) and petiole length decreased by 0.5 mm (5%). Index of leaf shape (ratio of leaf length to leaf width) was very similar in early flushing and late flushing trees, and it was not related to the elevation (Table 4). In both phenological forms of beech a significant relationship between leaf length and leaf width was found both in early flushing (r = 0.9773) and late flushing trees (r = 0.7595), while the relationship between leaf length and petiole length was statistically significant only in early flushing beeches (r = 0.9085) (Table 6).

Table 4. Beech leaves features

Number		Form	Length of blades		Width of blades		Area index (lenght x width : 1000)		Shape index (lenght : width)		Lenght of petiole	
exp.	plot		[mm]	average	[mm]	average		average		average	[mm]	average
1	1	W	86.0^{a}	83.0^{a}	53.2^{a}	51.6^{a}	4.58^{a}	4.29^{a}	1.62	1.61	10.1^{a}	9.6^{a}
		P	80.0^{b}		50.0^{b}		4.00^{c}		1.60		9.1^{b}	
	2	W	87.1^{a}	78.0^{b}	49.1^{b}	43.6^{b}	4.28^{b}	3.46^{b}	1.77	1.77	10.0^{a}	8.4^{b}
		P	69.0^{c,d}		38.1^{d,e}		2.63^{d}		1.78		6.9^{f}	
	3	W	73.0^{c}	70.6^{c}	43.4^{c}	41.7^{c}	3.17^{d}	2.95^{c}	1.68	1.69	8.7^{c}	8.4^{b}
		P	68.3^{d,e}		40.0^{d}		2.73^{e}		1.71		8.2^{d}	
	4	W	65.6^{d,e}	65.3^{d}	39.4^{d}	39.6^{d}	2.59^{f}	2.59^{d}	1.66	1.64	8.3$^{c, d}$	8.4^{b}
		P	65.0^{e}		39.9^{d}		2.59^{f}		1.63		8.5^{c}	
	5	W	57.4^{f}	54.9^{e}	36.3^{e,f}	34.4^{e}	2.08^{g}	1.89^{e}	1.58	1.60	7.5^{e}	6.9^{c}
		P	52.5^{g}		32.5^{g}		1.71^{h}		1.62		6.3^{g}	
	6	W	57.6^{f}	55.8^{e}	34.9^{f}	34.6^{e}	2.01^{g}	1.93^{e}	1.65	1.61	6.3^{g}	5.8^{d}
		P	54.1^{f,g}		34.4^{f,g}		1.86^{g,h}		1.57		5.4^{h}	
	7	W	57.1^{f}	54.2^{e}	36.4^{e,f}	35.8^{e}	2.08^{g}	1.95^{e}	1.57	1.52	6.7^{f}	6.1^{d}
		P	51.4^{g}		35.3^{f}		1.81^{h}		1.46		5.5^{h}	
	LSD P=0.05		3.54	2.94	2.33	1.66	0.23	0.16		n	0.23	0.58
	Mean	W	69.1^{a}	66.0	41.8^{a}	40.2	2.96^{a}	2.72	1.65	1.63	8.2^{a}	7.6
		P	62.9^{b}		38.6^{b}		2.47^{b}		1.62		7.1^{b}	
	LSD P=0.05		1.86		1.05		0.1		n		0.37	

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3	9	W	59.9^{a}	55.2	37.6^{a}	34.7	2.25^{a}	1.93	1.59	1.59	7.0^{a}	6.5
		P	50.5^{b}		31.8^{b}		1.61^{b}		1.59		6.0^{b}	
	LSD P=0.05		7.0		5.2		0.52		n		0.8	

W - early form of beech
P - late form of beech
a, b - homogenous groups
N - insignificant

Table 5. Damage indices of one-year old shoots in different forms of Fagus sylvatica after freezing in refrigerator

Experiment 1																			
No. of plot	Form	Freezing date																	
		December 16th 1996			March 14th 1997				April 18th 1997					May 9th 1997					
		Freezing temperature																	
		-25°C	-33°C		-10°C	-20°C	-33°C		-15°C	-25°C		-33°C		-10°C		-15°C		-25°C	
			%	φ			%	φ		%	φ	%	φ	%	φ	%	φ	%	φ
1	W	at the back-ground level	60.5	51.3^{c}	at the back-ground level	at the back-ground level	15.1	22.8$^{d.e.f}$	at the back-ground level	2.6	9.4$^{a.b.c}$	58.5	49.9^{f}	18.3	25.4^{d}	40.7	39.7^{e}	50.6	45.4$^{e.f}$
	P		58.6	50.2$^{b.c}$			5.6	13.6$^{a.b}$		0	0^{a}	51.8	46.0$^{e.f}$	7.4	15.7^{c}	11.2	19.4^{c}	49.7	44.8^{e}
2	W		57.9	49.6$^{b.c}$			24.0	29.3$^{f.g}$				48.9	44.4$^{d.e}$						
	P		41.4	39.9^{a}			16.2	23.5$^{d.e.f}$				38.0	38.1$^{b.c}$						
3	W		56.8	48.9$^{b.c}$			33.6	35.5^{g}		17.6	24.5^{f}	53.6	47.1$^{e.f}$	21.2	27.3^{d}	42.0	40.4^{e}	59.7	50.6^{f}
	P		51.8	46.1$^{b.c}$			15.5	23.1$^{d.e.f}$		8.7	17.0$^{d.e}$	42.8	40.9$^{c.d}$	3.9	11.4$^{b.c}$	16.6	24.0$^{c.d}$	49.2	44.5^{e}
4	W		53.1	46.8$^{b.c}$			27.9	32.1^{g}		14.5	22.4$^{e.f}$	51.7	46.0$^{e.f}$	5.0	12.9$^{b.c}$	22.3	28.1^{d}	54.5	47.6$^{e.f}$
	P		58.8	50.1$^{b.c}$			13.1	21.1$^{c.d.e}$		9.2	17.3$^{d.e}$	41.9	40.0$^{b.c}$	3.2	11.4$^{b.c}$	16.4	23.8$^{c.d}$	37.5	37.7^{d}
5	W		50.6	45.4^{b}			6.1	14.2$^{a.b.c}$		7.0	13.9$^{c.d}$	34.8	36.2^{b}	1.3	6.6$^{a.b}$	4.1	11.4^{b}	22.3	28.2^{c}
	P		51.6	46.0$^{b.c}$			9.3	17.3$^{b.c.d}$		4.2	9.8$^{b.c}$	37.5	37.8$^{b.c}$	0	0^{a}	0	0^{a}	6.2	14.4^{a}
6	W		55.2	48.0$^{b.c}$			3.3	10.3^{a}		8.5	16.6^{d}	42.3	40.6$^{c.d}$	3.0	10.5$^{b.c}$	0.7	4.8^{a}	34.4	36.0^{d}
	P		51.7	46.0$^{b.c}$			9.9	18.2$^{b.c.d.e}$		1.7	6.4^{b}	25.3	30.1^{a}	0	0^{a}	4.2	11.8^{b}	24.3	29.4^{c}
7	W		52.5	46.5^{b}			15.6	24.3$^{e.f}$		11.1	19.8$^{e.f}$	40.5	39.5$^{b.c}$	0	0^{a}	3.2	10.0^{b}	38.1	37.2^{d}
	P		58.6	49.9$^{b.c}$			14.1	22.0$^{d.e}$		0	0^{a}	23.5	28.8^{a}	0	0^{a}	0	0^{a}	12.9	20.9^{b}
LSD P=0.05			5.37					7.02			5.84		4.0		6.95		5.02		5.79
Average	W		55.2	48.1			18.2	25.2^{b}		10.0	19.5^{b}	47.2	43.4^{b}	8.1	13.8^{b}	18.8	22.4^{b}	43.3	41.0^{b}
	P		54.4	47.2			11.9	20.3^{a}		4.0	10.1^{a}	37.2	37.5^{a}	2.5	6.4^{a}	8.1	13.2^{a}	30.0	31.9^{a}
LSD P=0.05				n				4.0			3.92		2.81		4.94		6.82		5.64

Experiment 2					
No. of plot.	Form	November 17th 1999		March15th 2000	
		Freezing temperature -33°C			
		%	φ	%	φ
9	W	38.3	38.2	53.2	46.9^{b}
	P	37.9	38.0	43.7	41.2^{a}
LSD P=0.05			n		3.2

Experiment 3			
No. of plot.	Form	Damage of shoots by a late frost (May 28, 1997) (mean values for 8 provenances)	
		%	φ
8	W	42.3	40.6^{b}
	P	26.5	31.0^{a}
LSD P=0.05			7.51

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Table 6. Values of correlation coefficients "r" (Experiment 1)

Features	Beech forms		
	early	late	early + late
A. Between elevation above sea level (x) and y:			
• date of bud swelling	0.9652[c]	0.9233[c]	
• date of flushing	0.9591[c]	0.9663[c]	
• length of blades	-0.9811[c]	-0.9213[c]	-0.9727[c]
• width of blades	-0.9583[c]	-0.7533[a]	-0.8993[c]
• length of petiole	-0.8953[c]	-0.6452[n]	-0.8663[c]
• damage index of one-year old shoots after freezing Dec. 16th (-33°C)	-0.8340[c]	0.3400[n]	-0.0861[n]
• damage index of one-year old shoots after freezing March 14th (-33°C)	-0.3987[n]	0.0491[n]	-0.3530[n]
• damage index of one-year old shoots after freezing April 18th (-33°C)	-0.9603[b]	-0.7542[b]	-0.8067[b]
• damage index of one-year old shoots after freezing May 9th (-10°C)	-0.8311[b]	-0.9738[c]	-0.8931[c]
• damage index of one-year old shoots after freezing May 9th (-15°C)	-0.8860[c]	-0.6232[n]	-0.8534[c]
• damage index of one-year old shoots after freezing May 9th (-25°C)	-0.6159[n]	-0.8612[c]	-0.7783[b]
B. Between length of blades (x) and y:			
• width of blades	0.9773[c]	0.7595[b]	0.9154[c]
• length of petiole	0.9085	0.6243[n]	0.8346[c]
C. Between date of swelling in 1996 (x) and y:			
• damage index of one-year old shoots after freezing Dec. 16th 1996 (-33°C)			-0.0432[n]
• damage index of one-year old shoots after freezing March 14th 1997 (-33°C)			-0.5272[a]
• damage index of one-year old shoots after freezing April 18th 1997 (-33°C)			-0.7387[c]
• damage index of one-year old shoots after freezing May 9th 1997 (-10° C)			-0.8396[c]
• damage index of one-year old shoots after freezing May 9th 1997 (-15°C)			-0.8261[c]
• damage index of one-year old shoots after freezing May 9th 1997 (-25°C)			-0.8100[c]

Significant at:
c - 0.01 b - 0.05 a - 0.10 n - insignificant

Cold hardiness

In experiments no 1 and 3 (in experiment no 2 no such observations were conducted) in all times of twig collection (from autumn till spring) the percentage of electrolytes washed out from control (not frozen in refrigerartor) one-year old twigs was similar and amounted to 20%, indicating that in natural conditions no frost injuries occurred in winters 1996/1997 and 1999/2000.

In the experiment no 1 twigs collected on December 16, 1996, after being kept at the temperature of -33° C showed significant injuries (41.4 – 60.5%); no differences between the early flushing and late flushing trees were found (Table 5). In late winter (measurements on March 14, 1997) shoots were still quite frost-resistant, so that freezing them down to temperatures –10 and –20° C did not cause any measurable damages. Only after freezing down to –33° C did the shoots show substantial frost injuries (from 3.3 to 33.6%). In four (out of seven) sample plots the shoots of late-flushing beeches were significantly less damaged than the shoots of early-flushing form, and in two others there was a similar, although statistically insignificant tendency. Mean values of frost injuries in the entire experiment no 1 indicated, that in late winter the twigs of late-flushing beeches were significantly more resistant to frost damages than the twigs of the early flushing form (Table 5). Moreover, the percentage of frost injuries in twigs frozen to –33° C was correlated with the time of bud swelling in the former year (r = -0.5272). The next measurement, conducted on April 18, showed a relatively high level of cold-resistance in beech twigs. Freezing down to – 15° C did not cause any injuries, while after freezing down to -25° C and especially to -33° C the late-flushing form turned out to be significantly more cold-resistant (Table 5). Coefficients of correlation increased in that case to –0.7387 (Table 6). In the latest measurements, carried out on May 9, 1997, the degree of cold hardiness declined substantially, so that forest injuries were observed even after freezing twigs down to -10° C. At all temperatures – i.e. at -10° C, -15° C, and -25° C the shoots of late-flushing form were significantly less damaged than the early-flushing ones (Table 5). In mountain areas the process of losing cold-hardiness was much slower than in lower elevations. Coefficients of correlation between the degree of frost injuries and time of bud swelling and budbreak in the former year were statistically significant; in May they ranged from –0.8100 to –0.8396 (Table 6). Statistical analysis of the results indicated, that a negative correlation between the amount of frost injuries of one-year old shoots and elevation occurred in early winter (December 16, 1996) in the early-flushing form and in early spring (April 18, 1997) and middle spring (May 9, 1997) in both phenological forms (Table 6).

Results obtained in the season 1996/1997 (experiment 1) were corroborated in the season 1999/2000 (experiment no 3). In November 1999 one-year old twigs of both phenological forms of beech after freezing down to -33° C showed a similar amount of frost injuries, while in the late winter (March 15, 2000) the late-flushing form was significantly more frost-resistant than the early flushing one (Table 5).

In the experiment no 2 seedlings (representing eight different provenances of European beech from different parts of Poland) growing in the open near Krynica, were substantially damaged by a late frost which occurred on May 28, 1997. Early flushing beeches were injured much more than the late flushing ones (Table 5). A significant correlation between the amount of frost injuries and time of bud swelling was ascertained (r = -0.5302).

DISCUSSION

Investigations conducted using very heterogeneous material (trees in age ranging from 4 to 85 years, growing at elevations from 250 to 1050 m, in different geographic locations) indicated, that in sample plots early flushing and late flushing trees (differing in time of bud swelling and budbreak from 4 to 10 days) co-occur in the same stands. It agrees with other findings by different authors. For example, in Germany it was observed, that differences in spring phenological phases among beeches varied from 6 to 25 days [29]. In France these differences were from 1 to 21 days [4], in the Puszcza Bukowa near Szczecin from 5 to 15 days [33, 34] and in the Tatra Mountains from a few days up to twenty days [19, 20]. Differences were related to environmental conditions, and especially to the temperatures. In Eastern Carpathians, during a cool spring, the differences varied from 10 to 15 days, while after a rapid increase of temperature they went down to 5 days [18]. Usually the late form of beech begins bud swelling at the time when the early form already develops the leaves [15, 33].

In laboratory conditions the differences in timing of vernal phenological phases between the early and late forms of beech were maintained; in some instances (for example in case of twigs collected from sample plots no 2, 3, 5 and 7) they were even larger than in the field. (Table 2).

Time of bud swelling in beeches growing in the foothills and in the mountains got delayed with increasing elevation (Table 2), approximately by 2 – 2.5 days per each 100 m elevation gain (coefficient of correlation ranged from 0.9233 to 0.9663) (Table 6). This agrees with the findings of Molotkov [18] from Eastern Carpathians (delay of phenological phases by 2 days per each 100 m elevation gain). Also Myczkowski [22] found a delay of phenological phases in beeches growing in the Tatra Mountains as compared to the areas situated in lower elevations.

The environmental factors responsible for the delay of the beginning of growing season in the mountains are probably the later and cooler spring.

It seems interesting, that one-year old beech twigs collected in the late winter and kept in water in the laboratory maintained the phenological pattern typical for the locations, from which they were collected (Table 2). One can speculate, that the environmental condition of the locality, where buds were formed, affect their anatomy and result in phenological changes. For example, there are data indicating that high levels of light radiation (which occur in the mountains) during the time of bud formation cause the increase of the thickness of bud scales [8, 10], and thus increase the level of light and temperature necessary to break the bud dormancy, which causes the delay in bud development in spring [18, 34, 35]. One cannot also exclude the possibility, that the delay in development of buds from twigs coming from the mountains could be determined genetically, as a result of natural selection.

Our investigations on the dynamics of cold-hardiness indicated, that in autumn and in the beginning of winter the one-year old shoots of the early and late forms of beech did not differ in their frost-resistance (Table 5). Although in the early flushing form of beech the occurrence of lammas shoots was more common than in the late-flushing trees, but the shoot development was completed earlier in the early form than in the late one, and thus even the lammas shoots were fully lignified before the onset of winter. Moreover, leaf discoloration and leaf fall do occur earlier in the early form, which could contribute to the increase of cold-hardiness of shoots. On the other hand, in the late winter within few weeks before bud swelling, in the early flushing form of beech occur profound physiological and morphological changes in buds, causing loss of their cold-hardiness, as compared with the late-flushing form (Table 5). Thus in spring the differences in cold-hardiness between the early and late-flushing forms increase. In both phenological forms the loss of cold-hardiness occurred later in beeches growing in the mountains as compared with beeches growing in lower elevations; that was probably a result of a delay in the breaking of bud dormancy.

While determining the differences in morphological features between beeches flushing early and flushing late one should consider, that these differences could be secondary ones, caused – for example – by different degree of damage to buds and developing leaves by the late frosts. It is known, that after killing of developing leaves by late frost, a second generation of small and malformed leaves develops from dormant buds [19, 41]. Thus the measurements of leaves were conducted only in experiments no 1 and 3, in both cases after relatively mild winters and with no late frosts in spring; no such measurements were conducted in the experiment no 2.

The leaf samples analyzed in our study (900 leaves per tree from similar locations within the crown in 30 trees growing in tree stands of low density) seem to be representative. Our results (Table 4) suggest, that irrespectively of tree age (from 10 to 85 years), elevation (from 250 to 1050 m) and the year of study (1996, 1999) leaf and petiole sizes in early flushing trees were larger (at more than 10% on average) than in late-flushing trees, and that in both forms leaf sizes decreased with increasing elevation. Also Mišic [17], conducting investigations in the former Yugoslavia in the vicinity of Avel found, that the early flushing beeches had longer leaves than the late flushing ones. On the other hand, Molotkov [18] in Ukraine did not find differences in leaf sizes between the early and late forms of beech. Opinions concerning the influence of elevation on leaf dimensions are split. In most studies it was found, that the leaf sizes decrease with the increasing elevation; that was determined for example in Poland [42], in the Witosha Mountains in Bulgaria [2], in the Eastern Carpathians in Ukraine [15, 18]. On the other hand, no such relationship was observed in Slovakia [24] and in Czech Republic [40]. The negative influence of elevation on leaf sizes in beech can be explained by the increasing harshness of climatic conditions, decline in soil fertility as well as by the influence of the high intensity of short-wave radiation (especially the UV radiation), slowing down the processes of leaf growth.

CONCLUSIONS

The investigations conducted in southern Poland showed that:

1. Early flushing form of European beech had longer and wider leaves and longer petioles (on average 11-15%) as compared with trees belonging to the late form.
2. Leaf dimensions declined with increasing elevation of research plots.
3. In autumn both phonological forms did not differ in the degree of frost-hardiness, however, in the early spring, several weeks before bud break, the early flushing form showed a significant decline in frost-hardiness of shoots, as indicated by larger frost damages than in the late form.

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