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Pairwise Competition Among Progenies from Matings Within and Between Three Origins of Picea abies in a Nursery Trial

By F. VON EULER, I. EKBERG and G. ERIKSSON

Department of Forest Genetics, Swedish University of
Agricultural Sciences, P.O. Box 7027, S-750 07 Uppsala,
Sweden

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Summary

Picea abies (L.) KARST. full-sib progenies from a factorial mating design were classified into 8 types according to the origin of the parents: northern Sweden, central Sweden, or continental Europe. Seedlings were planted in 36-tree plots with 40 cm × 40 cm spacing, either a single mating type, or 2 types mixed (checker-board), on sandy, unfertilized soil. Seven out of the 28 possible pairwise mixtures were included. Height and stem diameter were assessed annually from age 2 (height) or 5 (diameter) through 9 years. The effects of direct mating type and of associate mating type were quantified by a factorial analysis of variance. For height, the direct effect was large at ages 2 to 4, as a result of juvenile free growth in the southern mating types. However, the direct effect declined and was smaller than the associate effect at age 9. An average mixed-plot superiority compared to pure plots was significant from age 3 through 6 for height, from age 6 through 8 for diameter. At most, this superiority was about 5%, both for height and for diameter. Similar competition effects have been reported for other conifers, with other types of genetic entries, when growing on nutrient-poor soils.

Key words: Competition, Provenance matings, Contrast plots, Narrow spacing, Mixture effects, Progeny test, *Picea abies* (L.) KARST.

Introduction

Many effects of competition between adjacent trees in the forest are obvious, and are the motives for silvicultural strategies such as various thinning and selective cutting regimes. With increasing intensity of cultivation and increasing control of the genetic set-up of entries, prediction of growth performance in mixtures of particular entries, or more generally, in defined competitive environments, becomes increasingly attractive. This would be possible through the identification of ideotypes (DONALD, 1968; CANNELL, 1982). A forest tree ideotype could be defined by different kinds of traits, e.g. phenological, morphological, or physiological. A highly heritable, narrow crown type of *Picea abies* in Finland, has been proposed as a crop ideotype that would yield more merchantable wood per unit area (PULKKINEN, 1991; PULKKINEN and TIGERSTEDT, 1992). However, for the ideotype concept to be useful, more knowledge and experimental data are required in areas such as sink dynamics, ageing, and competition processes (DICKMAN, 1985). Causes and effects of competition may depend on the type of competing entries (species, provenances, half-sibs, clones, etc), site conditions (soil fertility, spacing, etc.), age, and other factors. JOHANSSON and KEDDY (1991), working on a large number of wetland annual plant species, experimentally confirmed two general hypotheses related to competition, that (i) intensity, i.e. average growth depression, increases with the degree of similarity of the competing species, and that (ii) asymmetry, i. e. lack of balance between growth alterations of the competing species, decreases with increasing similarity. They also found that "competitive similarity" between species was difficult to measure, although a large number of traits, considered relevant for competition, were observed. This emphasizes the need for a better understanding of competitive mecha-

Table 1. — Provenance mating design: mating types (in brackets) and full-sib families [(⊗)].

	♂ parent								
	Northern N			Central C			Southern S		
♀ parent	1	2	3	1	2	3	Ukr.	Belg.	Ger.
Northern N	(N×N)			(N×C)			(N×S)		
1						⊗	⊗		
2		not included		⊗	⊗	⊗	⊗	⊗	⊗
3				⊗	⊗	⊗	⊗	⊗	⊗
Central C	(C×N)			(C×C)			(C×S)		
1	⊗			⊗	⊗	⊗	⊗	⊗	⊗
2	⊗	⊗		⊗					
3	⊗	⊗	⊗		⊗		⊗	⊗	⊗
Southern S	(S×N)			(S×C)			(S×S)		
Belg. 1	⊗	⊗	⊗	⊗	⊗		⊗	⊗	
Belg. 2	⊗		⊗	⊗	⊗				⊗
Belg. 3	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗	⊗

nisms, as argued by e.g. Weiner (1988) and Tilman and Wedin (1991). Most experimental evidence for the development over time of intra-specific competition between particular genetic entries under field conditions comes from a few, specially designed but mainly descriptive, studies (Wlérick, 1981; von Euler et al., 1992 and 1993). Strict tests of general hypotheses concerning competition processes could not be carried out with these data. On an infertile site, it has been observed that pairwise mixtures of half-sib families of *Pinus pinaster* Ait. grew better, compared to the average of the families in pure plots (overcompensation) (von Euler et al., 1992). A similar effect at the species level was found in mixed stands of *Abies alba* Mill. and *Picea abies* on sandy soils in Denmark (Jensen, 1983). These observations agree with hypothesis (i) above, and support the assumption that competition effects are similar for different kinds of genetic entries such as species, genotypes, and families.

The earlier focus on provenance hybrids of *Picea abies* in Swedish forest research stemmed from expectations of sizable heterosis effects. Ekberg et al. (1991) studied several phenological traits on 3 to 8-years-old provenance crosses in a nursery trial. For traits other than free growth, the additive effect of parent provenance was much larger than the non-additive effect. The present experiment was established on the same location as for Ekberg et al. (1991), and mainly the same seed material was used. The aim was to follow the development over time of various effects of competition among the provenance-mating types, until the age of selfthinning. In the light of the above-cited more recent findings, we further examined the data to see if the mixture effects of mating types resemble the effects observed for other conifer species with other kinds of genetic entries, and if competition patterns in large-scale field experiments can be reproduced on a smaller scale under nursery conditions, at a younger age and with closer spacing.

Materials and Methods

Six trees were chosen, 3 as female parents and 3 as male parents, from each of 3 geographically distant origins, or provenances: northern Sweden (N), approx. lat. 65° N, central Sweden (C), approx lat. 60° N, and continental Europe (S), approx. lat. 50° N (*Table 1*). The S "provenance" comprised 3 distinct origins: all females and 1 male came from a Belgian stand, while the other 2 S males originated from Germany and the Ukraine, respektively. The parents were selected as plus (superior phenotype) trees in mature, autochthonous stands, except for the Ukrainian male, which was selected in a central Swedish provenance trial (Ekberg et al., 1991). Crosses involving N females were carried out in northern Sweden, at lat. 64° N; other crosses were carried out at lat. 59°30' N. The provenance mating types (N×C, N×S, etc.) were each represented by 5 to 8 full-sib families (*Table 1*). The N×N type was not included, owing to lack of seeds.

Sowing was done in the greenhouse 1982, plantation in the nursery in spring 1983. The nursery soil is sandy, of low to moderate fertility. The experiment was not fertilized, only watered during dry periods. The plants were deployed in square 6×6-tree plots with 40×40 cm spacing. The plots were of 2 types: pure-mating-type plots, and contrast plots with 2 mating types mixed in a checkerboard arrangement. Within a plot, a mating type was represented by randomly selected trees from among the 5 to 8 families of that mating type. Thus, adjacent trees of the same mating type usually came from different families. All mating types were planted in pure plots; however, only 7 out of the 28 possible mixed plots were included (*Table 2*). The experiment was replicated in 3 adjacent, complete blocks, and was surrounded by 2 border rows. The total number of observations, neglecting mortality, was 1620. However, in all comparisons of competing mating types, only the inner 4×4 trees of each plot were used, corresponding to a total of 720 observations.

Total height was assessed every year from age 2 through age 9. Total stem diameter was assessed from age 5 through age 9. The diameter was measured at the stem base at ages 5 and 6, and after clear-felling at age 9. For practical reasons, 6 to 8-year diameters were measured at the middle of the stem section corresponding to the third year's leader. Basal diameter at age 7 and 8 could then be derived, using the relation between basal and

Table 2. — Competition diallel design, with pure plots (on the diagonal), and mixed plots indicated.

	Associate mating type							
Direct mating type	N×C	N×S	C×N	C×C	C×S	S×N	S×C	S×S
N×C	*pure*	mix1						
N×S	mix1	*pure*						
C×N			*pure*	mix2		mix3		
C×C			mix2	*pure*				mix4
C×S					*pure*			mix5
S×N			mix3			*pure*	mix6	
S×C						mix6	*pure*	mix7
S×S				mix4	mix5		mix7	*pure*

section diameters at age 6, assuming constant stem-form from age 6 through 8. Some information on growth rhythm was obtained by measuring leader lengths on 3 occasions during the shoot elongation period, from age 5 through age 8. Total leader length was recorded from age 5 through age 9; leader lenght at ages 3 and 4, and annual diameter increment, were calculated from the difference between consecutive assessments of cumulative growth. Relative growth rates were simply calculated as the difference between the corresponding, log-transformed values.

Reciprocal mating type mean values (e.g. N×S vs. S×N) were usually significantly different and hence, could not be pooled in subsequent analyses. It should be noted that the term "reciprocal" pertains to mating type, not tc full-sib families, since no single parent was used both as male and as female. In the ANOVA, the direct mating type and associate mating type (*Table 2*) represented crossed, independent effects:

$$y_{ijkl} = \mu + b_i + \delta_j + \varepsilon_k + (\delta \cdot \varepsilon)_{jk} + (b \cdot \delta \cdot \varepsilon)_{ijk} + e_{ijkl} \qquad [1]$$

Table 3. — Ranks of mating type means at ages 5 and 9 (bold figures) in pure plots (italics) and mixed plots, for height and diameter.

	Associate mating type							
Direct mating type	N×C	N×S	C×N	C×C	C×S	S×N	S×C	S×S
	Height							
N×C	*21-21*	22-22						
N×S	20-20	*17-18*						
C×N			*19-10*	15-16		16-13		
C×C			12- 4	*14-11*				18-19
C×S					*7 - 3*			9 -17
S×N			5 - 1			*6 - 6*	11-12	
S×C						2 - 2	*13-15*	8 - 9
S×S				3 - 7	1 - 5		4 - 8	*10-14*
	Diameter							
N×C	*21-22*	22-21						
N×S	20-20	*17-18*						
C×N			*12- 9*	14-15		11-13		
C×C			6 - 8	*10-15*				19-19
C×S					*3 - 7*			16-17
S×N			4 - 1			*5 - 6*	9 -14	
S×C						1 - 3	*18-12*	13-11
S×S				8 - 4	2 - 2		7 - 5	*15-10*

where

u = general mean

b_i = effect de to block i (2 df)

δ_j = additive effect of the j^th^ direct mating type (6 df)

ε_k = additive effect of the k^th^ associate mating type (6 df)

$(\delta\cdot\varepsilon)_{jk}$ = direct × associate interaction effect (8 df)

$(b\cdot\delta\cdot\varepsilon)_{ijk}$ = block × direct × associate interaction effect (error) (42 df)

e_{ijkl} = residual term (509 df to 597 df)

Type II sums of squares (each effect adjusted for all main effects) were used when computing F-ratios. This model is basically similar to those employed by VON EULER et al. (1992 and 1993), but with a slightly different formulation mainly due to the very strong non-orthogonality of direct and associate effects.

Results

Mortality was less than 1% until age 8, but increased to 5.8% at age 9. Height and diameter overall mean values for the N×C mating type were significantly smaller than for other mating types at all ages (*Fig. 1*). The N×S type

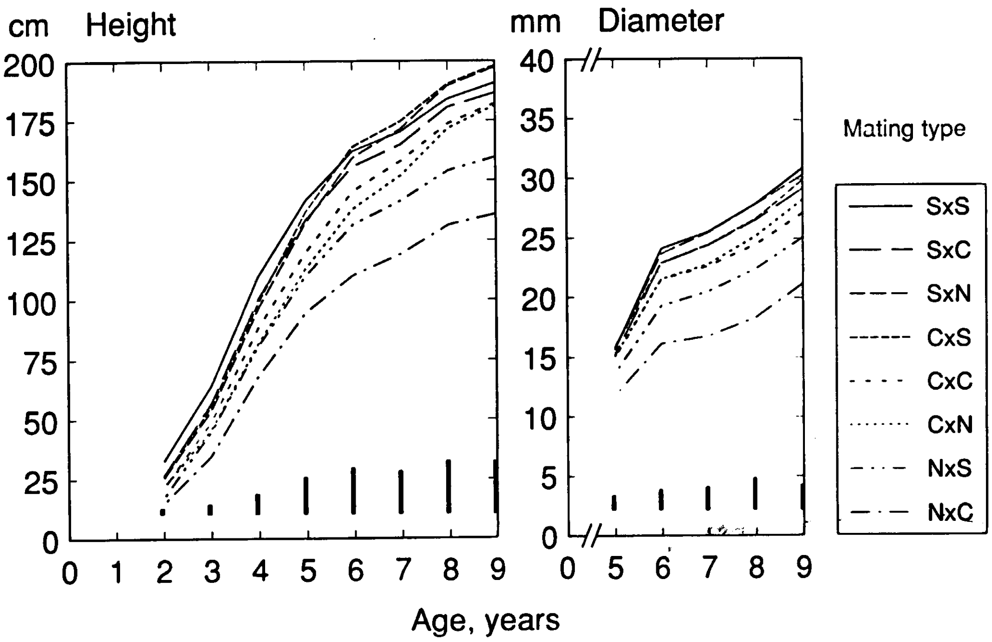

Figure 1. — Change of mating type means with age, across pure and mixed plots, of height and basal stem diameter. Vertical bars indicate the least significant difference between mating types ($p < 0.05$).

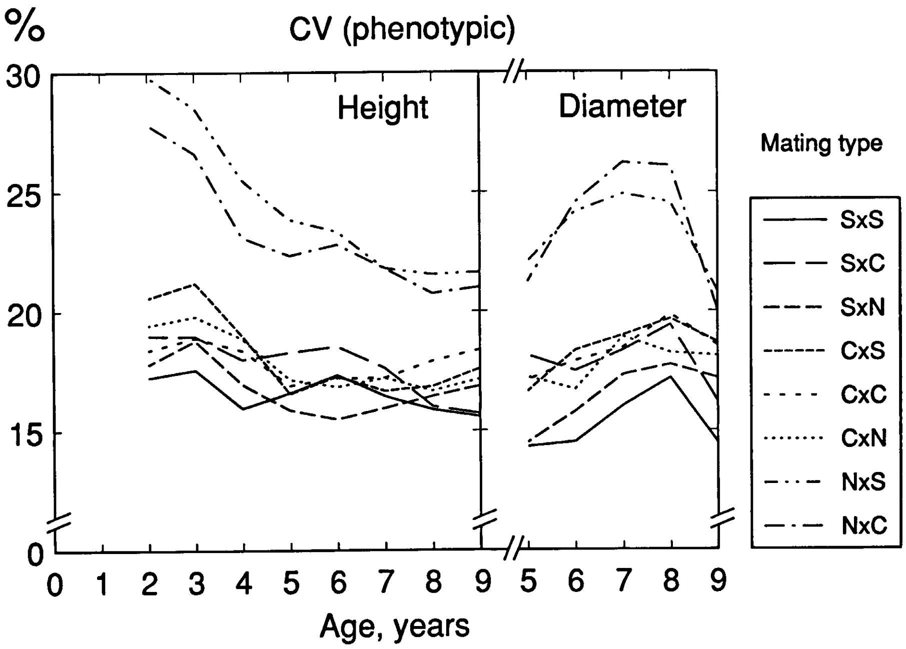

Figure 2. — Change of the coefficient of phenotypic variation (CV) with age, for mating types across pure and mixed plots.

Table 4. — F-ratios for the ANOVA model effects.

Trait	Age	*F*-value Block (b)^a	Direct (δ)^b	Associate (ε)^b	δ·ε ^{b}	b·δ·ε ^{a}	Residual MS
Height	2	7.69	43.83***	2.32	2.19*	1.25	21.50
	3	4.36	26.92***	3.05*	4.19***	1.02	103.32
	4	14.45	20.83***	2.64*	4.05**	1.01	285.10
	5	51.05	9.04***	2.70*	1.56	1.97	440.81
	6	122.28	5.22***	2.83*	1.08	2.48	610.34
	7	134.32	4.18**	3.54**	0.93	2.50	641.06
	8	115.59	3.28**	3.53**	0.55	2.69	741.38
	9	107.61	3.10*	4.00**	0.71	2.49	831.18
Basal stem diameter	5	47.24	2.59*	5.19***	1.36	1.93	5.54
	6	27.55	6.76***	5.92***	1.53	1.49	13.08
	7	21.37	6.56***	5.70***	1.41	1.36	17.46
	8	22.77	6.80***	5.56***	1.00	1.22	22.82
	9	13.09	5.76***	6.04***	0.49	1.80	21.11

a) F-ratio denominator: residual MS (level of significance not shown)

b) F-ratio denominator: (b·δ·ε) MS (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$)

was likewise below average, while the C×N and S×N types were close to, or better than the average mating type. At about age 5, the height-growth rate of the S×S and S×C types declined. After age 6, there was a general decrease of the diameter growth rate and a similar, but smaller, decrease of the height growth rate. The rank order of the mating type means in different plots (*Table 3*) appeared quite consistent with the overall mating type means. The hierarchy of the 2 mating types in a mixed plot was not correlated with their ranks in pure plots. The N×C and N×S mating types were distinguished by high coefficients of phenotypic variation (CV, *Fig. 2*). The height CV declined, while the diameter CV rose from age 5, and fell after age 7. For most mating types, however, the CV varied between 15% and 20%. The CV was quite similar in mixed and pure plots.

For height and diameter, both the direct and associate effects of mating type were largely significant (*Table 4*). During the first 3 years, the direct effect for height was an order of magnitude larger than the associate effect, but declined rather steeply. The associate effect increased slowly and was larger than the direct effect during the last 2 years. For diameter, both effects were strongly significant. Except for height at ages 2 to 4, no significant direct × associate interaction effect occurred. Block effects were large, even very large for height after age 4. For growth rhythm (age 5 to 8), the direct effect of mating type was usually strong at all 3 leader elongation assessments, while there were no associate or interaction effects (data not shown). For annual growth and growth rates, however, neither the direct nor the associate effect of mating type was significant after age 3. Therefore, these characters were not considered further.

Except for the mix N×C — N×S, mixes were usually superior to the mean of the corresponding pure plots (*Fig. 3*). Separate differences were too small to be significant, but the average mixed-plot superiority (omitting the N×C — N×S mix) was significant from age 3 through 6 for height (max. 4.7%), from age 6 through 8 for diameter (max. 5.8%) (*Fig. 4*). With the N×C — N×S mix included, the effect was only significant at age 4 (height) and 6 to 7 (diameter). Sometimes, mixed plots were superior to the best of the corresponding pure-mating-type plots (*Fig. 3*). The number of pure-mixed plot comparisons was not the same for all mating types. To check the importance of this bias, the mean of all pure plots was compared to the mean of all mixed plots (again omitting plots involving mating types N×C and N×S). The mixed-plots superiority was then significant at age 4 (height) and age 6 to 7 (diameter), consistent with earlier results. The superiority of mixed plots in separate comparisons was uncorrelated to the difference between the 2 constituents of the mixed plot, and to the difference between the corresponding pure plots.

Discussion

As usual with this kind of competition experiment, constraints on the design necessitate a cautious interpretation of the results. Only 25% of all possible pairwise mixtures were included. The competition diallel design was disconnected and non-orthogonal with respect to the genetic effects of the ANOVA model. Another disturbing

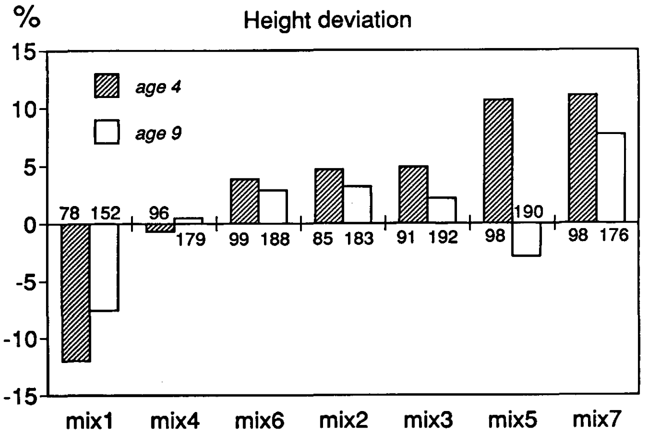

Figure 3. — Height deviation (%) of the mixed mating type plots (see *Tab. 2*), relative to the mean of the 2 corresponding pure mating type plots (zero), at ages 4 and 9. The actual mean values of the pure plot pairs are indicated (cm).

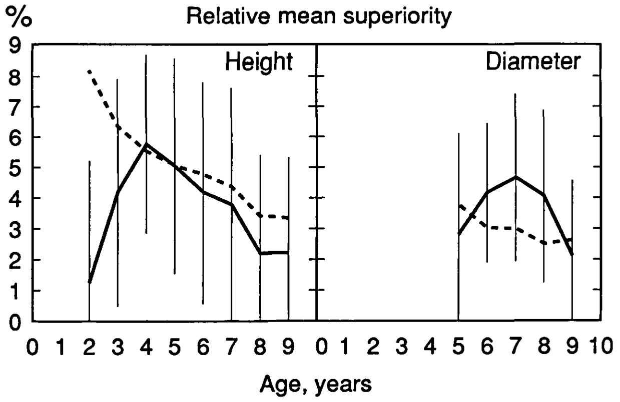

Figure 4. — Change of the average (mating types N×C and N×S excluded) superiority with age, of mixed plots (solid line), and of the best of the 2 pure plots corresponding to each mixed plot (hatched line). The reference zero) level is the average mean of 2 pure plots corresponding to each mixed plot. Vertical bars indicate confidence intervals ($p < 0.05$) for the mixed plot superiority.

circumstance is the very strong blocking effect, indicating that soil conditions were rather heterogeneous at some depth. The poor height and diameter, and the high phenotypic variability of mating types for which crossings were made in northern Sweden, compared to their reciprocal mating types, might be due to parental-environment aftereffects and/or maternal effects (Dormling and Johnsen, 1992; Johnsen et al., 1989).

Juvenile free growth is a probable reason for the strong direct mating-type effect, and also for the small associate mating-type effect for early height in the ANOVA. Juvenile free growth disappears rapidly after the age of 5 (Ekberg et al., 1991; Ununger et al., 1988). Among the best 6 mating types, the height-growth rate declined most in those with the highest frequency of juvenile free growth (Ekberg et al., 1991). Small effects of associate family compared to direct family effects, in particular for height, have been reported by Wlérick (1981) for 12-year-old *Pinus pinaster* full-sib families, and by von Euler (1993) for 15-year-old *Pinus sylvestris* L. varieties. Unlike the present experiment, however, those experiments were located on relatively fertile soil, or fertilized.

A likely explanation for the general growth decrease is that easily accessible nutrients in the sandy soil were depleted. Compared to many *Pinus* species, *Picea abies* is less of a pioneer species, has a greater ability to efficiently utilize low light intensities for photosynthesis, and has higher soil fertility requirements (Schmidt-Vogt, 1977). This implies a relatively stronger influence of root competition. Competition for nutrient resources is more symmetric than competition for light, and is consistent with stable or decreasing phenotypic variability in the population (Weiner, 1988). Since in the present experiment there was no increasing trend for the coefficient of phenotypic variation, light was probably not a limiting resource for height growth. However, competitors may have reduced the photosynthetic activity in sub-apical parts of the crown of neighbors, thereby affecting the ability of roots to grow and extract nutrients necessary for height growth. Competition effects on stem diameter and volume growth in some young, even-aged plantations of *Pinus* species were approximately linearly related to neighbor height dominance (Magnussen, 1989; von Euler, 1993). The pyramidal crown shape of *Picea abies* would act to strengthen such a relationship. Since the carbohydrate "pools" of the root system and the stem base are both located below the photosynthetically active parts of the crown, the transport-resistance model of forest growth and partitioning (Thornley, 1991) predicts that light competition effects on roots and stem are qualitatively similar.

In the present experiment, the direct and associate mating-type effects in the ANOVA were of approximately equal size during the last 3 to 4 years, when competition was most severe. A favourable growth effect of mixtures was then observed for diameter. Similar competition effects have been reported for half-sib family mixtures of *Pinus pinaster* at age 16 in an experiment (von Euler et al. 1992) where, in concordance with the present experiment, the height: spacing ratio was relatively high and the soil fertility was low. The development over time of positive mixture effects appears to be coupled to the faster acquisition of soil nutrients. The maximum mixture effect for diameter appeared late, when the effect for height was declining. This may be due to a high priority of height growth in resource utilization (Caldwell, 1987). It seems likely that the mixture superiority disappeared as a result of intensified competition for light.

In conclusion, the results of the present and the few comparable studies suggest that competition processes in even-aged conifer stands are strongly influenced by site conditions. Given comparable site conditions, age seems to be of little importance. For the low degree of control of growth factors that can be achieved in field experiments, the effect of mixing genetic entries, as compared to growing entries in pure plots, also appears to be the same at different taxonomic levels. For example, mixing families within population, or mixing provenance matings (or provenances) within species, or mixing species within guilds, yield qualitatively similar results. This is counterintuitive in that "similarity" at different taxonomic levels may be expressed in terms of traits with different kinds of adaptive significance (growth rhythm, architecture, etc.), with different relevance for between-entry competition. However, it must be emphasized that the small number of competition experiments still is a strongly limiting factor for general conclusions.

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Influence of the Genotype on Growth of Norway Spruce (Picea abies L.) in in Vitro Meristem Culture

By IRENE KUNZE

Institute of Plant Genetic and Crop Plant Research,
Corrensstraße 3, D-06466 Gatersleben, Germany

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Summary

The influence of the genotype for long term cultivation of meristematic tissues of *Picea abies* was investigated. For this aim, different *in vitro* clones were compared concerning their behaviour during (i) establishment, (ii, iii) their efficiencies to propagate and to elongate and (iv) their reaction to application of IAA.

Apparent phenotypical differences among individual clones could be observed. They remained stable during long term culture (4 years).

Induction of elongation of the shoot buds could be achieved with different success up to 100 %. This is the 1st report which describes an efficient induction of shoot elongation for *Picea abies* although the morphology of elongated shoots is still unsatisfactory.

Key words: Picea abies, genotype, *in vitro* clones, permanent multiplication, shoot buds.

Zusammenfassung

Es wurde der Einfluß des Genotyps auf die *In-vitro* Langzeitkultivierung von meristematischem Gewebe von *Picea abies* untersucht. Zu diesem Zweck wurden einige *In-vitro* Klone hinsichtlich ihres Verhaltens während ihrer Etablierung (i), (ii, iii) der Effizienz, mit der sie sich vermehren bzw. ihre angelegten Sproßknospen strekken und (iv) der Reaktion auf IAA-Applikation verglichen. Dabei zeigten die untersuchten Klone z. T. sehr auffällige Unterschiede, die während der Langzeitkultivierung (4 Jahre) stabil erhalten blieben.

In Abhängigkeit vom Genotyp konnten bis zu 100 % der angelegten Sproßknospen zur Streckung induziert werden. Es konnte damit zum ersten Mal eine effiziente Induktion der Sproßstreckung bei *Picea abies* erreicht werden.

Abbreviations

BA — 6-benzylaminopurine; KIN — N^6-furfuryladenine; ZEA — zeatin; 2ip, 6-(γ, γ-dimethylallyl)-aminopurine; IAA — indoleacetic acid; NAA — 1-naphthaleneacetic acid.

Introduction

The importance of the genotype for the regeneration potential of *in vitro* cultures of conifers has been described repeatedly. For example, explants like zygotic embryos or segments of seedlings of different genotype were stimulated by single application of growth regulators (PEREZ-BERMUDEZ and SOMMER, 1987; MOHAMMED and VIDAVER, 1988; AITKEN-CHRISTIE et al., 1988; SEN et al., 1989; VON ARNOLD et al., 1988). The effect of the genotype on permanently growing shoot bud cultures of *Picea abies* has not yet been described.

Meristematic cultures can be established and permanently subcultured according to the method depeloped by KUNZE et al. (1993). The principle of this method is the cultivation of segments of seedlings in 2 phases (without and with growth regulators) which alternate permanently. During the long term cultivation apparent phenotypical differences among individual clones were visible. The behaviour of genotypically different clones concerning their morphology, establishment, multiplication rates, reaction to IAA application and efficiency of induction of shoot elongation are described in the present paper.

Material and Methods

Material

Seeds of Norway spruce (*Picea abies* L) were kindly supplied by the Institute for Breeding of Forest Plants in