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The IUFRO 1964168 Provenance Test with Norway Spruce (*Picea abies* (L.) Karst.)

By PETER KRUTZSCH

Department of Forest Genetics
Royal College of Forestry
S 104 05 Stockholm 50
Sweden

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In the southern parts of Sweden *Picea abies* is the economically most important tree species. Since the last decades of the 19th century it was more or less commonly known, that in lower altitudes of these regions natural spruce is inferior to provenances of Central European origin. Trials in the beginning of this century made it clear that Norway Spruce is a typical provenance species, showing a great genetic variability in climatic adaptive traits and growth rate and consequently a great variability in economic value.

The first large attempt of investigation was the IUFRO international trial with Norway Spruce in 1938. Sweden participated very actively: All 36 provenances were planted in three well designed field experiments in South, Central, and North Sweden (LANGLET, 1953, 1960, 1963, 1964 a, 1964 b).

Results from this international series have been published in quite a number of reports mostly based on single experiments in the participating countries, but some attempts have also been made for overall evaluations of different experiments (EDWARDS & LINES 1970).

The practical results of the 1938 IUFRO experiment are important in most European countries with regard to choice of provenance or at least with regard to attention to the question of provenances. As for Sweden, the results have been of an almost revolutionary character. Seed imports from certain regions of Central Europe for use in Southern Sweden have become an institution — well guarded by rules of control of origin as well as by recommendations for the use of certain provenances for different regions within Sweden.

The 1938 IUFRO experiments, though enormously encouraging for the use of "provenances" in forest practice, have a couple of disadvantages: We all agree that the number of provenances tested is too small, and we all have some doubts whether these provenances may be taken for true representatives of whole regions.

In 1959, on the initiative of professor OLOF LANGLET, Royal College of Forestry, Stockholm, Sweden, an inventory

provenance test was started as a second step in provenance research on a promising species. The test was meant to be inventory, as the purpose was to test as many provenances as possible, regardless whether the seed sources were autochthonous or not, and regardless whether the seed stands were within or outside the borders of the natural distribution of Norway spruce.

An intensive period of seed collecting stretched over the following 4 years. It would be quite a task to compile a list of all the kind contributors to this Stockholm collection, which in 1962 had come to the number of 1012 seed samples and in 1964 to the number of 1615.

The seed sources of this collection are of very different kinds. First the seeds are collected in different years. Second, there are seed lots 1) from single tree collections; 2) from a number of single tree collections within a stand and 3) from mixed collections from 10 to 20 trees per stand; 4) from collections within single stands for practical purposes, and 5) from collections from a number of adjacent stands. Finally there are samples from commercial collections, where the origin is given by the name of the forest district and the elevation above sea level in figures "from — to" or "above" etc. We are well aware that this standard of seed collection is not the ideal form. The costs, however, for collections with all desirable restrictions would have been tremendous. The standard of collection for the different samples has been filed in 6 "seed classes" and can be taken into account in the evaluation of data.

An investigation on the variation within Norway Spruce was of course the general aim of this experiment. Do regions of specific types of Norway Spruce exist, and how great is the variation between and within these regions? For practical purposes, it was urgent to find the best regions or provenances for seed supply. The final goal is to test a great number of genotypes as different as possible in a great number of localities, and to select among them for further tree breeding.

In 1962, a first nursery test with 1012 seed samples was sown at Lugnet in the vicinity of Stockholm. The results of this 4-year-test are published in mimeograph: Die Pflanzschul-Ergebnisse eines inventierenden Fichtenherkunftversuches (PETER KRUTZSCH 1968). The following traits were examined:

Seed characters	Weight of 1000 grains
	Weight of 1000 grains adjusted for filled seed
	Seed size (as number of seeds/ccm)
Growth	Height of 2/1 plants
	Height of 2/2 plants
Phenology	Time of budburst in the fourth spring season

In 1963, the plans for an international trial with this seed material were made in collaboration with Professor KLAUS STERN and Professor WOLFGANG LANGNER from Schmalenbeck, Germany. In the spring of 1964, 1300 samples were sown in the nurseries of the Schmalenbeck Institute. In 1966, the seedlings were transplanted in the nurseries of Pein & Pein at Halstenbeck. Neither in sowing, nor in transplanting were replications used. It seemed unnecessary with regard to uniformity of nursery conditions and we planned no assessments on the seedlings. Moreover: the stock amounted to 1.1 million of seedlings.

The Schmalenbeck — Halstenbeck campaign was a tremendous task. We are deeply indebted to Professor WOLFGANG LANGNER and his people, especially E. MASCHNING who was in charge of the practical details. The Pein & Pein Co. with Dr. WALTER NEUGEBAUER who was in charge of the transplanting work, and the labelling, lifting, assorting and shipping of the material had an essential part in the success of this trial and helped us skilfully in the most admirable way.

In 1967 samples of 389 provenances were examined with regard to spring frost damage, the formation of late wood, stem diameter and the time of hardening off (DIETRICHSON, 1969).

The planning of the international series, and the design of the field experiments were worked out in cooperation with Professor KLAUS STERN. Single tree plots seemed the only possibility to deal with the vast number of treatments, i. e. provenances.

The prediction of experimental accuracy for this new experiment is based on the three Swedish experiments of the 1938 series with Norway spruce. We assumed, that variance within and between provenances should be the same in the new material and calculated the required number of replications according to this. The demand, that differences of 10% of the experimental mean should be significant at 90% level is met by 20 single tree replications. As a precaution against uncontrolled plant losses during the first years after plantation the number of 25 replications was chosen.

Due to plant losses and for some other reasons 1100 provenances were available at the end of the nursery period. This number was split up into 11 groups of 100 provenances each. As strata in the applied stratified randomization, geographical regions were chosen, assuming that neighbouring provenances should be equal or similar in performance. Thus the experimental unit of this trial is the block of 100 provenances with 25 plants each. The blocks are independent of each other, and each block can be regarded as a complete provenance trial in itself, containing material from the entire range of the collection.

In theory the 11 blocks should be equal in mean and variance within, thus being comparable.

The plan was proposed at the 1967 Provenance Meeting of IUFRO at Pont à Mousson near Nancy and all institutions interested were invited to participate in orthogonal field trials. From then on our trial obtained IUFRO status after having been a rather private enterprise. The costs for one set of experimental material — 1100 provenances with 27 500 plants — were 5000 DM, transport fees excluded.

The planting out of the field trials was successful and all reports were positive.

20 field trials were established in 13 countries:

No	Country	Locality	In charge of
01	Canada	New Brunswick	D. P. FOWLER
02	Ireland	SW of Dublin	J. O. DRISCOLL
03	England	SW of London	L. PEARCE
04	Norway	near Haugesund	H. ROBAK
05		near Kongsvinger and Tönsberg	J. DIETRICHSON
06	Sweden	near the west coast	P. KRUTZSCH
07		central Sweden	
08		in the North 63° 25'	
09		near Helsinki (non experimental)	L. KÄRKI
10	France	near Nancy	P. BOUVAREL
11	Belgium	(blocks 2, 4 and 6)	A. NANSON
12	Belgium	(blocks 1, 3 and 5)	A. JAMBLINNE
13	BRD	near Kaiserslautern	Schmalenbeck
14		near Hildesheim-Kassel	
15		N-W-Germany	
16	Scotland	(blocks 8, 9, 10 and 11)	R. LINES
17	CSSR	SE of Praha	B. VINŠ
18	Austria	blockwise, throughout country	L. GÜNZL
19	Poland	Kraków	S. BALUT
20	Hungary	NE of Budapest	L. SZÖNYI

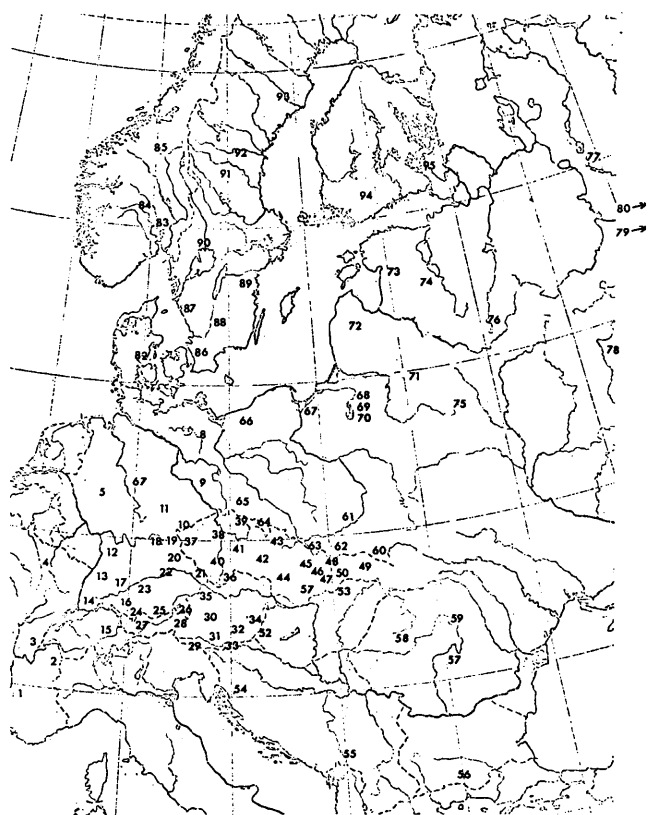


Fig. 1. — IUFRO 64/68. Regions of provenances (Stockholm 1972). The numbers approximately indicate the centre of provenance clusters.

From surplus material at Halstenbeck, Dr. W. KNABE from Landesanstalt für Immissionsschutz at Essen established field trials with 200 provenances at 4 localities in Germany for investigations on resistance to industrially polluted air. Dr. VINŠ from Brno established an extra provenance trial with 49 provenances testing the material in multi tree plots.

At an early stage of the collection about 400 seed samples were sent to Dr. A. FRÖHLICH at Hessische Forstliche Versuchsanstalt, Hann. Münden, Germany for parallel experiments. This material was planted out into 4 major field trials in Germany (BRD).

The documentation of provenance data has been provided from Stockholm. Decks of 80 columns punch cards were sent to all participants in the trial in order to guarantee uniformity.

In order to facilitate the handling of the material a suggestion of assortment of provenances into regions has been made.

IUFRO — 64/68. — Assortment of Provenances into Regions (Stockholm 1972)

Regions and number of provenances/region			
1	5		54
2	13		55
3	5		56
4	5	France	57
5	9		58
6	7		59
7	12	NW-Germany	60
8	12		61
9	2		62
10	11		63
11	9	DDR	64
12	7		65
13	19		66
14	16		67
15	18	(Switzerland)	68
16	15		69
17	28	SW-Germany	70
18	11		71
19	11		72
20	7		73
21	58		74
22	31		75
23	35		76
24	13		77
25	14		78
26	26	SE-Germany	79
27	16		80
28	21		81
29	5		82
30	24		83
31	24		84
32	49		85
33	7		86
34	12		87
35	3		88
36	17	Austria	89
37	12		90
38	8		91
39	7		92
40	9		93
41	19	Bohemia	94
42	25		95
43	10		96
44	11		
45	24	Moravia	
46	5		
47	23		
48	25		
49	3		
50	7		
51	2	Slovakia	
52	7		
53	4	Hungary	

This assortment is meant as a working hypothesis and suggested for common use until a better and more logical grouping of provenances can be worked out. It was not intended to make up an a-priori classification of delimited ecotypes.

The IUFRO 64/68 field trial no 06 near Halmstad at lat. 56° 56', long 12° 44' and 65 m above sealevel in southern Sweden has been assessed for total plant height in autumn 1972 at an age of 8 years after sowing, and 5 years after planting. The data have been processed with the Stockholm Single Tree Plot Series of Computer Programmes.

The development of the experiment

The planting out in the spring of 1968 was successful, due to excellent plant quality. The initial losses were less than 2% and are negligible.

On September 7th, severe plant damage was caused by an extremely early frost. Only about 20% of the plants were free from visible injuries. Almost 10% of the plants in this field trial were reported as dead in the autumn of 1969. It is assumed that most of the losses are direct sequelae of the frost. It is obvious, that provenances with late cessation of annual growth were more exposed to damage than others.

Just as the severe early autumn frost of 1968 was not normal for the test site, the complete lack of late spring frosts during the first years was not normal either. So, as a consequence of these particular climatic conditions it is clear that:

Early flushing provenances have not been hampered, whereas late flushing provenances have had no chance to gain relatively. —

and — Early cessation has been of extreme advantage, whereas late cessation has been punished in excess.

The results

The results are recorded as means within regions. The figures on the map (mean height in cm) indicate the centre of regions. The limit between superior and average plus inferior regions has been chosen to give the most perspicuous view.

Findings with regard to evaluation

1. Surprisingly high values for inter-class-correlations: Provenances within Blocks. All values are above .9, indicating small variation within provenances compared with variation between provenances.
2. In general, surprisingly low values for F-ratios: between Provenances within Regions: A few exceptions only indicate significant differences within regions. (See list)
3. Surprisingly small differences between the highest and the lowest provenances. In the Swedish nursery test on 1012 provenances the ratio was 1 : 6, in the original plant-stock of this series differences of 1 : 5 and 1 : 6 have been observed and reported.

At the age of 8 (5) in southern Sweden the average of the 11 blocks is 1 : 1.9 (with max. 1 : 3.04).

Findings with regard to provenance performance

1. The regions indicated as superior by the IUFRO trial of 1938 in South Sweden: White Russia, NE-Poland, S-Poland, Slovakia, the Eastern Carpathes and the Bihor Mountains in Romania prove to be superior also in the new trial.
2. An area comprising the Baltic states and the northern

parts of White Russia, which was not represented in 1938 shows high superiority.

3. A region in South Scandinavia: Denmark, the most southern parts of Sweden and the coastal strip up to Norway shows above average growth. The Danish material and a great part of the provenances from the very South of Sweden are not autochthonous, they originate from Central Europe.
4. With regard to the climatic conditions of this first test period, it is assumed that the future development will change the results: West European provenances will suffer from both late and especially early frosts and lose height relatively.

East European provenances will, for the same reason, gain in superiority.

The South Scandinavian provenances will share the fate of the West European ones, in spite of their relative hardiness to early frosts.

Acknowledgement

The initial work on this inventory provenance-test has been supported by grants from the Swedish Council for Forestry and Agricultural Research.

EXPERIMENT NO 06 SOUTH SWEDEN PLANT HEIGHT
1972, CM
COMPILATION OF REGIONS MEANS AND F-VALUES

RG H72

01	89.028	1.984	46	90.805	1.557
02	81.947	1.745	47	98.938	1.915
03	83.169	2.306	48	103.240	3.344
04	90.107	.418	49	102.001	2.534
05	88.874	1.058	50	97.222	2.971
06	89.100	1.886	51	93.665	8.582
07	88.978	.964	52	86.557	1.830
08	88.877	.938	53	87.176	2.055
09	83.790	.085	54	83.726	.664
10	90.894	2.377	55	75.767	10.191
11	85.915	1.180	56	83.032	2.815
12	77.933	1.858	57	92.339	2.463
13	83.531	1.165	58	105.920	1.719
14	87.994	1.670	59	99.432	1.638
15	30.034	2.221	60	103.760	2.868
16	85.046	1.866	61	90.972	.378
17	86.113	.738	62	97.150	1.569
18	87.837	2.032	63	98.501	1.684
19	93.233	2.196	64	95.393	2.139
20	88.359	3.047	65	94.038	.976
21	87.022	2.093	66	103.484	1.289
22	86.476	1.460	67	92.241	1.341
23	87.678	1.022	68	105.523	2.284
24	87.711	1.602	69	105.847	1.782
25	83.113	1.895	70	101.189	2.493
26	87.344	2.269	71	100.970	2.306
27	84.574	1.777	72	110.024	1.398
28	83.413	3.082	73	111.626	1.649
29	80.504	.494	74	103.879	.703
30	84.416	1.321	75	100.053	1.266
31	84.456	2.537	76	102.967	.261
32	87.069	1.458	77	86.537	7.974
33	85.289	3.014	78	96.878	.840
34	87.362	1.583	79	88.907	.634
35	82.101	.513	80	84.269	2.038
36	88.829	1.940	81	105.054	6.098
37	93.127	.977	82	100.372	.183
38	90.971	1.352	83	100.226	4.210
39	92.033	.900	84	89.647	1.023
40	88.221	.155	85	81.686	2.999
41	89.922	1.411	86	97.010	.401
42	91.304	1.434	87	99.520	.597
43	95.143	3.761	88	92.176	2.217
44	92.230	1.196	89	90.574	3.466
45	96.098	2.110	90	96.511	1.430
			91	81.724	5.423
			92	77.980	3.138
			93	68.630	3.147
			94	92.813	1.182
			95	85.138	1.839
			96	97.879	.000

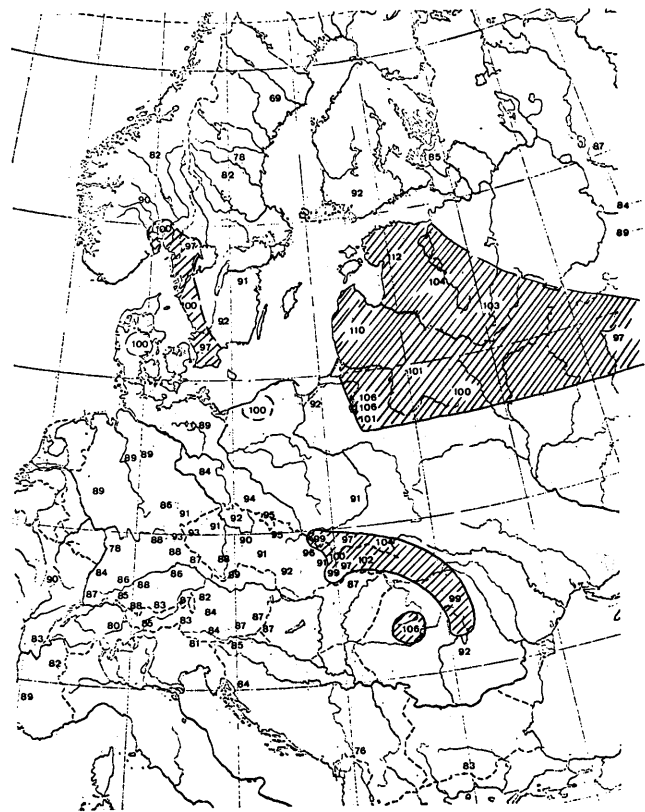


Fig. 2. — The IUFRO Provenance Test with Norway Spruce of 1964/68. Experiment 06, South Sweden. Plant height in autumn 1972. Regional means (cm) indicate the centre of the regions. Experimental mean = 90.2.

Abstract

In 1968 field trials with 1100 provenances of Norway Spruce (*Picea abies* (L.) KARST.) were established in 20 localities in 13 different countries. In this paper the background and performance of this inventory provenance test is reported. The series is now one of the major activities of the IUFRO Working Party for provenance research on Norway spruce (IUFRO S 2.02.11).

In experiment 06, near Halmstad in the south west of Sweden, total plant height was measured at the age of 8 years in autumn 1972. The results are discussed with regard to the very particular climatic conditions during the short of the field trial.

Key words: Norway spruce, inventory provenance test, Sweden, growth, frost hardiness.

Zusammenfassung

Im Jahre 1968 wurden 20 Feldversuche in 13 verschiedenen Ländern mit 1100 Herkünften der Fichte (*Picea abies* (L.) KARST.) angelegt. Hier wird über den Hintergrund und die Durchführung dieses inventierenden Herkunftversuches berichtet. Diese Serie von Versuchen ist nunmehr einer der Hauptpunkte der IUFRO Arbeitsgruppe für Provenienzforschung mit Fichte (IUFRO S 2.02.11).

Im Versuch Nr. 06 dieser Serie, in der Nähe von Halmstad im südwestlichen Schweden, wurden Pflanzenhöhen im Alter 8, im Herbst 1972 gemessen. Die Versuchsergebnisse werden unter Berücksichtigung der anomalen Witterungsbedingungen während der ersten Versuchsjahre besprochen.

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The application of ecological genetics principles to forest tree breeding

By P. M. A. TIGERSTEDT¹⁾

Department of Plant Breeding
University of Helsinki, Finland

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Definitions

Ecological genetics, a synthetic discipline, is difficult to define. It draws heavily on population genetics, quantitative genetics, population biology (itself an interdisciplinary science) and ecology. It is, however, justifiable to breed plants on an ecological genetic basis as the ecological basis is a model example of the interdisciplinary approach so essential in almost all fields of modern biology. Applied biology, in this case forest tree breeding, just does not advance if not approached wisely. It seems as though ecological genetics has finally advanced to a point of refinement which makes it imperative for all kinds of plant breeding. Forest trees with their long generation intervals, and often quite complicated natural ecosystems, stand out as particularly interesting organisms for ecological genetic studies. Emphasis has changed in recent years from more orthodox quantitative genetic approaches to ecological genetics. Heritability studies and the like are, of course, important components in the design of breeding programs but they are quite unreliable if not studied within a wider ecological framework. All these statements can of course be met with a laconic "so what" and it is our intention to penetrate a little the smooth surface into the maze of the ecosystem (food web) beneath.

Self-organizing systems relying largely upon feedback effects are inherent in all phenomena constituting our present world, be it mechanical or biological. These systems occasionally go astray — the results: severe distortion of the balance and input-output nonlinearity. The difference between a mechanical and a biological system is basically one of adaptation. To quote DOBZHANSKY (1956 and later) adaptation is the process of becoming adapted, adaptedness is a status of being adapted, i.e. of being able to live and reproduce in a given environment, while adaptability is an ability to become adapted to a certain range of environments.

A new situation in a biological system causes gradual genetic change in that system until a new optimum condition is attained. This change occurs gradually and almost

unnoticed as it is accompanied by invariant reproduction (MONOD 1970). Adaptation in a strictly mechanical system does not in fact occur. At the most such a system adjusts itself through feedback. This, however, does not bring the mechanical system closer to optimality, but merely protects it against damage caused by adverse operating conditions. An optimal yield system in biology is a system in which a certain input, in terms of energy gives a maximum return through growth. An ecosystem is by definition a community of plants (and animals) and its environment treated together as a functional system of complementary relationships, and transfer and circulation of energy and matter (WHITTAKER 1970). The balance of an ecosystem depends on the details of birth, growth, reproduction and death of individuals in the system, i.e. on its demography. Generally, ecosystems follow the diversity-stability rule which means that stability increases with diversity. This rule is valid not only when concerning ecological food-webs but also when diversity is measured as heterozygosity within populations. Just as a last introductory remark we can conclude that biological systems which function adaptively may adjust themselves in basically three different ways; they may tend towards maximum yield within time limits, they may tend towards maximum sustainable yield or they may tend towards yield optimality. It is a matter of species strategy (r- and K-strategists) and ecological succession which of these ways is chosen. A system close to yield optimality, however, is most reliable. It is ecologically stable, it operates under conditions of low energy dissipation and it is highly diversified both inter- and intra-specifically. It is precisely this optimality principle that form the basis for new thinking in forest tree breeding. Ecological genetics gives answers to the many aspects involved in this interdisciplinary science.

Provenance research — the oldtimer in ecological genetics

Genecology is a synthetic discipline combining ideas and methods from genetics, taxonomy and plant physiology (HESLOP-HARRISON 1964). Provenance research means approximately the same, i.e. genecological observations of species variability that are made from a plant breeder's utilitarian point of view. Actually, the term has been

¹⁾ Address of the author: P. M. A. TIGERSTEDT, Department of Plant Breeding, University of Helsinki, SF-00710 Helsinki 71, Finland.