Phenology differs among Norway spruce populations in relation to local variation in altitude of maternal stands in the Beskidy Mountains

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Abstract. An investigation of phenological and growth traits was conducted in a lowland planta-tion, comprised of 23 Norway spruce (*Picea abies* (L.) Karst.) seed stands from the Istebna region in the Beskidy Mountains of Poland. Significant differences were found among population in growth initiation, growth termination and the length of shoot elongation period. The two latter traits were highly correlated and were attributed to the altitude of the maternal stand. The tested populations were grouped based on phenology. Progeny of lower-alttitude stands ceased growth later, had a longer duration of shoot growth and greater current leader length compared to progeny of higher-altitude stands. Individual populations, however, did not differ in current-year growth and total tree height, implying higher within-population variation in growth traits than in phenology. The similar growth capacity of all tested populations suggests considerable gene flow between maternal stands, although differences in phenology imply the adaptation of progenies to the altitudinal environment of seed origin. These results suggest that within tested populations, selection is possible based on phenology alone, without considerable reduction of early height growth; final decisions, however, should be based on the environmental conditions of the planting site.

Introduction

As an economically important tree species, Norway spruce (*Picea abies* (L.) Karst.) is grown in many European countries. In Poland, regeneration of this species is largely accomplished by planting, and most seeds used for seedling production are collected in seed stands. An increased demand for timber products requires an intensification of forest production. Consequently, there is an increasing need to identify the best sources of planting material, suitable for growing in a broad spectrum of environmental conditions.

Norway spruce has been widely tested in many provenance experiments; hence, its diversity at the species level is relatively well known. Norway spruce exhibits clinal variation in most adaptive traits reflecting latitudinal or altitu-dinal changes in environmental conditions. Populations from high latitudes and/or high elevations, growing in common-garden experiments show earlier growth initiation (Ekberg et al. 1985; Skrøppa and Magnussen 1993; Danus-evičius and Persson 1998; Hannerz 1998), earlier growth cessation, a shorter

period of shoot elongation (Eriksson et al. 1978; Holzer 1993; Modrzyński 1995; Hannerz and Westin 2000) and a reduced frequency of Lammas growth (Ekberg et al. 1991, Holzer 1993). High-elevation populations also exhibit lower growth capacities, so their height and diameter increments are usually smaller than lowland seed sources (e.g. Modrzyński 1995; Oleksyn et al. 1998, Hannerz and Westin 2000). Trait variation associated with longitude of seed source origin is also observed in that eastern provenances cease growth earlier than western ones (Hannerz 1998). However, not all variation seems to be clinal in Norway spruce. Lagencrantz and Ryman (1990) concluded that genetic variation, correlated with variation in some morphological traits, reflects the history of postglacial migration of the species. Much within-population variation in the above-mentioned traits has been reported (Skrøppa 1991; Ekberg et al. 1994), thus selection for growth phenology is possible in this species.

The Carpathian Mountains are a region of origin of many valuable Norway spruce provenances (Krutzsch 1974; Giertych 1976, 1998; Vinš and Vančura 1979; Balut and Sabor 1993). Several Polish populations from the Beskidy Mts, especially stands from the Istebna and Wisla vicinity, have proven their high genetic quality in many national and international common-garden experiments (Giertych 1984; Rau et al. 1998; Barzdajn and Kowalkowski 2001; Matras 2002). However, not all populations from this region are equally good and suitable for all environments with regard to height growth (Giertych 1978, 1984) and volume production (Lundgren and Persson 2002). This variability might be a consequence of numerous introductions of non-native planting material during forest regeneration in the past.

Comparative results obtained in different growth environments imply that there might be a considerable differentiation in phenological traits and adaptability among populations that originate in the Beskidy Mts. the Istebna spruce flushed later than other Polish provenances, but those from Wisla flushed earlier (Giertych 1972). Trees of both provenances, however, were intermediate (Sabor 1984) or late (Giertych 1984) in flushing among provenances from the whole European range of the species. Those results might also depend on the choice of particular maternal stands and their progeny represented in the experiments. Thus, there is a need to investigate causes and consequences of variability existing in Norway spruce from this area.

Regeneration success is tightly linked with the use of proper planting material adapted to local environmental conditions in terms of developmental phenology. Planting early-flushing genetic entries on frost prone sites is frequently a reason of regeneration failure. Seedlings in the bud-burst stage are particularly vulnerable to injuries caused by late spring frosts (Danusevičius and Persson 1998; Hannerz et al. 1999) and their growth is greatly reduced, especially in response to injuries occurring throughout several consecutive years (Langvall et al. 2001). Therefore, recognizing the seed sources exhibiting suitable phenological rhythm and maintaining high growth capacity is critical.

The objective of this study was to examine differences in phenology and growth traits and their determinants among Norway spruce populations from

Istebna region in Beskidy Mountains. More precisely the research questions were: (i) are there differences in height growth, its dynamics and phenology among the tested populations?; (ii) if there is variation among populations originating from the limited geographical area, what might be its possible cause?; (iii) is it possible to identify Norway spruce populations exhibiting superior growth characteristics and phenological rhythm suitable for regeneration on sites of frequent late frost occurrence?

Materials and methods

Open pollinated seeds were collected from twenty-three seed stands, hereafter referred to as populations, from the Wisla Forest District in the Beskidy Mountains. The stands are permanent seed stands selected by the Forest Service, based on their superior phenotypic traits. The area of origin of populations lies between 49° 30′ and 49° 40′ N and 18°50′ and 19°00′ E encompassing an area approximately 18 km latitudinally and 12 km longitudinally. The maternal stands occupy an altitudinal range of 260 m from 540 to 800 m a.s.l.

The experimental site was located in the ''Zwierzyniec'' Experimental Forest near Kórnik in midwestern Poland (52°15′ N,17°04′ E, 70 m a.s.l). Historically, Norway spruce did not naturally occur on this area (Boratyńska 1998), but is commonly planted. The experiment was established in 1995 in three randomized complete blocks using 2-year-old seedlings. Each block contains all populations planted in 49-tree plots (14×14 m) at 2 m×2 m spacing. Block 1 was located separately from the other two and was established on abandoned agricultural land. Blocks 2 and 3 are located together on the size of a former poplar stand. Mean survival at age 8 in the experiment was above 70% and varied from 56 to 86% among populations. Natural mortality occurred in earlier stages after planting and no new dead trees were recorded during the study period; however, the causes of early mortality were not studied.

During the 8th annual growth period, the current height increment of the terminal leader was measured weekly with 1 mm accuracy. The first measurement was made on April 20, 2000 starting with a measurement of the length of the dormant bud. Subsequent measurements were obtained weekly on 11 to 18 trees per populations (3 to 7 trees in the middle row of a plot) up to the end of active growth, when the difference between consecutive measurements was less than 2 mm. Only the first flush was examined (frequency of lammas growth was very low). In total 346 trees were measured. At the end of growing season (October 2000), the total height of all trees was measured.

Individual tree data were fitted with the Richards function using statistical software (JMP Version 4.0 SAS Institute Inc., Cary, NC, USA). Data fitted with this model are more biologically meaningful than those fitted with polynomial exponentials, especially with respect to derived functions (Venus and Causton 1979). The formula of the function (Hunt 1982) was:

$$L = a(1 + e^{(b-cx)})^{-1/d}, \tag{1}$$

where L is the leader length, a is a maximum length, b, c and d are estimated parameters, and x is the day of year.

The fitted Richards functions described the data reasonably well with all values of $r^2 > 0.990$, thus they were considered to be highly reliable for derivation of following traits:

DAY5 – the number of days (from the beginning of the year) to complete 5% of the final leader length as an indication of growth initiation,
DAY95 – the number of days to complete 95% of the final leader as an indication of growth cessation,
GPL – the length of the shoot growth period in days, calculated as (DAY95 – DAY5),
TLH – total leader height.

Mean absolute growth rate (G; cm day^{-1}) over the whole growth period was calculated using parameters derived from a fitted Richards function as $ac/[2(d + 2)]$ (Hunt 1982).

The temperature sum (degree days) to bud burst was calculated as the sum of accumulated daily mean temperature above a 5 °C base from January 1st. Air temperature was recorded in the weather station in Kórnik, about 2 km away from experimental site and daily mean temperatures were calculated as:

$$T_{mean} = (T_{min} + T_{max} + T_{7am} + T_{7pm})/4, \tag{2}$$

where T_{min} – minimum temperature, T_{max} – maximum temperature, T_{7am} – temperature at 7 a.m., T_{7pm} – temperature at 7 p.m.

Statistical analysis

For all examined traits, an analysis of variance was conducted on the plot means according to the model:

$$Y_{ij} = \mu + a_i + b_j + e_{ij}, \tag{3}$$

where Y_{ij} is a plot mean, μ is a overall mean, a_i is the random effect of ith population, $i = (1, ..., 23)$, b_j is a fixed effect of jth block, $j = (1, 2, 3)$ and e_{ij} is the residual. The EMS (expected mean squares) method for random effects was used.

To analyze bivariate trait relationships and trait relationships to altitude, a correlation analysis was performed on the population means. Based on traits accounting for most of the between-population variation (DAY5, DAY95 and GPL), populations were clustered using hierarchical Ward's minimum variance method. This method combines clusters so that the within-group increase in sum of squares is minimized for a given connection of clusters (Everitt 1980).

For each cluster the mean Richards growth function was computed and mean values of all traits for groups were compared using Tukey–Kramer HSD test.

Results

The Norway spruce population differed significantly in shoot growth phenology, including day of growth initiation (DAY5), growth cessation (DAY95) and length of growth period (GPL) (Table 1). The populations differed in their height growth patterns with mean GPL ranging from 43 to 63 days. On average, the trees started growth on May 10th (day 131) with population means ranging from day 120 to 136. The mean date of growth cessation was July 3rd (day 185), and population means fell within a 20-day-period (from day 174 to 194). Mean values of traits for each population are presented in Table 2.

The date of growth initiation (DAY5) was highly positively correlated with date of growth cessation (DAY95; Table 3), indicating that populations that began growth earlier also tended to stop growth earlier. The length of the growth period (GPL) was positively correlated with DAY95, but was not correlated with growth initiation (DAY5, Table 3). GPL and DAY95 each showed strong positive correlations with final leader height (TLH, Table 3).

Mean growth rate (G) was quite uniform among populations and ranged only from 0.7 to 1 cm day^{-1}. All phenological traits were weakly correlated with growth rate, but TLH was strongly related to this trait (Table 3).

Both DAY95 and GPL were negatively correlated with the altitude of seed origin (ALT), indicating that spruce populations from lower elevations had a longer growth period, which extended later in the summer. The correlation between TLH and ALT was weaker but still statistically significant, whereas ALT was unrelated to DAY5, growth rate (G) and final tree height (H) (Table 3) and survival (data not shown).

Although the tested Norway spruce populations differed in phenology, there were no significant differences in a current-year leader growth (TLH) and total tree height (H), based on plot means. Mean tree height for the experiment was 207 cm and means varied from 165.3 to 239.1 cm among seed sources.

Table 1. Analysis of variance F and p (below) values for phenologic and growth traits of 23 populations of Norway spruce in a plantation trial in western Poland.

Source of variation	Day of growth initiation (DAY5)	Day of growth cessation (DAY95)	Growth period length (GPL)	Total leader height (TLH)	Absolute growth rate (G)	Tree height (H)
Block	2.77	17.00	15.33	41.25	36.97	137.69
	0.0736	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Population	4.58	3.72	2.25	0.91	0.88	1.30
	< 0.0001	0.0001	0.0109	0.5880	0.6199	0.2235

d.f. – degrees of freedom for blocks = 2, populations = 22, and error = 4.

Table 2. Mean values and standard errors (in brackets) for phenologic and growth traits of 23 populations of Norway spruce grown in a common-garden experiment.

Group	Population	ALT [m] a.s.l	Total leader initiation [cm]	Day of growth initiation (DAY5)	Day of growth cessation (DAY95)	Growth period length [days]	Absolute growth rate [cm day^{-1}]
1	31	630	36.27(4.71)	130(2.39)	181(4.90)	51(3.64)	0.744(0.07)
1	35	660	52.27(6.02)	133(1.79)	186(3.18)	53(2.48)	0.992(0.08)
1	5	700	43.58(4.09)	132(2.13)	182(4.15)	49(3.00)	0.880(0.06)
1	7	740	48.08(4.36)	136(1.71)	186(3.54)	50(2.96)	0.997(0.07)
1	10	800	38.43(3.43)	134(1.83)	177(2.84)	43(2.24)	0.943(0.04)
Mean			43.73 b	133 a	182 b	49 c	0.911 a
2	12	540	60.35(6.67)	131(2.36)	192(4.72)	61(2.95)	0.982(0.08)
2	11	560	54.19(5.09)	134(2.33)	193(3.82)	59(2.17)	0.904(0.07)
2	15	580	53.69(5.70)	136(1.36)	191(3.52)	55(2.84)	0.958(0.06)
2	34	595	42.83(5.53)	129(2.17)	186(3.76)	57(3.07)	0.751(0.07)
2	13	630	52.13(7.77)	136(2.25)	193(5.56)	57(4.21)	0.912(0.08)
2	29	630	50.97(6.99)	131(2.14)	187(4.19)	56(3.50)	0.890(0.08)
2	39	640	61.50(7.10)	127(2.50)	189(5.43)	63(3.26)	0.973(0.10)
2	40	640	51.02(4.31)	134(2.19)	194(4.48)	60(3.01)	0.839(0.05)
2	36	650	56.56(7.42)	135(1.18)	192(4.10)	57(3.56)	0.945(0.09)
2	16	660	53.91(4.00)	131(2.24)	187(3.53)	56(2.51)	0.991(0.05)
2	9	670	51.26(6.42)	133(2.01)	191(3.77)	58(2.86)	0.872(0.08)
2	17	720	55.20(4.36)	133(2.32)	189(4.09)	56(3.55)	0.997(0.06)
Mean			53.63 a	132 a	190 a	58 a	0.918 a
3	32	630	45.86(3.60)	128(2.00)	180(2.95)	52(1.85)	0.901(0.07)
3	38	650	43.37(6.53)	120(2.19)	174(3.32)	54(2.15)	0.813(0.09)
3	8	700	52.13(4.99)	126(1.97)	178(2.52)	52(1.67)	0.998(0.08)
3	41	750	48.92(4.90)	124(2.40)	177(3.40)	53(2.00)	0.930(0.06)
3	6	760	47.14(4.12)	123(1.41)	176(2.54)	53(2.06)	0.898(0.06)
3	18	760	40.20(5.19)	129(2.91)	183(4.83)	54(3.22)	0.750(0.07)
Mean			46.27 b	125 b	178 b	53 b	0.882 a
Overall mean			49.56	131	185	55	0.907

Groups are based on cluster analysis; groups designated with the same letter are not different at α = 0.05 level (Tukey–Kamer test). Populations within groups are ordered by altitude (ALT).

The grouping of the population was based on DAY5, DAY95 and GPL, which accounted for most differences between populations. The three cluster groups of populations differed significantly in all traits, except *G* and *H* (Table 2). Interestingly, a comparison of group means revealed a significance of differences in total leader height (TLH; Table 2), while among populations differences in this trait were not significant. Despite those differences, the group ranges overlapped considerably in TLH as did their maternal stand elevations.

In contrast, variation among groups in phenological traits was smaller than between individual populations, but group differences were still statistically significant and groups did not overlap to such an extent as in the other traits (Table 2). Growth patterns differed among the groups with mean DAY95

Table 3. Pearson's correlation coefficients between growth and phenologic traits among 23 Norway spruce provenances and their *p* values (below).

	Day of growth cessation (DAY95)	Growth period length (GPL)	Total leader height (TLH)	Absolute growth rate (G)	Tree height (H)	Altitude (ALT)
Day of growth Initiation (DAY5)	**0.72** 0.0001	0.01 0.9602	0.22 0.3195	0.27 0.2140	0.20 0.3512	− 0.20 0.3664
Day of growth Cessation (DAY95)		**0.71** 0.0002	**0.66** 0.0006	0.20 0.3531	**0.43** 0.0397	**−0.59** 0.0030
Growth period Length (GPL)			**0.72** 0.0001	0.02 0.9382	0.41 0.0509	**−0.65** 0.0009
Total leader Height (TLH)				**0.69** 0.0003	**0.43** 0.0387	**−0.43** 0.0392
Absolute growth Rate (G)					0.16 0.4550	0.07 0.7428
Tree height (H)						−0.28 0.1961

Bold values are significant at the $\alpha = 0.05$ level or lower.

varying more (12 days) than mean DAY5 (8 days). The fastest-growing trees (group no. 2) flushed on average only one day earlier than the group of slower-growing ones (group no. 1), but had significantly later growth cessation and a longer growth period than both other groups.

Discussion

Considerable variation in phenological traits was found among populations of Norway spruce of the Istebna provenance from the Beskidy Mts. in Poland. The positive correlation between DAY5 and DAY95 indicates that populations that begin growth earlier also tend to cease growth earlier. This result is in accordance with the findings of Ekberg et al. (1985, 1994), but contrary to those of Skrøppa and Magnussen (1993). Changes in the length of the growth period was more related to the termination of shoot growth that to growth initiation, as indicated by the strong positive correlation between DAY95 and GPL. This finding confirms those reported earlier by von Wuehlisch and Muhs (1987, 1991), Ununger et al. (1988), and Hannerz (1998).

Both growth cessation and growth period length were highly dependent on the altitude of seed origin, indicating adaptation of the tested populations to the environment of the maternal stands. Progeny of higher-altitude populations terminated growth earlier and had a shorter period of leader growth than populations from lower elevations, which is a similar pattern to that described earlier by Skrøppa and Magnussen (1993), and Modrzyński (1995). However, contrary to the results reported by Modrzyński (1995), but in accordance with

those by Skrøppa and Magnussen (1993), a higher elevation of the maternal stand did not promote earlier growth initiation in the present study.

Trees which ended height growth later in the season, also tended to have a longer growing period and longer leader shoot than those ending growth early. Surprisingly, despite the positive correlation between leader length and these phenological traits, the differences among populations in final leader length were not significant, probably as a result of higher within-population variation in growth than in phenology.

A strong control of the duration of the growth period on final leader length was confirmed by the fact that growth rate did not vary among populations. Skrøppa and Magnussen (1993) found that growth capacity at the population level in Norway spruce was attributed mainly to growth duration, whereas within populations growth was equally related to growth duration and growth rate. In contrast, Ununger et al. (1988) and Ekberg et al. (1994) claimed that growth rate accounted for differences in leader length more so than did shoot growth duration. In this study, however, growth rate was not a significant factor and differences in growth pattern seem to be linked to phenology.

Clustering of populations based on phenological traits revealed the existence of three groups. Interestingly, the groups differed not only in phenology, but also in total leader height, whereas individual populations did not. One possible explanation of this discrepancy is that ANOVA was performed on the plot mean values, whereas cluster analysis was conducted on the population means. Thus, in the case of cluster analysis, within-cluster variation was reduced compared to within-population variation. Consequently, differences in growth traits among groups are probably less reliable than differences among individual populations. However, the groups were distinct with regard to phenology, which confirms that the tested populations differ considerably in those traits. Thus, the distinguished groups should have practical use in identifying populations exhibiting particular phenological traits.

The use of proper planting material, which exhibits phenology adjusted to local environment, is one of the most important factors determining regeneration success, because plants can fully exploit favorable conditions for growth both at the beginning and at the end of the growing season. Late frosts occurring during bud-burst may injure newly developing shoots, which might reduce growth or, in severe causes, kill trees. Such damage can be avoided by the use of late-flushing trees (Hannerz et al. 1999), but the probability of occurrence of frost-related damages should be assessed for individual sites. If the goal is to find late flushing populations that avoid spring frost injury, the approach and findings here provide a basis for choosing appropriate populations.

To predict spring frost injury risk for a particular seed source, Hannerz (1999) recommends using accumulated heat sum (degree days) rather than day of year. For the populations in this experiment, the mean heat sum for bud-burst was 352 degree-days and ranged from 236 to 413 among seed sources. These values are higher than those reported by Hannerz (1999) and Langvall et al. (2001) and reflect the criterion used to rate bud-burst. In those studies,

bud-burst was defined as stage 3 of the Krutzsch index (emergence of needle tips, Krutzsch 1973), whereas DAY5, regarded as bud-burst in this experiment, was comparable to stage 5 or 6 of the Krutzsch scale (first spread of needles – "painter's brush" or shoot elongation, respectively). However, even if tested populations seem to be late flushing, the risk of frost injury depends on the probability of occurrence of frost events after bud burst at the particular site.

According to Hannerz et al. (1999), at the family level in Norway spruce, selection of only the latest flushing families was less effective, with regard to height response and frost damage reduction, than selection based on phenology and growth traits together. In contrast, it seems that in the environmental conditions of our experimental site, selection might be based on phenology alone, without significant reduction of height growth in selected progenies. Based on the above-mentioned recommendations, selection should be made within group 2, if there is also risk of early frosts in fall, or within group 1, though the latter group has slightly poorer height growth performance. However, the climatic conditions at this test location did not permit discrimination of frost-susceptible populations from resistant ones as might be expected on sites prone to late spring or early fall frosts. Therefore these results cannot be generalized to other environments.

In a limited geographic area of origin, such as presented here, one might expect considerable gene flow between populations. It seems to be the case in terms of growth capacity, which was not significantly different among examined populations of Norway spruce from within the Istebna region in the Beskidy Mts in Poland. In contrast, even in that geographically confined area, phenology differed considerably among populations in relation to the elevation of seed source. This finding confirms that adaptation of progenies to the altitudinal environment of origin has a larger influence on phenology than on grow capacity. Elevational climate gradients are similar to the changes in climatic conditions occurring in lowland areas with increasing latitude. Plants exhibit adaptation to both gradients in a similar way, but the spatial scale is usually much smaller in the case of altitude. The results presented here confirm the importance of the influence of the maternal environment during sexual reproduction on the phenological performance of progeny, reported earlier for Norway spruce (see Johnsen and Skøppa 1997 for review).

The obvious constraint of this investigation, making more general conclusions impossible, is its restriction to one experimental site and one year only. Rankings of populations and their stability throughout time need further investigation. The examination of performance in other, especially frost prone sites also will help to clarify the present conclusions.

Acknowledgements

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