A Revised Classification of Geographic Varieties in Scots Pine[1])

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Introduction

The original description of Scots or Scotch pine ***Pinus sylvestris*** L.) by Linnaeus was brief and cuntained no reference to the great amount of variability in the species. The first geographic variety to be described in the taxonomic literature was P. ***sylvestris*** var. ***haguenensis*** Loudon, named in 1838. Since Loudon's work, 51 other geographic varieties and numerous cultivars have been described, and Carlisle's (1958) book included 144 different names for infraspecific taxa of various categories.

Early in the present century Schott (1907) wrote a paper summarizing the races of Scots pine in which he recognized nine varieties, some described by him for the first time. A year later Elwes and Henry (1908) also recognized nine varieties, but only two were the same as described by Schott. Both workers covered only a part of the species' range. Other writers of taxonomic manuals (Beissner, 1909; Beissner and Fitschen, 1930; Rehder, 1940, 1949; Dallimore and Jackson, 1948, 1966) have also covered parts of the species' range and have recognized from four to 14 varieties. Even when two authors recognized the same varieties, they often differed as to varietal limits.

Svoboda (1953) of Poland was the first to attempt a complete monograph of the species. To information gained from phenotypic descriptions of natural forests, he added biometrical data gathered from mass collections made in several parts of the range. He recognized 35 geographic varieties, several described by himself. Next was Gaussen (1960) of France, who stressed pollen characteristics as well as other traits and recognized 30 geographic varieties. Third was Staszkiewicz (1960, 1961, 1062, 1970) who made biometrical studies and summarized the classification schemes of his predecessors.

Most authors were aware of provenance test data and attempted to use genetic concepts in limiting varieties. However, with the exception of Langlet's (1936) comprehensive study of Swedish material, the provenance tests available to these authors did not involve sufficient seedlots to serve as the basis for a genetic classification scheme. Thus, all the classification schemes mentioned above are based upon phenotypic data.

We became interested in the problem and wanted to learn how well the classical taxonomic or phenotypic classification schemes agreed with one based on genetic information derived from large replicated provenance tests. Part of the results have been presented in a previous paper by the senior author (Ruby, 1967). In the present paper we present the basis for the genetic classification, the most suitable taxonomic names, and descriptions of the varieties based upon genetic data.

Description of the genetic experiments

The genetic data used in this paper are derived principally from the NC-99 (formerly NC-51) provenance tests of Scots pine which were started in 1958 with the importation of seed. These tests are made up of two separate experiments which include altogether trees grown from seed collected from 164 natural stands in nearly all parts of the species' natural range in Europe and Asia ***(Figs.*** *1 and 2).* An additional 24 seedlots were obtained from plantations or dealers. Nearly all seedlots were collected from several unselected trees in a stand.

The seedlings were grown for two years in an experimental nursery in East Lansing and then transferred to permanent test plantations. The plantations were established in 1961—62 for the first experiment and 1962—63 for the second experiment. In all, 49 test plantations were established in 11 states. The present report is based primarily on data from 12 plantations in Michigan and 7 in other north central states. Most of these 19 plantations contain 72 to 108 seedlots each, and were replicated 10 times with 4-tree plots. Nearly all seedlots were represented in four or more plantations.

Several traits (height, foliage color, winter damage, needle length, etc.) were measured while the seedlings were still in the nursery. These same traits have been measured one to several times in each of the 19 best-studied plantations, the last time in 1974. Additionally, resistance to pests, date of bud formation, stem form, mineral nutrient content ob the foliage, and monoterpene content of the cortical oleoresin has been measured in one or more test plantations. The results have been summarized in a series of papers by Wright and Bull (1963), Steinbeck (1965), Wright, Pauley ***et al.*** (1966), Wright, Wilson and Randall (1967), Wright and Wilson (1972), Tobolski and Hanover (1971) Steiner (1974), Wright, Wilson and Bright (1976), Wright, Lemmien ***et al.*** (1976) and Brown (1967, 1970).

The nursery data from the first of the two experiments were subjected to a multivariate analysis which served as the basis for the provisional classification into geographic ecotypes used in Wright and Bull (1963). Three years later, using data from all plantations, the provisional classification was revised slightly and variety names were substituted for the letters used earlier to denote ecotypes (Wright, Pauley ***et al.*** 1966).

Further refinements have since been made. Each set of measurement data, whether for a single plantation or combined for several plantations, has been subjected to analysis of variance. For these analyses, the seedlots have been grouped by regions in such a manner as to maximize the amount of genetic variation accounted for by between-region differences and to minimize the amount accounted for by within- region differences. We attempted to make the groupings as natural as possible. Also, we attempted to arrive at a final grouping applicable to the largest possible number of diverse traits.

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Correspondence between phenotypic and genetic classification schemes

As the previously mentioned taxonomic classifications schemes were based on phenotypic data, it seemed desirable to learn whether the taxonomic groupings had a genetic basis. This was done by the senior author, who wrote cooperators in Europe and asked that leaves and cones be collected from several individual trees in each of many natural stands. The samples were to be collected in a standard manner from trees of a prescribed size class growing under prescribed conditions in order to minimize the amount of environmentally induced variation. Response was good, and samples were obtained from 35 different stands. For these samples, several leaf and cone characteristics were measured and the data were subjected to statistical analysis. The main conclusions were based upon analysis of variance, conducted in such a manner as to separate the variation into between-region, between-stand-within-region, and between-tree-within-stand components. The methods used were similar to those used by Svoboda and Staszkiewicz.

The 35 stands sampled in this manner were among those represented by offspring in the NC-99 provenance tests. This provided an opportunity to compare a phenotypic classification scheme with a genetic one based upon nursery data available at the time. The results of such a comparison are presented in a paper by Ruby (1967). Those results can be summarized as follows: (1) There was a close correspondence between the phenotypic and genetic grouping of populations, and (2) The phenotypic data derived from European stands provided few clues as to the probable performance of the offspring of those stands in Michigan. In other words, one could learn from the phenotypic analyses which stands were apt to be the most similar or most different genetically, but one could not learn which stands produced progeny which might grow the best (or have the best color or be straightest) in Michigan.

The concept of a geographic variety of Scots pine

The concept of a geographic variety has varied with time, and also differs among taxonomists. Therefore, it is desirable to define the concept specifically as it is used in this paper.

(1) A geographic variety has a distinctive geographic range. It may also be termed a geographic race, geographic ecotype, or portion of a cline. The geographic ranges of some isolated varieties such as those inhabiting Spain and southern France can be delimited exactly. Where varieties intergrade with each other, as in Scandinavia, the boundaries can only be approximated.

It is possible theoretically to have altitudinal as well as geographic races. We found no cases, however, in which high- and low-elevation seedlots from a limited geographic area differed consistently. Langlet (1936) did find consistent elevational differences in Sweden, but his high- and low-elevational seedlots were from different geographic regions.

(2) A variety is a taxonomic unit and therefore should be named in accordance with the International Code of Botanical Nomenclature. Among other things, this means adherence to the rules of priority, under which the first validly published name is the proper one. Fortunately, many names in common use have priority and will therefore continue to be accepted. It is also fortunate that most of the acceptable names are descriptive and might be considered most suitable even if they lacked priority.

(3) Being taxonomic units and presumably of some use in the field as well as in genetic studies, varieties should differ phenotypically as well as genetically. Very often, however, the most distinctive features of a naturally growing variety are so much under environmental control as to be of little use in characterizing the variety away from its natural habitat. For example, Elwes and Henry (1908) described var. *rigensis* as having cylindrical stems with few lateral branches and var. *haguenensis* as having stems not so tall or clear with numerous lateral branches. Those de-

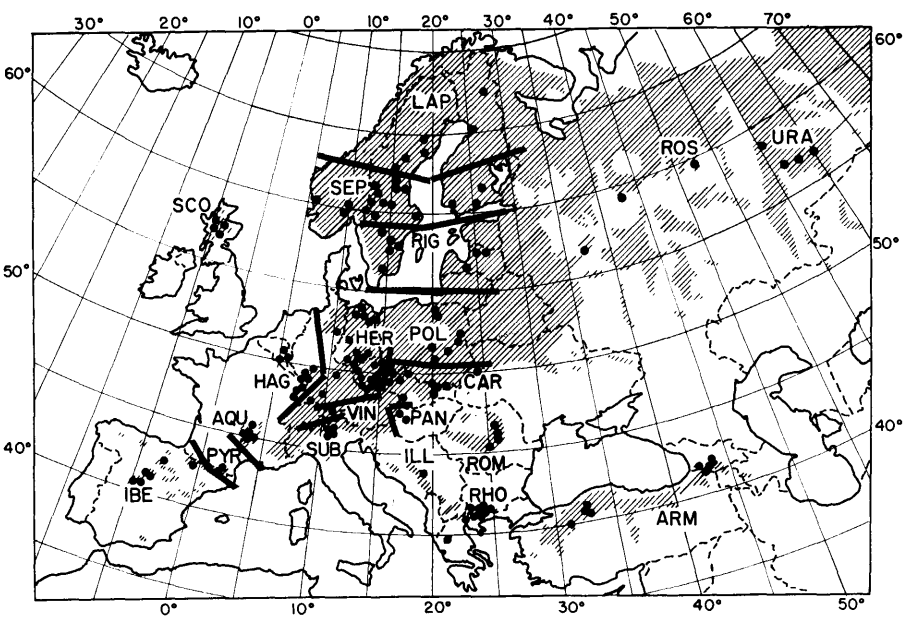

Figure 1. — Natural distribution (shaded), location of natural stands tested in the provenance studies (dots) and geographic varieties of Scotch pine in Europe and western Asia. The varietal abbreviations are as follows: *AQUitana, ARMena, CARpatica, HAGuenensis, HERcynica, IBErica, ILLyrica, LAPponica, PANnonica, POLonica, PYReneica, RIGensis, RHOdopaea, ROManica, ROSsica, SCOtica, SEPtentrionalis, SUBillyrica, URAlensis, VINdelica.* (Distribution after Critchfield and Little, 1966).

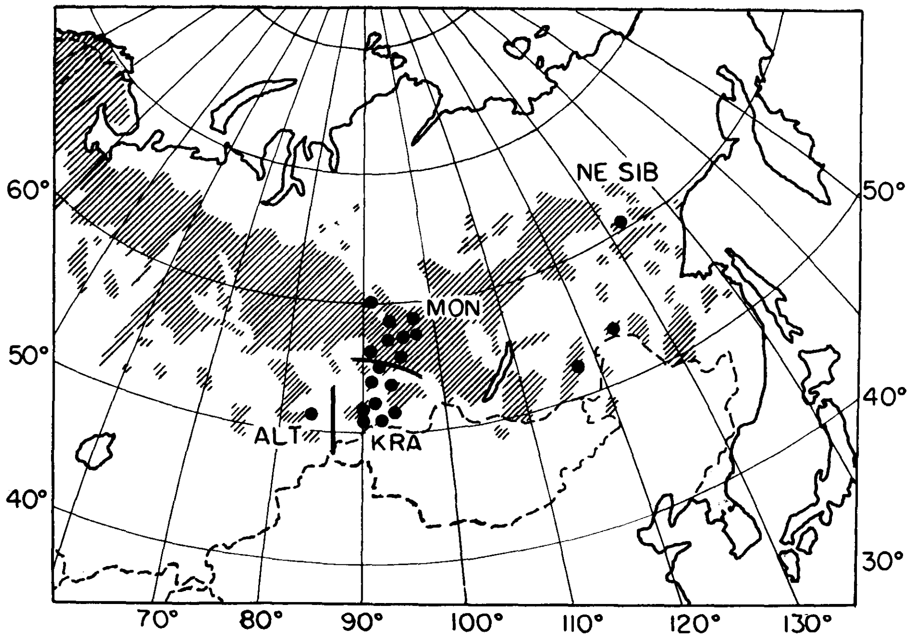

Figure 2. — Natural distribution, shaded), location of natural stands tested in the provenance studies (dots) and geographic varieties of Scotch pine in central and eastern Asia. Abbreviations are as follows: *NE SIBeria, MONgolica, KRAsnoyarsk, ALTaica.* Other valid varieties may exist in unsampled areas. (Distribution after CRITCHFIELD and LITTLE, 1966).

scriptions obviously reflected cultural practices and environmental conditions around Riga and Hagenau, respectively, but do not necessarily reflect the genetic potential of the varieties.

Descriptions based upon biometrical studies have the advantage of more nearly reflecting genetic differences among varieties. However, the differences among varieties are often based upon such obscure characteristics as to be of little practical value.

(4) A geographic variety has a genetic basis. In our delimitation of varieties we have relied most heavily on the genetic data from the NC-99 experiments in Michigan For Scandinavian populations, LANGLET's (1936) paper has been useful.

We based the decision on whether to recognize one or two varieties in a particular area on the pattern of variation rather than on the size of the differences. Two varieties were recognized if a line could be drawn such that nearly all seedlots from one side of the line behave differently from nearly all seedlots from the other side of the line. One variety was recognized if no such line could be drawn. In Czechoslovakia, for example, most seedlots from east of longitude 15° E. grew faster than most seedlots from west of that line. Accordingly, var. *carpatica* (eastern Czechoslovakia) was recognized as different from var. *hercynica* (western Czechoslovakia, parts of East Germany and parts of West Germany).

(5) For the Michigan experiments, differences among varieties accounted for 70 to 85% of the total genetic variation in most traits. Varieties which differed considerably in one trait were apt to differ markedly in other traits. There was no such tendency within a variety, and individual seedlots which differed in one trait were apt to be similar in other traits.

Distribution and characterization of varieties

The following list includes the varieties we recognize, their synonyms, geographic distribution (see also *Figs. 1 and 2)* and distinguishing characteristics. The textual descriptions are supplemented by tabular material *(Tables 1 through 4).* Our classification scheme is genetic and is based mainly on the results of experiments in Michigan. Among the phenotypic classification schemes, it is most similar to that of Svoboda. Therefore we follow SVOBODA where genetic data are lacking.

As the classification scheme is genetic, the descriptions and tables are also genetic. Genetic data are necessarily the results of experiments performed in one habitat or

Table 1. — Growth characteristics of Scotch pine varieties in Michigan.

Variety	Relative Height age 13		Winter Foliage color	Leaf length, age 4	Date of first year bud set	Trees having winter injury in northern Michigan
	South. Mich.	North. Mich.				
	---% of mean---		grade (0= yellowest) (10= greenest)	mm	day of year	%
SCANDINAVIAN VARIETIES						
lapponica	56	57	1.2	40	220	1
septentrionalis	81	86	2.3	47	220	0
rigensis	95	108	3.0	52	240	0
NORTH RUSSIAN AND SIBERIAN VARIETIES						
'NE Siberia'	40	45	0.0	45	200	0
mongolica	76	79	1.5	48	220	1
'Krasnoyarsk'	86	89	2.9	53	225	1
altaica	116	99	3.3	--	230	0
uralensis	95	104	1.1	52	220	0
rossica	84	87	2.4	--	220	0
CENTRAL EUROPEAN VARIETIES						
polonica	114	125	4.6	58	245	0
hercynica	118	125	6.6	56	245	1
haguenensis	126	125	7.6	71	255	1
carpatica	125	127	5.6	59	245	0
pannonica	114	115	6.5	60	255	0
vindelica	100	106	6.3	51	245	0
romanica	107	112	--	--	--	0
VARIETIES FROM BRITISH ISLES, SOUTHERN EUROPE AND SOUTHWEST ASIA						
scotica	98	94	7.6	48	230	4
'E. Anglia'	112	118	8.3	62	240	3
iberica	87	66	10.0	43	265	55
aquitana	104	85	9.6	42	250	5
pyreneica	80	60	10.0	42	255	25
subillyrica	101	98	6.4	52	265	1
illyrica	108	107	7.3	54	250	1
rhodopaea	103	97	8.2	52	250	2
armena	96	90	8.8	54	255	4

Table 2. — Differences among Scotch pine varieties in fruitfulness at early ages ans susceptibility to bird and insect pests.

Variety	Cone-bearing trees Age 7–14	Proportion of trees attacked by				
		Pine Grosbeak	European pine sawfly	White pine shoot borer	Pine root collar weevil	Zimmerman moth
	%	-------% attacked-----			----% dead----	
SCANDINAVIAN VARIETIES						
lapponica	8	77	0	7	14	15
septentrionalis	11	64	2	21	38	11
rigensis	14	30	6	31	45	40
SIBERIAN VARIETIES						
'NE Siberia'	0	50	0	5	0	30
mongolica	8	32	1	18	12	30
'Krasnoyarsk'	3	33	1	18	42	42
uralensis	13	25	3	19	40	25
CENTRAL EUROPEAN VARIETIES						
polonica	9	5	19	37	67	0
hercynica	16	10	21	34	69	5
haguenensis	20	7	26	38	65	27
carpatica	10	7	20	42	43	16
pannonica	10	0	20	47	45	23
VARIETIES FROM BRITISH ISLES, SOUTHERN EUROPE AND SOUTHWEST ASIA						
scotica	24	46	7	41	31	3
'E. Anglia'	34	28	27	36	55	39
iberica	8	7	11	58	17	6
aquitana	26	11	10	49	11	6
pyreneica	6	--	10	--	16	--
subillyrica	17	21	12	44	11	3
illyrica	10	20	19	56	10	9
rhodopaea	7	21	9	53	19	5
armena	12	20	7	51	12	6

Table 3. — Cortical monoterpene composition of Scotch pine varieties (after Tobolski and Hanover, 1971).

Variety	Concentration of						
	α-Pinene	β-Pinene	Myrcene	3-Carene	Limonene	β-Phellandrene	Terpinolene
	---------------% of total monoterpenes---------------						
SCANDINAVIAN VARIETIES							
lapponica	9	17	6	41	9	11	3
septentrionalis	8	17	8	44	6	10	4
rigensis	7	14	8	47	6	11	4
SIBERIAN VARIETIES							
'NE Siberia'	15	29	12	9	16	16	1
mongolica	11	17	7	26	14	17	4
uralensis	9	20	11	25	11	17	3
CENTRAL EUROPEAN VARIETIES							
polonica	10	22	9	38	8	6	3
hercynica	10	25	13	32	8	8	3
haguenensis	10	20	10	42	5	5	3
carpatica	8	15	8	40	7	7	4
pannonica	8	13	6	50	6	9	5
VARIETIES FROM BRITISH ISLES, SOUTHERN EUROPE AND SOUTHWEST ASIA							
scotica	11	22	12	40	5	5	3
'E. Anglia'	17	32	11	26	4	3	2
iberica	46	15	13	1	7	15	Trace
aquitana	18	50	19	5	9	4	Trace
pyreneica	21	32	15	2	24	2	1
subillyrica	17	42	22	4	6	4	1
illyrica	12	24	18	20	13	8	2
rhodopaea	12	35	12	6	23	8	1
armena	19	43	18	4	10	3	1

Table 4. — Foliar mineral content of eight elements studied by Steinbeck (1965), expressed as a percentage of the overall 3-plantation mean for each element.

Variety	Relative Concentration of Element							
	N	P	Na	Ca	Mg	Fe	B	Zn
	--------------% of overall mean----------------							
SCANDINAVIAN VARIETIES								
lapponica	103	104	88	104	92	115	86	98
septentrionalis	104	100	92	105	87	94	107	103
rigensis	100	102	98	100	97	94	100	96
SIBERIAN VARIETIES								
mongolica	99	106	99	106	69	89	85	109
uralensis	97	102	81	103	87	94	92	103
CENTRAL EUROPEAN VARIETIES								
polonica	105	103	105	99	118	106	103	105
hercynica	101	103	80	94	118	116	107	98
haguenensis	104	105	110	99	119	113	99	107
pannonica	88	90	94	88	110	101	97	104
VARIETIES FROM BRITISH ISLES, SOUTHERN EUROPE AND SOUTHWEST ASIA								
scotica	100	98	97	90	96	133	92	94
'E. Anglia'	99	97	117	85	100	114	101	108
iberica	94	89	116	92	96	90	107	96
aquitana	97	96	133	101	101	102	106	96
rhodopaea	99	101	124	110	98	107	102	108
armena	99	102	103	103	107	105	96	83
Absolute average content, expressed on a dry weight basis	1.87	.21	67	.41	.08	78	32	63
Units	%	%	ppm	%	%	ppm	ppm	ppm

one series of habitats. Since the NC-99 experiments are the only ones in which most of these varieties have been compared with each other, they are the principal sources of descriptive material. The papers from which the descriptions were compiled are cited in the earlier section "Description of the Genetic Experiments".

The other alternative would have been to prepare phenotypic descriptions of the varieties as they occur in their natural habitats. Such descriptions would be valuable for many purposes, but would not reflect the genetic differences among varieties and would not apply if the trees were to be grown in other habitats. Also, we are not well qualified to produce such descriptions.

A few words about stem form are in order. In Michigan, form proved to be a function of susceptibility to a particular pest and relative abundance of that pest, and was under indirect genetic control. Thus, some varieties such as var. *rigensis* which have been widely regarded as having excellent stem form under all circumstances proved to be straight-stemmed in some test areas and to be very crooked in other areas containing pests to which these varieties were susceptible.

Scandinavian varieties. The Scandinavian varieties are similar to each other in several respects. In Michigan they grew slowly to very slowly, had yellow winter foliage, flushed 2—3 days earlier than central European varieties, had high concentration of β-phellandrene, and were very susceptible to the pine root collar weevil. These varieties are probably portions of a north-south cline.. Langlet (1936) found that northern seedlings of this cline had higher dry matter contents than southern seedlings when grown in Sweden. We found no consistent east-west differences to support Svoboda's recognition of separate Norwegian, Swedish and Finnish varieties. The three varieties we recognize are:

P. sylvestris var. *lapponica* (Fries) Hartman. Synonyms: *P. frieseana* Wichura, *P. lapponica* Fries, *P. s.* var. *borealis* Svoboda, *P. s.* var. *frieseana* (Wichura) Caspary. Distribution: north of latitude 63° N in Norway, Sweden, Finland and probably the USSR. Two seedlots from north of latitude 65° N grew even more slowly than the others and are possibly entitled to separate status. Performance in Michigan: very slow growth, very yellow winter foliage, irregular crowns.

P. sylvestris var. *septentrionalis* Schott. Synonyms: *P. s.* var. *suecica* Svoboda, *P. s.* var. *fennica* Svoboda, *P. s.* var. *norvegica* Svoboda. Distribution: latitudes 59 to 63° N in Norway, Sweden and Finland. Performance in Michigan: slow growth, yellow winter foliage, narrow regular crowns, high susceptibility to attack by the pine grosbeak.

P. sylvestris var. *rigensis* Loudon. Synonyms: *P. rigensis* Desfontaines, *P. s.* var. *baltica* Svoboda, *P. s.* var. *septentrionalis* Schott (in part). Distribution: southern Sweden, Latvian SSR, Estonian SSR. Latvian and Swedish provenances differed significantly in the New Hampshire experiment reported by Wright and Baldwin (1957) but not in the NC-99 experiments. Performance in Michigan: moderate growth rate, yellow winter foliage, narrow regular crowns, straight stems except where attacked by Zimmerman pine moth or the pine grosbeak.

North Russian and Siberian varieties. Like the Scandinavian varieties, those from European and Asiatic USSR are characterized by slow growth, yellow winter foliage, early flushing, high concentration of β-phellandrene, and low resistance to pine root collar weevil. Trees from the USSR have high resistance to European pine sawfly and in Michigan produce very few flowers prior to age 18. These varieties are incompletely known.

'Northeast Siberia' race. One seedlot from the Yakutsk ASSR, extreme northeastern Siberia, grew very slowly. It resembles seedlots from extreme northern Finland in growth traits but not in cortical monoterpenes. This race has not been formally described as a variety.

P. sylvestris var. *mongolica* Litvinof. Synonyms: *P. s.* var. *jakutensis* Sucacz., *P. funebris* Komarov, *P. yamazutai* Uyeki, *P. takahasii* Nakai. Distribution: latitudes 50 to 55^0 N in eastern Siberia and 55 to 60^0 N in central Siberia (Amur Province and Krasnoyarsk Region). Performance in Michigan: slow growth.

'Krasnoyarsk' race. Distribution: south of latitude 55^0 N in Tuvinsk Oblast and Krasnoyarsk Region of central Siberia. Performance in Michigan: several seedlots of this race consistently grew 10% faster and averaged one color grade greener in winter than did seedlots from north of latitude 55^0 N.

P. sylvestris var. *altaica* Ledeb. Synonyms: *P. s.* var. *sibirica* Ledeb. (in part), *P. padufia* Ledeb. ex Gord. (in part). Distribution: Altai Mountains of south-central Siberia, south to Kirghiz and Sungaria. Performance in Michigan: 25% faster growth than var. *mongolica.*

P. sylvestris var. *uralensis* Fischer. Synonyms: *P. s.* var. *obensis* Svoboda, *P. s.* var. *sibirica* Ledeb. (in part), *P. padufia* Ledeb. ex Gord. (in part). Distribution: Ural Mountains between European and Asiatic USSR. Performance in Michigan: moderate growth rate, narrow regular crowns with ascending branches, high resistance to European pine sawfly, foliage very yellow during the winter but dark green in summer.

P. sylvestris var. *rossica* Svoboda. Central European Russia. Slightly faster growth than in var. *mongolica.*

Other possibly valid varieties: *P. s.* var. *baschirica* Svoboda, *P. s.* var. *sarmatica* Zapalowicz, *P. s.* var. *scythica* Svoboda, *P. s.* var. *kasachstanica* Svoboda, *P. s.* var. *ucrainica* Svoboda. These were recognized by Svoboda. Provenance data are insufficient to make firm decisions on their genetic distinctness.

Central European varieties. The central European varieties are so similar to each other as to indicate they became differentiated from a common ancestor in post-Pleistocene times. In north central United States they grew at moderate to fast rates, produced long needles, had green winter foliage, produced cones at early ages, and had low resistance to European pine sawfly and pine root collar weevil.

P. sylvestris var. *polonica* Svoboda. Distribution: Poland. Performance in Michigan: slightly yellower during winter than var. *hercynica* and doubtfully distinct from that variety.

P. sylvestris var. *hercynica* Münch. Synonym: *P. s.* var. *genuina* Heer. Distribution: West Germany except for the Pfalz, East Germany, Czechoslovakia west of longitude 15^0 E. Performance in Michigan: rapid growth. Linnaeus' herbarium contains specimens collected in Germany, and it is likely that this should be considered as the type variety.

P. sylvestris var. *borussica* Schott. Distribution: lowlands of northeastern East Germany. Performance in Michigan: slightly slower growing than var. *hercynica* and doutbfully distinct from that variety.

P. sylvestris var. *haguenensis* Loudon. Synonyms: *P. s.* var. *superrhenana* Schott, *P. s.* var. *rubra* Endlicher, *P. s.* var. *batava* Schott, *P. s.* var. *genuina* subvar. *haguenensis* Elwes and Henry. Distribution: Vosges Mountains of eastern France, Pfalz, Land of adjacent West Germany, and many plantations in Belgium. Performance in Michigan: more stem crooks than in other varieties, very rapid growth, heavy cone production on young trees, long needles, green foliage during the winter.

P. sylvestris var. *carpatica* Domin. Synonyms: *P. s.* var. *subcarpatica* Staszkiewicz, *P. s.* var. *meridionalis* Staszkiewicz (in part). Distribution: Czechoslovakia east of longitude 15^0 E. Performance in Michigan: as rapidly growing but better form than in var. *haguenensis.*

P. sylvestris var. *pannonica* Schott. Synonyms: *P. s.* var. *bohemica* Siman, *P. s.* var. *meridionalis* Staszkiewicz (in part). Performance in Michigan: slower growth and coarser branches than in var. *hercynica.*

P. sylvestris var. *vindelica* Schott. Synonyms: *P. s.* var. *reflexa* Heer, *P. s.* var. *engadinensis* (Heer) Hegi, *P. s.* var. *vulgaris* Bauhin, *P. s.* var. *vocontiana* Guinier and Gaussen, *P. s.* var. *brigantiaca* Gaussen, *P. genevensis* hort. Distribution: Switzerland, western Austria. Performance in Michigan: one *bona fide* seedlot from the Austrian Tyrol grew much less rapidly than var. *hercynica.* Two other 'Austrian' seedlots obtained from dealers differed so much from other central European trees as to indicate they were collected from plantations of diverse origins.

P. sylvestris var. *romanica* Svoboda. Distribution: Romania. Performance in Michigan: 10% slower growth than in var. *hercynica.*

Varieties from the British Isles. The Scottish population resembles south European varieties so much as to indicate it is a post-Pleistocene derivative of southern rather than central or northern stock. The "East Anglia" race is probably a hybrid derivative of Scottish and German origin. The hybridization probably took place several generations ago, for that race is as stable as any natural variety. Trees from the British Isles were green to dark green in winter, had high concentrations of 3-carene, grew at moderate to rapid rates, and flushed 1—2 days earlier than trees from central Europe.

P. sylvestris var. *scotica* Beissner. Distribution: four small areas in the Scottish highlands. Performance in Michigan: moderate growth rate, high frequency of branched terminal buds. This resembles southern varieties in foliage color, needle length and resistance to pine root collar weevil; it resembles northern varieties in monoterpene composition, phenology and resistance to Zimmerman pine moth.

"East Anglia" race. Distribution: certain plantations in East Anglia, England. Performance in Michigan: rapid growth, heavy cone production at early ages, high susceptibility to three serious insect pests.

Varieties from southern Europe and Turkey. These are characterized by green to very dark green foliage during the winter, large seeds, slow to medium growth rate, high concentrations of α-pinene or β-pinene, low concentrations of 3-carene (except var. *illyrica)*, high resistance to pine root collar weevil and Zimmerman pine moth, and late flushing (2—3 days later than for trees from central Europe. Most southern varieties have isolated ranges and do not intergrade with each other.

P. sylvestris var. *iberica* SVOBODA. Synonym: *P. s.* var. *catalaunica* GAUSSEN. Distribution: mountains of Spain with the possible exception of the Sierra Nevada in the extreme south. Performance in Michigan: very dark green winter foliage color, moderate growth rate, susceptibility to winter cold in northern areas, very high concentrations of α-pinene and β-phellandrene.

P. sylvestris var. *nevadensis* CHRIST. Synonym: *P. s.* var. *hispanica* SVOBODA. Distribution: Sierra Nevada Mountains of southern Spain. Doubtfully distinct from var. *iberica.*

P. sylvestris var. *aquitana* SCHOTT. Synoyms: *P. s.* var. *avernensis* BAYER, *P. s.* var. *caussicola* STASZKIEWICZ. Distribution: Massif Central of southern France. Performance in Michigan: slight susceptibility to winter cold damage in northern Michigan, dark green foliage color during the winter, very heavy cone and pollen production at early ages; high concentration of β-pinene.

P. sylvestris var. *pyreneica* SVOBODA. Distribution: French Pyrenees. Performance in Michigan: intermediate between vars. *iberica* and *aquitana*, high in limonene. Only one seedlot was tested.

P. sylvestris var. *subillyrica* CORONA. Synonym: *P. s.* var. *alpina* SVOBODA. Distribution: Trentino Province of Italy and possibly other parts of Italy and southern Switzerland. Performance in Michigan: resembling central European varieties in general appearance but slower growing and later flushing; resembling southern varieties in concentration of α-pinene, 3-carene and terpinolene, lateness of flushing, growth rate and resistance to pine root collar weevil.

P. sylvestris var. *illyrica* SVOBODA. Synonym: *P. s.* var. *balcanica* SVOBODA (in part). Distribution: mountains of central Yugoslavia. Performance in Michigan: resembling central European varieties in general appearance, phenology and monoterpene composition; resembling southern varieties in winter foliage color, resistance to pine root collar weevil, and resistance to Zimmerman pine moth.

P. sylvestris var. *rhodopaea* SVOBODA. Distribution: mountains of southern Bulgaria, northern Greece. Performance in Michigan: moderate growth rate, low concentrations of 3-carene and terpinolene, dark green winter foliage color, moderate leaf length.

P. sylvestris var. *armena* K. KOCH. Synonyms: *P. s.* var. *hamata* (STEVEN) KOMAROV, *P. kochiana* KLOTZSCH ex C. KOCH, *P. s.* var. *caucasica* FISCHER, *P. altissima* LEDEB. ex GORDON, *P. sosnowskyi* NAKAI. Distribution: Crimean SSR, Turkey, Armenian SSR, Georgian SSR. Performance in Michigan: similar to var. *rhodopaea* but fruiting more heavily.

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Summary

Genetic data derived from range-wide provenance tests were used to subdivide Scots pine into geographic races or portions of clines. These equal geographic varieties as described by taxonomists. The taxonomic varieties of *Pinus sylvestris* with a proven genetic basis are *lapponica, septentrionalis* and *rigensis* from Scandinavia; *mongolica, altaica* and *uralensis* from Siberia; *polonica, hercynica, haguenensis, carpatica, pannonica* and *romanica* from central Europe; *scotica* from Scotland; *iberica, aquitana, pyreneica, subillyrica, illyrica, rhodopaea* and *armena* from southern Europe and Asia Minor. Three additional races, not described taxonomically but distinct enough to war ant varietal status, are "NE Siberia", "Krasnoyarsk" and "East Anglia". Geographic distribution and performance of the varieties in Michigan are described.

Key words: Pinus sylvestris, phenotypic variation, provenance, intraspecific variation.

Zusammenfassung

In den Jahren 1961 bis 1963 wurden in 11 Staaten der nördlichen USA 49 Provenienzversuche mit 164 Herkünften von *Pinus sylvestris* aus dem gesamten natürlichen Verbreitungsgebiet angelegt. Es wird hier über die Entwicklung, Nadelfarbe, Frostgefährdung, Nadellänge usw. der Herkünfte in 12 Provenienzversuchen in Michigan und 7 in anderen nördlichen Zentralstaaten berichtet. Danach kann die Art in folgende geographische Rassen bzw. Varietäten eingeteilt werden:

Skandinavien = *lapponica, septendrionalis* und *rigensis,* Sibirien = *mongolica, altaica* und *uralensis,* Zentraleuropa = *polonica, hercynica, haguenensis, carpatica, pannonica* und *romanica,* Schottland = scotia, Südeuropa und Kleinasien = *iberica, aquitana, pyrenaica, subillyrica illyrica, rhodopaea* und *armena.* Dazu werden drei bisher nicht beschriebene geographische Rassen ausgeschieden: Ne Siberia, Krasnojarsk und East Anglia.

Literature Cited

BEISSNER, L.: Handbuch der Nadelholzkunde. Paul Parey, Berlin. 742 pp. (1909). — BEISSNER, L. and FITSCHEN, J.: Handbuch der Nadelholzkunde, ed 3. Paul Parey, Berlin. 765 pp. (1930). — BROWN, J. H.: Patterns of variation in root systems of Scotch pine provenances. Ph. D. thesis, Mich. State Univ. 161 pp. (1967). — BROWN, J. H.: Seedling growth of three Scotch pine provenances with varying moisture and fertility treatments. Forest Sci. 16: 43—45 (1970). — CARLISLE, A.: A guide to the named variants of Scots pine (*Pinus silvestris* LINNAEUS). Forestry 31: 203—224 (1958). — CRITCHFIELD, W. B. and LITTLE, E. L. JR.: Geographic distribution of the pines of the world. US Dept. Agri. Misc. Pub. 991. 97 pp. (1966). — DALLIMORE, W. and JACKSON, A. B.: A handbook of Coniferae including *Ginkgoaceae*, ed. 3. Edward Arnold & Co., London 682 pp. (1948). — DALLIMORE, W. and JACKSON, A. B.: A handbook of Coniferae and *Ginkgoaceae*, ed 4, rev. by S. G. Harrison. Edward Arnold & Co., London (1966). — ELWES, J. H. and HENRY, A.: The trees of Great Britain and Ireland. Edinburgh (1908). — GAUSSEN, H.: Les Gymnospermes, actuelles et fossiles. Generalites, Genre *Pinus*. Trav. du Lab. Forest. de Toulouse Tome II, sec. 1, v. 1, pt. 2 272 pp. (1960). — LANGLET, O.: Studier över tallens fysiologiska variabilitet och des samband med klimatet. Medd. f. Statens Skogsförsökanstalt 29: 219—470 (1936). — REHDER, A.: Manual of cultivated trees and shrubs. Macmillan, N. Y. 996 pp. (1940). — REHDER, A.: Bibliography of cultivated trees and shrubs hardy in the cooler temperature regions of the northern hemisphere. Arnold Arboretum of Harvard Univ. (1949). — RUBY, J. L.: The correspondence between genetic, morphological and climatic variation patterns in Scotch pine. I. Variations in parental characters. Silvae Genetica 16: 50—56 (1967). — SCHOTT, P. K.: Rassen der gemeinen Kiefer, *Pinus silvestris* L. Forstwiss. Cbl. 29: 199—218, 262—279 (1907). — STASZKIEWICZ, J.: Zmienność współczesnych i kopalnych szyszek sosny zwyczajnej (*Pinus silvestris* L.). (Variation in recent and fossil cones of *Pinus silvestris* L.). Floristica et Geobotanica 7 (1): 97—160 (1960). — STASZKIEWICZ, J.: Biometric studies on the cones of *Pinus silvestris* L. growing in Hungary. Acta Botanica 7: 451—466 (1961). — STASZKIEWICZ, J.: Badania biometryczne nad zmiennośćia szyszek sosny szwyczajnej (*Pinus silvestris* L.) w Masymywie Centralnym we Francji. (Recherches biométriques sur la variabilité des cones du pin sylvestre (*Pinus silvestris* L.) du Massif central en France). Floristica et Geobotanica 9 (2): 175—187 (1962). — STASZKIEWICZ, J.: Sosna zwyczajna, *Pinus silvestris* L., systematyka i zmiennosć. (Scotch pine, systematics and variability). Zaklad Dendrologii i Arboretum Kornickie, Polskiej Akad. Nauk, Nasze Drzewa Lesne, Tom I, 55—77 (1970). — STEINBECK, K.: Foliar mineral accumulation by several Scotch pine (*Pinus sylvestris* L.) provenances. Ph. D. thesis, Mich. State Univ. 115 pp. (1965). — STEINER, K.: Genetic differences in resistance of Scotch pine to the eastern pineshoot borer. The Great Lakes Entomologist 7: 103—107 (1974). — SVOBODA, P.: Lesni dreviny a jejich porosty. Cast 1. (Forest trees and shrubs and their stands, part 1). Statni Zem. Nakl. Praha. 411 pp. (1953). — TOBOLSKI, J. and HANOVER, J. W.: Genetic variation in the monoterpenes of Scotch pine. Forest Sci. 17: 293—299 (1971). — WRIGHT, J. W. and BALDWIN, H. I.: The Interantional Union Scotch pine provenance test in New Hampshire. Silvae Genetica 6: 2—14 (1957). — WRIGHT, J. W. and BULL, W. I.: Geographic variation in Scotch pine. Silvae Genetica 12: 1—25 (1963). — WRIGHT, J. W., LEMMIEN, W. L., BRIGHT, J. N., DAY, M. W. and SAJDAK, R. L.: Scotch pine varieties for Christmas tree and forest planting in Michigan. Mich. Agri. Exper. Sta. Res. Rpt. 293. 15 pp. (1976). — WRIGHT, J. W., PAULEY, S. S., POLK, R. B., JOKELA, J. J. and READ, R. A.: Performance of Scotch pine varieties in the north central region. Silvae Genetica 15: 101—110 (1966). — WRIGHT, J. W. and WILSON, L. F.: Genetic differences in Scotch pine resistance to pine root collar weevil. Mich. Agri. Exper. Sta. Res. Rpt. 159. 5 pp. (1972). — WRIGHT, J. W., WILSON, L. F. and BRIGHT, J. N.: Genetic variatiton in resistance of Scotch pine to Zimmerman pine moth. The Great Lakes Entomologist 8: 231—236 (1975). — WRIGHT, J. W., WILSON, L. F. and RANDALL, W. K.: Differences among Scotch pine varieties in susceptibility to European pine sawfly. Forest Sci. 13: 175—181 (1967).

Two-Level Diallel Cross Experiments
II. Incomplete Environmental Designs*)

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1. Introduction

As a possible experimental procedure for studying and evaluating interpopulation crosses (to be understood in a very general sense), HINKELMANN (1974) proposed a two-level diallel cross experiment. The mating design for this experiment, involving m populations and n individuals per population, calls for m(m—1)/2 "population crosses" and n^2 "individual crosses" for each population cross. This may lead to a rather large number of crosses and hence to a large number of seedlings that have to be grown.

It is here then that we have to give attention to the second design aspect for a genetic experiment: the environmental design (for a more general discussion of design aspects we refer to HINKELMANN, 1975). In this paper we propose a practical and workable plan for the layout of the field experiment for the two-level diallel cross. This environmental design is an incomplete block design of a special type reflecting the particular structure of the underlying mating design.

2. The environmental design

As pointed out earlier, in order to accommodate the generally large number of crosses and adequately control environmental effects one will need to use some form of incomplete block design. Rather than using the most general approach to this end, *i.e.*, identify the crosses with treatments and use any available incomplete block design, we shall consider a design that takes into account the fact that the crosses have a two-level structure. This allows us to affect a reduction in block size at both levels either separately or simultaneously. From the point of view of simplicity of experimentation it seems fairly obvious here to consider a reduction in block size through the population crosses as follows.

For a two-level diallel in a randomized complete block design each block would consist of $m(m—1)n^2/2$ crosses, *i.e.*, n^2 individual crosses for each of the $t = m(m—1)/2$ population crosses. One way to reduce the block size is to reduce the number of population crosses occurring in a block. We achieve this by relating the t population crosses to the treatments of an incomplete block design as illustrated in *Fig. 1* for m = 4. This triangular array tells us that, for example, population cross $P_2 \times P_4$ corresponds to treatment 5, etc. We now look for an appropriate balanced incomplete (BIB) or partially balanced incomplete block (PBIB) design with blocks of size k as listed in COCHRAN and COX (1957) or CLATWORTHY (1973). Each block of the resulting environment-

	P_1	P_2	P_3	P_4
P_1	*	1	2	3
P_2		*	4	5
P_3			*	6
P_4				*

Fig. 1. — Correspondence between population crosses and treatments of an incomplete block design.

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