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Flowering and cone bearing of *Picea abies* grafts in second-generation seed orchards

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Abstract: In 2004, abundant flowering of Norway spruce (*Picea abies* (L.) Karst.) was observed in two second-generation seed orchards: (1) 'Outbreeding', promoting crossing between clones of five geographically distant populations; and (2) 'Kolonowskie', restoring a population whose offspring exists only in an international experiment (IUFRO 1964/1968). In both seed orchards, female strobili were produced by 91.3% and 91.7% of clones, represented by 64.1% and 55.5% of grafts, respectively, and statistically significant differences between clones were found in the number of mature cones. In the case of the seed orchard 'Outbreeding', the number of mature cones in individual clones was significantly correlated with latitude of the origin of maternal populations ($r = 0.8826$, $p = 0.0470$). The majority (95%) of cones in seed orchards 'Outbreeding' and 'Kolonowskie' were produced by only 28.2% and 38.5% of all clones, and 21.4% and 25.7% of all grafts, respectively. These data attest to a disparity between the level of genetic diversity in seed orchard progeny resulting from the observed numbers of cone-bearing clones and grafts and the genetic diversity expected from the actual participation of clones and grafts in seed orchard composition. The estimated seed production per 1 ha of seed orchard area in 2004 reached 21.05 kg for 'Outbreeding' and 21.72 kg for 'Kolonowskie'.

Additional key words: Norway spruce, cone yield, seed production

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Introduction

The main objective of second-generation seed orchards is to produce seeds of higher genetic quality, as compared to the maternal populations (Giertych 1997). Such seed orchards are established by means of vegetative propagation of plus trees, selected on the basis of collected information on the genetic value of their offspring. Thus the selected trees transmit to their offspring some desirable traits, which have a genetic background and are only minimally affected by the environment (Chałupka 2003).

In the Experimental Forest 'Zwierzyniec' (N52°14' E17°04'), owned by the Institute of Dendrology, Polish Academy of Sciences, Kórnik, the oldest Polish second-generation seed orchards of Norway spruce (*Picea abies* Karst.) were established in 1981. The one called 'Outbreeding' includes five geographically distant spruce populations, selected from a group of 1100 provenances from all parts of Europe, participating in the international IUFRO 1964/1968 experiment (Table 1). In an evaluation of results of these experiments, which was carried out in 1976, these five populations proved to be the most plastic, as they proved to be the best in various countries in terms of both growth traits and adaptability (Giertych 1978). On the basis of assessments of individual trees in an IUFRO 1964/1968 experimental area in Poland (Experimental Forest in Krynica, owned by the Forestry Faculty, Agricultural Academy, Kraków, Poland), a group of the best trees was selected in each of the populations. From the selected trees, scions were taken for grafting, to create the clonal second-generation seed orchard called 'Outbreeding'. Numbers of clones and grafts from each population are given in Table 1. This seed orchard was aimed to produce a highly genetically diverse offspring of geographically distant populations distinguished by high adaptability (Giertych 1993, 1999).

Another second-generation seed orchard ('Kolonowskie') was created to restore the highly valuable population Kolonowskie IUFRO 0293, which no longer exists in the wild. Seeds from the original Kolonowskie population were collected for the IUFRO 1964/1968 experiment. The offspring of that population developed from those seeds proved to have the highest breeding value among the 1100 progeny populations compared during the experiment mentioned above (Giertych 1978). Thanks to international scientific cooperation, vegetative plant materials in the form of scions were collected in 11 countries in 1979, where IUFRO 1964/1968 experimental plantations were located. From the grafted scions, a restitution seed orchard was created. It includes 109 spruce clones of the population Kolonowskie, deriving from maternal trees selected on 14 research plots located in 11 countries (Table 2) (Giertych 1993, 1999).

The aims of the study performed in 2004 were: (1) to analyse quantitatively the flowering abundance and cone production in those two seed orchards; (2) to assess the participation of individual clones in cone production; and (3) to compare the seed yield of the orchards.

Material and methods

Flowering abundance (i.e. production of young strobili) was analysed in both seed orchards in early May 2004. In this study, we used the term 'strobili' when referring to young generative structures, and the term 'cones' when referring to mature, seed-bearing cones. The abundance of female strobili on indi-

Table 1. Provenance of five populations of Norway spruce in the second–generation seed orchard 'Outbreeding' in the Experimental Forest 'Zwierzyniec' in Kórnik (updated in November 2004)

IUFRO no.	Population name	Geographic location			Clone symbols
		latitude	longitude	altitude [m]	
0253	Serwy	N 53°50'	E 23°02'	120	04–106 to 04–129
0266	Karnieszewice	N 53°20'	E 15°50'	150–200	04–150 to 04–170
0293	Kolonowskie	N 50°39'	E 18°23'	150–200	04–130 to 04–149
1045	Istebna 148–149	N 49°34'	E 18°51'	540	04–83 to 04–105
1062	Jasina	N 48°18'	E 24°20'	800–1000	04–171 to 04–189

Table 2. Origin of clones (i.e. scion collection sites) of Norway spruce population Kolonowskie (IUFRO no. 0293) in the second-generation restitution seed orchard 'Kolonowskie' in the Experimental Forest 'Zwierzyniec' in Kórnik (updated in November 2004)

Country	Location	Geographic location			Clone symbols
		latitude	longitude	altitude [m]	
Poland	Krynica	N 49°21'	E 20°58'	750	04–130 to 04–149
Canada	Bronson N.B.	N 46°11'	W 65°47'	70	22–01 to 22–04
France	Amance	N 48°47'	E 06°18'	240	24–01 to 24–09
Sweden	Lisjö	N 59°43'	E 16°05'	65	26–01 to 26–08
Sweden	Abild	N 59°56'	E 12°44'	60	26–09 to 26–18
Czech Rep.	Zahradka	N 49°38'	E 15°15'	390	27–01 to 27–04
Belgium	Herbeumont	N 49°48'	E 05°15'	410	29–01 to 29–03
Norway	Overud	N 60°10'	E 11°04'	200	31–01 to 31–07
Norway	Ilsvig	N 59°31'	E 05°49'	150	31–08 to 31–11
England	Salisbury	N 51°04'	W 01°47'	n.d.	34–01 to 34–15
Hungary	Mátrafüred	N 47°50'	E 19°55'	580	37–01 to 37–18
Ireland	Knocktopher	N 52°29'	W 07°13'	n.d.	38–01 to 38–22
Germany	Brüggen	N 51°14'	E 06°06'	40	39–01, –02, –07
Germany	Branscheid	N 50°30'	E 06°40'	620	39–03 to 39–06, –08, –09

n.d. = no data available

vidual grafts was assessed on a scale of 0–3 (0 ÷ no strobili; 1 ÷ 1–20 strobili; 2 ÷ 21–50 strobili; 3 ÷ more than 50 strobili). The abundance of male strobili was only roughly estimated on a scale of 0–2 (0 ÷ no strobili; 1 ÷ strobili present; 2 ÷ strobili abundant). In mid-November 2004, cones were collected in both seed orchards, and seeds of each graft (i.e. each tree) were extracted and weighed in January 2005. Cone production data were subjected to analysis of variance, and only clones represented by three or more ramets (i.e. grafts) were included into analysis. Because of the experimental design and uneven numbers of observations in individual sources of variation (provenances and/or origins, clones, grafts), the analysis was multivariate, hierarchical and nonorthogonal. Calculations were made according to the model developed by Giertych (1991) for nonorthogonal data (Table 3), using Hicks' (1973) method for estimation of expected mean squares. In the analysis we took into account the highest possible variability (individual variability between grafts as a component of variance for error).

Results and discussion

Flowering

Abundant flowering and cone production was observed in both studied seed orchards in 2004 (Tables 4–6), and also in other experimental plantations of Norway spruce in the experimental forest of the Institute of Dendrology in Kórnik. This confirmed the prognosis for Poland prepared at the Forestry Research Institute in Warsaw (Załęski and Kantorowicz 2004). The main factor that determines the flowering abundance of Norway spruce is the duration of direct solar irradiation in June in the preceding year, i.e. when the generative structures are initiated. Large numbers of strobili are initiated in this species if the

Table 3. Model of analysis of variance used in this study (after Giertych 1991)

Source of variation	DF	Expected mean square	F
Total	kpq–1		
Clones	r–1	$A = V_Q+qV_R$	A/D
Provenances (or Origins)	k–1	$B = V_Q+qV_P+pqV_K$	B/C
Clones in provenances (or in Origins)	k (p–1)	$C = V_Q+qV_P$	C/D
Error (grafts in clones in provenances or in origins)	kp (q–1)	$D = V_Q$	

r = no. of clones
k = no. of provenances (or origins)
p = no. of clones in provenances (or in origins)
q = no. of grafts in clones in provenances (or in origins)
V_R = variance of clones
V_K = variance of provenances (or origins)
V_P = variance of clones in provenances (or in origins)
V_Q = variance of grafts in clones in provenances (or in origins)
DF = degrees of freedom
F = test F

Table 4. Flowering abundance in the second-generation seed orchard 'Outbreeding' in Kórnik in 2004. Italics show percentages

Provenance	Total no. of clones in seed orchard	Total no. of grafts in seed orchard	Clones with strobili	Clones with cones	Grafts with strobili			Grafts with cones	Total no. of cones	Cones per graft	Cones per cone-bearing graft
					male	female	total				
Serwy	24	110	22	22	73	73	85	69	3942	35.8	57.1
	23.3	*24.5*	*91.7*	*91.7*	*66.4*	*66.4*	*77.3*	*62.7*			
Karnieszewice	21	104	19	17	55	60	68	39	2210	21.2	56.7
	20.4	*23.2*	*90.5*	*85.0*	*52.9*	*57.7*	*65.4*	*37.5*			
Kolonowskie	18	57	14	10	18	16	24	12	230	4.0	19.2
	17.5	*12.7*	*77.8*	*55.5*	*31.6*	*28.1*	*42.1*	*21.0*			
Istebna 148–149	21	86	20	12	37	37	48	23	733	8.5	31.9
	20.4	*19.2*	*95.2*	*57.1*	*43.0*	*43.0*	*55.8*	*26.7*			
Jasina	19	91	19	9	51	52	62	20	140	1.5	7.0
	18.4	*20.3*	*100*	*47.4*	*56.0*	*57.1*	*68.1*	*22.0*			
All	103	448	94	70	234	238	287	163	7255	16.2	44.5
	100	*100*	*91.3*	*68.0*	*52.2*	*53.1*	*64.1*	*36.4*			

Table 5. Flowering abundance in the second-generation seed orchard ‘Kolonowskie’ in Kórnik in 2004. Italics show percentages

Origin of scions		Total no. of clones in seed orchard	Total no. of grafts in seed orchard	Clones with strobili	Clones with cones	Grafts with strobili			Grafts with cones	Total no. of cones	Cones per graft	Cones per cone-bearing graft
Country	Locality					male	female	total				
Poland	Krynica	19	18	17	98	58	50	61	44	1110	11.3	25.2
		17.4	*94.7*	*89.5*	*18.8*	*59.2*	*51.0*	*62.2*	*44.9*			
Canada	Bronson N.B.	2	2	2	10	3	5	5	5	106	10.6	21.2
		1.8	*100*	*100*	*1.9*	*30.0*	*50.0*	*50.0*	*50.0*			
France	Amance	7	6	6	32	23	22	26	22	1369	42.8	62.2
		6.4	*85.7*	*85.7*	*6.1*	*71.9*	*68.7*	*81.2*	*68.7*			
Sweden	Lisjö	7	6	5	34	18	16	18	15	275	8.1	18.3
		6.4	*85.7*	*71.4*	*6.5*	*52.9*	*47.1*	*52.9*	*44.1*			
Sweden	Abild	7	6	6	38	16	12	17	11	344	9.0	31.3
		6.4	*85.7*	*85.7*	*7.3*	*42.1*	*31.6*	*44.7*	*29.0*			
Czech Rep.	Zahradka	3	3	1	13	6	5	7	2	13	1.0	6.5
		2.7	*100*	*33.3*	*2.5*	*46.1*	*38.5*	*53.8*	*15.4*			
Belgium	Herbeumant	3	2	1	10	2	2	2	1	3	0.3	3.0
		2.7	*66.7*	*33.3*	*1.9*	*20.0*	*20.0*	*20.0*	*10.0*			
Norway	Orerud	6	6	4	30	16	9	17	9	433	14.8	49.2
		5.5	*100*	*66.7*	*5.8*	*53.3*	*30.0*	*56.7*	*30.0*			
Norway	Iesråg	4	4	4	18	10	7	11	7	66	3.7	9.4
		3.7	*66.7*	*66.7*	*3.4*	*55.5*	*18.9*	*61.1*	*18.9*			
England	Salisbury	11	8	7	42	16	12	17	11	103	2.4	9.4
		10.1	*72.7*	*63.6*	*8.1*	*38.1*	*28.6*	*40.5*	*26.2*			
Hungary	Mátrafüred	17	16	12	82	26	29	32	24	2332	28.6	97.6
		15.6	*94.1*	*70.6*	*15.7*	*31.7*	*35.4*	*39.0*	*29.3*			
Ireland	Knocktopher	15	15	14	73	43	40	49	36	1541	22.3	45.1
		13.8	*100*	*93.3*	*14.0*	*58.9*	*54.8*	*67.1*	*49.3*			
Germany	Brüggen	3	3	3	15	8	8	9	7	335	22.3	47.9
		2.7	*100*	*100*	*2.9*	*53.3*	*53.3*	*60.0*	*46.7*			
Germany	Brandscheid	5	5	4	26	16	14	18	13	680	26.1	52.3
		4.6	*100*	*80.0*	*5.0*	*61.5*	*53.8*	*69.2*	*50.0*			
All		109	521	100	86	261	231	289	207	8710	16.7	42.1
		100	*100*	*91.7*	*78.9*	*50.1*	*44.3*	*55.5*	*39.7*			

Table 6. Comparison of cone yield in second-generation seed orchards ‘Outbreeding’ and ‘Kolonowskie’ in Kórnik in 1993 and 2004. Italics show percentages

Seed orchard	Year	Total no. of clones	Clones with female strobili	Clones with cones	Total no. of grafts	Grafts with female strobili	Grafts with cones
Outbreeding	1993	104	101	98	497	271	262
		100	*97.1*	*94.2*	*100*	*54.5*	*52.7*
	2004	103	83	70	448	238	163
		100	*80.6*	*68.0*	*100*	*53.1*	*36.4*
Kolonowskie	1993	109	100	100	553	239	237
		100	*91.7*	*91.7*	*100*	*43.2*	*42.9*
	2004	109	93	86	521	231	207
		100	*85.3*	*78.9*	*100*	*44.3*	*39.7*

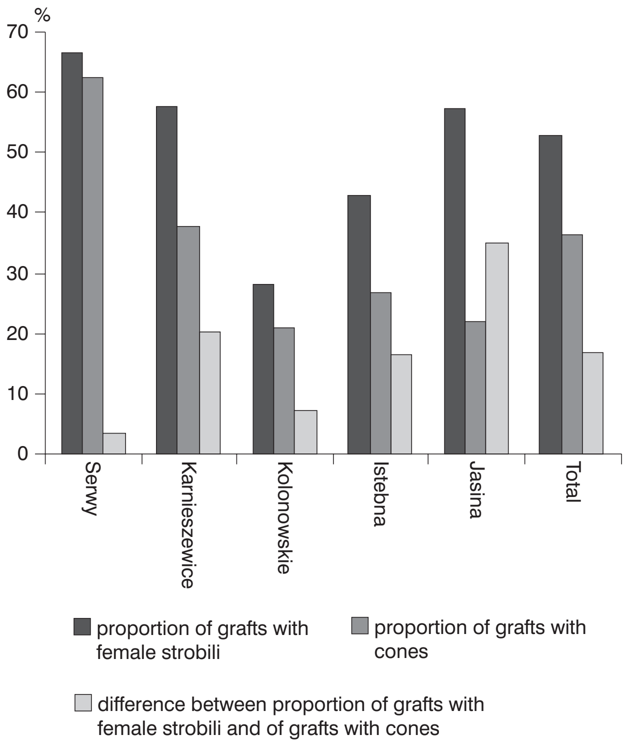

Fig. 1. Proportion of grafts with young female strobili and with mature cones (in relation to the total number of grafts) in the second-generation seed orchard 'Outbreeding' in Kórnik in 2004

mean daily duration of direct solar irradiation exceeds 9 hours (Chałupka 1975). In June 2003, its duration reached 10.4 hours, and this resulted in abundant flowering and cone production in Norway spruce in 2004. A similar phenomenon was observed in 1993, because the mean daily duration of direct solar irradiation in June 1992 reached 10.5 hours (Chałupka 1997).

Table 4 compares data on flowering of individual clones and grafts in the second-generation seed orchard 'Outbreeding'. Generally in that seed orchard, female and/or male strobili were formed by 91.3% of all clones and 64.1% of all grafts. The highest proportions of grafts with strobili were recorded in clones of both northern provenances: in Serwy 77.3% (29.6% of all flowering grafts), in Karnieszewice 65.4% (23.7% of all flowering grafts), and in the montane population Jasina 68.1% (21.6% of all flowering grafts). This situation is probably related to the previously reported favourable influence exerted on flowering and cone production in Norway spruce by the transfer of clones southwards from their place of origin (Koski 1987; Melchior 1987; Schmidtling 1987; Efimov 1993; Chałupka 1988) or from mountains to lowlands (Skrøppa and Tutturen 1985). This favourable effect seems to be due to improved climatic conditions.

A comparison of data on flowering of the second-generation seed orchard 'Kolonowskie' is presented in Table 5. In that orchard, we observed female and/or male strobili in 91.7% of all clones and 55.5% of all grafts. No significant correlation was found between flowering abundance and latitude of scion collection site (r = –0.265; p = 0.359). Thus it can be concluded that spruce trees growing for 10–15 years in varied environmental conditions did not acquire any traits affecting the flowering abundance and cone yield.

Cone production

Detailed data on cone production in the studied second-generation seed orchards are shown in Tables 4 and 5. The mean cone yield of Norway spruce in 2004 in Poland (34% of full bearing) was not as high as predicted (Załęski and Kantorowicz 2005). A comparison of cone production data for 1993 and 2004 shows also that the number of cone-bearing trees was markedly higher in 1993. Despite the younger age of the seed orchard at that time, cones were produced by more grafts in 1993 than in 2004 (Table 6). In both seed orchards, many female strobili were aborted in 2004, so the number of grafts with cones was markedly lower than the number of grafts that produced female strobili (Figs 1 and 2).

In the seed orchard 'Outbreeding', the proportion of grafts with cones declined by 16.7% (in relation to the total number of grafts), as compared with the proportion of grafts with female strobili during the spring assessment. Finally, cones matured on 36.4% of the total number of grafts and 68.0% of the total number of clones. Abortion of female strobili and their premature shedding might result from many factors. Sarvas (1962, 1968) suggested that the most important cause of this phenomenon is an insufficient amount of pollen. In the seed orchard design, pollen insufficiency was most likely in clones of the populations whose shoots developed earlier. This was confirmed in the seed orchard 'Outbreeding', as the greatest losses (35.1%) as compared with the proportion of flowering grafts was recorded in clones of the montane population Jasina, whose shoots developed the earliest in spring (Sabor 1984) and in clones of the population Karnieszewice (20.2%), whose shoots develop 8 days before clones of the next ranking population Istebna (16.3%) and 3 weeks before clones of the population Kolonowskie (7.1%), whose development started the latest (Kamińska-Rożek and Pukacki in print). The lowest losses of female strobili (3.7%) were observed in clones of the population Serwy.

Some of the developing cones were injured by insects, mainly by *Dioryctia abietella* Schiff. and *Laspeyresia strobilella* L., which also caused premature cone shedding. According to Kiełczewski et al. (1967), such injuries are observed on about 10% of strobili. Abortion of the Norway spruce cones can be also due to late spring frost during pollination (Sarvas 1968).

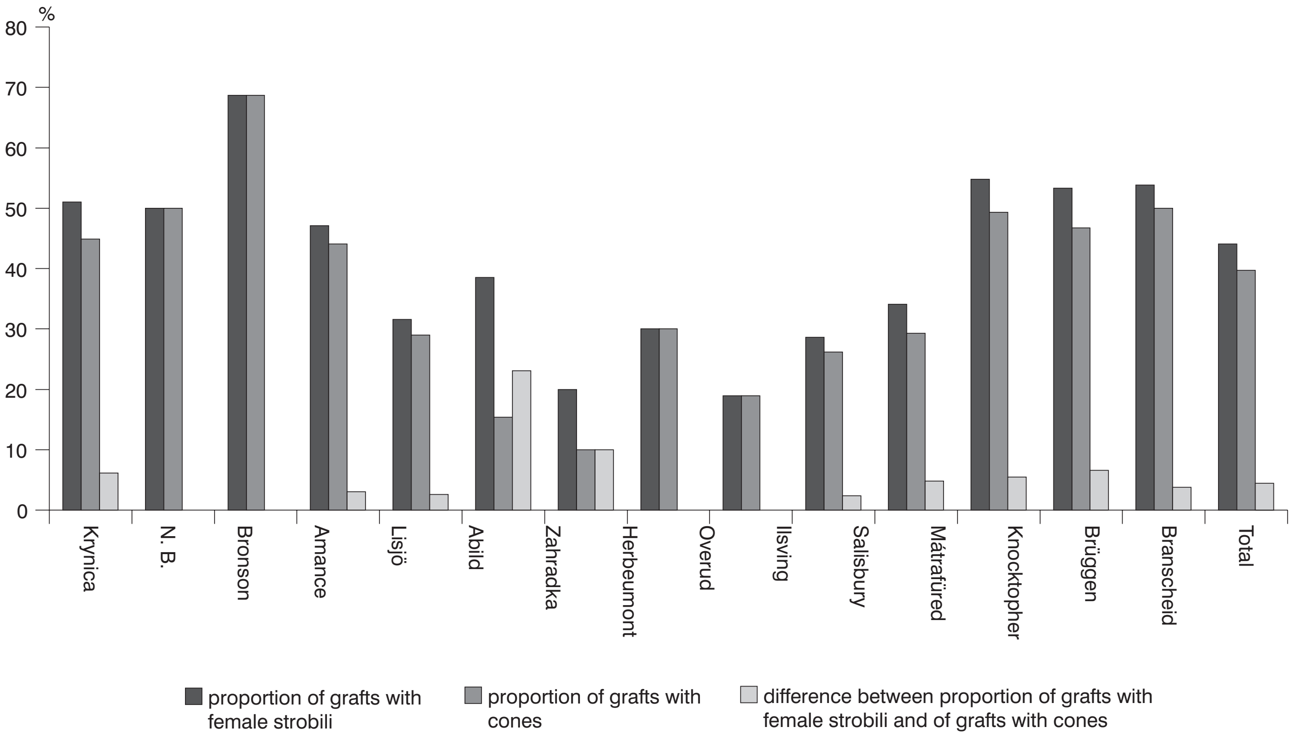

Fig. 2. Proportion of grafts with female strobili and with cones (in relation to the total number of grafts) in the second-generation seed orchard 'Kolonowskie' in Kórnik in 2004

Cone yield from individual maternal populations in the seed orchard 'Outbreeding' was significantly correlated with the latitude of provenance of maternal populations (r = 0.8826; p = 0.0474) (Fig. 3).

In the seed orchard 'Kolonowskie' (Fig. 2), cones were collected from 39.7% of the total number of grafts and from 78.9% of the total number of clones. The difference between the proportion of grafts with female strobili and the proportion of grafts with cones was smaller than in 'Outbreeding', as it reached on average 4.6% (in relation to the total number of grafts). In clones derived from 4 locations (Bronson N.B., Amance, Overund and Ilsvig), the difference was close to 0%, while in clones from Zahradka the difference was the highest and reached 23.1%. This

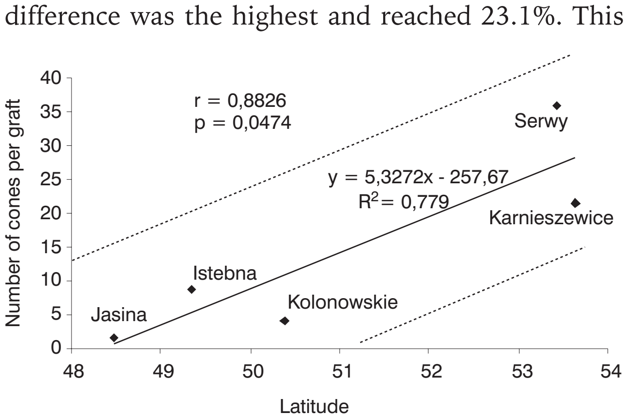

Fig. 3. Relationship between the latitude of provenance of maternal populations and mean number of cones per graft in those populations in the second-generation seed orchard 'Outbreeding'

may be explained by the fact that only 5 grafts from Zahradka produced a small number of female strobili, so the risk of their accidental loss was higher.

Clonal variation in cone yield

A significant factor affecting cone yield is interclonal variation (Nilsson and Wiman 1967; Eriksson et al. 1973; Wesoły et al. 1984; Skrøppa and Tutturen 1985; Chałupka 1988). The analysis of variance performed for each of the studied spruce seed orchards in Kórnik also confirmed that variation between clones was significant both in general and within individual provenances. In the case of the seed orchard 'Outbreeding', significant differences were also found between provenances (Table 7).

All cones collected in the seed orchard 'Outbreeding' derived from 163 grafts representing 70 clones (Table 4), but it is noteworthy that about a half of all cones (51.9%) were produced by only 24 grafts of 4 clones (5.4% of all grafts and 3.9% of all clones in the seed orchard), whereas 95.2% of cones were collected from 96 grafts representing 29 clones (21.4% of all grafts and 28.2% of all clones in the orchard) (Fig. 4A).

In the seed orchard 'Kolonowskie', cones were harvested from 207 grafts deriving from 86 clones (Table 5). However, about half of the total number of collected cones (51.2%) originated from only 38 grafts (7.3% of all grafts in the seed orchard), representing 10 clones (9.2% of all clones). As many as 95.2% were found on 134 grafts (25.7% of all grafts) belong-

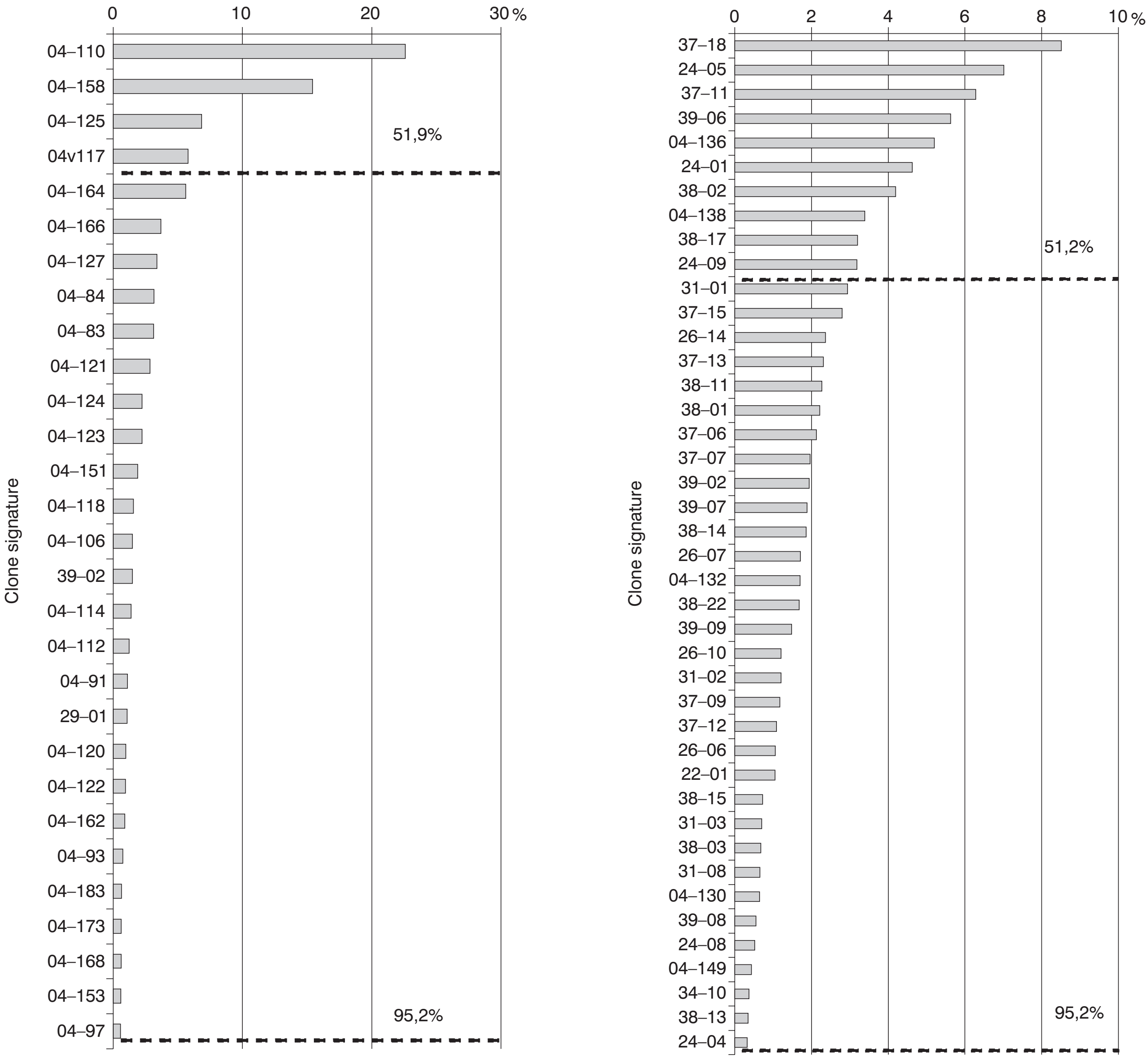

Fig. 4. Contribution of individual clones to the total number of cones in second-generation seed orchards ‘Outbreeding’ and ‘Kolonowskie’ in 2004

ing to 42 clones (38.5% of all clones in ‘Kolonowskie’ (Fig. 4B).

Our results confirm that only some clones and grafts participate in production of mature cones in second-generation seed orchards. This may result in limitation of the genetic diversity of the offspring (seeds) in relation to the theoretical expectations of the breeder, resulting from the true number of clones

Table 7. Analysis of variance of Norway spruce cone yield in second-generation seed orchards ‘Outbreeding’ and ‘Kolonowskie’ in Kórnik in 2004

Outbreeding			Kolonowskie		
Source of variation	DF	F	Source of variation	DF	F
Total	415		Total	502	
Clones	85	4.31**	Clones	99	1.46**
Provenances	4	2.52*	Origins	13	1.55
Clones in provenances	81	4.02**	Clones in origins	86	1.36*
Error	330		Error	403	

*significant at 0.05 level
**significant at 0.01 level

in the seed orchard (Chałupka 1988; Chałupka and Rożkowski 2004).

Estimated seed production

On the basis of some justified presumptions (Chałupka and Rożkowski 1995) and the number of collected cones, we estimated the total seed production in the studied seed orchards in 2004. According to Sarvas (1968), the mean number of seeds per cone in Norway spruce is 236, and the mean 1000-seed weight is about 7.5 g in Poland (Dutkiewicz 1968). In this way, we estimated that the seed orchard 'Outbreeding' (0.61 ha) produced 12.84 kg of spruce seed, i.e. 21.05 kg per ha, while 'Kolonowskie' (0.71 ha) produced 15.42 kg, i.e. 21.72 kg per ha. Similar values of Norway spruce seed yield, ranging approximately from 20 to 40 kg/ha, were recorded also in over 20-year-old seed orchards in good cone crop years in Norway and Poland (Skrøppa and Tutturen 1985; Chałupka and Rożkowski 1995).

Conclusions

1. In 2004, abundant flowering and cone production was observed in second-generation seed orchards 'Outbreeding' (91.3% of all clones and 64.1% of all grafts produced male and/or female flowers) and 'Kolonowskie' (91.7% of all clones and 55.5% of grafts with flowers) in Kórnik. However, due to abortion of female strobili, the cones matured only on 68.0% and 78.9% of all clones and 36.4% and 39.7% of all grafts, respectively.
2. In the seed orchard 'Outbreeding', cone yield of individual clones was positively correlated with the latitude of provenance of maternal populations ($r = 0.8826$, $p = 0.047$).
3. In the restitution second-generation seed orchard 'Kolonowskie', no significant correlation was observed between flowering abundance or cone yield of individual clones and the latitude of scion collection sites (i.e. plantations of this Norway spruce population in other locations in Poland and abroad).
4. In both seed orchards, significant variation was observed in cone yield within clones and within provenances and/or origins. In the seed orchard 'Outbreeding', significant differences were also observed between provenances of maternal populations.
5. About 50% of cones in seed orchards 'Outbreeding' and 'Kolonowskie' were produced by 3.9% and 9.2% of all clones and 5.4% and 7.3% of all grafts, respectively. About 95% of cones were produced by 28.2% and 38.5% of all clones and 21.4% and 25.7% of all grafts, respectively. These data indicate that genetic diversity of the offspring (seeds) from both seed orchards in 2004 was much narrower than expected from the composition of the seed orchards.
6. The estimated seed production per hectare in 2004 reached 21.05 kg in the seed orchard 'Outbreeding' and 21.72 kg in 'Kolonowskie'.

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