Variability of Beech Provenances in Spring and Autumn Phenology

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Abstract

Time of flushing and growth cessation of beech (Fagus sylvatica L.) provenances is important on sites with frequently occuring late or early frosts. The 35 beech provenances growing in a trial in Choczewo in northern Poland were examined as regards flushing (FLUSH) and growth cessation (CESS) in two growing seasons (1997 and 2001). We conclude that in these traits an ecotypical variation pattern exists between provenances. Longitude had the most important influence on FLUSH and CESS – more eastern provenances tending to flush and cease growth earlier. Latitude and altitude also significantly affected phenology – northern populations flushed and ended growing season later as well as those from lower altitudes. In the environmental conditions of the experiment selection for late flushing has little importance.

Key words: Fagus sylvatica, flushing, bud-burst, growth cessation, provenances.

Introduction

Common beech (Fagus sylvatica L.) is one of the most important broadleaved species in Europe. Its natural range spans from Spain in the west to the Black Sea in the east, and from Sicily in Mediterranean to southern parts of Sweden and Norway (Boratyńska and Boratyński, 1990). In southern Europe beech is confined to montane regions whereas in the north it occupies lowland areas. Such extended area of distribution, involving latitudinal and altitudinal zonality, should be reflected in natural diversity. The best way to test genetic variation within a species are provenance experiments in which populations from different locations are grown in a common environment. First such experiments with beech were started at the end of nineteenth century in Germany. Since this time numerous trials were established in European countries on national as well as international level. Good reviews of the hitherto results regarding beech variability were given by PAULE et al. (1984) and GIERTYCH (1990) indicating that for most growth traits there are no distinct geographical patterns, so ecotypical variation prevails rather than clinal. Genetic diversity of beech populations was also studied using genetic markers. Employing various numbers of polymorfous isoenzymatic loci it was found that differences within and between populations increase towards Southern Europe. However only PX1 and PX2 (peroxidases) allelic frequency variations seem to be related to environmental changes associated with latitudes or altitudes (Barrière et al., 1985; Comps et al., 1990, 1991; PAULE, 1995). Such a pattern of diversity reflects the history of postglacial migrations of this species.

Beech is vulnerable to very low temperatures in the winter even at a mature age (Pukacki, 1990) but seedlings are most sensitive to late frosts. Especially those flushing too early in spring are exposed to frost damage which leads to reduction in height and diameter increment (Hristov and Botev, 1981) and irregularities in stem form (Myczkowski, 1955). Thus most selection programmes are directed at choosing late flushing provenances and individuals to protect them against those injuries. This matter is of increasing importance since global warming tends to enlarge frost damage risk in trees by increas-

ing winter temperatures which could lead to earlier dehardening (SAXE et al. 2001).

In Poland some provenance trials were established by RZEŹNIK (1976). He observed diversity of 7 Polish beech provenances and concluded on the basis of morphological and phenological traits that there are two ecotypes of beech—montane and lowland. Another series of provenance experiments with beech was started in Poland in the years 1992 to 1995. In this paper we present results regarding phenological traits obtained on one of these sites. Our purpose was to find out whether the recognition of two beech ecotypes is justified based on a bigger set of provenances compared with the earlier one or whether some other variation pattern exists among beech populations in Poland. Knowledge of the phenological behaviour of the tested provenaces will help in transfers of planting material to sites with a known frost injury risk.

Material and Methods

The experiment contains 38 provenances of beech from its natural distribution range in Poland. The provenances cover a $5^{\circ}38'$ of latitudinal and a $8^{\circ}57'$ of longitudinal gradient (Fig. 1, Table 1). The experimental site was established in April 1996 with three-year-old seedlings in the Choczewo Forest District in Northern Poland on an open flat area. Each provenance has 100 or 50 trees (1.5 x 1.3 m spacings) plots in 1 to 6 replications. This area is a part of project testing diversity of beech in Poland (GC 2234 1992–1995). Similar trials were also planted in five other locations (BARZDAJN, 1999).

In this experiment we examined flushing on 28 to 104 trees per provenance at the beginning of the fifth (1997 – FLUSH 5) and ninth (2001 – FLUSH 9) growing period using a 7 point scale developed by Teissier du Cross (1981). On the same trees in the autumn we observed growth cessation rate (CESS 5 and CESS 9 respectively) using an 8 point scale (Stachak, 1965). These observations were done on one day when distinct differences between trees were noticeable. Such a method of scoring data gives relatively precise results (Giertych, 1972; von Wuehlisch et al., 1995).

Analysis of variance was done (standard least squares procedure, JMP 4. SAS Institute Inc. Cary) to determine differences between provenances. Due to an unequal number of replicates only the provenance component significance could be tested using the model:

$$Y_{ij} = \mu + P_i + e_{ij} \tag{1}$$

where Y_{ij} is the individual observation, μ is the overall mean, P_i is the effect of i^{th} provenance and e_{ij} is the residual. Each provenance had from two to five replicates. Three provenances (29 Milicz, 35 Tomaszów and 45 Losie) were excluded from analysis because of insufficient number of replicates.

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Table 1. – Geographical origin of maternal stands and average values of phenological phases (s.d.) for populations. * – provenances present in the experiment but excluded from analysis. See text for terms explanation.

number	population	Latitude (N)	Longitude (E)	Altitude ([m] a.s.l.)	FLUSH 5	FLUSH 9	CESS 5	CESS 9
1	Gryfino 1	53 18	14 43	80	2.35 (0.13)	2.13 (0.51)	6.45 (0.64)	5.13 (0.38
2	Gryfino 2	53 20	14 42	80 -95	2.41 (0.10)	2.12 (0.21)	6.23 (0.57)	5.17 (0.44
3	Bierzwnik	53 05	15 54	193	1.85 (0.14)	1.81 (0.12)	6.47 (0.41)	4.85 (0.43
4	DrawieńskiPN	53 05	16 55	193	2.00 (0.06)	1.86 (0.34)	6.63 (0.59)	5.02 (0.25
5	Karnieszewice	54 17	16 22	20	1.79 (0.15)	1.84 (0.23)	6.31 (0.56)	4.69 (0.37
6	Wejcherowo 1	54 40	17 06	60	2.06 (0.23)	2.06 (0.14)	6.66 (0.21)	4.85 (0.2
7	Wejcherowo 2	54 37	18 18	115	1.83 (0.33)	1.97 (0.29)	6.57 (0.51)	4.57 (0.4)
8	Szczecinek 1	53 40	16 40	130	1.68 (0.25)	1.64 (0.38)	6.33 (0.79)	4.63 (0.3
9	Szczecinek 2	53 45	16 30	130	1.64 (0.19)	1.89 (0.06)	6.47 (0.39)	4.91 (0.3
10	Lipusz	54 11	17 40	190	1.89 (0.28)	1.98 (0.38)	6.53 (0.45)	5.00 (0.3
11	Gdańsk	54 23	18 31	70	1.83 (0.16)	1.86 (0.11)	6.40 (0.61)	4.82 (0.2
15	Kwidzyn 1	53 39	19 06	30	2.15 (0.22)	2.37 (0.18)	6.56 (0.17)	5.54 (0.4
16	Kwidzyn 2	53 39	19 06	30	2.29 (0.05)	2.42 (0.07)	7.07 (0.25)	5.73 (0.4
17	Kwidzyn 3	53 51	19 10	40	2.02 (0.16)	2.06 (0.34)	6.92 (0.34)	5.45 (0.7
18	Młynary	54 01	19 56	148	2.13 (0.17)	2.14 (0.22)	6.73 (0.48)	5.47 (0.2
19	Wipsowo	53 58	20 57	175	2.38 (0.16)	2.21 (0.17)	7.05 (0.51)	5.49 (0.6
21	Lutówko	53 29	17 26	140	1.71 (0.05)	1.72 (0.11)	6.52 (0.32)	4.73 (0.2
23	Krucz	52 52	16 30	120	2.01 (0.22)	2.11 (0.34)	6.82 (0.57)	4.56 (0.2
24	Świebodzin 1	52 28	15 30	150	2.09 (0.21)	2.40 (0.15)	7.20 (0.21)	4.96 (0.8
25	Świebodzin 2	52 30	15 30	100	1.94 (0.12)	1.88 (0.14)	6.65 (0.32)	5.01 (0.3
26	Grodzisk	52 23	16 16	95	2.14 (0.19)	1.98 (0.22)	6.43 (0.50)	5.06 (0.3
27	Pniewy	52 30	16 20	95	2.11 (0.27)	1.62 (0.33)	6.86 (0.59)	4.86 (0.7
28	Łopuchówko	52 35	17 05	110	1.96 (0.31)	1.78 (0.22)	6.60 (0.50)	4.92 (0.3
29	Milicz *	51 27	17 16	230	1.74	1.71	7.11	5.06
30	Lipinki	51 37	15 18	200	1.77 (0.23)	1.93 (0.26)	6.37 (0.55)	4.76 (0.2
31	Prudnik	50 20	17 20	425	2.30 (0.33)	1.91 (0.46)	6.27 (0.33)	5.04 (0.4
32	Brzeziny	51 50	19 36	200 - 250	1.70 (0.09)	1.72 (0.29)	6.42 (0.58)	4.72 (0.2
34	Łagów	50 50	20 59	350	2.59 (0.09)	2.81 (0.31)	6.72 (0.38)	5.53 (0.1
35	Tomaszów *	50 50	23 00	180 - 300	2.00	2.25	8.53	5.63
37	Leżajsk	50 23	22 17	170	2.60 (0.18)	2.74 (0.30)	6.19 (0.11)	5.21 (0.3
38	Zdroje	50 17	16 30	740 - 840	2.37 (0.24)	2.11 (0.01)	7.34 (0.70)	5.50 (0.5
39	Ustroń	49 39	18 54	550	2.28 (0.19)	2.19 (0.45)	6.58 (0.40)	4.85 (0.3
41	Lesko	49 28	22 16	520	2.62 (0.35)	2.63 (0.32)	6.50 (0.52)	5.97 (0.4
42	Bieszczadzki PN1	49 07	22 29	700 - 920	2.11 (0.08)	2.00 (0.31)	6.85 (0.19)	5.27 (0.7
43	Bieszczadzki PN2	49 07	22 29	740 -980	2.11 (0.08)	2.34 (0.08)	6.84 (0.52)	5.67 (0.0
44	Bieszczadzki PN3	49 07	22 29	780 - 1030	2.00 (0.00)	2.17 (0.23)	6.64 (0.33)	5.53 (1.2
45	Łosie *	49 36	21 07	400 - 520	2.85	2.44	7.50	5.68
47	Rymanów	49 34	22 00	350 - 400	2.14 (0.12)	2.09 (0.11)	6.80 (0.58)	5.19 (0.3
	mean				2.08	2.07	6.63	5.10

Pearson's moment correlations based on provenance means were also calculated to examine relationships between traits in respective years and geographical coordinates of the maternal stands (LAT-latitude, LONG-longitude and ALT-altitude a.s.l.).

Results

Analysis of variance showed significant differences between provenances in all phenological traits except for CESS 5 (*Table 2*).

The greater the FLUSH value the earlier do trees tend to flush in the spring. Average FLUSH for provenances ranged from 1.64 (9 Szczecinek 2) to 2.68 (41 Lesko) in the first investigation and from 1.62 (27 Pniewy) to 2.81 (34 Lagów) in the second (Table 1). There were some populations which were stably early (34 Lagów, 37 Leżajsk, 41 Lesko) or late flushers (8 Szczecinek 1, 21 Lutówko, 32 Brzeziny) in the experimental site conditions for both growing periods, while some others changed their flushing behaviour either to earlier (e.g. 24 Świebodzin 1) or to later bud burst (e.g. 27 Pniewy) from one season to another (Table 1). These unstable provenances however have no effect on the strong linear relationship of FLUSH between both years. Flushing stage was also correlated with LAT (negatively) and with LONG (Fig. 2; Table 3). Relationship of flushing with ALT is not linear and shows a similar pattern in both seasons but only at the age of 5 it is significant (P=0.0382; Fig. 2).

Similarly to FLUSH the greater are the CESS values the earlier trees stop their growth in autumn. This average trait fluctuates from 6.19 (37 Leżajsk) to 7.34 (38 Zdroje) at the end of $5^{\rm th}$ growing period and from 4.56 (23 Krucz) to 5.97 (41 Lesko) at the $9^{\rm th}$ but differences between provenances were significant only in the second term (Table~2). CESS is weakly correlated between the two years since there were changes in rank of early and late ceasing growth provenaces between these years. A close correlation of CESS with LAT, LONG and ALT was observed only at age of 9 (Fig.~3). It is also strongly correlated with FLUSH (Table~3) which means that trees from earlier flushing provenances also ceased growth early.

Multiple regressions of FLUSH 9 and CESS 9 with LAT, LONG and ALT are significant (R^2 =0.30; P=0.0106 and R^2 =0.40; P=0.0011, respectively):

FLUSH
$$9 = 3.64 - 0.05 \text{ LAT} + 0.06 \text{ LONG} - 0.0003 \text{ ALT}$$
 (2)

CESS
$$9 = 2.03 + 0.03 \text{ LAT} + 0.07 \text{ LONG} + 0.0005 \text{ ALT}$$
 (3)

LONG was the most important parameter for prediction of both traits (P=0.0116 and P=0.0099, respectively).

Since FLUSH and CESS are strongly related in 2001, provenances were grouped basing on both of them with Ward's minimum variance method. Other method (centroid) gave almost the same results except for provenance 12 Świebodzin. Provenances were divided into two groups (Fig. 1). The group of early flushing and early completing growth populations con-

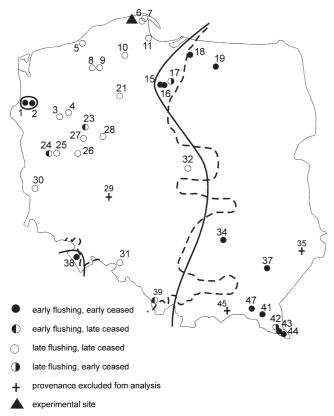


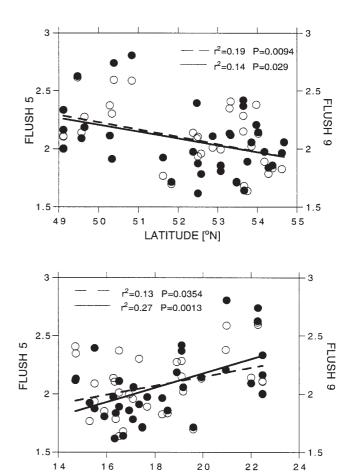
Figure 1. – Beech provenances growing in the Choczewo experimental area (triangle). See Table 1 for details. Dashed line shows the January isotherm –3°C (Wiszniewski, 1973). Solid line shows division between provenances which have different phenological behaviour.

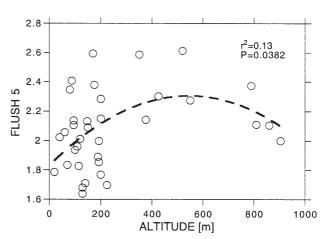
tains mainly those from eastern and south-eastern Poland. However in this group are also populations from the most western part of the country.

FLUSH 9 and CESS 9 show a strong positive relationship with survival rate and weaker with height growth (data not presented) in the experimental conditions. These correlations imply that in Choczewo, time of budburst and growth cessation may have an influence on survival and growth performance of beech.

Discussion

The origin of beech populations grown in Choczewo affected their flushing and autumnal leaf discoloration. Longitude had the most important influence in our investigation. This is visible from the significance of this parameter in multiple regression equations (2 and 3). However, LAT and ALT of provenances taken separately also have an influence on both flushing and growth cessation. Thus earlier flushing and earlier ceasing growth populations came from eastern Poland (Fig. 1) and also those from more southern provenances flushed and ceased growth early. These findings correspond well with results obtained in trials with the same provenances grown in central and southern Poland (SABOR et al., 1999; SABOR and ŻUCHOWSKA, 1999; TARASIUK et al. 1998) and with other beech provenances from Poland (RZEŹNIK, 1976) but they are contrary to evidence of earlier flushing of nothern beech populations in Italy (FALUSI and CALAMASSI, 1996). Stability of flushing throughout different evironments shows that this feature is under strong genetical control as was also claimed before (Teissier du Cros et al., 1988; Giertych, 1990). Elevational





LONGITUDE [°E]

Figure 2. – Geographical effects on flushing stage for beech provenances in the Choczewo experimental site. Open symbols and dashed lines reffer to $5^{\rm th}$ growing period, closed symbols and solid lines reffer to $9^{\rm th}$ growing period.

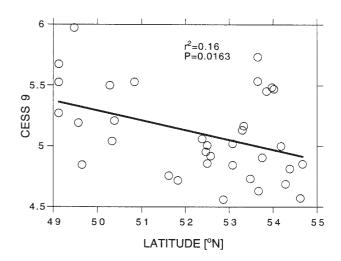
effect on the spring phenology of beech in Choczewo is not linear, implying that the earliest bud-bursting provenances are from the uplands in south-eastern Poland while those from the highest altitudes flushed slightly later. This trend existed in both years but in the second term it was not significant. Further observations are needed to find out whether this altitudinal effect on beech flushing is stable. Many other

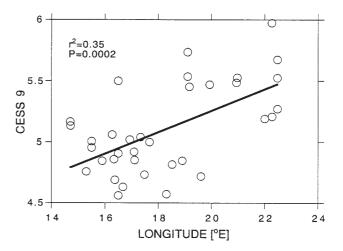
authors have also found a relationship of beech flushing with altitude but not consistently (Muhs, 1985; Teissier du Cross et al., 1988; von Wuehlisch et al., 1995; Falusi and Calamassi, 1996). Correlation of CESS with ALT is more distinct than for FLUSH in this experiment, with populations from lower elevations ceasing growth later (Fig. 3), though this effect was not broadly discussed in the literature.

However, strict separation of geographical effects in this experiment is difficult, because maternal stands from the eastern part of country tend to be also located in the south and at higher elevations. Grouping of provenances with respect to spring and autumn phenology shows a strong longitudinal pattern. The division line between early flushing, early ceasing growth provenances and late flushing, late ceasing growth ones corresponds well with the January isotherm -3°C (Wiszniew-SKI, 1973) (Fig. 1). Only two beech provenances from Gryfino (1 and 2) are outside of this range. Maybe they are not native to their sites and were introduced there from other locations. Such grouping suggests that beech from eastern provenances has lower requirement for temperature sum than that from the north-western part of the country. This phenomenon seems to be the same as found by VON WUEHLISCH et al. (1995). They examined samples from 158 beech stands from most parts of Europe and concluded that with increasing longitude and altitude, and decreasing latitude beech provenances have lower heat demands for bud-burst, however longitude had the strongest effect. In view of our results it is obvious that this response can also be found in beech provenances from a much less extended area. The territory of Poland lies in the transitive zone between a maritime climate in the west and a continental one in the east. The earlier start of growth and its earlier completion in populations from eastern Poland may reflect their adaptation to continental conditions with shorter intermediate seasons (spring and autumn).

Weather conditions in the consecutive years influenced a change in the autumn behaviour of beech provenances. Figure 4 shows Gaussen – Walter's climadiagrams (WALTER and LEITH, 1960) for both growing seasons for the weather station Leba, the nearest to the experimental site. The monthly mean temperatures and the sums of monthly precipitation are presented in the scale 1:2. If the line of precipitation goes below the line of temperature, as was in midsummer 1997 (Fig. 4), this indicates a drought period. That water shortage probably caused earlier growth cessation in this year which is reflected in lack of significant differences among provenances in CESS 5 and lack of correlation of FLUSH 5 and CESS 5 (Table 2 and 3).

In this trial we found that earlier flushing and earlier ceasing growth provenances have better survival and higher trees (data not presented). If this tendency lasts in the future, it will imply that for the Choczewo environmental conditions selection of beech for late flushing is not appropriate. Early flushers took advantage from the less frequent occurence of late frosts in the mild, maritime climate and grew faster than those which flushed later and prolonged their growing season. PAULE (1982) also found that in beech provenances from Slovakia most height growth takes place in the spring (until June 15th). We could expect even greater profits from early budbursting trees growing under stand shelter where young trees are protected from late frosts as is usual in forestry practice. Also earlier growth cessation of eastern provenances may be to their advantage. They are adapted to earlier start of winter in a more continental climate, as was stated above, and early end of the growing season allows them to avoid the early autumn frosts.





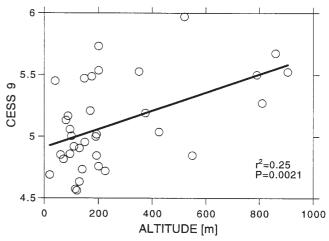
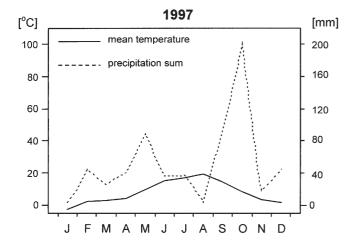


Figure 3. – Geographical effects on growth cessation stage for beech provenances in the $9^{\rm th}$ growing period.

The observed differences in spring and autumn phenology between beech provenances grown in Choczewo confirm an ecotypical variation of these traits. However distinction between montane and lowland beech ecotypes proposed earlier by RZEŹNIK (1976) should be verified, especially regarding populations from 15–17 Kwidzyn, 18 Młynary and 19 Wipsowo (see Table 1 and Fig. 1).



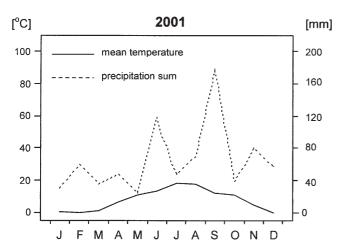


Figure 4. — Climadiagrams for the Leba weather station in 1997 and 2001. Left axis shows the monthly mean temperature and right shows monthly sum of precipitation. In 1997 there is drought period when dotted line goes under the solid line in midsummer.

Table 2. – Population effects in analysis of variance. See text for terms explanation.

Trait	d.f. (error d.f.)	MS	F	Prob > F
FLUSH 5	34 (105)	0.29	7.62	< 0.0001
FLUSH 9	34 (105)	0.31	3.92	< 0.0001
CESS 5	34 (105)	0.25	1.04	0.4244
CESS 9	34 (105)	0.48	2.60	0.0001

Further investigations on this trial are needed however to check the likely interaction of phenological traits with age and their influence on growth and qualitative traits of beech.

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 $\begin{tabular}{lll} \it Table 3. - Pearson's correlation coefficients and P values (below), \\ N = 35. Bold values are statistically significant. See text for terms explanation. \\ \end{tabular}$

	FLUSH 9	CESS 5	CESS 9	LAT	LONG	ALT
FLUSH 5	0.78 0.0000	0.21 0.2347	0.68 0.0000	-0.43 0.0094	0.36 0.0354	0.29 0.0891
FLUSH9		0.22 0.2017	0.69 0.0000	-0.37 0.0290	0.52 0.0013	0.29 0.0870
CESS 5			0.39 0.0198	-0.11 0.5170	0.16 0.3449	0.31 0.0719
CESS 9				-0.40 0.0163	0.60 0.0002	0.50 0.0021

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