Site, Height, and Mineral Nutrient Content Relations of Scotch Pine Provenances[1])

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Introduction

Scotch pine *(Pinus sylvestris* L.) varies in numerous morphological characteristics. Height growth (WRIGHT and BULL, 1963; JENSEN and GATHERUM, 1964; GATHERUM and JENSEN, 1964; and KING, 1965 a), needle length (WRIGHT and BULL, 1963; KING, 1965 b), increase in dry matter (LANGLET, 1936). and needle color (GERHOLD, 1959; WRIGHT and BULL, 1963; KING, 1965 b) all have been demonstrated to vary among origins from different parts of the geographic range. It is generally accepted that these differences are genetically controlled, but the pathway from gene or genes to morphological expression remains obscure.

In agronomically important crops ~differencesin yields among varieties have sometimes been related to differences in their mineral contents. VOSE (1963) reviewed the work dealing with varietal differences in plant nutrition, and commented that breeders of crop plants have to take so many agronomic and commercial factors into account that little inducement exists to take yet another factor – nutritional efficiency – under consideration. The forester, however, may be well advised to investigate this factor. Forestry is nearly always relegated to sites which are not fertile enough for agricultural exploitation. The value of the forest crop and the length of rotation justifies the manipulation of soil fertility only under rare circumstances. Therefore, a small difference in the ability to accumulate nutrients may make the difference between stagnation and growth of plantations

EPSTEIN and JEFFERIES (1964) reviewed the evidence for the genetic basis of selective ion transport in plants. They mentioned that plant physiologists 'have investigated relatively few species, most of them economic crop plants, and that these highly selected varieties may be less competent in absorbing nutrients from a given substrate than wild species. Scotch pine, though regarded as a crop by foresters, is a wild species in the sense of EPSTEIN and JEFFERIES. Because it has such a large geographic range *(Figures 1 and 2),* and is relegated in that range mostly to the less fertile, sandy sites, it may have evolved a highly efficient nutrient accumulation mechanism.

GERHOLD (1959), working with the then 19-year-old IUFRO Scotch pine provenance test, found that six seedlots differed significantly in their foliar levels 04 nitrogen, calcium, magnesium, and iron. STEINBECK (1965) found that five seedlots of 4-year-old Scotch pine differed significantly in their needle concentrations of nitrogen: phosphorus, magnesium, iron, zinc, and aluminum. He also reported significant seedlot X site interactions for potassium, phosphorus, sodium, iron, boron, zinc, and aluminum.

One purpose of the investigation reported here was to cxplore the possibility that mineral levels of Scotch pine needles are correlated with height growth. Such a relationship can indicate the lines along which the pathway from gene to expression of the gross character (i. e., height growth) should be investigated. Furthermore, this study was designed to determine the effects of site on nutrient accumulation and the interactions between seedlots and sites.

Methods

The provenance plantations established with the nursery stock described by WRIGHT and BULL (1963) were sampled in this investigation. At each site, 70 to 110 seedlots had been planted in a randomized block design. There were 7 to 10 blocks at each site; plots consisted of four trees on an 8-by 8-foot spacing. At the time of sampling the trees had completed the fourth growing season.

The outplantings chosen for study are located in the Higgins Lake State Forest (10–61),[3]) the Fred Russ Memorial Forest (7–61), and the Newaygo Experimental Forest (9–61). All plantations are located in the lower peninsula of Michigan.

Soils and Soil Sampling: The Higgins Lake planting grows on a Grayling sand which grades to a Graycalm sand. This Brown Podzolic soil has developed in deep glacial drift containing little or no limestone. The site is an abandoned field which has 0 to 2 percent slopes.

Trees at Newaygo are growing in a Sparta sand, an intergrade between the Brown Podzolic and Brunizem Great Soil Groups. It developed in deep glacial drift containing little limestone. The site once supported prairie vegetation, but wind erosion has removed the organic matter. The planting is located on an old field with 0 to 2 percent slopes. The stand contains two windblows each about 200 to 300 square feet in area.

The Russ planting is located on a site fornerly occupied by a forest tree nursery which had been maintained at a high level of fertility. The soil is a Fox sandy loam, a well-drained Gray Brown Podzolic soil developed in silty or lcamy materials. It is underlain by stratified, calcareous gravel and sand at 24 to 80 inches. In the autumn before planting, 20 pounds of Dalapon per acre were applied to the planting strips to reduce sod competition. Since then 4 pounds of simazine per acre have been applied for additional weed control. The site also has 0 to 2 percent slopes.

In May, 1964 the soils of all three plantations were sampled on essentially a grid pattern. There were 26 sampling stations at each site, at each station the soil layer from 0 to 8 and from 8 to 14 inches in depth was collected. Soil samples were analyzed for P (Bray's no. 1) and exchangeable K, Ca, and Mg (flame photometer). The pH, cation exchange capacity, and base saturation were determined. Total nitrogen was determined for 10 samples per site, five each for the 0 to 8 inch and the 8 to 14 inch layer.

Tissue sampling: Forty-five seedlots encompassing the geographic range of Scotch pine and which were represented at all three locations were chosen for study *(Table 1).*

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[3]) Map number of *Figure* 3.

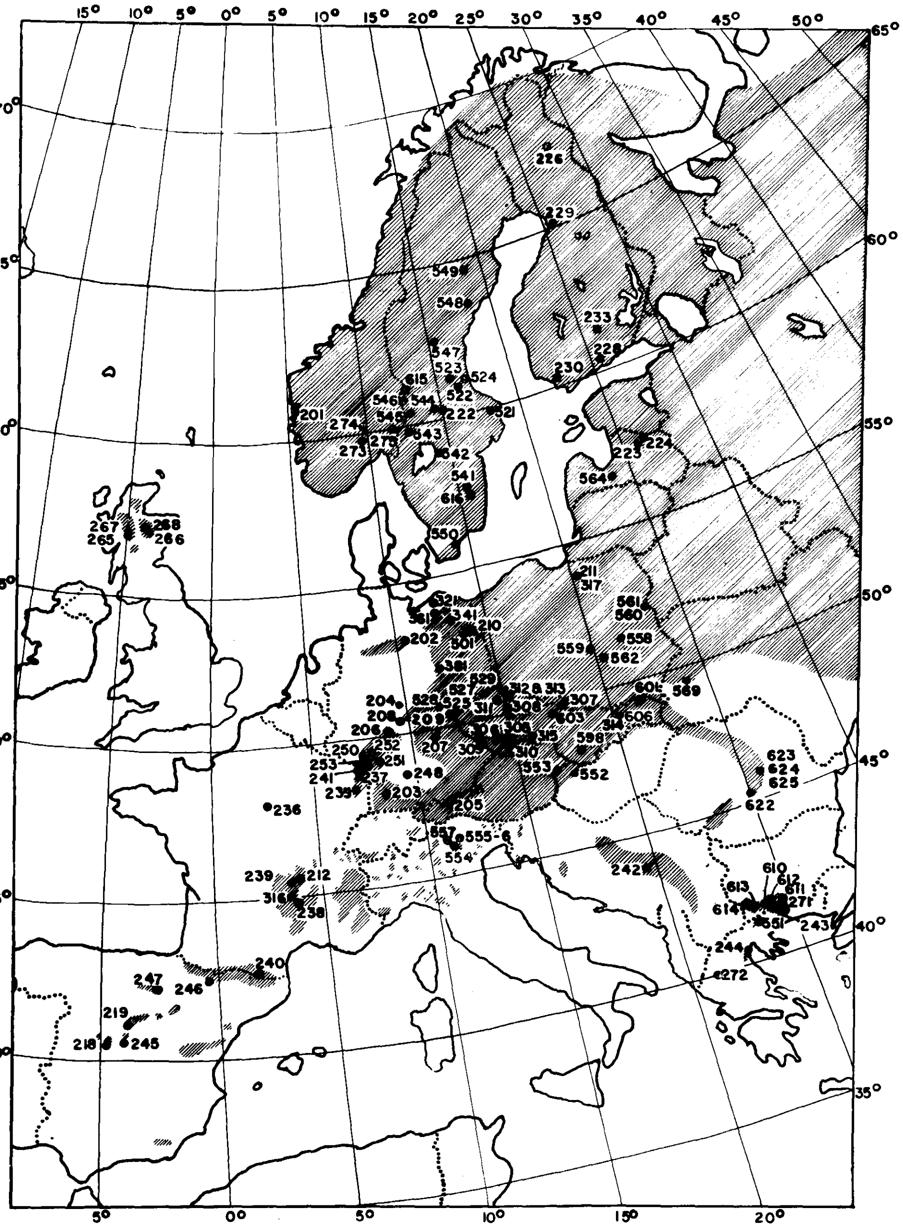

Figure 1. — Natural distribution of Scotch pine in Europe (shaded) and provenances included in WRIGHT and BULL (1963) tests (numbered dots).

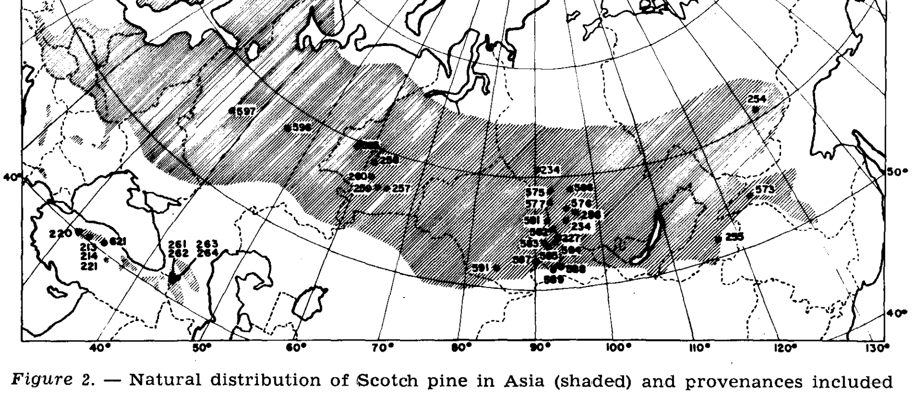

Figure 2. — Natural distribution of Scotch pine in Asia (shaded) and provenances included in WRIGHT and BULL (1963) test (numbered dots).

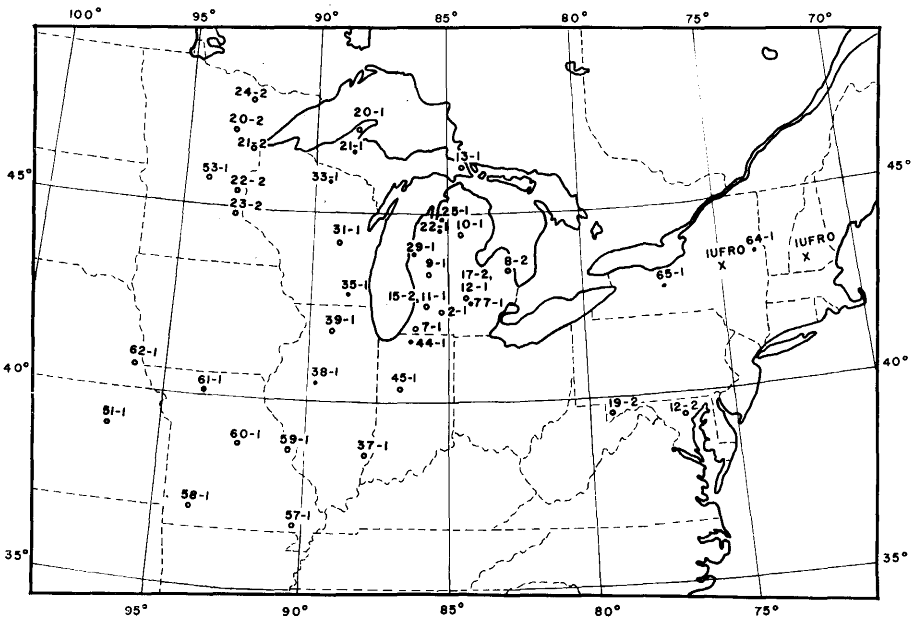

Figure 3. — Location of the outplantings (solid dots).

Additional seedlots were sampled at Russ Forest in order to obtain as complete a picture as possible of the range-wide variation in Scotch pine *(Table 1).*

Tissue samples were collected during late November and early December 1963. One upper lateral branch was clipped from each of the four trees constituting a plot. All replications at each site were sampled and all sample branches for one seedlot at each site were composited. Thus, each composite sample represented up to 40 trees of one seedlot in a particular plantation.

The mean of such a composited sample must be the same as the average of the subsamples were they analyzed separately. However, it was also necessary to determine the reliability of these composite-sample means if there was to be an estimate of seedlot × plantation interaction. Five seedlots were chosen to measure interaction. For each seedlot the tissue samples for the first and second half of the Russ, Newaygo, and Higgins Lake plantings were composited separately. Separate analyses of these provided estimates of the standard error of a seedlot-within-plantation mean and the seedlot × plantation interaction.

Sample preparation and analysis: Current needles were separated from the stems and dried at 70° C for 48 hours.

After drying the needles were ground in an intermediate Wiley mill to pass a 20-mesh sieve. The samples were analyzed by photoelectric spectrometer for P, Ca, Mg, Mn, Fe, Cu, Zn, B, Al, and Na; for N by the KJELDAHL method, and for K with the flame photometer.

Internode growth: The growth increment for 1963 was measured at Russ and Newaygo to the nearest one-half inch. Because heavy weevil attack had partially or completely destroyed the youngest whorls at the Higgins Lake planting, KING's (1965 a) measurements of the 1963 growth increment were used.

Statistical Analyses: All computations involved in the analysis of variance, correlation, and regression techniques were performed by the CDC 3600 computer with library programs at Michigan State University.

Results and Discussion

The soil analyses were performed to obtain a general picture of the nutrient supplying capacities of the sites *(Table 2).* Should large deviations in the tissue levels of some elements have occurred, a reasonable estimate of the degree to which soil factors were causing these deviations could have been made.

The abandoned nursery on the Russ Forest was the most fertile of all three sites. With the exception of total nitrogen, the soil levels of all nutrients were highest there. The significant differences among plantations in the quantities of available P, K, Ca, and Mg were largely due to the fact that their soil levels at Russ were higher than at both other plantings. Russ was the only site where soil magnesium levels were as high as 75 pounds per acre, a level considered adequate for agricultural crops by soil scientists in Michigan (MSU, 1963). WILDE (1958, p. 360) considers about 120 pounds of exchangeable magnesium per acre adequate for Scotch pine nurseries and therefore even Russ was deficient in soil magnesium by his standards.

Higgins Lake was intermediate in fertility. Soil magnesium was deficient and total nitrogen was the lowest of all three sites. The other nutrients appeared adequate for growth.

Newaygo was the least fertile site despite the relatively high total nitrogen content shown in *Table 2.* This is probably not a reflection of soil nitrogen available for plant growth. The soil of the Newaygo site developed under prairie vegetation and much of the nitrogen remaining in the soil today is probably immobilized in ligno proteins of the remains of grass roots. Soil magnesium was almost non-existent at Newaygo. Calcium and potassium were low by WILDE's (1958) standards.

Determinations of seedlot × site interaction: Seedlot × site interaction was measured for all elements in five seedlots. The values obtained for those seedlots were used as an estimate of the interaction for all seedlots. Seedlots interacted with site in regard to their magnesium, copper, and aluminum contents *(Table 4).* Of these, only magnesium

Table 1. — Seedlots sampled and geographic data for their collection areas.

Region, country of origin, MSFG No.	North lat.	East long.	Elev.	Plantings sampled[1]
	Degrees		100's of ft.	
A FIN[2] 229	65.2	25.5	0	3
SIB 254	60.8	131.6	25	2
B SWE 546	60.9	13.4	15	3
SWE 547	62.5	15.7	7	2
SWE 548	63.5	18.7	7	2
C NOR 201	60.5	3.2	1	1
NOR 273	59.7	9.5	6	3
SWE 222	60.2	15.0	8	3
SWE 521	60.0	18.0	1	1
SWE 522	60.9	16.5	7	3
SWE 523	61.3	16.0	7	1
SWE 524	61.3	17.9	1	1
SWE 543	59.9	12.9	7	3
SWE 544	60.4	14.9	8	3
SWE 545	60.4	12.9	8	1
FIN 228	60.4	25.4	1	1
FIN 230	60.5	22.4	1	3
FIN 232	60.3	25.4	--	1
FIN 233	61.5	26.0	--	1
D LAT 223	57.5	25.8	--	3
LAT 224	57.7	26.3	--	3
SWE 541	57.0	15.6	5	3
SWE 542	58.8	14.3	4	3
SWE 550	55.9	14.1	1	3
E SIB 227	54.0	94.0	5	3
SIB 234	56.0	95.0	--	1
SIB 255	52.4	117.7	20	3
SIB 256	56.7	96.3	13	3
URA 257	56.8	65.0	5	1
URA 258	58.8	60.8	3	3
URA 259	56.9	63.2	3	3
URA 260	57.0	61.4	5	1
F POL 211	53.8	20.3	--	3
POL 317	53.7	20.5	--	3
G GER 202	53.-	10.6	4	3
GER 203	48.2	8.3	--	3
GER 204	50.8	9.7	13	3
GER 207	49.7	11.2	--	3
GER 208	50.6	9.7	--	3
GER 210	53.2	14.3	--	1
GER 525	50.4	12.2	15	1
GER 526	50.4	12.2	17	1
GER 527	50.9	13.7	18	3
GER 528	50.6	12.0	15	1
CZE 305	49.-	14.7	13	1
CZE 306	49.2	14.-	15	1
CZE 307	49.9	17.9	8	1
G CZE 308	50.2	15.0	7	1
CZE 309	49.1	13.3	22	1
CZE 310	48.7	14.9	18	1
CZE 311	50.5	14.7	10	1
H NYOp 225	43.-	75.-	--	1
FRA 237	43.8	7.8	5	1
FRA 241	49.1	7.4	8	3
GER 250	49.4	7.6	13	1
GER 251	49.1	8.1	5	3
GER 252	49.3	7.9	13	1
GER 253	49.1	7.8	13	3
BEL 318p	51.2	5.5	--	1
BEL 530p	50.0	5.0	10	3
HUN 553	47.7	16.6	10	3
ITA 554	46.0	11.2	25	1
ITA 555	46.3	11.3	31	1
ITA 556	46.3	11.3	33	1
ITA 557	46.3	11.0	26	1
I ENG 269p	51.2	0.8	7	2
ENG 270p	51.2	0.8	7	2
J GER 209	50.3	12.2	62	2
FRA 235	48.2	9.2	22	3
YUG 242	43.9	19.4	40	3
K TUR 213	40.5	32.7	49	3
TUR 214	40.5	32.7	49	1
TUR 220	40.0	31.3	47	3
TUR 221	40.5	32.7	49	3
GRE 243	41.5	24.3	49	3
GRE 244	40.2	22.1	55	3
GRE 272	39.9	21.2	45	1
GEO 261	41.7	42.7	36	1
GEO 262	41.7	43.0	39	1
GEO 263	41.8	43.4	37	1
GEO 264	41.8	43.5	52	1
L SCO 266	57.2	-3.7	8	1
SCO 267	57.2	-4.8	9	1
SCO 268	57.2	-3.8	--	1
M FRA 212	45.-	4.-	--	2
FRA 238	44.7	3.8	31	3
FRA 239	45.3	3.7	33	3
FRA 240	42.6	2.1	50	1
N SPA 218	40.3	-5.2	37	3
SPA 219	40.8	-4.0	49	3
SPA 245	40.7	-4.2	49	3
SPA 246	41.8	-2.8	39	3
SPA 247	42.3	-0.5	37	3

[1] A '1' indicates that the seedlot was sampled at Russ, a '2' that it was sampled at Russ and Newaygo, and a '3' that it was sampled at Russ, Newaygo, and Higgins Lake.

[2] BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgia SSR, GERmany, GREece, HUNgary, ITAly, LATvia, NORway, NYO (New York), POLand, SCOtland, SIBeria, SPAin, SWEden, TURkey, URAl Mountains, YUGoslavia.

p Seeds obtained from planted stands.

showed significant among-seedlot-differences. The foliar magnesium × site interaction of five Scotch pine seedlots grown at three sites will therefore be considered *(Table 3)*.

The soil-test data for the magnesium levels at the plantings should be recalled. Russ was highest, Higgins Lake intermediate, and Newayo low to the point of deficiency

Table 2. — Mean values for the 0 to 8 inch and 8 to 14 inch soil horizon parameters[1]) for the three sites.

Parameter	Russ Forest		Newaygo Forest		Higgins Lake		F-value due to Plantings[3])	
	0—8"	8—14"	0—8"	8—14"	0—8"	8—14"	0—8"	8—14"
pH	5.3	5.1	5.6	5.9	6.1	6.2	25.32**	47.08**
Lbs N/acre[2])	1620.0	860.0	1660.0	1060.0	1180.0	640.0	26.80**	22.38**
Lbs P/acre	240.9	194.5	28.6	35.5	80.1	79.7	192.86**	88.49**
Lbs K/acre	161.4	141.5	34.8	21.5	75.4	33.4	103.62**	54.17**
Lbs Ca/acre	652.8	778.5	104.3	103.7	489.6	257.4	11.54**	40.00**
Lbs Mg/acre	55.0	80.4	6.5	5.0	34.6	10.7	10.97**	45.66**
C.E.C.	10.1	9.8	9.3	5.1	5.8	2.5	4.38*	76.89**
% base sat.	19.8	25.8	2.3	5.2	23.8	32.1	18.26**	18.69**

[1]) — Nitrogen by Kjeldahl, phosphorus by extraction with Bray's no. 1, potassium, calcium, and magnesium by extraction with ammonium acetate and flame photometer

[2]) — Nitrogen on the basis of five samples for each of the two horizons. There were 2 degrees of freedom for plantings and 14 for error.

[3]) — There were 2 degrees of freedom for plantings and 72 for error (not applicable to nitrogen F-values).

Table 3. — Differences in foliar magnesium levels of Scotch pine seedlots grown at three sites.

MSFG Origin and Home Country	Percent foliar magnesium		
	Russ Forest	Newaygo Forest	Higgins Lake
SWE[1]) 541	.080	.045	.125
URA 258	.075	.030	.100
GER 251	.090	.055	.105
TUR 221	.095	.045	.135
SPA 219	.060	.055	.100
Average	.080	.046	.113

[1]) — GERmany, SPAin, SWEden, TURkey, URAl Mountains.

in soil magnesium *(Table 2)*. The seedlots from Germany, Turkey, and Spain interacted with site *(Table 3)*. The German seedlot was above the mean magnesium content both at Russ and Newaygo but below the mean at Higgins Lake. Considering the low soil-magnesium levels at Newaygo, these tissue levels indicated that this fast growing seedlot has the ability to extract the nutrient from the soil when the element is present in only small quantities. Once the needs of this German seedlot for foliar magnesium are met, however, it does not accumulate the element *(Table 3)*. This is demonstrated by the fact that it was only 11 percent above average at the Russ Forest, where soil magnesium was high, and that it was slightly below average at Higgins Lake, where foliar magnesium levels of other seedlots were very high. In contrast, the Turkish seedlot had the highest magnesium levels of all five seedlots at Russ and at Higgins Lake, both plantings at which soil magnesium levels were higher than at Newaygo. At Newaygo this Turkish seedlot was below average in its tissue magnesium content, indicating that it is a poor absorber of the element when it becomes limiting. In contrast, the Spanish origin was lower than average in magnesium content at both Russ and Higgins Lake, but was well above average at Newaygo, indicating that it can extract magnesium from the soil when the element is low.

Because of the significant seedlot × plantation interaction established for magnesium, the significant among-seedlot-differences for the element *(Table 4)* should be interpreted cautiously.

Tissue Analysis: The foliar levels of all elements are presented in *Table 4*. Comparison with tissue concentrations reported by other authors (Leyton, 1955; Irmak, 1958; Irmak and Cepel, 1959; Gerhold, 1959; Tamm, 1963) shows that the nitrogen levels encountered in this study were generally the same; potassium and magnesium levels were lower, iron, copper and boron were generally higher than the values found in the literature.

The phosphorus and calcium levels determined by other workers and the manganese levels in this study *(Table 4)* vary too much to permit comparison.

The tissue levels of all mineral elements varied to a highly significant degree among locales *(Table 4)*. This points out the high degree in which the substrate affects the mineral composition of Scotch pine. Evolution probably has shaped this characteristic. The species is relegated to

Table 4. — Mean foliar mineral contents (percent oven-dry weight) of 45 Scotch pine origins grown at three locations.

Element	Units	Location			F-value due to		
		Russ Forest	Newaygo Forest	Higgins Lake	Site	Seedlot[1])	s × p Interaction[2])
N	%	2.00	1.86	1.77	64.59**	1.57*	1.34
K	%	.53	.44	.57	135.26**	1.30	2.52
P	%	.22	.22	.19	71.88**	1.78*	.37
Na	ppm	62.62	62.09	78.60	11.26**	2.40**	2.38
Ca	%	.40	.36	.48	50.65**	.70	1.46
Mg	%	.07	.05	.11	376.76**	1.85*	3.20*
Mn	ppm	898.22	1007.78	275.78	256.31**	.68	1.10
Fe	ppm	95.96	77.40	60.73	94.32**	1.40	2.22
Cu	ppm	9.46	7.50	7.76	14.65**	.90	4.79**
B	ppm	35.84	37.89	22.29	252.52**	2.18**	.45
Zn	ppm	62.87	57.89	67.33	6.41**	.82	.83
Al	ppm	984.89	1376.44	1131.11	87.43**	1.49	3.24*

*, ** — Indicates significance at the five and one percent level, respectively.

[1]) — There were 44 degrees of freedom for seedlot and 88 for the error term.

[2]) — Determined in a separate experiment as described under "Methods". There were 8/12 degrees of freedom for s × p interaction.

the less fertile sites throughout its range and has apparently developed a very efficient mechanism for nutrient accumulation. When man plants it on fertile sites, this characteristic — efficient nutrient accumulation — may easily create nutritional imbalances within the trees when the soil nutrient levels are out of balance.

The pronounced effect of substrate on foliar composition makes tissue level comparisons of field-grown Scotch pine difficult. But what KENWORTHY (1961) stipulated for fruit trees is also true for Scotch pine. He wrote, "The differences found in tissue composition values for different regions, states or countries reflect differences in nutrient supply, sampling technique and analytical methods rather than changes in physiological requirements of the plants." The physiological requirements of Scotch pine must be determined by experiments under controlled conditions.

The tissue levels of nitrogen, phosphorus, sodium, magnesium, and boron varied significantly among seedlots (*Table 4*). Among-seedlot-differences for nitrogen and phosphorus were reported in an earlier paper (STEINBECK, 1965), but other elements accumulated differently by seedlots in the earlier investigation did not differ in this study and vice versa. Various factors may account for this discrepancy. The number of seedlots, the sites, and the years all varied between the studies. Differences in the significance of F-values for among-seedlots for both studies may indicate a departure from randomness in the seedlots selected in the earlier investigation. The present study represents an approximation of the entire Scotch pine population. It is possible that departures from randomness caused some of the differences between the studies. The strong effect of site on foliar composition has already been mentioned. When the foliar levels of N, K, P, and Mg for the five seedlots sampled in 1962 (STEINBECK, 1965) were compared to their levels in 1963, significant yearly fluctuations existed for K and P.

Multiple Regression with 1963 Internode Growth as the Dependent Variable

Growth averaged 8.20 inches at Russ Forest, 4.53 inches at Newaygo, and 3.08 inches at Higgins Lake.

The coefficients for the regression equations which relate 1963 internode growth at the three plantings to the foliar levels of twelve mineral elements were calculated (*Table 5*). These equations by themselves give no direct information about the significance of the contributions made

Table 5. — Partial regression coefficients for the mineral element (percent oven-dry weight) contents when 1963 internode growth is the dependent variable.

Element	Unit	Partial regression coefficients		
		Russ Forest	Newaygo Forest	Higgins Lake
N	%	—5.045	4.572	.727
K	%	16.796	1.760	2.974
P	%	—5.966	25.582	—15.561
Na	ppm	.011	—.003	—.006
Ca	%	—4.107	—2.393	—2.008
Mg	%	73.340	46.502	36.394
Mn	ppm	—.001	—.030	—.004
Fe	ppm	—.003	.011	.042
Cu	ppm	—.248	.094	—.107
B	ppm	.015	—.023	.010
Zn	ppm	.040	.018	.006
Al	ppm	—.006	.004	—.003
		Regression constant		
		6.303	—11.026	—1.566

by the individual elements. An F-test was used to determine whether an element had an effect in the regression. In order to perform the test, the regression was calculated twice, once with the element in the regression and once without it. An F-value was then calculated as follows:

(1) Obtain the difference between the error sums of squares for the two regressions.
(2) Divide by 1 (= degrees of freedom) to obtain the difference-mean-square.
(3) For the complete regression divide the error sum of squares by degrees of freedom to obtain an error-mean-square.
(4) Divide the difference-mean-square by the complete-regression-mean-square.

Table 6. — The significance of the contribution of the mineral elements (percent oven-dry weight) to the regression equations for 1963 internode growth.

Element eliminated from the regression	Percent of variation accounted for by element		
	Russ Forest	Newaygo Forest	Higgins Lake
N	3.1*	3.7*	.2
K	5.5**	.1	1.4
P	.0	2.0	2.7
Na	.6	.1	1.5
Ca	.4	.2	.6
Mg	14.8**	11.5**	17.0**
Mn	.0	5.3*	.0
Fe	.0	.5	14.8*
Cu	1.6	.6	3.5
B	.0	.2	.1
Zn	1.7	.5	.4
Al	.0	.1	.1
Amount of total variance accounted for by regression[1])			
	46.9%	69.7%	60.1%

*, ** — Indicate significance at the five and one percent level, respectively. There were 72 degrees of freedom at Russ, 39 at Newaygo and 21 at Higgins Lake.

[1]) — Due to interactions between elements, the sum of the variations accounted for by individual elements is not equal to the amount of total variance accounted for by the regression.

Table 6 presents the results of that F-test, the amount of total variance in internode growth explained by the regression equations, and the relative contributions of each element to the regression.

At Russ, N, K, and Mg made significant contributions to the regression equation for internode growth (*Table 6*). The nitrogen content was inversely related to internode growth. This might have been due to excess nitrogen in the trees or some other cause. Tissue nitrogen levels were higher than at the other two plantings (*Table 4*), but when Russ nitrogen levels are compared with concentrations reported by other investigators they do not appear to be sufficiently high to be detrimental to growth. The inverse relationship between nitrogen and internode growth does not appear to be due to nitrogen toxicity or to an imbalance caused by high N.

Plants deficient in potassium usually contain a higher percentage of amino acids and amides (WALL, 1940) than those adequately supplied with the nutrient. Although the soil potassium levels at Russ were substantially higher than at the other two plantings (*Table 2*) and the foliar levels were intermediate (*Table 4*), multiple regression analysis indicated that potassium made a highly significant, positive contribution to internode growth at Russ (*Table 6*). It appears that the level of nutrition at Russ was so high that a foliar level of potash sufficient at the other plantings was deficient at Russ. This in turn may have caused the accumulation of nitrogen.

There was a distinct trend in nitrogen accumulation at Russ. Slow growing northern seedlots tended to accumulate the nutrient; thus the negative relation between height and nitrogen. It may mean that northern seedlots are either poorer potassium or better nitrogen accumulators than the other seedlots. The former seemed to be the case because northern seedlots averaged about .51 percent tissue potash as compared to an overall mean content of .54 percent at Russ. Sodium, an element which can help ameliorate potash deficiencies, also was lower in the northern than in the other seedlots.

Why are the northern seedlots such poor potassium accumulators? The predominantly coarse textured soils of the native, north European region of these seedlots are often low in both potash and nitrogen and probably in balance. But at Russ, where the trees did not absorb sufficient potash and where nitrogen was adequate, the relatively poor capacity of these origins to absorb potassium accentuated the accumulation of nitrogen. Nothing is known about the cause for differences in the ability to accumulate nutrients, whether they are to be sought in the size of the exchange capacity of the root system, the efficiency of translocation within the plant, or differences in the metabolism of the trees which allow the more efficient utilization of an element.

At both other plantings, Higgins Lake and Newaygo, potash seemed adequate. The fast growing, central European origins had relatively higher nitrogen levels than either the northern or southern seedlots. At Newaygo this trend was especially pronounced. Nitrogen made a significant, positive contribution to internode growth *(Table 6)*, probably indicating that at that site this nutrient was one of the growth limiting factors.

Magnesium was one of the key elements for growth at all three locations. German foresters (MÖLLER, 1904; BRÜNING, 1959) observed that a fertilizer containing both potash and magnesium accelerated Scotch pine growth on infertile sites in eastern Germany. BRÜNING (1959) applied nitrogen, phosphorus, potash, and magnesium to Scotch pine plantations and reported that potash and magnesium were most effective in increasing growth. He believed that the sites on which he worked were more severely depleted in potash and magnesium than nitrogen. In this study soil magnesium at Newaygo was low to the point of deficiency (about 5.7 pounds per acre, *Table 2)* and may well have been the element most limiting to growth. At both other plantings magnesium also made significant contributions to internode growth *(Table 6)*.

Foliar manganese levels were highest at Newaygo *(Table 4)* and the partial regression coefficient for this nutrient made a significant negative contribution to the regression equation for internode growth *(Table 6)*.

Multiple Regression of Mineral Content Expressed as Weight per Needle with 1963 Internode Growth

Multiple regressions for internode growth dependent on mineral content per needle and the contributions of the individual elements to the regression were calculated *(Tables 7 and 8)*. The transformation from a percent to a weight per needle concentration resulted in regression equations similar to the ones obtained when the foliar levels were expressed on a percentage basis. No new relationships were discovered. Rather, seven of the sixteen significant contributions of elements shown in *Table 6* (based on percent oven-dry weight content) do not appear in *Table 8* (based on weight per needle). Significant contributions of sodium at Russ, manganese and iron at Newaygo and iron at Higgins Lake were eliminated by the transformation. Whether this represents a loss of information or an improvement in the method cannot be decided here. The amount of the total variance in internode growth accounted for by the regression equations generally was greater when weight per needle rather than percent content was used as the independent variable.

Table 7. — Regression coefficients for the mineral elements (weight per needle) when 1963 internode growth is the dependent variable.

Element	Unit	Partial regression coefficients		
		Russ Forest	Newaygo Forest	Higgins Lake
N	mg	—40.48	34.22	—6.22
K	mg	163.92	—60.41	33.72
P	mg	31.58	41.30	—155.16
Na	10^{-4}mg	.15	—.01	—.07
Ca	mg	—19.80	31.26	—18.29
Mg	mg	540.35	291.49	215.65
Mn	10^{-4}mg	—.24	—.09	.14
Fe	10^{-4}mg	.05	—.06	.16
Cu	10^{-4}mg	—1.30	.70	—.32
B	10^{-4}mg	.02	.57	.13
Zn	10^{-4}mg	.02	—.16	.02
Al	10^{-4}mg	.05	—.19	.01
		Regression constant		
		4.00	.44	2.11

Table 8. — The significance of the contribution of the mineral elements (weight per needle) to the regression equation for 1963 internode growth.

Element eliminated from the regression	Percent of variation accounted for by element		
	Russ Forest	Newaygo Forest	Higgins Lake
N	4.0**	1.8	.5
K	16.3**	1.3	3.6
P	.1	.1	4.6
Na	2.1**	.0	5.1
Ca	.2	.2	1.3
Mg	12.3**	1.7	16.8**
Mn	1.6	.3	.5
Fe	.2	.1	5.7
Cu	.8	.3	1.1
B	.0	.9	.3
Zn	.1	.3	.1
Al	.1	2.5	.0
Amount of total variance accounted for by regression[1])	59.6%	72.8%	56.4%

*, ** — Indicate significance at the five and one percent level, respectively. There were 72 degrees of freedom at Russ, 39 at Newaygo, 21 at Higgins Lake.

[1]) — Due to interactions between elements, the sum of the variations accounted for by individual elements is not equal to the amount of total variance accounted for by the regression.

Conclusions

The foliar levels of all twelve minerals investigated in this study varied significantly among three plantations. This points up the high degree to which the substrate affected the mineral composition of Scotch pine. It is suggested that Scotch pine has evolved an efficient mechanism to extract nutrients from the infertile sites to which it is relegated in its native range. Transplanting to more fertile sites may easily create nutritional imbalances within the trees when the soil nutrient levels are out of balance.

This study demonstrated significant among-seedlot differences in the ability to accumulate nitrogen, phosphorus, sodium, magnesium, and boron.

The pronounced differences among seedlots in height growth are under genetic control (Wright and Bull, 1963; King, 1965 a). Multiple regressions between internode growth and the mineral content of the foliage were calculated in an attempt to elucidate the pathway from gene to the morphological expression of the difference.

Internode growth was selected as an index to genetic differences in total height because yearly fluctuations in nutrient content are more closely associated with current than total height growth. Various nutrients were significantly associated with 1963 internode growth at each of the three plantings, probably because of differences in fertility. Of the elements shown to differ significantly between seedlots, nitrogen and magnesium were related to internode growth.

Nitrogen was positively related to internode growth at one planting and negatively at another. The association of higher nitrogen accumulation with better internode growth at the first planting probably is one of the pathways in which genes control growth. But the mechanism of the pathway remains obscure. It might be sought in the size and cation exchange capacity of the root system, translocational differences resulting in different nutrient concentration gradients, or in variations in the efficiency with which different seedlots metabolize nutrients. Of course, a combination of any or all of these factors is possible. The negative association of nitrogen levels with growth at the other planting was probably the result of limited potash uptake by slow growing, northern seedlots. Potash deficiency has been associated with organic nitrogen accumulation in plants (Wall, 1940). The negative association was therefore probably not caused by high nitrogen levels but rather by low potash concentrations.

Magnesium was one of the key minerals in the nutrition of Scotch pine at all sites. Seedlots varied significantly in their ability to accumulate magnesium and fast growing seedlots accumulated high foliar magnesium levels. Future studies should investigate whether this is a cause and effect relationship.

The demonstration of differences in the ability of Scotch pine provenances to accumulate nutrients and a relationship between nutrient levels and growth points up a line of investigation as yet scarcely followed by foresters. Research may eventually lead to the selection of certain genotypes of forest tree species which are particularly suited for specific sites in terms of nutrient accumulation and utilization.

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Summary

It was the objective of this study to investigate the effect of site on the foliar nutrient accumulation of Scotch pine seedlots and to relate differences in the seedlots' nutrient content to internode growth.

Scotch pine seed, collected from 122 native stands throughout the species' range, was sown in the Michigan State University forest tree nursery in the spring of 1959. In 1961, 2-year-old stock from this collection was used to establish test plantations throughout Michigan and the central United States. Each planting followed a randomized block design with seven to ten replications. Each plot consisted of four trees. The number of seedlots at each planting varied from 50 to 100.

Foliage samples from 45 seedlots common to three test plantations in the lower peninsula of Michigan were collected after the completion of the trees' fifth growing season, during the winter of 1963. An additional 46 seedlots were sampled at one of the plantations in order to cover the species' range as completely as possible. Samples from each of the 4-tree plots were composited over all replicates at each planting. An estimate of plantation × seedlot interaction was obtained by compositing the samples of five seedlots separately for the first half and for the second half of each planting.

The foliage was analyzed for twelve minerals — N, K, P, Na, Ca, Mg, Mn, Fe, Cu, B, Zn, and Al. Internode growth for the previous growing season was measured at each plantation.

The foliar levels of all twelve minerals varied to a highly significant degree among the three plantings. This points up the high degree to which substrate affects the mineral foliar composition of Scotch pine. It is suggested that the species has evolved an efficient mechanism to extract nutrients from the infertile sites to which it is usually relegated in its native range.

The present investigation demonstrated significant among-seedlot differences in the ability to accumulate N, P, Na, Mg, and B.

Various nutrients were significantly associated with 1963 internode growth at each of the three plantings, probably because of among-site differences in fertility. Of the elements differing significantly among seedlots, nitrogen and magnesium were related to internode growth.

Nitrogen was positively related to internode growth at one planting and negatively at another. The association of higher nitrogen accumulation in the faster growing seedlots at the first planting may be one of the pathways in which genes control growth. The negative association of nitrogen levels with growth at the second planting was probably the result of limited potash uptake by slow growing, northern seedlots. Low potassium levels could have caused an accumulation of organic compounds in the leaves.

Magnesium was one of the key minerals in the nutrition of Scotch pine at all plantations. Seedlots varied significantly in their ability to accumulate it and fast growing seedlots were associated with high foliar magnesium levels. Research to determine whether this is a cause and effect relationship should be fruitful.

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Needed: a New Approach to the Study of Pollen Dispersion

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As genetics assumes more importance in forestry, the need for accurate information on pollen dispersion becomes critical. In recent years forest geneticists have made many studies of pollen dispersal. And their results have been used to determine safe isolation distances around seed orchards and to estimate distances across which populations may interbreed.

The usual approach to the study of pollen dispersal is to measure the pollen density of the air a few feet above the ground, at various distances from a known source, usually the edge of a forest or isolated trees.[2]) Typically these counts describe a gradient in which the frequency of airborne pollen declines rapidly as the distance from the source increases (*figure 1*). This rapid decline has led to the belief that relatively narrow isolation strips (0.25 to 0.7 miles) are satisfactory barriers to pollen contamination in seed orchards (STRAND 1957; WANG *et al.* 1960). WANG *et al.* (1960) admit that under certain conditions (e. g. atmospheric turbulence and strong winds) foreign pollen may penetrate the barrier, but it is expected that such pollen will be greatly outnumbered by pollen produced within the seed orchard.

WRIGHT (1953) has extrapolated short-distance dispersion data in estimating long-distance migration rates of pollen. He concluded that pollen transported more than 10 miles is ineffective in preventing genetic differentiation, largely because of the very small number of viable grains that he estimates would be present.

Departures from the Model

Because of the reliance that has been placed on the results of short-distance dispersion studies, it is important to explain departures from the model depicted in *figure 1*. The magnitude of such departures is evidenced by the following:

(a) SILEN (1962) monitored Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) pollen in the center of a 3×14.5-mile treeless area in the Willamette Valley, Oregon. He recorded up to 246 pollen grains per $inch^2$ per 24 hours during a 5-day period. The count would probably have been higher if counts had been made daily, thus showing peaks in the capture pattern. This view is based on the assumption that, as SARVAS' data (1955, 1962) show, peaks lasted only a few hours.

(b) MESHKOV (1950) observed a deposit of pine pollen sufficiently heavy to color the soil of the main street in a village on the steppes of the USSR after a rainstorm. The nearest pine stands were 6—7 miles distant.

(c) FLORENCE (1958) monitored slash pine (*Pinus elliottii* ENGELM.) pollen in a seed orchard that was 2.5 miles from the pollen source and surrounded by a 2-mile wide screen of hardwoods 100 feet tall. In a period of calm weather, and a fairly heavy pollen crop, he found pollen density was more than 6 percent of the density at the source. In the

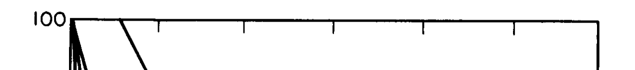

Figure 1. — Typical pollen dispersion curves derived from studies of short-distance transport, from several sources cited in *footnote 2*.

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[2]) BUELL 1947, COLWELL 1951, FLORENCE 1958, SILEN 1962, STRAND 1957, WANG *et al.* 1960, WRIGHT 1953, etc.