Adaptation of Progenies of a Norway Spruce Provenance Test (IUFRO 1964/68) to Local Environment

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Abstract – Adaptability of open pollinated offspring of different Norway spruce provenances has been studied in a progeny test. 38 superior and 10 inferior mother trees were selected in the Inventory Provenance Test with Norway Spruce (IUFRO 1964/68). The mother trees originated from different European regions from different geographical distances. Local sources were introduced as controls both in the provenance test and in the progeny test. Survival and height growth of 13 years old half-sib families were used for assessing the adaptability. Survival of families has shown small differences, the average amounted to 91 %. The family mean heights were more equalized than expected but significant differences could be shown among the families. Offspring of the superior mother trees performed well, most of them exceed the local control. The offspring of inferior mother trees showed reduced growth. A highly significant correlation (P = 1 %) was found between the height of mother trees and mean height of their progenies. Correlation between provenance mean of mother trees and the family mean was also significant.

***Picea abies* / mother tree / open pollinated offspring / progeny test / half-sib family**

Kivonat – A nyírjesi IUFRO lucfenyő származási kísérlet utódnemzedékeinek alkalmazkodása a helyi környezethez. A tanulmányban különböző származású lucfenyő anyafák szabad beporzású utódnemzedékeinek alkalmazkodó képességét vizsgáltuk egy mátrai utódvizsgálati területen. A Leltározó Lucfenyő Származási Kísérletben (IUFRO 1964/68) 38 kiváló növekedésű és 10 növekedésben elmaradt anyafát jelöltünk ki. Az anyanövények eltérő földrajzi távolságból, különböző európai régiókból érkezetek, kontrollként helyi – észak-középhegységi – populáció szolgált. Az alkalmazkodó képesség meghatározásához az utódok megmaradását, valamint 13. évben elért magassági növekedésüket vettük alapul. Az utódnemzedékek átlagos megmaradása 91% volt. Magassági növekedésüket tekintve a családok között bizonyos kiegyenlítődés mutatkozott, de a varianciaanalízis szignifikáns különbségeket igazolt. A helyi populációhoz viszonyítva 3 család szignifikánsan jobb növekedésű, 5 pedig szignifikánsan gyengébb volt. A jó növekedésű anyafák utódnemzedékeinek többsége megtartotta fölényét, az anyafák és utódok között szoros, P = 1%-os szinten szignifikáns korrelációt mutattunk ki. Ugyancsak szoros korrelációt találtunk a szülői származásátlag és az utódnemzedék átlagmagassága között.

***Picea abies* / anyafa / utódnemzedék / utódvizsgálat / féltestvér populáció**

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1 INTRODUCTION, BACKGROUND OF THE RESEARCH

Hungary has participated in numerous provenance tests organized by IUFRO (International Union of Forest Research Organisations). One set of a large-scale, international project, the Inventory Provenance Test with Norway Spruce (IUFRO 1964/68) was established in Hungary in 1968 (Szőnyi – Ujvári 1970). That time the main objective of the research was the selection of the best suitable populations and seed import sources to increase growth and yield (Szőnyi – Ujvári 1975).

During the study of the provenance test not only the provenances but also the individuals within the provenance showed a high phenotypical variation mainly in growth. The outstanding phenotypic and genetic variation of the Norway spruce can be explained with its wide natural range.

Having observed the first cone yield in the IUFRO provenance test, we selected mother trees and in 1985, out of the 13 participant countries, we were the first to introduce a progeny test. The offspring originated from open pollination. We therefore assumed that the adaptability of the progenies would show a great variation also within family.

The main objectives of this study were to study the implications of selection in a provenance trial and compare the performance of the progenies of selected mother trees that originate from geographically distant sites and from different ecologic environments with that of the local control. As the selection was done for both superior and inferior phenotypes in the provenance test, it was also of interest to see how well these characteristics were inherited by the progeny.

2 MATERIALS AND METHODS

Having started in 1968, the Inventory Provenance Test with Norway Spruce (IUFRO 1964/68) in Mátra mountains, Hungary, is part of a series that consists of 20 experiments with the participation of 13 countries. The 1 100 geographical provenances were collected from 96 regions (Krutzsch 1974). The trial layout followed the internationally recommended design. These 1 100 sources were grouped into 11 groups (blocks) of 100 provenances each, which have been planted in a 1 ha block. Each provenance was represented by 25 plants. For the experimental layout single tree plots with 2 meter by 2 meter spacing was applied. The whole experiment extends over 11 hectares (Szőnyi – Ujvári 1970). Each block of 100 sources is a complete trial. Due to stratified sampling, the blocks are estimated to be equal in mean and variance, thus easily comparable (Krutzsch 1992).

Having observed the first cone yield we have selected a number of the tallest, superior, vigorous mother trees based on their phenotypic performance in the provenances that showed a good or average performance. This first, sporadic seed yield enabled only the selection of few mother trees and because of the high ratio of empty seed the number of offspring was less than expected. The mother trees that produced enough seedlings to be included in a progeny test significantly exceeded the provenance and block means. The selection intensity varied between 2.2 – 2.8. For the sake of comparison we also selected 10 short, inferior but healthy mother trees, mostly from the poorer provenances. In *Table 1* we indicate the origin of the mother trees in the IUFRO experiment, and the growth in decreasing order of the height of the mother trees (we used a darker background to mark the mother trees that showed an inferior performance). The data of the local population (no. 796. Bükkszentkereszt, K1) is also included.

Table 1. Geographic origin and height performance of mother trees, block means, provenance means and control (K1) in the provenance trial IUFRO 1964/68.

No. and location of mother trees		Geographic origin					Height at 10 year			Rank[1]
No.	block	prov. no.	country	lat.	long.	alt. m	mother tree cm	block mean cm	prov. mean cm	
1	8	835	DEN	54º 50'	9º 19'	70	680	441	482	26
2	8	870	GER	47º 52'	10º 38'	800	680	441	477	33
3	7	781	POL	50º 30'	16º 40'	400	670	450	470	40
4	10	1075	BEL	49º 46'	5º 28'	400	670	417	444	32
5	6	675	GER	49º 06'	13º 28'	600	640	396	422	31
6	6	691	POL	54º 17'	20º 30'	150	640	396	416	35
7	7	742	GER	48º 53'	13º 36'	1000	640	450	442	60
8	7	791	CZE	49º 47'	14º 10'	450	640	450	500	15
9	8	877	CZE	50º 30'	16º 30'	550	640	441	502	6
10	4	471	GER	50º 56'	10º 36'	200	630	360	386	35
11	6	648	GER	51º 47'	10º 09'	300	630	396	513	2
12	7	736	CZE	49º 20'	18º 15'	800	630	450	478	29
13	7	741	GER	47º 44'	10º 24'	1000	630	450	453	52
14	7	751	CZE	50º 37'	15º 37'	750	630	450	472	38
15	7	755	ROM	47º 45'	25º 45'	670	630	450	516	4
16	7	755	ROM	47º 45'	25º 45'	670	630	450	516	4
17	7	786	POL	49º 38'	19º 08'	700	630	450	501	16
18	8	815	AUT	47º 05'	14º 09'	1200	630	441	478	32
19	8	830	AUT	47º 05'	14º 09'	1150	630	441	442	59
20	9	928	POL	49º 35'	18º 55'	650	630	420	497	3
21	6	695	GER	50º 41'	10º 50'	800	620	396	437	18
22	8	859	CZE	49º 35'	16º 05'	580	620	441	502	7
23	9	976	SVK	49º 08'	20º 30'	800	620	420	456	17
24	10	1048	GER	48º 04'	11º 53'	620	620	417	449	29
25	10	1079	CZE	49º 33'	17º 43'	500	620	417	482	7
26	3	331	POL	52º 40'	23º 50'	130	610	362	405	15
27	6	600	CZE	49º 15'	15º 50'	550	610	396	432	23
28	6	606	BLR	54º 05'	26º 30'	230	610	396	451	9
29	6	691	POL	54º 17'	20º 30'	150	610	396	416	35
30	10	1030	GER	54º 10'	12º 30'	100	610	417	423	49
31	10	1061	GER	49º 54'	11º 20'	500	610	417	428	45
32	2	252	POL	53º 40'	16º 45'	100	580	336	354	33
33	2	273	CZE	49º 15'	15º 50'	550	580	336	377	16
34	11	1147	BLR	53º 40'	30º 00'	150	580	381	418	23
35	11	1198	POL	49º 35'	18º 55'	500	580	381	432	12
36	11	1199	GER	50º 47'	10º 44'	650	580	381	375	63
37	11	1160	GER	50º 26'	12º 54'	980	570	381	377	60
38	2	230	LAT	56º 40'	26º 40'	90	550	336	397	5
39	3	310	GER	47º 41'	7º 57'	850	400	362	353	64
40	8	838	SWE	58º 12'	12º 55'	90	380	441	373	91
41	8	820	SWE	59º 18'	14º 41'	100	350	441	367	92
42	8	873	GER	48º 20'	9º 30'	800	350	441	465	43
43	9	927	NOR	58º 20'	8º 20'	100	320	420	323	93
44	10	1083	SWE	59º 05'	16º 21'	75	310	417	337	94
45	8	897	RUS	58º 00'	39º 00'	100	290	441	361	93
46	8	875	SWE	62º 47'	14º 23'	350	280	441	282	99
47	9	981	FIN	61º 41'	27º 15'	100	250	420	292	97
48	8	876	SWE	57º 22'	13º 12'	180	200	441	402	81
K1	**7**	**796**	**HUN**	**48º 04'**	**20º 38'**	**615**		**450**	**474**	**35**
K2			**HUN**	**48° 20'**	**20° 50'**	**700**				

[1] Rank of the provenance within the block (1 – 99; 1. = the best)

Selected slow growing mother trees (no. 39 – 48)

K1 Local control for mother trees (provenance in IUFRO provenance trial)

K2 Local control for progenies (commercial seed lot from Telkibánya)

We selected the mother trees in an area of large extension, in 9 blocks of the provenance test. Since there were great differences in the site conditions (e.g. exposure, slope and mainly the depth of the soil), the block effect could significantly influence the performance of the mother trees. To eliminate this, for the analysis of the correlations of the height performance between the mother trees and their progenies we chose 12 mother trees in block 8located in a nearly flat area, where site conditions could be regarded as more or less homogenous.

To analyse the performance of the offspring, we used a commercial seed lot from a domestic seed extractory (Telkibánya, K2) as control. The lot was collected in Norway spruce stands in the Zemplén mountains in the Northern mountain range. *Table 1* contains the provenance data of the control populations.

The cone collection and the growing of the seedlings took place separately for each tree. We established a progeny test with the half-sib progenies of 48 mother trees and the control lot. In each plot we planted out 24 seedlings in 7 x 7 simple lattice design, with 2 replications. The 2 ha experiment is located in forest sub-compartment Nagybátony 8 E in the Mátra mountains, at an altitude of 400 m above sea level. In the experiment located on a slope, the depth of the soil is unfortunately uneven. Some plots are therefore located on shallow soil.

The field assessment was carried out at the age of 13 after planting. The assessment included the measurement of the diameter at the breast height (DBH), the total height, the survival and the recording of damages.

The statistical analysis was based on plot means. A weighting factor was used to obtain the adjusted treatment totals. For the testing of significance an *F*-test of the adjusted treatment totals was completed (Cochran – Cox 1956),

3 RESULTS

3.1 Evaluation of progenies

Numerous scholars recommended the analysis of the biomass (dendromass) for the evaluation of adaptation to the climate (e.g. Callaham 1964). Adaptedness can be characterized well by growth traits over a longer period (height, tree volume, etc.) because they combine the effects of several factors. The height growth is an eminent component of tree production capacity, which is best determined genetically (Mátyás 2002). In our investigations we gave preference to the method of Mátyás – Yeatman (1987) applied for jack pine. For the characterization of adaptive variation we used the height data measured at the age of 13.

The analysis of variance showed significant differences among the families at P=0.1% level (*Table 2*). The adjusted F-value$_2$ showed a greater accuracy so we used the adjusted family means for the further calculations.

During the analysis of the adjusted family means we found that the height growth of the progenies was more equalized than expected. Surprisingly, the test mean (637.2 cm) was nearly the same as the mean of the local population – K2, Telkibánya (636.4 cm) – that was used as control. In *Table 3* the ranking follows the decreasing order of the family mean heights. Comparing it to the original rank according to the height of the mother trees, it can be stated that ranks are somewhat modified. It can be, nevertheless, said that the overwhelming majority of the progenies of the superior mother trees also showed a performance above the average. In the first third of the rank according to height we can find only progenies of the superior mother trees. The families of the inferior mother trees – with two exceptions – failed to reach the average of the local population. Further, in the last third of the table we can mainly find the progenies of the inferior mother trees.

Table 2. Analysis of variance of family mean heights at the age of 13 in the 7 x 7 simple lattice experiment

Source of variance	DF	MS	$F\text{-value}_1$	$F\text{-value}_2$
Replications	1	3.30		
Families	48	35.06	3.27***	3.55***
Block within replication (adj)	12	12.71		
Intra-block error	36	10.04		
Total	97			

$F\text{-value}_1$ = of originally measured and calculated family means
$F\text{-value}_2$ = of adjusted family means
*** significance level P = 0.1 %

Three families – all of them progenies of the selected mother trees – were significantly higher (P = 5%) than the local population (SD = 66.0 cm). Five families – mostly the progenies of the inferior mother trees – performed significantly worse than average.

In the evaluation of the progenies we have to take into account the survival too. In spite of the droughty weather that preceded the field assessment the vitality of the progenies was also impressive besides their good height performance. We did not experience significant damages apart from game damage. As compared to our other field tests, the survival was excellent, 91% on average. Only few families were exceptions (e.g. number **2**) where severe game damage caused the loss of several seedlings (*Table 3*).

3.2 Relationship between growth characteristics

For the comparison of the performance of the provenances, mother trees and their progenies we chose block 8 of the IUFRO experiment. We tested 12 – 6 superior and 6 inferior – mother trees out of the examined 48 trees in this block. The assessment of the height of the mother trees and of the progenies took place at different ages (at the age of 10 and 13, respectively). Therefore we compared relative heights (*Figure 1*). The height of the local control population in the Northern mountain range represented 100%. For the mother trees, the mean of the Bükkszentkereszt provenance was used (K1 = 474.0 cm), while the mean of the Telkibánya seed lot served for comparison of progenies (K2 = 636.4 cm).

Figure 1 illustrates the large differences among the mother trees. At the same time the performance of the open pollinated progenies were rather equalized. As already discussed, the progenies of the vigorous mother trees had the best performance, all of them exceeding the control. In case of the families marked **2** and **18** the difference is statistically significant. The progenies of the inferior mother trees showed results that were better than expected but with one exception (St. Johann marked **42**, from the Swabian Alb region) they failed to surpass the control. This provenance also exceeded the block mean in the IUFRO experiment. The families marked **40**, **45** and **48** were the shortest. All of them significantly differed from the control.

The correlation analysis (*Table 4*) showed a significant correlation at P = 1 % level between the mean heights of the mother trees and of the progenies (R = 0.81).

We examined the relationship between the provenances and their progenies, too. We also found a significant correlation at P = 1 % level between the mean heights of the provenances and of the progenies (R = 0.73).

Table 3 Results of the half-sib progeny test (Nagybátony 8 E) at the age of 13. Family mean heights (ranking trait), coefficient of variation (CV) and survival

Rank	Mother tree (family)	Provenance no.	Provenance name	Family mean height cm	Sign. diff.[1]	CV %	Survival %
1	**21**	695	ELGERSBURG	723.2	*	10.0	91.7
2	**2**	870	KAUFBEUREN	717.0	*	12.8	77.1
3	**18**	815	EMMACH/MURAU	708.0	*	9.7	91.7
4	**9**	877	ZAMBERK	686.9		10.3	95.8
5	**16**	755	MARGINEA	679.0		10.6	91.7
6	**36**	1199	CRAWINKEL	677.3		12.1	93.8
7	**26**	331	BIALOWIEZA	676.2		11.2	93.8
8	**1**	835	GRAASTEN	674.0		14.7	95.8
9	**12**	736	VELKE KARLOVICE	673.3		10.0	93.8
10	**31**	1061	NEUWIRTSHAUS	672.9		10.7	89.6
11	**35**	1198	ISTEBNA	672.9		12.7	87.5
12	**28**	606	WOLOZIN	672.3		9.2	85.4
13	**5**	675	ZWIESEL OST VI/11	668.0		12.9	93.8
14	**4**	1075	MELLIER	666.8		11.6	89.6
15	**3**	781	KLODZKO	663.8		11.9	89.6
16	**10**	471	MECHTERSTAEDT	662.0		12.3	91.7
17	**22**	859	MORAVEC	656.3		11.6	87.5
18	**11**	648	WESTERHOF 50/58	655.2		11.2	93.8
19	**24**	1048	LANDSBERG	654.9		13.8	93.8
20	**42**	873	ST. JOHANN	654.6		11.7	91.7
21	**38**	230	VARAKALANI REV.	651.9		10.2	91.7
22	**17**	786	WEGIERSKA GOR.	647.3		11.0	85.4
23	**27**	600	TREBIC	642.6		17.7	83.3
24	**19**	830	EMMACH/MURAU	639.8		11.2	95.8
25	**37**	1160	TELLERHAEUSER	638.5		10.3	95.8
26	**44**	1083	FLODA	636.6		12.7	93.8
27	**K2**		*TELKIBÁNYA*	**636.4**		**11.5**	**97.9**
28	**15**	755	MARGINEA	635.5		11.7	95.8
29	**25**	1079	HRANICE	632.4		10.4	100.0
30	**41**	820	VILLINGSBERG	632.2		11.6	91.7
31	**34**	1147	MOGILEVSK. OBL.	631.3		12.2	79.2
32	**8**	791	DOBRIS	621.3		14.4	93.8
33	**6**	691	GOROWO	618.2		13.1	91.7
34	**7**	742	MAUTH OST	618.1		12.1	93.8
35	**30**	1030	ROSTOCK	616.5		12.4	95.8
36	**14**	751	VRCHLABI	611.8		15.2	79.2
37	**39**	310	TODTMOOS	611.2		12.3	95.8
38	**13**	741	BETZIGAU	609.2		12.7	83.3
39	**46**	875	BERG BEV.	606.0		13.1	91.7
40	**32**	252	SZCZECINEK	605.0		14.2	87.5
41	**33**	273	TREBIC	598.0		14.2	93.8
42	**29**	691	GOROWO	597.4		15.7	77.1
43	**47**	981	MIKKELIN	593.2		12.9	97.9
44	**23**	976	PODOLINEC	588.0		15.8	89.6
45	**20**	928	ISTEBNA	570.7	*	19.2	95.8
46	**48**	876	BJOERLIDA	566.9	*	13.9	89.6
47	**40**	838	HILLET	557.4	*	18.2	85.4
48	**43**	927	AUSTAGDER	550.7	*	16.4	93.8
49	**45**	897	JAROSLAWL	543.2	*	15.5	95.8
			TEST MEAN	**637.2**			**91.0**

* Families that significantly differ from the average mean height of the local populations (P = 5%)

▢ Inferior mother trees and their progenies (**39 – 48**)

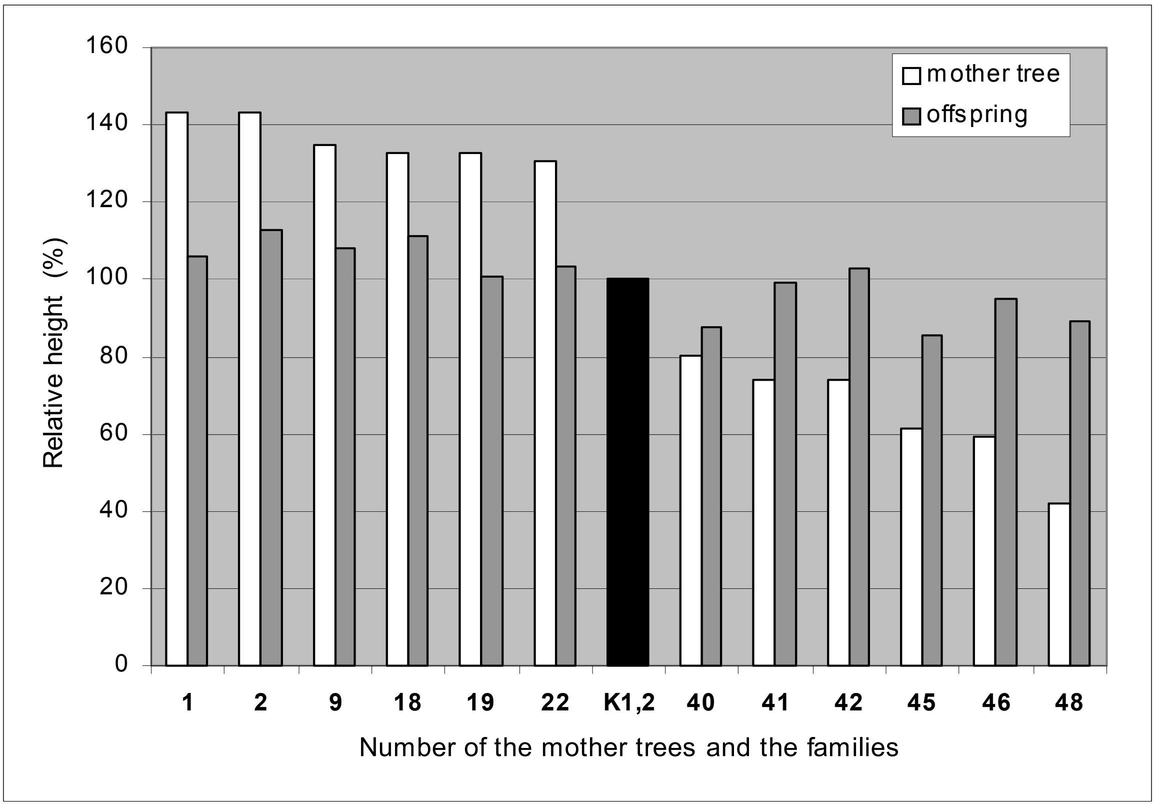

Figure 1. Relative height of mother trees and their half-sib progenies. Identification numbers are the same as in tables 1 and 3. (K1 and K2 represent the local sources for the mother trees and the progenies, respectively)

Table 4. Results of correlation analysis on height increment (provenance means, mother trees and their progenies)

Generation	Provenance	Mother tree
Provenance	1	
Mother tree	0.79**	1
Open pollinated progeny	0.73**	0.81**

** Correlation is significant at the P=1% level

4 DISCUSSION

The results of the progeny tests confirmed the general impression that Norway spruce has an outstanding adaptability and plasticity. The progenies originating from very different ecological environments had shownlow mortality, which did not significantly differ from the mortality of the control. This is perhaps not surprising because the populations of the mother trees already went through a selection for fitness in the Hungarian IUFRO experiment. We can mention here the example of a provenance from the West Siberian Plain (Timirjas), which disappeared from the experiment within 30 years. The selected mother trees can already be regarded as "survivors" of juvenile fitness selection

There was no opportunity to examine the tolerance to biotic and abiotic damages because fortunately, there was no significant damage in the experiment apart from the game damage.

We found that height growth of several progenies significantly exceeded the local (control) population. This is a well known phenomenon. In the IUFRO provenance test we could show that the 11 Hungarian provenances had a performance above the average (Ujvári – Ujvári 1980), but the best originated from relatively distant locations, e.g. from the Eastern Carpathians, from the region of the Beskids (Ujvári – Ujvári 1979). Namkoong (1969) and many other researchers formulated the opinion that at a given site it may not be the local population that grows best. For example, for jack pine (*Pinus banksiana*) Mátyás – Yeatman (1987) could statistically prove, that autochtonous populations are not necessarily the best growers at a given site.

The relatively low number of the Norway spruce progenies did not allow to identify general relationships. We could, nevertheless, show a strong correlation (R = 0.81) between the mother trees and their offspring when selection was made both for good and poor height growth. The experiment supported earlier information that the mother trees of the best progenies originate from Swabia, Thuringian Forest, Sudeten, Eastern Carpathians, Western Beskids, etc.

We included intentionally the mother trees of provenances showing extreme performance in our experiment. Therefore we had an opportunity to identify further relationships. In the progeny tests we also have shown that there is a highly significant correlation (P = 1%) between the mean heights of the provenances and their open pollinated progenies.

The analysis of growth traits has proven that even though the differences among the families were smaller than expected, the phenotypic variation of the individuals within a family was large. Particularly the coefficient of variation (CV) of the inferior progenies was higher than the control (*Table 3)*.

We have found also some remarkable correlation breakers. While very distant provenances, e.g. Floda and Villingsberg (Southern Sweden) originating from the 59th degree of latitude were among the poorest growers in the IUFRO experiment, the height growth of the progenies from these provenances approached or even reached the performance of the local population. Thus the differences between the two groups of selected provenances were considerably larger in the original provenance trial than they were in the progeny test.

Two factors may have contributed to these results. The first relates to the pollination in the provenance trial. Different trees may have contributed in varying degrees and random mating can therefore not be expected to have taken place. Most likely trees from the best growing, and more southern provenances contributed more to the pollen cloud and thus became the pollen parents of the open pollinated families. Inferior trees from inferior provenances may have contributed to a less extent as their flowering was presumably less abundant due to their position among better growing trees. In addition, there could be background pollination from local spruce stands. Thus, the contribution from the pollen parent may be one factor that caused the unexpectedly good performance of families from poorly growing provenances (Skrøppa pers. comm.).

Another important factor may be the effect of the climatic conditions at the site where the seeds were produced. Studies with Norway spruce in Northern Europe have shown that both day length and temperature during seed production can affect the annual growth rhythm and growth of the progenies (Skrøppa – Johnsen 1999; Johnsen et al. 2005a, b). It has also been demonstrated that seedlings from seeds collected in stands of transferred provenances have changed their annual growth rhythm towards that of the local provenance (Tollefsrud et al. in prep.). Such effects could have a common influence in particular on provenances that have been transferred from northern latitudes and may explain that some of the Nordic provenances perform surprisingly well and better than they do in the original provenance trial (Skrøppa pers. comm.).

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