Seed Source x Environment Interactions in Scotch Pine

II. Needle length and color[1])

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Introduction

The rising popularity of Sootch pine (*Pinus sylvestris* L.), particularly among Christmas tree growers, has resulted in an increasing interest in the genetic improvement of this species.

In 1959 a 122-origin provenance study was started in the Michigan State University forest tree nursery in East Lansing, Michigan. This study was a part of Regional Study NC-51 of the U. S. Department of Agriculture entitled "Tree Improvement through Selection and Breeding of Forest Trees of Known Origin", and involves the active cooperation by the State Experiment Stations of 10 states in the north central states.

In 1961 and 1962 seedlings from this study were used to establish 41 permanent test plantations throughout Michigan, Wisconsin, Minnesota, Illinois, Indiana, Missouri, Kansas, Nebraska, New York, and Maryland.

The present author has described the results of height growth measurements made at the end of the 1962 and 1963 growing seasons in 7 Michigan plantations and 1 Illinois planting (KING, 1964, 1965).

This paper covers the results of needle length measurements made in 5 Michigan plantations in 1962 and 4 Michigan plantations in 1963. Color scorings made in 6 Michigan plantings in 1962 are also reported.

Methods

Materials

Seed source data, seed procurement, nursery procedures. and seedling performance have 'been described in detail by WRIGHT and BULL (1963).

Plantation, location and size are shown in ***Table*** 1. All of these plantings follow a randomized complete block design.

Only seedlings which had been in the field at least two years were measured. No seedlings were measured which showed the stunted growth characteristic of Scotch pine in the first season following transplanting.

Measurernent

One needle fascicle from the middle of the current terminal growth was removed from each tree and measured to the nearest millimeter. The average length of the fascicles from all living trees was recorded.

Large samples of ten to fifteen fascicles per tree were collected at several plantings in 1962 for comparison with results of the single fascicle measurement. This comparison showed that a single fascicle per tree gave almost identical results as obtained with a larger sample of fascicles. This was due to the small within-tree variation in needle length.

Color was scored on the basis of ten color grades – grade 1 being the yellowect in the planting and grade 10 the bluest. This scoring system permits within-planting analysis but may bias between-planting comparisons. To determine the constancy of color grades between plantings, several samples were scored in the field and then brought immediately into the office for comparison with Munsell color charts. The following tabulation shows the entire range of Munsell color grades and the field score of the selected samples:

Munsell Color	Plantation and date sample taken: Higgins Lake October 20, 1962	Newaygo October 22, 1962	Russ Forest November 13, 1962
	Field Score[1])		
2.5 Y		1	1
5.0 Y	1		
7.5 Y			
10.0 Y	2		2
2.5 GY			
5.0 GY		6	6
7.5 GY	5		
10.0 GY		9	
2.5 G	9		9
5.0 G			

[1]) 1 = Yellowest; 10 = Darkest Green.

There is good general agreement between plantings among the greener shades. However, there are indications that the observer recognized fewer shades of yellow than of green.

The color scorings were mede over a fairly wide range of dates. However, subsequent analyses showed that the date of scoring was relatively unimportant. Because of a heavy snowstorm in early December of 1962, it was not possi'ble to score the plantings when color differences would be at their peak – about mid-December.

One special color scoring was made the first week of December. This scoring was designed to provide precise between-planting comparisons with the effect of date of scoring held constant. Samples of nineteen cources com-

Table 1. — Summary of plantation location and size.

Name	County, State	North Lat. (Degrees)	West Long. (Degrees)	Seed Sources	Replications Number	Trees Plot
Kellogg Forest	Kalamazoo, Michigan	42.3	85.3	108	10	4
Higgins Lake	Crawford, Michigan	44.5	84.7	72	7	4
Allegan	Allegan, Michigan	42.5	86.0	72	10	4
Rose Lake	Shiawassee, Michigan	42.8	84.3	70	8	4
Houghton	Houghton, Michigan	47.1	88.4	80	8	4

[1]) This paper is part of a dissertation submitted to the Graduate School of Michigan State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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mon to three plantings were collected. The needles were removed from each tree, stapled onto a white card with plot identification on the back, and then brought into the laboratory for direct comparison under uniform light. Collection and scoring were completed within two days. Using this system it was possible to recognize nineteen color grades.

Analysis

The number of seed sources used in the analyses was determined by the number of seed sources the measured plantations had in common. There were 42 seed sources common to the 5 plantings measured for needle length in 1962, and 55 seed sources common to the 4 Michigan plantings measured in 1962 and 1963. There were 57 sources common to the six plantations scored for color.

Data for each plantation were subjected to analysis of variance using plot means. Plantation analyses were then grouped into various combined analyses as described by Cochran and Cox (1957). Components of variance were determined by setting the computed mean squares equal to their expected mean squares and solving for the components.

Needle Length

Sources from central Europe (Groups F, G and H) had the longest needles and sources from the southern extremes of the Scotch pine range had the shortest needles *(Table 2)*.

Group C, from southern Norway and central Sweden, had relatively longer needles in 1963 than in 1962 (note significant seed source × year interaction in ***Table 3***). However, these sources still averaged intermediate in needle length for both years.

At the Houghton plantation the Spanish sources consistently had longer needles than at any other planting. The Scandinavian sources on the other hand tended to have relatively shorter needles at Houghton. As a result, in 1962 the Spanish sources were longer needled than the Scandinavian sources at Houghton, while in 1963 the Spanish, Greek-Turkish, and Scandinavian groups did not differ in needle length.

At the Kellogg plantation, however, the opposite trend was observed. While in 1962 the Scandinavian sources were intermediate in needle length; in 1963 these sources were nearly equal to the long-needled German-Belgium-Czechoslovakian sources.

Thus, there was a tendency in both years for sources from the southern part of the range to have relatively longer needles in the northernmost plantation, while sources from the northern part of the range had longer needles at the southernmost plantation.

There were large year-to-year changes in the mean plantation needle length. Houghton, which had the lowest mean needle length in 1962, had, with Higgins Lake, the highest mean needle length in 1963. While the mean needle length increased at Houghton in 1963, it decreased at all the other plantations. The ratio of mean 1963 needle length to mean 1962 needle length was .74 for Kellogg Forest; .82 for Allegan; .94 for Higgins Lake; and 1.11 for Houghton. That the differences in these ratios are real is shown by the significant plantation × year interaction *(Table 3)*.

The amount of variation due to seed source × plantation interaction *(Table 4)* in 1962 was small compared to the variation due to seed source differences. However, this interaction component showed a definite increase between

Table 2. Needle length of Scotch pine seed sources.

Region, Country of origin, MSFG No.	Kellogg Forest 1962	Kellogg Forest 1963	Allegan 1962	Allegan 1963	Higgins Lake 1962	Higgins Lake 1963	Houghton 1962	Houghton 1963	Rose Lake 1962
	Percent of plantation mean								
C NOR[1] 201	86.9	94.0	94.6	94.0	83.5	82.3	86.7	90.5	92.3
SWE 222	98.9	99.8	99.3	105.0	93.9	88.3	92.5	93.8	82.3
FIN 230	77.7	89.5	79.6	89.0	78.6	80.1	69.0	81.2	--
NOR 273	95.0	105.6	91.9	102.7	94.6	98.0	85.9	92.5	86.7
NOR 274	86.4	99.1	85.1	91.8	88.3	96.5	79.3	94.5	84.8
SWE 521	91.5	101.1	93.2	104.0	98.1	99.4	88.9	99.7	87.9
SWE 523	91.5	105.0	89.1	106.0	88.3	92.0	88.9	93.8	79.8
SWE 524	92.8	100.4	100.7	99.0	91.1	92.8	87.4	88.5	88.6
SWE 543	92.4	110.7	88.5	99.3	96.7	91.3	83.7	101.7	89.8
SWE 544	96.7	108.8	91.2	97.3	96.0	98.0	86.7	95.1	84.2
SWE 545	85.9	93.2	86.4	100.5	86.2	86.1	81.5	89.2	--
Average	90.5	100.7	90.9	99.0	90.5	91.3	84.6	92.8	86.3
D LAT 223	93.7	94.0	92.5	94.3	106.4	98.0	104.3	99.7	94.8
LAT 224	95.0	90.1	90.5	95.8	96.0	92.8	99.1	101.1	90.5
SWE 541	104.1	109.4	105.5	106.3	109.2	104.6	101.4	103.0	101.8
SWE 542	99.7	116.5	100.0	102.6	96.7	112.8	99.1	103.7	92.3
SWE 550	98.0	103.0	104.1	102.8	94.6	96.5	100.0	107.0	--
Average	98.1	102.6	98.5	100.4	100.6	100.9	100.8	102.9	94.9
E SIB 227	102.3	119.1	108.2	113.8	110.6	99.4	119.7	108.3	--
URA 258	98.9	120.4	102.7	109.8	96.0	103.1	97.7	99.7	98.0
Average	100.6	119.8	105.5	111.8	103.3	101.3	108.7	104.0	98.0
F POL 211	113.6	108.8	123.8	110.7	105.0	110.6	109.4	104.4	121.2
POL 317	112.7	101.7	110.2	104.0	100.8	115.0	102.8	114.3	125.6
Average	113.2	105.3	117.0	107.4	102.9	112.8	106.1	109.4	123.4
G GER 202	117.9	104.3	108.2	109.6	107.1	122.4	100.6	104.4	119.3
GER 203	101.5	95.3	104.8	102.6	102.9	98.7	102.8	99.1	94.8
GER 208	114.9	101.7	106.8	104.0	109.2	106.9	110.2	106.3	--
GER 210	124.8	109.4	112.3	113.8	109.9	122.4	127.1	116.2	128.1
CZE 305	111.4	112.6	112.3	106.3	102.2	111.3	95.5	101.7	--
CZE 306	108.4	101.7	102.1	105.3	99.5	104.6	118.2	105.0	108.0
CZE 307	114.4	108.1	117.0	116.6	105.7	113.5	110.9	105.0	--
CZE 308	106.2	103.0	117.0	106.9	112.7	113.5	110.9	106.3	--
CZE 309	104.5	104.3	107.5	96.0	100.8	104.6	102.8	104.4	100.5
CZE 310	113.1	106.1	108.2	102.1	113.4	115.8	96.2	102.4	111.8
CZE 311	113.1	102.3	109.6	98.6	110.6	109.1	107.2	106.3	--
CZE 312	114.0	110.7	109.6	108.2	113.4	105.7	109.4	105.7	118.7
GER 525	98.9	97.2	102.1	97.5	104.3	103.1	110.2	108.3	104.9
GER 527	99.3	97.8	103.4	100.2	118.2	103.9	96.2	101.1	99.9
Average	110.2	103.9	108.6	104.8	107.9	109.7	107.0	105.2	109.5
H GER 206	117.4	104.0	118.4	110.0	121.0	106.1	121.2	107.7	117.5
FRA 241	122.2	120.4	108.2	110.8	109.9	116.5	113.1	107.7	--
GER 251	117.0	102.4	113.6	117.6	111.3	122.4	126.3	110.3	130.6
GER 253	119.2	112.7	109.6	111.5	118.9	106.9	117.5	119.6	137.6
BEL 318	121.3	108.8	120.4	113.1	115.5	115.8	118.2	111.6	127.5
BEL 530	125.5	114.6	116.4	115.1	112.0	111.3	117.5	110.3	136.9
HUN 553	107.5	97.1	107.5	109.3	114.1	111.3	116.8	109.0	--
NY 225	102.8	96.6	100.0	99.7	111.3	102.4	108.7	103.7	103.6
Average	116.6	107.1	111.8	110.9	114.3	111.6	117.4	110.0	130.0
J FRA 235	102.3	100.7	100.7	95.8	95.3	92.0	112.4	103.7	99.9
YUG 242	106.6	98.5	102.7	87.9	106.4	105.4	105.8	100.4	110.5
Average	104.5	99.6	101.7	91.9	100.9	98.7	109.1	102.1	105.2
K TUR 213	86.4	77.3	91.2	84.2	93.2	93.5	90.3	86.5	92.0
TUR 220	89.4	95.3	95.3	92.3	93.9	87.6	106.5	99.1	94.2
TUR 221	86.9	84.3	87.1	83.9	88.3	76.4	80.8	83.9	98.0
GRE 243	84.2	81.1	83.7	78.0	85.5	87.6	69.0	78.6	79.8
GRE 271	77.3	86.9	83.0	87.0	87.6	88.3	85.2	91.1	--
GRE 551	82.9	79.2	85.1	82.7	81.4	78.0	77.8	89.8	--
Average	84.5	84.0	87.6	84.7	88.3	85.2	84.9	88.1	91.0
N SPA 218	77.7	77.2	86.4	88.1	86.2	86.1	93.3	93.8	77.9
SPA 219	79.9	83.7	85.7	83.0	81.4	77.2	107.2	94.5	74.7
SPA 245	85.9	75.3	83.7	85.0	82.8	83.1	89.6	89.8	80.4
SPA 246	69.5	76.0	77.6	80.4	79.3	77.2	91.1	85.9	74.1
SPA 247	82.9	76.0	86.4	88.5	94.6	78.7	89.1	87.9	81.7
Average	79.2	77.6	84.0	85.0	84.9	80.5	94.1	90.4	77.8
Mean plantation needle length (millimeters)	57.91	42.92	45.93	37.64	51.36	48.03	42.54	47.30	49.81
Standard error of seed source mean as a percent of plantation mean	4.09	4.17	4.03	3.16	4.38	4.02	5.83	4.06	4.68

1/ BELgium, CZEchoslovakia, FINland, FRAnce, GERmany, GREece, HUNgary, LATvia, NORway, POLand, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

1962 and 1963 (*Table 3* — note significant seed source × plantation × years interaction). Although never accounting for more than eight percent of the total variance, in some instances the interaction component was more than one-quarter the seed source component in 1963.

The plantations were all very similar in seed source needle length *(Table 5)*. As in the case of height growth (King, 1964), there is no consistent relation between interaction variance and between-plantation correlations. For ex-

Table 3. — Combined analysis of variance for 1962 and 1963 needle length of 55 Scotch pine seed sources grown in four Michigan plantations.

Source of Variation	Degrees of Freedom	Mean Square	Component variance as a percent of total variance
Years	1	6518.83**	7.94
Plantations	3	3185.03**	7.27
Seed Sources	54	273.93**	12.78
Years × Seed Sources	54	16.19**1)	.73
Years × Plantations	3	2170.14**1)	31.06
Seed Sources × Plantations	162	12.40*1)	1.36
Seed Sources × Years × Plantations	162	8.88**2)	2.78
Error	3186	5.36	36.08

** Significant at the one percent level.
* Significant at the five percent level.
1) Based upon seed sources × years × plantations interaction as error term.
2) Based upon seed sources × replication-within-plantation as error term.

ample, both the Kellogg Forest-Higgins Lake and the Houghton-Higgins Lake interactions increased from 1962 to 1963 (*Table 4*), but in one case the correlation decreased and in the other it increased.

Color

Field Measurements. — The color differences between seed sources closely followed the results reported by Wright and Bull (1963) as well as the 1961 plantation scorings[3]) (*Tables 6 and 7*).

Northern seed sources were the yellowest and southern seed sources the most blue-green. This trend was not completely related to latitude however. Group E from the Ural Mountains of Russia — an area of intermediate latitude — was the yellowest in all plantations. Sources from Spain (Group N) and southern France (Group M) were the darkest green in all plantations.

The plantings at Higgins Lake and Newaygo — the two northernmost plantations scored for color — showed the greatest color differentiation. These plantation means were lower and they show the greatest range in plot means. Allegan — the next northernmost plantation — showed the least differentiation. Since Allegan was one of the last plantations measured, this suggests that the plantation itself is a more important source of color variation than the date of scoring.

There was a small but significant seed source × plantation interaction among the plantings (*Table 8*). But this interaction never accounted for more than six percent of the total variation and was very small in relation to the variation due to seed source differences.

Sources from southern Scandinavia (Group C) were much more yellow at Higgins Lake than at any other planting. Source MSFG 521 from southern Sweden was about 1½ grades yellower at Higgins Lake than at any other planting.

3) The 1961 color scorings were made by J. W. Wright.

Table 4. — 1962 and 1963 components of needle length variance as a percent of total variance — from 55 seed sources.

Plantations in combined analysis	Variance Component							
	σ^2_p		σ^2_s		σ^2_{ps}		σ^2_e	
	1962	1963	1962	1963	1962	1963	1962	1963
	Percent of total variance							
Kellogg Forest Higgins Lake Allegan Houghton	37.4**	34.3**	25.7**	25.4**	3.3**	5.0**	33.6	35.3
Kellogg Forest Allegan	44.3**	26.7**	26.6**	30.3**	1.4*	3.3**	27.7	39.7
Kellogg Forest Higgins Lake	17.5**	18.8**	38.8**	32.7**	2.0*	8.2**	41.7	40.3
Kellogg Forest Houghton	52.6**	16.3**	18.1**	26.2**	3.9**	7.1**	25.4	50.4
Houghton Higgins Lake	33.7**	0.2NS	24.9**	43.2**	2.1*	6.6**	39.3	50.0

σ^2_p, σ^2_s, σ^2_{ps}, and σ^2_e are the components of variance due to differences between plantations, differences between seed sources, seed source × plantation interaction, and random variations between plots within plantings respectively.
NS = Non-significant.
* = Significant at the five percent level.
** = Significant at the one percent level.

Table 5. — Between-plantation correlation coefficients based on seed source mean needle length.

		Kellogg Forest 1962	Kellogg Forest 1963	Allegan 1962	Allegan 1963	Higgins Lake 1962	Higgins Lake 1963	Houghton 1962	Houghton 1963
Kellogg Forest	1962	1.00	.74	.92	—	.88	—	.74	—
	1963		1.00	—	.84	—	.72	—	.70
Allegan	1962			1.00	.82	.83	—	.75	—
	1963				1.00	—	.79	—	.77
Higgins Lake	1962					1.00	.83	.70	—
	1963						1.00	—	.81
Houghton	1962							1.00	.86
	1963								1.00

All values are significant at the 1 percent level where r = .35 with 53 degrees of freedom.
— not computed.

Table 6. Color grades and date of scoring Scotch pine seed sources.

Region, Country of origin, MSFG No.		Rose Lake	Higgins Lake	Newaygo	Kellogg Forest	Allegan	Russ Forest
		Date of scoring					
		Oct. 10	Oct. 20	Oct. 22	Oct. 31	Nov. 6	Nov. 13
		Percent of plantation mean					
A	SIB[1/] 254	41	33	23	44	52	38
C	NOR 201	74	64	72	88	81	71
	SWE 222	74	50	47	62	84	57
	NOR 273	83	59	76	79	89	68
	NOR 274	83	50	49	64	84	50
	SWE 521	67	33	70	54	84	59
	SWE 522	63	42	52	51	81	47
	SWE 523	52	39	56	39	71	45
	SWE 524	63	42	49	56	71	52
	SWE 543	80	53	43	64	87	57
	SWE 544	70	56	54	62	87	57
	SWE 545	70	56	68	64	86	51
	Average	70.8	49.5	57.8	62.1	82.3	55.8
D	LAT 223	72	43	70	61	83	57
	LAT 224	80	47	60	78	81	63
	SWE 541	87	73	93	76	87	71
	SWE 542	67	53	51	54	76	54
	Average	76.5	54.0	68.5	67.3	81.8	61.3
E	SIB 255	37	36	21	34	45	37
	URA 258	46	36	33	37	65	35
	Average	41.5	36.0	27.0	35.5	55.0	36.0
F	POL 211	100	92	99	91	89	91
	POL 317	102	81	107	95	94	96
	Average	101.0	86.5	103.0	93.0	91.5	93.5
G	GER 202	91	98	130	106	110	104
	GER 203	117	103	130	118	110	118
	GER 207	115	95	134	113	109	120
	GER 208	111	111	113	115	109	117
	GER 210	109	95	103	103	107	96
	CZE 305	115	86	113	99	99	110
	CZE 306	120	106	144	101	105	110
	CZE 308	102	111	115	105	102	111
	CZE 309	106	103	126	110	99	96
	CZE 310	106	103	117	105	102	108
	CZE 311	111	98	124	99	107	111
	CZE 312	106	81	113	99	104	113
	GER 525	104	106	146	113	104	115
	GER 527	93	95	107	86	102	98
	Average	107.6	99.4	122.5	105.1	104.9	109.1
H	GER 206	109	120	122	113	110	120
	N Y 225	115	114	142	135	115	131
	FRA 241	117	137	136	113	115	129
	GER 251	117	134	147	128	107	127
	GER 252	115	117	134	124	107	125
	GER 253	111	125	132	126	109	115
	BEL 318	117	125	151	115	109	116
	BEL 530	120	111	138	117	107	122
	HUN 553	106	109	122	113	104	103
	Average	114.1	121.3	136.0	120.4	109.2	120.9
J	FRA 235	122	131	146	122	113	139
	YUG 242	120	122	124	115	105	122
	Average	121.0	126.5	135.0	118.5	109.0	130.5
K	TUR 213	122	167	151	138	117	134
	TUR 220	117	167	134	128	112	127
	TUR 221	128	151	130	133	113	141
	GRE 243	115	139	146	121	112	120
	GRE 244	115	111	132	120	109	123
	Average	119.4	147.0	138.6	128.0	112.6	129.0
M	FRA 238	135	164	163	145	133	141
	FRA 239	122	159	175	149	125	151
	Average	128.5	161.5	169.0	147.0	129.0	146.0
N	SPA 218	137	176	175	149	131	157
	SPA 219	132	176	157	147	123	148
	SPA 245	132	176	175	149	130	150
	SPA 246	122	164	151	128	118	137
	SPA 247	135	173	167	145	125	139
	Average	131.6	173.0	165.0	143.6	125.4	146.2
Mean plantation color grade[2/]		5.75	5.13	5.65	5.92	6.17	5.75
Standard error of seed source mean as a percent of plantation mean		5.39	8.19	7.08	5.57	3.57	4.70

1/ BELgium, CZEchoslovakia, FRAnce, GERmany, GREece, HUNgary, LATvia, NORway, POLand, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

2/ Color grades: 1 = yellowest; 10 = darkest green.

The Spanish sources appeared bluer at Higgins Lake than anywhere else, but this was probably a result of the scoring method.

Laboratory Measurements. — As mentioned previously (see *Methods — Measurement*) a special color scoring was made in the laboratory under uniform lighting conditions. This was done to eliminate observer bias when evaluating color at different times and places.

The results of this laboratory test *(Table 9)* strongly confirms the conclusions from the plantation measurements. There are real differences between plantations. Southern Scandinavian sources are more yellow at Higgins Lake than at any other plantation. Source MSFG 521 from southern Sweden does show a distinctly different color at Higgins Lake.

Furthermore, the components of variance expressed as a percent of total variance differ by less than two percent between the laboratory scoring and the combined plantation analyses of the same three plantation scorings.

Applicability of results to other areas

Needle length measurements made on four-year-old trees of a New Hampshire study (Wright and Baldwin, 1957) are in general agreement with the results of this study. Sources from Belgium and Germany had the longest needles while sources from southern Sweden were slightly shorter. Although there were no needle length measurements of northern Scandinavian sources in this present study, both the three-year Michigan nursery study (Wright and Bull, 1963) and the New Hampshire study indicated that sources from northern Sweden had shorter needles than sources from southern Sweden.

However, Langlet (1936) found a striking seed source × plantation interaction for needle length when sources from northern and southern Sweden were tested in Sweden. Langlet reported on 26 Swedish Scotch pine seed sources ranging in latitude from 56° 07' N. to 70° 0' N. The sources were grown at three Swedish locations: Tönnersjöheden (56° 40' N. Lat.); Kulbacksliden (64° 10' N. Lat.); and Gaillivare (67° 8' N. Lat.). At the southernmost plantation the northern sources all had much shorter needles than the southern sources. At Kulbacksliden, the intermediate site, there were only slight differences in needle length between all seed sources, while at the northernmost planting the northern sources had the longest needles. Thus, it seems that southern Swedish sources are longer-needled than northern Swedish sources only in areas south of southern Sweden.

Color results are probably applicable over the widest range of sites and regions. The present study, the Michigan nursery study (Wright and Bull, 1963) and the New Hampshire study (Wright and Baldwin, 1957), all reported the same pattern of color differences. Moreover, both the New Hampshire study and a Swedish study (Langlet, 1936) reported the same differences between sources from northern and southern Sweden.

Further evidence of the constancy of Scotch pine seed source color may be inferred from advertisements of tree seed dealers. Many dealers have long advertised "French green" or "golden yellow" strains of Scotch pine in nationally distributed publications. Such advertising would not be profitable for very long unless the seed produced the color advertised wherever the buyer grew them.

Table 7. — Between-plantation correlation coefficients using the mean seed source color grade for the 1961 and 1962 measurements.

	1961 Measurements Kellogg Forest	Russ Forest	Newaygo	Higgins Lake	Michigan State Nursery	1962 Measurements Kellogg Forest	Russ Forest	Newaygo	Higgins Lake	Allegan	Rose Lake
1961 Measurements											
Kellogg Forest	1.00										
Russ Forest	.91	1.00									
Newaygo	.92	.91	1.00								
Higgins Lake	.90	.86	.88	1.00							
Michigan State Nursery	.91	.88	.93	.82	1.00						
1962 Measurements											
Kellogg Forest	.96	.92	.94	.87	.95	1.00					
Russ Forest	.95	.94	.95	.87	.95	.97	1.00				
Newaygo	.95	.90	.95	.89	.93	.96	.97	1.00			
Higgins Lake	.91	.89	.94	.82	.96	.95	.95	.93	1.00		
Allegan	.95	.88	.93	.89	.93	.94	.94	.94	.91	1.00	
Rose Lake	.95	.91	.93	.89	.92	.96	.96	.95	.91	.95	1.00

All values are significant at the 1 percent level where r = .35 with 53 degrees of freedom.

Table 8. — 1962 components of color variance as a percent of total color variance — from 57 seed sources.

Plantations in combined analysis	σ^2_p	σ^2_s	σ^2_{ps}	σ^2_e
	Percent of total variance			
Russ Forest, Allegan, Kellogg Forest, Newaygo, Higgins Lake, Rose Lake	3.18**	69.15**	5.73**	21.94
Russ Forest, Allegan, Kellogg Forest, Newaygo, Higgins Lake	3.34**	69.43**	5.84**	21.39
Russ Forest, Allegan, Kellogg Forest, Newaygo, Rose Lake	2.28**	69.42**	5.63**	22.67
Newaygo, Rose Lake, Higgins	2.22**	68.48**	5.59**	23.71
Kellogg Forest, Newaygo, Russ Forest	0.25NS	77.05**	0.80*	21.90
Kellogg Forest, Russ Forest	0.21NS	80.04**	0.22NS	19.53

σ_p^2, σ^2_s, σ^2_{ps}, and σ^2_e are the components of variance due to differences between plantations, differences between seed sources, seed source × plantation interaction and random variations between plantings respectively.

NS = Non-significant.

* = Significant at the five percent level.

** = Significant at the one percent level.

Table 9. — Results and analysis of laboratory color measurement.

Region, Country of origin, MSFG No.			Plantation: Newaygo	Higgins Lake	Rose Lake
			Mean color grade[1]		
C	NOR[2]	201	6.6	6.2	7.8
	NOR	273	7.0	5.2	11.6
	SWE	521	5.8	3.8	8.6
D	LAT	223	9.6	3.8	8.0
E	SIB	256	3.4	6.2	4.6
	URA	258	3.8	3.8	3.8
G	GER	202	10.8	10.8	12.4
	GER	208	10.6	13.2	14.8
	CZE	310	11.0	12.2	13.2
H	FRA	241	13.0	13.6	15.6
	GER	251	15.2	15.2	15.0
	BEL	530	14.4	12.4	16.2
	HUN	553	12.0	13.2	13.6
J	YUG	242	12.6	14.8	14.6
K	TUR	213	15.4	14.4	16.4
	TUR	221	17.2	17.6	17.6
M	FRA	239	17.0	17.6	16.0
N	SPA	218	18.2	18.0	17.6
	SPA	219	17.2	17.6	15.6
Plantation mean			11.36	11.25	12.68

Analysis of variance

Source of variation	Degrees of freedom	Mean square	Component of variance as a percent of total variance
Plantation	2	60.48**	2.1
Seed source	18	283.92**[3]	70.9
Seed source × Plantation	36	10.65**[4]	3.6
Error	216	6.00	23.4

** = Significant at the one percent level.

[1] 1 = Yellowest; 19 = Darkest Green.

[2] BELgium, CZEchoslovakia, FRAnce, GERmany, HUNgary, LATvia, NORway, TURkey, URAl Mountains, SIBeria, SPAin, SWEden, YUGoslavia.

[3] Based on seed source × plantation interaction as error term.

[4] Based on seed source × replicate within-plantation as error term.

Discussion

An exceptionally large portion of the total needle length variance was due to the years × plantation interaction. There was a late spring frost in 1963. All four Michigan plantations had below freezing temperatures on May 23. This suggests the following explanation for the large year × plantation needle length interaction.

WRIGHT and BULL (1963) reported that all sources began growth together in early May at East Lansing. If we assume the southernmost plantation would begin growth first and the northernmost plantation begin last, then there would be large between-plantation, but little within-plantation (among-seed source) variation in foliage condition at the time of the late frost. The needles at the southernmost plantation would be elongating and exposed while the needle fascicles at the northern plantation would still be protected by the bud scales. As a result, there would be little effect on among-seed source needle reduction, large between-planting differences in needle reduction, and the amount of needle length reduction would decrease as we move north.

This is exactly the pattern that was found. The seed source interactions show little variation between plantings while Kellogg Forest (the southernmost plantation) shows the greatest needle length reduction, Allegan the next greatest reduction, Higgins Lake next, and Houghton (the northernmost plantation) shows no reduction in needle length.

The size of the seed source × environment interactions encountered throughout this study have been relatively small. This is not surprising. The material in this test represents a wide range of genetic variation. This large range of variation would make all but the most extreme interactions seem small by comparison. Moreover, the sources themselves are from stand collections and contain a diversity of genotypes. Certain genotypes within each source may do better in one environment than another environment, while other genotypes from the same source may perform in an opposite manner. Such within-source genotype × environment interactions would produce a somewhat buffered population that would not respond sharply to changes in environment.

The existence of seed source × environment interactions has important implications in population studies. A researcher studying Scotch pine needle length at Kellog Forest or Allegan in 1962 would have concluded that Groups C, D, and G all differed in average needle length and, therefore, each group was from a different population (race, ecotype, etc.). However, the same researcher studying the same characteristic on the same trees in the same plantations in 1963 would have found practically no differences in needle length among the same groups and, therefore, might have concluded that the groups all represented a single population. However, if in both 1962 and 1963, the researcher also took into account height growth at the same two plantations (*Table 7*, King, 1964 and 1965), differences between the groups would be apparent in both years.

Thus, studies intended to determine the pattern of genetic variation within a species must be carried out in more than a single environment in order to accurately assess the variation pattern. Furthermore, correlations between seed source growth characters and seed source climatic characters (mean temperature, length of growing season, latitude, etc.) must be carefully interpreted. It is quite conceivable that correlations between, for example, height growth and seed source latitude could be positive, negative, or non-significant depending upon the test environment. Just such a situation has already been reported in the Southwide Pine Seed Source Study (Wakeley, 1961).

And finally, delineation of populations on the basis of more than a single plant characteristic (multi-character analysis) is less subject to the pitfalls of seed source × environment interactions than single character analysis.

Practical applications

Whether it is advantageous to test at several locations rather than a single location depends not only upon the size of the interaction, but upon the nature of the interaction and the characteristic under selection.

The effect of selecting for short-needled trees in one environment on the basis of performance in a different environment is shown in *Table 10*.

Selecting short-needled sources for Higgins Lake in 1962 on the basis of 1962 needle length at Kellogg Forest was quite effective. These plantations had 9 of their 10 shortest-needled sources in common. But in 1963, because of the relatively longer needle growth of the intermediate length Scandinavian sources, selection at Kellogg Forest for short needles in the Higgins plantation was not nearly so effective. Only 6 sources were common to the 10 shortest-needled sources in these two plantings. Note also that the percent of interaction variance between Kellogg Forest and Higgins Lake increased between 1962 and 1963 *(Table 4)*.

The interaction variance between Houghton and Higgins Lake also increased between 1962 and 1963, but selection for Houghton on the basis of needle length at Higgins Lake was more effective in 1963 than in 1962. The same picture — increased interaction with an increase in the number of best sources in common — is also seen between Kellogg Forest and Houghton. This occurred because the 1962 seed source × environment interaction, though small, involved the usually short-needled Spanish sources. In other words, the interaction takes on a greater significance if it involves the sources with the desired character.

That there was a significant amount of seed source × plantation interaction would have little practical significance in a breeding program designed to obtain a tree with darker green foliage because the interaction involved only the medium and yellower sources. If one selected the greenest seed sources in *Table 6*, he would choose sources 218,

Table 10. — Selecting the ten shortest-needled seed sources in each plantation and comparing the number of short-needled sources in common between plantations demonstrates the effect of selecting for one environment on the basis of performance in another environment.

In selecting the ten shortest-needled sources at:		The following number were also among the ten shortest-needled sources at:							
		Kellogg Forest		Allegan		Higgins Lake		Houghton	
		1962	1963	1962	1963	1962	1963	1962	1963
		Number of sources							
Kellogg Forest	1962	10	7	10	7	9	8	5	7
	1963		10	8	9	7	6	4	7
Allegan	1962			10	7	9	8	5	7
	1963				10	7	6	4	6
Higgins Lake	1962					10	8	6	6
	1963						10	5	7
Houghton	1962							10	5
	1963								10

219, 238, 239, 245, and 247. One could select for color almost any place in Michigan for planting at almost any other place.

When the between-plantation needle length correlations *(Table 5)* are compared with the number of best sources in common between the plantations *(Table 10)*, it is apparent that there is no consistent relation between the two. This is not surprising if it is remembered that $1 - r^2$, the unaccounted for variation, includes both interaction variance and experimental error variance. Low correlations may indicate either a high interaction variance due to differential growth response between environments, or a high experimental error due to non-genetic factors. The same applies to year-to-year correlations within the same environment (juvenile-mature tree correlations).

In sum, neither the absolute size of the interaction variance, nor the absolute size of the between-environment seed source correlations are in themselves effective criterion for judging the effectiveness of seed source selection from measurements made at another time or another place.

Acknowledgement

The author is deeply grateful to all members of Regional Project NC-51, U. S. D. A., who made their test plantations available for this study. He is especially indebted to Dr. J. W. Wright who guided the entire study.

Summary

A comprehensive seed source test of Scotch pine was started at Michigan State University in 1959. Provenances from 122 stands in 19 Eurasian countries are represented in the original study. Most of these provenances have been established in permanent test plantations throughout Michigan and the central United States.

Needle length measurements were made in 5 Michigan plantations in 1962 and 4 Michigan plantations in 1963. Color was scored in 6 Michigan plantings in 1962.

Sources from central Europe had the longest needles and sources from either the northern or southern extremity of the Scotch pine range had the shortest needles. However, while the Scandinavian sources were relatively short-needled in the northernmost Michigan plantation, they had relatively long needles in the southernmost plantation. The Spanish sources all had relatively longer needles at the northernmost plantation.

The mean needle length for all sources combined differed sharply with site and year. In 1963 the mean needle length decreased by twenty-five percent at Kellogg Forest while it increased by ten percent at Houghton. It is suggested that this year × plantation interaction was the result of a late frost in May 1963.

The Spanish, Greek-Turkish, and southern France sources were the darkest green, and sources from the Ural Mountains and Scandinavia were the most yellow in all plantations. Sources from Scandinavia showed more yellowing at Higgins Lake than at any other plantation, but were still not as yellow as the Ural Mountain sources.

The component of variance resulting from seed source × plantation interaction was small compared to the seed source component. The largest interaction component encountered was about ¼ the seed source component for needle length, and about $^1/_{12}$ the seed source component for color.

The effect of these interactions on a selection program for improving needle length and color are also discussed.

Résumé

Titre de l'article: *Interaction provenance × environnement chez le pin sylvestre. II. Longueur et couleur des aiguilles.*

Une plantation comparative de provenances de pin sylvestre très complète fut établie à l'Université de l'Etat de Michigan en 1959. Des provenances de 122 peuplements de 19 pays d'Europe et d'Asie sont représentées dans l'étude originale. La plupart de ces provenances ont été mises en place dans des plantations comparatives permanentes dans tout le Michigan et le centre des Etats-Unis.

Les longueurs d'aiguilles ont été mesurées dans 5 plantations du Michigan en 1962 et 4 en 1963. Des observations ont été faites sur la couleur dans 6 plantations du Michigan en 1962.

Les provenances d'Europe centrale ont les aiguilles les plus longues et celles de l'extrémité septentrionale ou de l'extrémité méridionale de l'aire du pin sylvestre ont les aiguilles les plus courtes. Cependant, bien que les provenances scandinaves aient des aiguilles relativement courtes dans les plantations du Michigan les plus septentrionales, elles sont relativement longues dans les plantations du sud du Michigan. Les provenances espagnoles ont toutes des aiguilles relativement plus longues dans les plantations du Nord.

La longueur moyenne des aiguilles pour toutes les provenances ensemble varie nettement suivant la station et suivant l'année. En 1963, la longueur moyenne est réduite de 25% à Kellogg Forest tandis qu'elle augmente de 10% à Houghton. On pense que cette interaction entre l'année et la plantation est le résultat des gelées tardives de mai 1963.

Les provenances d'Espagne, de Grèce, de Turquie et du sud de la France ont les aiguilles les plus foncées et les provenances de l'Oural et de la Scandinavie ont les aiguilles les plus jaunes dans toutes les plantations. Les provenances de Scandinavie ont tendance à être plus jaunes à Higgins Lake que dans toutes les autres plantations, mais cependant elles ne sont pas aussi jaunes que les provenances de l'Oural.

La composante de la variance qui vient de l'interaction entre la provenance et la plantation est faible, comparée à la composante relative à la provenance. La composante d'interaction la plus élevée représente environ ¼ de la composante de la provenance pour la longueur des aiguilles et environ $^1/_{12}$ pour la couleur.

On discute également l'effet de ces interactions sur un programme de sélection pour l'amélioration de la longueur des aiguilles et de la couleur.

Zusammenfassung

Titel der Arbeit: *Interaktionen von Herkunft × Umwelt bei Pinus silvestris. II. Nadellänge und Farbe.*

1959 begann man bei der Michigan State University mit einem umfassenden *Pinus silvestris*-Herkunftsversuch. Er enthält Provenienzen von 122 Beständen aus 19 eurasischen Ländern. Mit den meisten Provenienzen sind langfristige Testpflanzungen in Michigan und in den mittleren U. S. A. begründet worden.

Nadellängen wurden in Michigan bei 5 Pflanzungen 1962 und bei 4 Pflanzungen 1963 gemessen. Die Farbe wurde bei 6 Pflanzungen in Michigan 1962 bonitiert.

Die Herkünfte aus Mitteleuropa hatten die längsten Nadeln; die Herkünfte vom Nord- bzw. dem Südrand des Kiefernareals besaßen die kürzesten Nadeln. Die skandi-

navischen Herkünfte waren auf der nördlichsten Fläche Michigans relativ kurznadelig; auf der südlichsten besaßen sie aber relativ lange Nadeln. Alle spanischen Herkünfte hatten auf der nördlichsten Fläche relativ längere Nadeln.

Die kombinierte mittlere Nadellänge aller Herkünfte unterschied sich scharf je nach Standort und Jahr. 1963 nahm die mittlere Nadellänge im Kellogg-Forst um 25% ab, während sie in Houghton 10% anstieg. Es wird angenommen, daß diese Interaktion von Jahr × Pflanzung das Ergebnis eines Spätfrostes vom Mai 1963 gewesen war.

Die spanischen, griechisch-türkischen und die südfranzösischen Herkünfte waren am dunkelsten grün, Herkünfte vom Ural und von Skandinavien waren in allen Pflanzungen am meisten gelb. Die Skandinavier zeigten in Higgins Lake mehr Gelbfärbung als in anderen Pflanzungen, waren aber noch nicht so gelb wie die Ural-Herkünfte.

Der Varianzanteil an der Interaktion Herkunft × Pflanzung war gering, verglichen mit der Herkunftskomponente. Die größte gefundene Interaktionskomponente war zu etwa ¼ der Anteil der Samenherkunft bei der Nadellänge und zu etwa 1/12 der Anteil der Herkunft bei der Farbe.

Die Auswirkung solcher Interaktionen auf ein Selektionsprogramm zur Nutzung der Nadellänge und Farbe wurde diskutiert.

Literature cited

Cochran, William G., and Cox, Gertrude M.: Experimental designs. 2nd ed. John Wiley & Sons, New York, 1957, 611 pp. — King, James P.: Seed source × environment interactions in Scotch pine. Thesis for degree of Ph. D., Mich. State Univ., East Lansing, 1964. (Unpublished.) — King, James P.: Seed source × environment interactions. I. Height growth. Silvae Genetica 14, 105—115 (1965). — Langlet, Olof: Studier över tallens fysiologiska variabilitet och des samband med klimatet. Meddel. Stat. Skogsförsöksanstalt 29, 219—470 (1936). — Wakeley, Philip C.: Results of the southwide pine seed source study through 1960—1961. South Conf. Forest Tree Impr. Proc. 6: 10—24 (1961). — Wright, Jonathan W., and Baldwin, Henry J.: The 1938 International Union Scotch pine provenance test in New Hampshire. Silvae Genetica 6: 2—14 (1957). — Wright, Jonathan W., and Bull, W. Ira: Geographic variation in Scotch pine. Silvae Genetica 12: 1—25 (1963).

Über die Vegetativvermehrung von Bombacopsis quinata (Jaq.) Dugant[1])

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(Eingegangen am 15. 1. 1965)

1. Vorkommen und Bedeutung

Die baumförmigen Bombacaceen sind eine in den Tropen beheimatete Pflanzenfamilie zu der u. a. auch die Gattung *Bombacopsis* zählt (Aristigueta 1954). Sie enthält einige bekanntere Arten, die alle gradschäftige, hohe Bäume sind und beträchtlichen Durchmesser erreichen. Ihr Vorkommen ist auf das nördliche Südamerika und Zentralamerika bis Honduras beschränkt (Hueck 1961).

Bombacopsis quinata, eine dieser Arten (s. Lamprecht und Hueck 1959, Hueck 1961), wächst auch in den Regengrünen Wäldern der heißen Zone Venezuelas (Höhenlage bis 500 m). Dieser Passatwald stellt eine Parallele zu dem Monsunwald Indiens dar und ist durch den Wechsel von Trocken- und Regenzeit außerdem durch gleichmäßig hohe Temperaturen während des ganzen Jahres gekennzeichnet *(Abb. 1,* Hueck 1961, Lamprecht 1961, Veillon 1964).

Vier große Waldgebiete dieses Typs sind in Venezuela zu unterscheiden: Der Passatwald in den westlichen Hoch-Llanos[3]) Venezuelas stellt das wirtschaftlich wichtigste dar *(Abb. 2,* Ziffer 1). Es ist vom Gebiet des östlichen Tropophilwaldes in der venezolanischen Guayana *(Abb. 2,* Ziffer 2) und vom nördlichen, südlich des Karibischen Meeres *(Abb. 2,* Ziffer 3) durch weite Savannen sowie von den Regengrünen Wäldern um den Maracaibosee *(Abb. 2,* Ziffer 4) durch die Anden getrennt (Hueck 1960, Lamprecht 1964, MAC 1961).

Im trockenen Typ des Regengrünen Waldes (mittl. Jahresniederschlag: 1361 mm; mittl. jährl. Anzahl von Trokkenmonaten: 4) findet *Bombacopsis* seine größte Verbreitung; aufgrund einer großen ökologischen Amplitude ist die Art aber auch im „sehr trockenen Tropophilwald", doch in weit geringerem Maße anzutreffen (mittl. Jahresniederschlag: 726 mm; mittl. jährl. Anzahl von Trockenmonaten: 7; Veillon 1964, s. auch Holdridge).

Die nachstehenden Versuche wurden in dem der Anden-Universität in Mérida gehörenden Waldgebiet „El Caimital" durchgeführt, das ökologisch als Regengrüner Trokkenwald zu klassifizieren ist (in wenig intensiver Form in den Jahren 1940 und 1951 exploitiert; s. Petit 1963). Es liegt 170 m ü. NN am Mittellauf des von NW nach SO von den Anden abströmenden Flusses Yuca in den westlichen, Hoch-Llanos auf wenig durchlüftetem, alluvialem, sandigem bis lehmigem Ton im Übergang zum Laterit (Castillo 1962). Der jährliche Niederschlag beträgt zwischen 1500 und 1600 mm (Vila 1963) und die Jahresmitteltemperatur 26—27° C (Castillo 1962).

Die Wälder dieser Region erreichen Oberhöhen von ungefähr 30 m und setzen sich aus rund 60 verschiedenen Baumarten aller Stärkeklassen zusammen (Hueck 1961, Lamprecht 1961, 1964, Veillon 1964). Aber nur wenige Arten dominieren nach Volumen und Stammzahl, unter ih-

[1]) Der experimentelle Teil der Arbeit wurde in der Zeit zwischen September 1961—1963 während der Zugehörigkeit des Autors zum Instituto de Silvicultura, Facultad de Ciencias Forestales, Universidad de los Andes, Mérida, Venezuela, durchgeführt und wird ausführlich in *„Revista Forestal Venezolana"* publiziert werden. — Allen Mitarbeitern am Institut, ohne deren kameradschaftliche Hilfe die vorliegende Arbeit nicht zustande gekommen wäre, danke ich herzlich. Hervorheben möchte ich besonders die vielfältigen Anregungen und freundschaftliche Unterstützung durch den damaligen Direktor des Instituts, Herrn Dr. Ing. For. H. Lamprecht und die Herren Ing. For. H. Finol U., G. H. Raets und Dr. H.-J. Tillmanns (Instituto Forestal Latino Americano); zu Dank verbunden bin ich außerdem dem Dekan der Fakultät, Herrn Ing. For. C. Liscano, für die stete Förderung und sein reges Interesse am Fortgang der Untersuchungen. Nicht zuletzt wird die wertvolle technische Hilfe von Herrn J. R. Gutierrez dankbar anerkannt und die Mithilfe all derer, die nicht namentlich aufgeführt wurden. — Herrn Prof. Dr. D. v. Denffer danke ich bestens für die kritische Durchsicht des Manuskripts.

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[3]) Als westliche Llanos bezeichnet man die ausgedehnten Ebenen zwischen Andenfluß und Orinoko. Sie werden in die Llanos Altos (Hoch-Llanos) zwischen 200—100 m. ü. NN und die Llanos Bajos (Tief-Llanos) zwischen 100—0 m ü. NN unterteilt.