ABSTRACT

FOLIAR MINERAL ACCUMULATION BY SEVERAL SCOTCH PINE (Pinus sylvestris L.) PROVENANCES

by Klaus Steinbeck

The objectives of this study were: (1) To investigate the effect of site on the foliar nutrient accumulation of Scotch pine, (2) To explore the possibility that seedlots react differently to the same site, and (3) To relate differences in the seedlots' nutrient contents to genetically controlled, morphological differences.

Scotch pine seed, collected from 122 native stands by co-operators throughout the species' range, was sown in the Michigan State University forest tree nursery in the spring of 1959. Each seedlot was collected from about ten trees per stand.

In 1961, 2-year-old stock from this collection was used to establish permanent test plantations throughout Michigan and the central United States. Each planting followed a randomized block design with seven to ten replications at each planting. Trees were planted in four-tree plots. The number of seedlots per planting varied from 50 to 100.

A preliminary investigation, conducted in 1962, demonstrated significant between-seedlot and between-plantation differences in the foliar mineral levels of five seedlots.

Foliage samples from 45 seedlots common to three plantations in the lower peninsula of Michigan were collected during the winter of 1963. An additional 47 seedlots were sampled at one of the plantations in order to cover the species' range as completely as possible. The samples from each of the 4-tree plots were composited over all replications at each

planting. An estimate of plantation x 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 needles were analyzed for 12 elements: Nitrogen, potassium, phosphorus, sodium, calcium, magnesium, manganese, iron, copper, boron, zinc, and aluminum. Internode growth for 1963, and needle length, weight, and color were measured at each plantation.

The foliar levels of all 12 elements varied to a highly significant degree between the three plantings. This points up the high degree to which substrate affected the mineral 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 relegated in its native range.

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

The non-chemical measurements taken in this study have been demonstrated to be under genetic control. Multiple regressions between these gross-characters and the mineral content of the foliage were calculated in an attempt to elucidate the pathway from gene to the expression of the difference.

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

The results of this study, as does most of the literature, indicate that the genetically controlled color differences between seedlots in winter are not caused by differences in the nutritional levels of the trees.

Needle length was influenced by more foliar minerals than any other physical characteristic measured. It is suggested that it could be a useful indicator of the general nutritional status of Scotch pine.

FOLIAR MINERAL ACCUMULATION BY SEVERAL SCOTCH PINE (*Pinus sylvestris* L.) PROVENANCES

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CHAPTER I

INTRODUCTION

The search for the "Principle of Growth" has been on for centuries. After Europe had shaken off the manacles of the Dark Ages, Van Helmont (1577 - 1644) conducted one of the classic studies to determine the "Principle of Vegetation." He planted a 5-pound willow tree in 200 pounds of soil and added nothing but rainwater. After 5 years he found that the tree weighed 169 pounds 3 ounces and that 2 ounces were lost from the soil. Van Helmont concluded that water is the "Principle of Vegetation."

Since then many great scientists, - Boyle, Bacon, Tull, Priestley, Boussingault, de Saussure, Lawes, Liebig, and others -, have added to and revised the concepts concerning growth. Today Davis *et al.* (1960) list more than sixty factors which affect the growth of crops and there are undoubtedly some as yet unknown. But basically the determinants of growth in green plants are: Light, oxygen, carbon dioxide, water, temperature, and the 16 elements which have been established as essential.

Through the manipulation and optimum combination of as many of the above factors as possible and the tremendous strides in the development of strains and hybrids of crop plants, modern agriculture produces higher yields on less area than ever before.

Forestry today stands on the threshold of an era similar to that of the beginning of the corn breeding program in agriculture. Wood yields will increase manyfold through manipulation of the growth determinants, especially water and light, and by the development of genetically superior

Figure 1.-- Natural distribution of Scotch pine in Europe (shaded) and provenances included in this study (numbered dots).

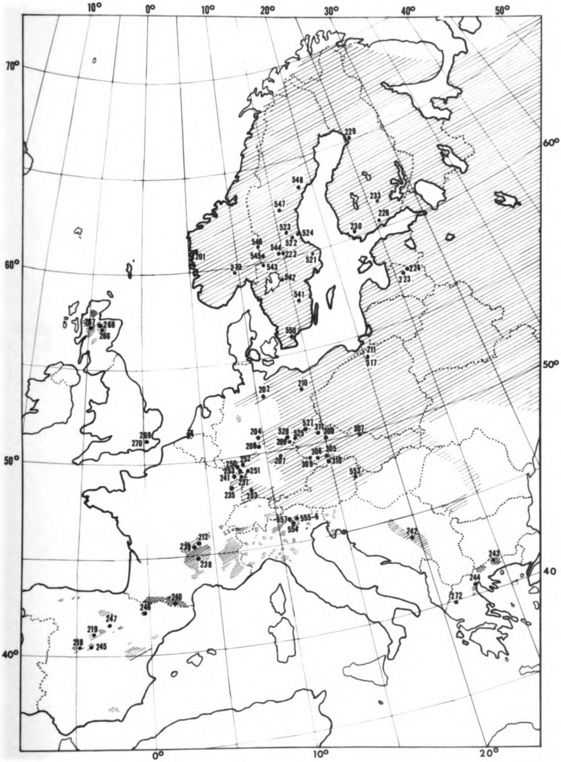

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Figure 2.-- Natural distribution of Scotch pine in Asia (shaded) and provenances included in Wright and Bull (1963) test (numbered dots).

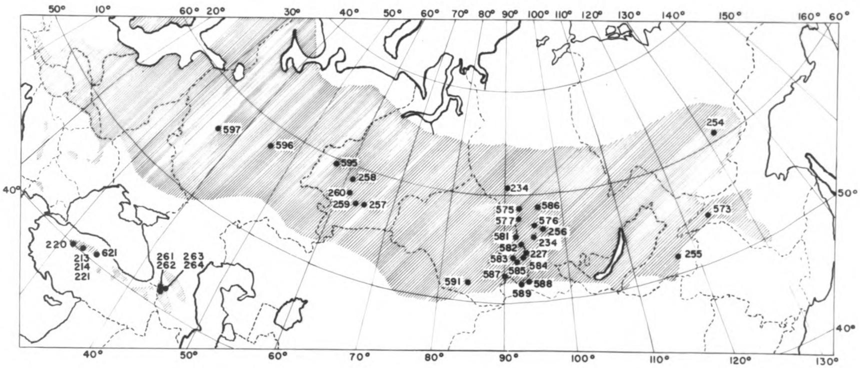
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Figure 3.-- Thirty-year-old Scotch pine (left) and 27-year-old red pine in a wind erosion control planting in Newaygo County, Michigan. Summer 1963.

Figure 4.-- Portion of the test planting on the Newaygo Forest; one of the two windblows on the site appears in the center. Spring 1964.

physiological responses to the climate, inherited genes which control the growth rate, or varying responses to the soils on which these trees grow? A combination of all three possibilities probably comes closest to explaining why, for instance, trees from Germany are so much taller than those of equal age from Sweden.

The main objective of this dissertation is to explore the possibility that provenances react differently to soils, or more specifically whether there is a difference between the abilities of the provenances to absorb and accumulate certain nutrients. Such differences will be demonstrated by relating nutrient contents to genetic differences. The effects of various sites on nutrient accumulation and interactions between ecotypes and sites will be investigated. Foliar composition values from this study may also aid in the establishment of 'normal' composition values useful for diagnostic purposes.

CHAPTER II

LITERATURE REVIEW

The Status of Current Knowledge of Mineral Nutrition - Gene Interaction

Herbaceous plants: A plant must carry on many thousands of chemical reactions in order to live. About 1,000 of them are known and more or less understood today. The life and vigor of the plant are to a very large degree dependent on the relative rates of these reactions in its cells.

Genes exert a controlling influences on reaction rates and the chemical composition of a plant. In the final analysis genes probably control the differences between certain reactions, their relative rates, and the chemical composition of the plant and thus determine that one fertilized egg cell grows into an oak and another into a Scotch pine.

One need not consider plants as different taxonomically as oaks and pines to find differences in metabolism. In fact, genetic differences should be studied in close relatives. Mostly since the late 1950's foresters, agronomists, and horticulturists have observed that varieties of the same species vary in their ability to accumulate certain mineral elements from the same substrate.

The objective of most of the following investigations was to demonstrate that differential accumulation of one or more elements was related to yield differences.

Robinson (1942) grew eight selected clones of white clover on each of five soils in the greenhouse. Percent calcium differed because of both soils and clones. The ranking of the clones by calcium content was essentially the same on all soils. Differences in the phosphorus content due to soils and clones were also highly significant. Moreover there was a highly significant interaction between soils and clones. Ranking of the clones by percent potassium was the same for all soils, and differences due to clones were highly significant.

Seay and Henson (1958) studied potassium, phosphorus, and percent dry matter in 30 clones of Kenland red clover. They found strong clonal differences in all three traits.

Brown and co-workers (1961) reported that seven winter oat varieties responded variously to several levels of fertilizer and gave significant variety x fertilizer interactions for grain yields, protein content of grain, and straw weight. Morris and Reese (1962) grew three rye varieties at various soil levels of nitrogen and obtained differential responses.

An aspect reflecting the atomic age with its fall-out problems and its role in nutrient accumulation was investigated by Rasmusson _et al_. (1963). They determined the effect of genotype in 48 barley and 50 wheat varieties on the accumulation of Sr^{89} added to the soil in the greenhouse. They found highly significant differences in the ability to accumulate Sr^{89} between barley and wheat varieties. This indicates that genotypic differences play an important role in controlling the absorption and/or translocation of the element. Unpublished data of Rasmusson show that varieties with a high ash content do not necessarily have a high Sr^{89} content. A mechanism for either active uptake or exclusion seems to be present, but they offered no theory as to the exact mechanism.

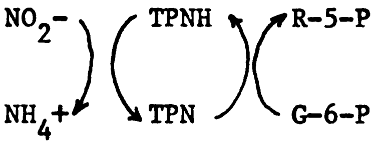
Gorsline _et al_. (1961) reported that differential ear-leaf accumulation of calcium and magnesium in maize was highly heritable and that the genetic variance was mostly additive. Inheritance of potassium accumulation involved non-additive variance. No relationship between the Ca, Mg, and K accumulation was reported.

As most of the literature concerning differences in nutrient accumulation, the above papers state that these differences exist but do not offer theories or experimental work as to how they are brought about.

A group of workers at the University of Illinois has started to determine the physiological and genetic implications of differential nutrient uptake. In a series of papers (Hageman _et al._, 1961; Knipmeyer _et al._, 1962; and Zieserl _et al._, 1963) they have investigated nitrogen metabolism of hybrid lines of maize, attempted to relate varietal differences to enzyme activity, and link the nitrogen and carbohydrate metabolism in the maize plant.

The work of the group was prompted by the fact that maize varieties showed different responses to light intensity (Hageman _et al._ 1961). Yields of hybrids that were tolerant of crowding were least affected by artificial shading. At the same time these tolerant hybrids consistently exhibited a higher level of nitrate reductase (NR) activity than those intolerant of competition. Assuming that nitrates were freely available for absorption by the plant, the accumulation of nitrates observed in shaded plants might have been the result of lower NR activity. Lower NR activity in turn could be cause by a lack of energy provided by carbohydrate breakdown. As in other plants, NR in corn is diphosphopyridine nucleotide (DPN) specific and the subsequent reduction of NO_2- to NH_4+ is in part dependent on reduced triphosphopyridine nucleotide (TPNH) for energy. At the same time the conversion of glucose-6-phosphate (G-6-P) to ribulose-5-phosphate (R-5-P) requires TPN and generates TPNH.

Hageman and his coworkers (1961) visualize the following relationship between carbohydrate and nitrogen metabolism:



The sequence $NO_3 \rightarrow NH_4 \rightarrow$ Amino Acids → More proteins → Higher yield for shade tolerant hybrids was naturally tempting. A diurnal variation of the NR activity, water soluble protein, and nitrate content was observed in the leaves. However, the intermediate metabolites between NO_3 and the amino acids, if such is indeed the primary pathway, did not appear to accumulate.

In the second paper of the series Knipmeyer _et al_. (1962) attempted to establish whether a lack of NR activity or carbohydrate substrate was the primary cause for yield reduction. The nitrogen and carbohydrate metabolisms are interlinked in that keto-acids, probably from the Krebs cycle, are required for amino acid formation. Because citric acid is a precursor and substrate for both keto-acid formation and energy generated in the mitochondria, it was selected as an indicator of carbohydrate supply. They reasoned that low levels of citric acid would reflect low levels of keto-acids and energy and either of the latter could cause nitrate accumulation. But citric acid was as high or higher in the shaded plants as in the unshaded controls. Thus neither energy nor keto-acid supply were the rate-limiting factors and the important role of NR in protein formation was established.

This aspect was elaborated in the third paper by Zieserl et al. (1963). They reasoned that a hybrid having a high level of NR would supply more reduced nitrogen throughout the season. If a certain level of amino acids must be maintained by the plant to initiate or permit normal ear development, the daily input of reduced nitrogen could be a limiting factor. When four hybrids were analyzed for their NR and protein contents, the protein content followed the same general ranking as the NR activity. There was no overall correlation between NR and protein content. However, the data indicate that a decrease in the reduced nitrogen input is a cause of low yields.

In summary of the Illinois papers, hybrid maize lines intolerant of shading exhibited an accumulation of nitrates under high population densities. This accumulation was probably due to a decrease in NR activity because the energy yielding carbohydrate metabolism was not affected by light intensity. The decrease in NR activity caused a decrease in the input of reduced nitrogen necessary for the production of amino acids. Lower amino acid levels reduced protein synthesis, which in turn diminished yields. Because these differences are exhibited by genetically different lines, genes must ultimately control the whole sequence from absorbed nitrate to grain yield.

Trees: Haas (1947) analyzed the pinnae of 15 varieties of date palms growing under the same environmental conditions in southern California. He found a wide range in the Ca, Mg, K, and total P contents of the varieties. Awad (1961) reported that different rootstocks and different varieties of apple trees affected leaf composition significantly. This included N, P, K, Ca, Mg, Mn, Fe, Cu, B, Zn, and Al. His findings indicate that root systems as well as stem and leaf metabolism effect differential mineral element uptake.

Gerhold (1959) worked with six seedlots of 19-year-old Scotch pine planted as part of the International Union of Forest Research Organizations (IUFRO) Scotch pine provenance study in the Vincent State Forest in New Hampshire. The seedlots came from the Netherlands (#19), Germany (#21), Poland (#55), Czechoslovakia (#42), Sweden (#46), and Norway (#4). He analyzed the current year's needles from the leaders of lateral branches in the second and third whorls for needle color, total chlorophyll, total corotenoids, N, P, K, Ca, Mg, Mn, Fe, Cu, and B.

Needle color, N, and Mg varied to a highly significant degree and total chlorophyll, Fe, and Ca varied significantly between the six seedlots. Table 1 presents the average foliar nutrient element contents for the February sampling date. Because of their importance in regard to the present study, Gerhold's (1959) data will be discussed in more detail in Chapters III and IV.

The Relationship Between Mineral Nutrition and Growth

In this section investigations dealing not with genetic but with physiological responses to mineral nutrition within the same genetic background will be discussed.

Before information on mineral concentrations in plants can be related to the understanding of the plant's metabolism, amounts and ranges regarded as deficient, optimum, and excessive must be determined. Experiments to determine optimum foliar levels for tree seedlings in sand cultures have

Table 1. Nutrient element contents of the current year's needles of six Scotch pine seedlots as reported by Gerhold (1959).

Seedlot, IUFRO No.	Concentration of elements								
	% dry weight					ppm			
	N	P	K	Ca	Mg	Fe	Mn	Cu	B
19	1.72	.12	.70	.33	.09	35	627	6.4	11.7
21	1.76	.12	.68	.34	.10	32	301	6.2	10.0
55	1.69	.12	.66	.57	.11	32	535	5.7	11.3
42	1.63	.12	.65	.33	.06	33	761	6.4	9.7
46	1.78	.11	.66	.46	.08	26	584	5.4	13.1
4	1.66	.11	.66	.37	.06	23	487	6.4	13.2
Avg.	1.71	.12	.67	.40	.08	30	549	6.1	11.5

been conducted with eastern white pine (Mitchell, 1939), loblolly pine (Fowells and Krauss, 1959; May _et al._, 1962), Virginia pine (Fowells and Krauss, 1959; Sucoff, 1962), longleaf and slash pine (May _et al._, 1962), western red cedar (Walker _et al._, 1955), and the Canadian pulpwood species of white spruce, black spruce, jack pine, and western hemlock (Swan, 1960). Height growth and needle color are the usual indicators of optimum seedling development.

Because all the above mentioned experiments were conducted in sand culture, they sidestep one of the major problems confronting the foliar analyst: Variation in nutrient concentration due to site. Once the upper part of the Mitscherlich curve, termed 'luxury range' by Smith (1962), is reached by an element, increases in the foliar concentrations of that particular element are not accompanied by increased growth. This problem can be largely overcome by sampling vigorous trees over large regions because "the differences found in 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." (Kenworthy, 1961).

One factor frequently overlooked when interpreting foliar concentrations is the effect of increased strength of nutrient concentrations. When strawberries were grown in different dilutions of Hoagland's solution (Roberts and Kenworthy, 1956), total growth was not affected but the tissue concentration of K, P, B, and Cu increased as the supply increased, Ca, Fe, and Mn decreased, and Mg was not affected. There seems to be no way to deduct soil nutrient concentrations from tissue concentrations and no way of predicting what effect a change in total supply of nutrients may have on tissue concentration.

A few attempts to correlate growth with foliar concentrations of nutrients in forest trees have been made. Leyton (1956) investigated the foliar composition of 10-year-old Japanese larch trees and found significant linear correlations between the height of the trees and the levels of N, P, K, and ash content.

Leyton and Armson (1955) calculated multiple regression equations for tissue levels of N, P, K, and Ca with the height of 10-year-old Scotch pine. Only in the case of nitrogen and potassium in the terminal needles were individual nutrients associated with significant partial regression coefficients. When all factors except nitrogen and potassium were excluded from multiple regression analysis, a highly significant multiple correlation coefficient ($R = .919$) was obtained. The authors postulated that due to interactions between nutrients the existence of a simple correlation between tree height and the concentration of a particular nutrient does not necessarily mean that the nutrient makes a significant contribution to the multiple regression.

Table 2 is compiled from data of authors working in various countries with Scotch pines of different origins and ages. Leyton and Armson (1955) analyzed current needles from the first whorl of 10-year-old trees in England. The medians of the ranges reported by them are given here. Irmak's (1958) data refer to 1 - 2 transplants in nurseries in Turkey. This probably accounts for their high nitrogen content. Irmak and Cepel (1959) were primarily interested in nutrient concentration changes in the course of a year and their data for the November sampling date for 25- to 30-year-old trees are given in Table 2. Gerhold's (1959) data

Table 2. Nitrogen, phosphorus, potassium, calcium, and magnesium composition of Scotch pine foliage as reported by several authors.

	Tissue content as percent dry weight				
Author	N	P	K	Ca	Mg
Leyton (1955)	1.22	.13	.86	.25	--
Irmak (1958)	2.32	.21	.82	.52	.26
Irmak and Cepel (1959)	1.85	.15	.86	.52	.23
Gehold (1959)	1.71	.12	.67	.40	.08
Tamm (1963)	1.31	.16	.59	.43	.09

are the same as the averages reported in Table 1. Tamm, working in Sweden, (1963) presented nutrient contents of needles of Scotch pine sampled over the entire crown. The values given in his paper as kilogram of nutrient per mass of needles per hectare were recalculated to percent of dry weight.

Table 2 illustrates the dilemma which besets forest researchers the world over. Because none of the workers used the same sampling procedure nor reported the provenance of their experimental material, this form of compilation can only convey a general idea of the tissue concentrations to the reader.

Provenance Testing of Scotch Pine

"Provenance in forestry refers to the population of trees growing at a particular place of origin. Provenance research defines the genetic and environmental components of phenotypic variation associated with geographic source. Information on provenance is important in assuring sources of seed to give well-adapted, productive trees and in directing breeding of interracial and interspecific hybrids toward adaptation to particular localities. Concepts of the species, of variation within species, of continuity in this variation, and of relation of variation to factors of the environment have developed over the past century." (Callaham, 1964).

Genetic differences attributable to differences in geographic origin has been demonstrated in more than 35 temperate zone species (Wright, 1962). De Vilmorin is credited with establishing the first Scotch pine provenance test between 1820 and 1850. Since then many European tests have been established. Among them those of Langlet (1939) and the IUFRO deserve special mention because unlike many others, they were well replicated and yielded results applicable to localities other than the test sites. Wright and Bull (1963) and Wettstein (1958) give good summaries of the history of provenance testing of Scotch pine.

Several varieties of Pinus sylvestris have been proposed by various taxonomists. Their studies proved valuable aids in planning provenance experiments. Both Ruby (1964) and Wright and Bull (1963) reviewed the taxonomy of Scotch pine extensively.

Wright and Baldwin (1957) reported on the 17-year-old IUFRO Scotch pine provenance planting established by Baldwin with 2-2 stock in 1942 on the Fox and Vincent State Forests in New Hampshire. They measured gross morphological differences -- height, branch and stem diameters, basal sweep, lean, small and large crooks, porcupine damage, and fruiting. Statistically significant correlations (R = .933 and R = .861, respectively) between 3- or 4-year-height and 17-year-height existed. The Latvian - Esthonian seedlots were moderately fast growing and had the best bole form. Seedlots from the Belgium and Germany - Poland - Czechoslovakia - Hungary regions grew faster but had less desirable growth characteristics. The Scandinavian provenances were generally the slowest growing trees. Scandinavian and Belgian Scotch pines fruited most heavily.

The New Hampshire planting with 50 provenances is one of the most complete IUFRO plantations. Wright and Baldwin grouped provenances into ecotypes, which were statistically different in some of their traits. Most of the dividing lines between regions ran roughly East - West indicating that environmental factors which vary from North to South, - temperature daylength, and light quality -, caused more genetic differentiation than rainfall, soil, or other factors. The boundaries of some ecotypes coincided with geographic breaks in the range. The Baltic Sea is an example of such a genetic migration barrier.

Wright and Baldwin found more significant differences between provenances in height than in any other character measured. They showed that the New Hampshire planting had growth rates comparable to some European provenance tests.

Gerhold's (1959) study of the mineral and pigment changes over a year in Scotch pine needles has already been mentioned. In the same New Hampshire planting Echols (1958) studied wood quality in 15 provenances. He found that tracheid length increased with tree height. Specific gravity varied inversely with growth rate. Thus, according to Echols' results, selection of Scotch pines for fast growth rate is equivalent to selection for longer tracheid length but not to selection for either high or low specific gravity.

Langlet (1936 and 1959) maintains that the entire Scotch pine population does not consist of more or less distinct ecotypes but is of the opinion that its variation is essentially clinal.

The potential of Scotch pine on the many infertile sites of the north-central region of the United States as well as inquiries by Christmas-tree growers in regard to origins best suited for their business prompted the NC-51 committee to initiate extensive provenance tests of the species. NC-51 is a part of the Cooperative State Research Service of the U. S. Department of Agriculture. The project is entitled "Tree Imporvement through Selection and Breeding" and involves active cooperation of numerous federal, state, and private agencies in the North Central United States.

The seed for these provenance tests was procured from European and Asian researchers who were requested to sample native Scotch pine stands in their vicinity. They sent 122 samples: 106 from native stands, 11 from unknown origin plantations, and 5 from dealers. These seeds were planted in the Bogue Nursery of Michigan State University at East Lansing and observed and measured for two years. Wright and Bull (1963) tentatively recognized 14 ecotypes over the whole range of the species. They are differentiated mainly on such characteristics as total height, autumn color, bud formation date and leaf length. Subsequent to nursery testing permanent outplantings were established in Michigan and other north central states. Details of plantation establishment are covered in Chapter III.

King (1965a, b) reported that the seed source x plantation interaction of the individual origins showed little relation to either seed source or plantation location. This interaction never accounted for more than 6 percent of the total variation between seed sources on eight planting sites in two years. Performance differences between plantings, according to King, seem to be more a result of temperature and moisture variations than between-plantation differences in soil or photoperiod. He recommends testing more seed sources at one location and replication of plantings of only the best seed sources.

Further indications that the gross differences of Scotch pine seedlots are little affected by plantation location within a region are given by Jensen and Gatherum (1964). They measured survival, and growth of 10 provenances in northeast Iowa and their color and height data are very similar to those obtained in Michigan studies. The same thing holds true for southeast Iowa (Gatherum and Jensen, 1964).

If nutrient contents of Scotch pine needles follow the same trends as gross genetic differences, the results of the analyses from the samples from these plantations should be applicable to most of the northeast and north-central region of the United States.

Needle Color Changes in Scotch Pine

Scotch pine exhibits striking seasonal foliage pigment changes. Northern provenances turn yellow in winter, trees from central Europe discolor less, and southern seedlots retain nearly the same, blue-green color throughout the year.

The time of year when discoloration begins is variable but the yellowing always increases from fall until the late winter or early spring months. The green color returns with the initiation of the growing period.

The tips of the needles discolor first, the basal portions change less. The upper side turns brighter yellow than the lower one; shaded needles discolor less than those exposed to full sunlight.

Gerhold (1959a) could not correlate degree of yellowing with the foliar content of nitrogen, phosphorus, potassium, calcium, magnesium, manganese, iron, copper, or boron. He investigated six seedlots (Table 1). He did find that the chlorophyll a and chlorophyll b content of trees from central Europe was lower than in trees from Norway and Sweden in August. In February the opposite was true: the chlorophyll content of the Scandinavian trees dropped as much as fifty percent. Carotenoids increased in winter in all trees regardless of origin and without differences between origins.

Plants in general become yellow or colorless because their leaf pigments undergo changes, presumably chemical decomposition. This process occurs when illumination becomes too strong (photoautoxidation) or when photosynthesis is inhibited by poisons or starvation. Rabinowitch (1945, p. 527) proposed as a working hypothesis that "the primary photochemical process of photoautoxidation in vivo is identical with the primary photochemical process in photosynthesis, but that it is coupled with secondary reactions catalyzed by heat resistant catalysts while, in photosynthesis, the same primary process is associated with secondary reactions catalyzed by true, heat sensitive enzymes." This suggests that the wavelengths which destroy chlorophyll are the same ones which are effective in photosynthesis.

When seven-year-old Riga Scotch pines were covered with black, blue, or clear polyethylene, they showed discoloration during the winter (Hacskaylo and Goslin, 1957). Trees covered with red plastic discolored much less and were much bluer-green than the greenest controls.

Gerhold (1959b) fitted sleeves of clear, blue, green, red, and yellow plastic over the twigs of the two upper whorls of seven-year-old trees and found that all treatments were somewhat effective in reducing yellowing. The effects of the blue, yellow, and clear plastics were not statistically different. The red was significantly more effective than the previous three colors and the green was significantly better than red in reducing discoloration. Red plastic screened wavelengths from 440 mu to 520 mu quite effectively; in addition to these, the green plastic shielded the needles also against the wavelengths from 600 mu to 650 mu. Both chlorophyll a and chlorophyll b have absorption peaks in these regions.

Wettstein and Grüll (1954) altered the photoperiod of two different origins of two-year-old Scotch pines. They found that trees of the same origin growing under normal day lengths were still actively growing and green in September whereas those trees which had been given only six hours of light daily had ceased to grow and were yellowing prematurely. When 7-year-old trees were subjected to shortened photoperiods at two temperature regimes, those growing with the higher temperature discolored only slightly. Trees subjected to the shorter day length discolored more severely at both temperature treatments.

CHAPTER III

PRELIMINARY INVESTIGATION

Methods

The objective of the Preliminary Investigation was to determine the magnitudes of the differences in the foliar composition in the various Scotch pine seedlots. Furthermore the effects of site and site x seedlot interaction on tissue composition were to be studied.

The plant material, as all experimental plant material used for this thesis, was collected from outplantings of the nursery stock described by Wright and Bull (1963). In the spring of 1959 they had sown the seeds from trees in 122 stands throughout the natural range of Scotch pine in the Bogue Nursery of Michigan State University at East Lansing, Michigan. This provenance test represents probably the most extensive and statistically best planned study of genetic variation in Scotch pine ever attempted. For further details of seed procurement cee Chapter II. A part of the seed was sown in a 4-replicated, randomized block design in the nursery to determine gross genetic differences. The remainder of the seed was broadcast on large, rectangular plots.

In the spring of 1961, 2-0 seedlings from the broadcast sown plots were distributed to cooperators throughout the north-central region of the United States and 41 permanent test plantations were established. Five plantations were selected from the permanent plantings for measurement (Figure 5). The details of plantation establishment are given in Table 3. Seedlings that did not survive the first year after outplanting were replaced in the spring of 1962. These replacements were easily identified by their tall, spindly appearance in the fall and winter of

Figure 5.-- Location of the outplantings (solid dots) which were sampled.

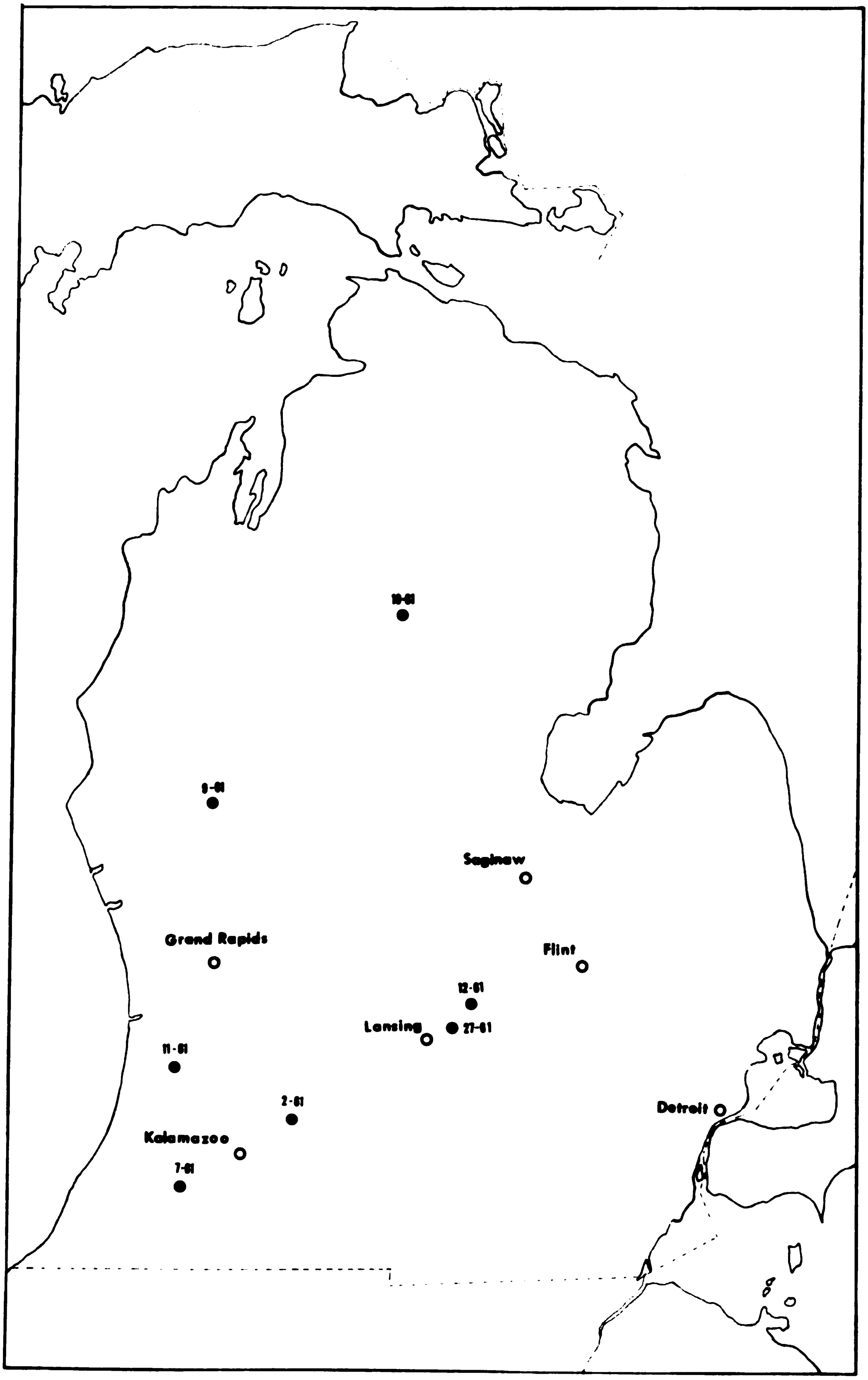

10-81
9-81
Saginaw
Grand Rapids
Flint
12-81
Lansing
27-81
11-81
2-81
Kalamazoo
7-81
Detroit

Table 3. Summary of plantation location and method of establishment.[1]

Map Number[2]	Name	Michigan County	North Lat.	West Long.	Method of Planting
2- 61	Kellogg Forest	Kalamazoo	42.3	85.3	FH [3]
7- 61	Russ Forest	Cass	42.0	85.9	CH
9- 61	Newaygo Forest	Newaygo	43.4	85.8	M
10- 61	Higgins Lake	Crawford	44.5	84.7	M
11- 61	Allegan Forest	Allegan	42.5	86.0	M
12- 61	Rose Lake	Shiawassee	42.8	84.3	M
27- 61	Bogue Nursery	Ingham	42.6	84.5	CH

[1] Seven to ten replication of 4-tree plots are planted at each site. Spacing is 8 by 8 feet on all sites.

[2] Map number of Figure 5.

[3] Furrowed, Hand planted, Machine planted, Chemical weed control.

1962 and 1963 and were not sampled. The collection areas of the seedlots used in both the Preliminary Investigation and Main Study are shown in Figures 1 and 2. Origin data for the five seedlots selected for the Preliminary Investigation are included in Table 4.

The foliage samples for the Preliminary Investigation were collected from five 4-year-old plantings located in the Allegan State Forest (11-61)[1/], Higgins Lake State Forest (10-61), Kellogg Forest (2-61), Bogue Nursery (27-61), and Rose Lake Wildlife Experiment Station (12-61), all in the lower peninsula of Michigan.

During the period between mid-November and mid-December, 1962, one upper lateral branch was clipped from each of the four trees in a plot and composited. The sampling procedures suggested by White (1954) in regard to time of sampling and age of tissue were followed. Cardinal aspect of the lateral sampled was ignored because the trees were essentially growing in the open at age four years and an 8 by 8 foot spacing.

Five origins which encompass the range of Scotch pine, one each from Spain (Michigan State Forest Genetics #219), Turkey (MSFG #221), Germany (MSFG #251), Russia (MSFG #258), and Sweden (MSFG #541) were chosen for study. Each belongs to a different ecotype according to Wright and Bull (1963). Five replications of each origin were sampled at each of the five sites so that 125 samples in all were collected.

The current needle tissue was separated from the stems and dried at 70°C for 48 hours immediately after the return to the laboratory from the collection trips. During the unavoidable delays the needle tissue was kept cool. The time from collection to drying for any sample never

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[1/] Map number of Figure 5.

Table 4.-- Seedlots sampled and geographic data for their collection areas.

Region,	Country of origin MSFG No.	North Lat.	East Long.	Elev.	Plantgs. sampled
		degrees		100's of ft.	
A	FIN[1] 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	7
	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	7
	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
	CZE 308	50.2	15.0	7	1
G	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	NYOp225	~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	7
	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	7
	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	7
	SPA 245	40.7	-4.2	49	3
	SPA 246	41.8	-2.8	39	3
	SPA 247	42.3	-0.5	37	3

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[1] BELgium, CZEchoslovakia, ENGland, FINland, FRAnce, GEOrgia SSR, GERmany, GREece, HUNgary, LATvia, NORway, POLand, SCOtland, SIBeria, SPAin, SWEden, YUGoslavia, URAl Mountains.

p Seeds obtained from planted stands.

exceeded two days.

After drying the needle tissue was ground in an intermediate Wiley mill to pass a 20-mesh sieve. The samples were analyzed by a photoelectric spectrometer in the Plant Analysis Laboratory of the Horticulture Department at Michigan State University for P, Ca, Mg, Fe, Mn, Cu, Zn, B, Al, and Na; for N by the Kjeldahl method, and for K with the flame photometer. The reading accuracy of the spectrometer is given below.

Reading accuracy of the spectrometer (from Kenworthy, 1960).

Element and unit of measurement	Reading accuracy
P - %	.003%
Ca - %	.020%
Mg - %	.010%
Mn - ppm	3.0 ppm
Fe - ppm	2.0 ppm
Cu - ppm	0.6 ppm
B - ppm	0.8 ppm
Zn - ppm	3.0 ppm
Al - ppm	3.0 ppm
Na - ppm	4.0 ppm

A survey of plant analysis laboratories which included the one at Michigan State University was conducted by Kenworthy et al. (1956). A comparison of the results of routine analyses showed good agreement for N, P, K, Ca, and Mg. The results for the other elements tabulated above did not show satisfactory agreement between laboratories. The results of this study in regard to the first five elements are therefore probably comparable with data reported by other authors. Analyses for the other elements, however, will reflect relative differences within this study. Care should be exercised when data for the latter elements are compared with analyses from other laboratories.

The data were analyzed for significance by analysis of variance. There were 4 degrees of freedom for plantations, 4 for seedlots, 4 for replications, 16 for replication x plantation interaction (= error term for replications or plantations), and 80 for seedlot x replication-within-plantation (= error term for seedlots and seedlot x plantation interaction).

Results and Discussion

Table 5 presents a summary of the foliar mineral contents for the five sites.

The Bogue Nursery was a long-established forest tree nursery with a high level of soil fertility on a Hillsdale loamy sand. It was maintained weed free and irrigated when necessary. Scotch pines outplanted in the nursery had a greater stem diameter and more leaf area than the trees on all other sites. The foliar contents of N, K, Mg, Fe, Cu, B, and Na were above average in the nursery grown trees, probably reflecting its high soil fertility. Nitrogen and potassium contents were the highest of any site. Conversely, manganese and aluminum contents of the foliage were abnormally low in the nursery-grown trees.

The four other sites are old field plantings on well drained, sandy soils of low fertility.

The foliage of trees growing on the Kellogg Forest is above the experiment average content in ten elements. A comparison between foliar mineral composition of trees grown at Higgins Lake and at Rose Lake reveals that height growth is not necessarily a reliable indicator of the nutrient status expressed in percentages or as parts per million. King (1965a) reported a mean height growth for 1963 of 19.6 cm at Higgins Lake and 10.9 cm at Rose Lake. But trees growing at Rose Lake have a higher foliar mineral content in 9 of 13 elements which were measured than the faster growing ones at Higgins Lake. Site components other than soil fertility, moisture in particular which may be a reflection of weed competition, probably explain this apparent discrepancy.

Table 5. Effects of site on the mineral content of the current year's foliage of Scotch pine seedlots. 1/

	Content as percent of experiment mean						F value due to	
	Bogue Nursery	Kellogg Forest	Higgins Lake	Rose Lake	Alle-gan	Expt. Mean	Site	Reps. Within Pltg.
N	104	103	98	101	93	1.79%	3.39*	.48
K	110	106	102	94	92	.50%	4.55*	.10
P	89	106	100	100	100	.18%	8.54**	.27
Na	134	104	108	80	75	27.9ppm	6.49**	.57
Ca	98	111	100	102	84	.44%	5.67**	.58
Mg	133	108	83	92	92	.12%	34.74**	2.36
Mn	27	137	72	170	94	406.6ppm	19.06**	.30
Fe	156	84	54	106	100	97.9ppm	35.06**	1.34
Cu	135	106	74	116	70	9.0ppm	44.49**	3.13*
B	106	98	66	125	105	24.9ppm	28.56**	1.98
Zn	87	104	98	121	91	58.8ppm	20.05**	1.89
Mo	98	117	103	102	81	2.0ppm	9.69**	.60
Al	22	96	97	138	147	600.4ppm	37.24**	.30

1/ Mean values of all five seedlots.

*, ** = Significant at the 5 and 1 percent levels respectively. There were 4/16 degrees of freedom for both site and replicate.

The Allegan Forest site was rated the poorest of all five sites for Scotch pine growth. Lichens, poverty grass (Danthonia spicata (L.) Beauv.), and a few cacti (Opuntia humifusa Raf.), all indicating a poor site, are part of the ground cover. The trees appear spindly and grew only 12.5 cm in 1963 (King, 1964). The foliar mineral content was below the experiment mean in 11 of 13 elements. The aluminum content was very high.

Differences in the five sites had highly significant effects on the foliar levels of 12 elements and significant effects on the 13th, nitrogen. In view of the uniformity of the differences in gross morphological characteristics in provenance plantings throughout Michigan, Illinois, and Iowa (Wright and Bull, 1963; King, 1965a, b; Jensen and Gatherum, 1964; Gatherum and Jensen, 1964), this strong influence of site on the mineral accumulation may be surprising. Roberts' and Kenworthy's (1956) strawberry experiment may be the key to this site influence on foliar mineral levels. Their plants, when grown in different strengths of Hoagland's solution, exhibited variations in the tissue concentrations of several elements while total growth was not affected. By the same token, differences in the tissue levels of the nutrients may not markedly affect gross characters of Scotch pine as long as the levels of the nutrients are above the critical range.

With the exception of copper levels there were no significant differences in the foliar composition values between replications on the same site (Table 5).

Table 6 shows the differences between the nutrient contents of the five seedlots. They are arranged in the order of increasing north latitude

Table 6. Mineral content of the current year's foliage of Scotch pine from five different seedlots. [1]

	Content as percent of experiment mean					F value due to	
	MSFG seedlot and home country					Seed-Lot	Seedlot x Site Interaction
	219 Spain	221 Turkey	251 Germany	258 USSR	541 Sweden		
N	96	97	99	102	104	5.46**	1.28
K	102	102	104	92	102	2.36	2.67**
P	94	100	100	106	100	5.09**	7.70**
Na	108	110	104	87	90	1.07	2.50**
Ca	96	96	96	105	105	2.40	1.76
Mg	100	108	100	92	100	3.45*	1.38
Mn	94	99	98	104	104	.36	.98
Fe	114	109	91	90	95	4.33**	3.81**
Cu	99	103	96	101	101	.42	.74
B	95	105	99	101	100	.60	3.40**
Zn	88	90	101	111	110	8.65**	3.06**
Mo	97	96	98	106	104	1.93	1.42
Al	75	123	94	106	102	6.06**	2.18*

1/ Mean values of all five sites.

*, ** = Significant at 5 and 1 percent levels respectively. There were 4/16 and 16/80 degrees of freedom respectively for seedlot and seedlot x site interaction.

of origin. The five seedlots differed to a highly significant degree in their percent N, P, Fe, Zn, and Al tissue levels and to a significant degree in their Mg content.

Tissue concentrations of K, P, Na, Fe, B, and Zn exhibited highly significant, and Al significant seedlot x site interaction. This means that an origin accumulating high levels of these elements on one site does not necessarily behave similarly on another site. This is demonstrated for phosphorus in Table 7. Table 7 shows that the phosphorus content of origin 541 demonstrates seedlot x site interaction. Trees of this origin growing on the Kellogg Forest were much below, and trees of the same origin growing at the Bogue Nursery were much above the average phosphorus content of all five origins growing at the same locations. Origins 251 and 221 show less pronounced seedlot x site interactions. But trees of seedlot 258 and 219 are consistently above and below the average phosphorus level, respectively. In other words, not all seedlots interact with the site on which they grow with regard to phosphorus. Reasons for the presence or absence of origin x site interaction for particular seedlots remain largely speculative at this point.

When separate statistical analyses were performed for each plot sample, the standard deviations of the mineral contents averaged from 11 percent (Phosphorus) to 59 percent (Aluminum) of the mean concentration. These large errors in single plot means necessitate more replications than are financially feasible to detect small differences in the mineral content between origins. A means to reduce this error other than by replication must therefore be found in the Main Study.

In summary, this Preliminary Investigation demonstrates that site

Table 7. Average percent phosphorus content of five Scotch pine seedlots growing on five sites.

MSFG Origin Number	Phosphorus content as percent of dry weight				
	Kellogg Forest	Higgins Lake	Allegan Forest	Rose Lake	Bogue Nursery
541	.159	.176	.191	.190	.196
258	.210	.183	.191	.186	.171
251	.210	.179	.193	.174	.154
221	.200	.189	.184	.179	.148
219	.191	.171	.161	.174	.134
Average	.194	.179	.184	.181	.161

has an influence on the foliar levels of 12 elements, that seedlots vary in the tissue concentrations of certain elements, and that certain seedlots respond differently to varying site conditions. Other seedlots exhibit no seedlot x site interaction. The Preliminary Investigation furthermore made it clear that an expansion of its statistical design will not provide adequate information and that a new approach to reduce the error involved in single plot analysis must be found.

CHAPTER IV

METHODS

Sampling Considerations

The Preliminary Investigation showed that considerable variation exists in the ability of Scotch pine from various seedlots to accumulate mineral elements from the same site. The Main Study was undertaken to determine the geographic pattern of this variation and to relate differences in mineral levels to growth characteristics.

The Preliminary Investigation demonstrated highly significant differences in foliar mineral content related to site. To preclude limiting the applicability of this study to one specific site, several sites were sampled. In this way predictions of the behavior of a specific seedlot on a particular site might be possible.

Seedlot differences were of primary interest; therefore, as many seedlots as possible were to be sampled. They were to be derived from stands throughout the range of Scotch pine and to give as complete a picture as possible of regional differences.

The Preliminary Investigation also demonstrated significant or highly significant seedlot x plantation (S x P) interactions for seven elements. More intensive study of this interaction would have necessitated the replication of sampling of each particular seedlot at each site. Only a few seedlots could be studied on a few sites. It would have been impossible to determine range-wide variation patterns with such a limited number of seedlots. Furthermore, the studies of King (1965a, b) showed that S x P interactions for height growth, needle length, and needle color accounted for no more than six percent of the total variance in those characters. Therefore it was decided to measure S x P interaction for 5 seedlots and to utilize the majority of the samples to determine between seedlot and regional differences.

Selection of Experimental Material and Analytical Methods

Locales: The permanent outplantings of Wright and Bull's (1963) nursery stock chosen for this thesis are located in the Higgins Lake State Forest (10-61) [2/], the Fred Russ Memorial Forest (7-61), and the Newaygo Experimental Forest (9-61). All plantations are located in the lower peninsula of Michigan.

The Higgins Lake planting is growing on a Grayling sand which grades into a Graycalm sand. Grayling soils are well drained Brown Podzolic soils which have developed in deep glacial drift that contains little or no limestone. The Graycalm soil series includes weakly developed Podzols formed in loamy sands or sand drifts. The site has 0 to 2 percent slopes. It is an abandoned field.

Trees at the Newaygo site are growing in a Sparta sand. This soil type is an intergrade between the Brown Podzolic and the Brunizem Great Soil Groups. It developed in deep glacial drift which contains little limestone. The site once supported prairie vegetation. The high organic matter soil enticed early settlement but wind erosion removed the organic matter and left deep, infertile sand. The test plantation is located on an old field with 0 to 2 percent slopes. Only two relatively small (200 to 300 square feet) windblows are now on the site.

2/ Map number of Figure 5.

The Russ planting is located on the site formerly occupied by a forest tree nursery. The soil is a Fox sandy loam. The Fox series includes well drained Gray Brown Podzolic soils developed in silty or loamy materials underlain by stratified, calcareous gravel and sand at depths of 24 to more than 80 inches. In the autumn before planting, 20 pounds of Dalapon per acre was applied to two foot wide strips where the trees were to be planted. Since then four pounds of simazine per acre have been applied. Russ is the only planting at which the trees were hand-planted rather than by machine.

<u>Soil sampling</u>: In May, 1964, the soils of all three plantations were sampled. Sampling followed 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 depth were collected. The soil analyses were performed by the Soil Analysis Laboratory of the Soil Science Department of Michigan State University. The pH, pounds of available phosphorus, potassium, calcium, and magnesium per acre, the cation exchange capacity, and base saturation were determined for each sample. Ten soil samples per site, five each from the 0 to 8 inch and 8 to 14 inch layer were chosen at random and analyzed for their nitrogen content in the Tree Nutrition Laboratory of the Department of Forestry at Michigan State University.

<u>Tissue sampling</u>: The seedlots to be sampled for the Main Study had to meet two requirements. First, in their entirety they must represent and encompass the geographical range of the species. Second, each seedlot must be represented at all three outplantings and show less than 25 percent mortality at each planting. Forty-five origins met both requirements.

They are listed in Table 4 and identifiable by the fact that they were sampled at three or seven plantations as indicated under the column-heading 'Plantings sampled.' These 45 seedlots constitute the Main Study.

In case the Main Study left any discontinuities in the genetic constitution of Scotch pine regions in doubt, a more complete picture of its variability had to be obtained. This was accomplished by sampling all origins represented and showing less than 25 percent mortality at Russ. The seedlots sampled in addition to the 45 origins of the Main Study at Russ are identified by the numeral "1" in Table 4 under the column heading 'Plantings sampled.' These additional seedlots also provide additional information on the between region differences because they furnish degrees of freedom for the statistical analysis.

Leaf samples were collected on the 29th and 30th of November, 1963, at Higgins Lake and Newaygo, respectively, and on the 9th and 10th of December, 1963, at the Russ Forest. One upper lateral branch was clipped from each of the four trees constituting a plot. All replications at each site were sampled and all tissue samples for one seedlot at each site were composited. Thus each composite sample represented leafy twigs from up to 40 trees of one seedlot in a particular plantation.

The mean of such a composited sample must be the same as if the samples were not composited and analyzed separtely. However, it was also necessary to determine the reliability of these composite-sample means if there were to be an estimate of plantation X seedlot interaction. The same five origins used in the Preliminary Investigation were chosen for this purpose. For each seedlot the samples for the first five and the second five replicates in 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 of the plantation X seedlot interaction.

Sample preparation: For each composite sample the current needle tissue was separated from the stems and dried at 70°C for 48 hours within three days of collections. The needle tissue was kept cool prior to drying.

Needle length: Needle length was measured after drying. Twenty unbroken needles were selected at random from each sample and placed alongside a meter stick. The length of 5, 10, 15, and 20 needles was recorded to the nearest millimeter.

Needle weight: Twenty entire needle fascicles (40 needles) were weighed after drying. This measurement permitted the conversion of relative concentrations in the tissue to a weight of element per needle basis.

Chemical analysis: The remaining sample component for each seedlot was ground to pass a 20-mesh sieve in an intermediate Wiley mill. The chemical analytical procedures are identical to those described for the Preliminary Investigation.

Needle color: Needle color was determined by scoring the ground needle homogenate in glass jars. By using uniform light conditions of the laboratory and scoring the samples for all plantings at the same time, light quality changes in the field and color perception changes in the eyes of the observer are greatly reduced as sources of error. A treatment error - oven drying - is introduced by the color scoring method used in this study. Two persons scored color independently under identical conditions. Eighteen color grades were recognized by each observer. The grades ranged from Munsell color 5.0Y 6/6 for grade 1 to 5.0Y 6/8 for grade 18. After an observer had categorized all samples, a few of them were taken at random out of the array, their positions noted, and the same observer was asked to return them to their proper place in the array. In only 6 of 23 cases did he replace the jars more than one color grade away from the original scoring.

Internode growth: The growth increment for 1963 was measured at Russ and Newaygo to the nearest one-half inch. Because of heavy weeviling in the Higgins Lake planting had partially or completely destroyed the 1963 whorl, King's (1965a) growth data for 1963 were used for that site.

Statistical analyses: All analyses of variance, regression, and correlation calculations were performed by the Control Data Computer 3600 with library programs at Michigan State University.

CHAPTER V

RESULTS AND DISCUSSION

In the analysis of the data of this study the regional groupings of Scotch pine derived by Wright and Bull (1963) were followed. Those groupings are based on multi-character analysis of gross morphological differences.

It should be pointed out that regions based on morphological characters may not completely coincide with groupings which might be derived on the basis of the mineral contents of needles from trees native to various regions of the range. No attempt was made in this study to establish such a grouping because the 45 seedlots used did not cover the range of the species to such an extent that either a continuous or discontinuous picture could emerge.

While perusing the results of this investigation, the reader should keep in mind that mineral analysis of plant tissue is at very best a rough picture of the constitutional and metabolic needs of the plant. The spectrometer analyzes a tissue homogenate. This means that the ground leaves are analyzed for the organic and in-organic, structural and non-structural, functional and superfluous substances within the tissue alike for its content of a certain element. This total mineral content is reported and analyzed statistically. No matter how good the statistics, the picture based on these analyses can only be incomplete. In time we hope to explain the empirical results, obtained today, on the basis of the plant's intricate structure and metabolism.

Differences in the Foliar and Soil Mineral Levels Between Plantings

Table 8 shows the between-plantation differences for the foliar mineral elements and other needle characters. Tables 9 and 10 present the soil data and their statistical significance.

The soil analyses were performed to obtain a general picture of the nutrient-supplying capacities of the sites. There were 26 sampling stations at each site. At each station the surface to 8 inch and the 8 to 14 inch soil layer were sampled. Thirteen samples from one-half of the site were then compared with the 13 from the other half to obtain the within-plantation differences for the soil tests. Nitrogen was determined on five topsoil and subsoil samples, randomly chosen, for each plantation. No correlations between soil and plant mineral levels were calculated.

Table 10 shows that there were significant differences between plantations for all soil characteristics. Russ had the highest nutrient supplying capacity of all sites except for the element nitrogen. Newaygo was slightly higher in that nutrient. The soil tests furthermore show that Newaygo was lowest in phosphorus, potash, and magnesium. Higgins Lake was intermediate between Russ and Newaygo in nutrient supplying capacity. Only in nitrogen did it drop below the level of both other sites.

There were some significant differences in the nutrient levels within the plantings (Table 10). These should not affect the results of this study, however, because samples for each origin were composited across each entire site.

Table 8. Differences in the mean foliar mineral contents (percent oven-dry weight) and needle color, length, and weight of 45 Scotch pine origins grown at three locations.

Character	Units	Location Russ Forest	 Newaygo Forest	 Higgins Lake	F-value due to site [a/]
N	%	2.00	1.86	1.77	64.59**
K	%	.53	.44	.57	135.26**
P	%	.22	.22	.19	71.88**
Na	ppm	62.62	62.07	78.60	11.26**
Ca	%	.40	.36	.48	50.65**
Mg	%	.07	.05	.11	376.76**
Mn	ppm	898.22	1007.78	275.78	256.31**
Fe	ppm	95.96	77.40	60.73	94.32**
Cu	ppm	9.46	7.50	7.76	14.65**
B	ppm	35.84	37.89	22.29	252.52**
Zn	ppm	62.87	57.89	67.33	6.41**
Al	ppm	984.89	1376.44	1131.11	87.43**
Color	1 - 18 [b/]	10.38	9.18	6.57	64.85**
Length of 20 needles	mm	787.78	585.78	872.22	200.59**
O.D. wt. 40 needles	g	.49	.32	.62	138.74**

** - Indicates significance at the one percent level.

a/ - There were 2 degrees of freedom for plantations and 88 for the error term.

b/ - Color was scored on the basis of 18 units. The first unit was the most yellow, unit 18 was the most green.

Table 9. Mean values for the 0 to 8 inch and 8 to 14 inch soil horizon parameters [a] for the three sites.

	Russ Forest		Newaygo Forest		Higgins Lake	
Parameter	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
Lb N/acre [b]	1620.0	860.0	1660.0	1060.0	1180.0	640.0
Lb P/acre	240.9	194.5	28.6	35.5	80.1	79.7
Lb K/acre	161.4	141.5	34.8	21.5	75.4	33.4
Lb Ca/acre	652.8	778.5	104.3	103.7	489.6	257.4
Lb Mg/acre	55.0	80.4	6.5	5.0	34.6	10.7
C.E.C.	10.1	9.8	9.3	5.1	5.8	2.5
% base sat.	19.8	25.8	2.3	5.2	23.8	32.1

a/ - Nitrogen by Kjeldahl, phosphorus by extraction with Bray's #1, potassium, calcium, and magnesium by extraction with ammonium acetate and flame photometer.

b/ - Nitrogen on the basis of five samples for each of the two horizons.

Table 10. F-values [a] for the 0 to 8 inch and the 8 to 14 inch soil horizon parameters for the three plantations.

Parameter	Plantings		Within plantings	
	0-8"	8-14"	0-8"	8-14"
pH	25.32**	47.08**	2.22	1.00
Lbs N/acre [b]	26.80**	22.38**	--	--
Lbs P/acre	192.86**	88.49**	23.36**	17.80**
Lbs K/acre	103.62**	54.17**	3.94*	4.42**
Lbs Ca/acre	11.54**	40.00**	2.21	.48
Lbs Mg/acre	10.97**	45.66**	2.83*	.26
C.E.C.	4.38*	76.89**	1.04	.84
% base sat.	18.26**	18.69**	3.67*	.59

*, ** - Indicate significance at the five and one percent level, respectively.

[a] - There were two degrees of freedom for plantings, three for within plantings (between halves of plantings), and 72 for error.

[b] - For the nitrogen soil test there were 2 degrees of freedom for plantings and 14 for error.

The foliar levels of all mineral elements as well as needle color, length, and weight varied highly significantly between locales (Table 8). This points out the high degree in which the substrate affects the mineral composition of Scotch pine. Evolution may have played a part in this characteristic because throughout its range this species is relegated to the poorer soils and must extract the nutrients necessary for survival from these infertile sites. When man plants it on fertile sites, this characteristic -- absorbing nearly as much as is supplied -- creates nutritional imbalances within the trees rather easily when the soil nutrient levels are out of balance.

Trees at Russ are growing on a site formerly occupied by a forest tree nursery which had been maintained at a high level of soil fertility. The high foliar nitrogen content at that site may be a response to the residual effect of earlier soil management. This leaves the question as to why foliar nitrogen levels at Newaygo are lower than those of Russ unanswered. It is true that total soil nitrogen at Newaygo was somewhat higher than at Russ (Table 9), but total soil nitrogen is not always a reflection of available nitrogen. The Sparta sand at Newaygo developed under prairie vegetation and much of the nitrogen present may be mineralizing only slowly. The nutrient may be tied up in ligno-proteins from the grass roots. But at Russ the nitrogen was supplied by man in the form of fertilizer salts. These salts are more readily available to the trees and thus the picture of available nitrogen at the two sites probably favors Russ.

Soil levels of both phosphorus and potassium were higher at Russ than at the other plantings (Table 9) but the high soil levels were not reflected in the leaf analysis (Table 8). Trees growing at that site were only intermediate in their potassium levels and their phosphorus content was equal to that of trees at Newaygo. But the soil test for Newaygo showed only about 33 pounds of available phosphorus per acre as compared to 220 pounds at Russ. The potash levels of trees analyzed in this study were generally lower than those reported by other authors. Table 2 shows that five other investigations have shown foliar potassium levels ranging from .59 to .86 percent. But the average potassium content of trees for all plantings in this study was only about .51 percent. The phosphorus levels of trees in this study were generally averaged .21 percent of foliar phosphorus whereas Table 2 shows a range of .13 to .21 percent in other investigations.

Magnesium levels in this study were low in samples from both Russ and Newaygo. Other workers have reported foliar levels from .08 to .26 percent magnesium (Table 2) but levels at Newaygo were .05, those at Russ .07, and contents at Higgins Lake averaged .11 percent. The low level of tissue magnesium at Newaygo seemed to be a reflection of the low soil magnesium levels (Table 9). But trees growing at Russ were lower in magnesium than those at Higgins Lake. Soil levels of the nutrient were exactly opposite from the foliar levels, about 72 pounds of magnesium per acre at Russ and about 22 pounds at Higgins Lake. The low magnesium concentrations in the foliage from all plantations affected all physical tree measurements as will be seen in subsequent sections. This nutrient seemed to be one of the key elements in the nutrition of Scotch pines grown in Michigan.

The low tissue levels of manganese at Higgins Lake were prevalent throughout the array of origins sampled there. Iron and copper tissue levels were higher, and those of aluminum lower at Russ than at the other two sites.

Needles, on the average, were more yellow (decreasing numbers in Table 8) as the latitude of the plantation location increased. This was probably caused by differing climatic conditions as the plantings are situated farther north. White and Wright [3] are finding in growth chamber experiments that yellowing is a reversible photo - temperature dependent reaction. Either, lower temperatures and shorter photoperiods alone, increase yellowing but they are most effective in combination. The same holds true for greening, only that higher temperatures and longer photoperiods are needed. Photoperiod changes only by about 15 minutes between the most southern (Russ) and the most northern (Higgins Lake) planting. But if the mean annual temperature can be taken as an index to the relative temperature differences between plantings in the fall and winter months, Higgins Lake is lowest (42.8°F), Newaygo intermediate (44.7°F), and Russ highest (48.3°F). The temperature and needle color trends are the same.

Needle length and needle weight each were highest in Higgins Lake, intermediate at Russ, and lowest at Newaygo (Table 8). The last site was the poorest in nutrient supplying capacity and trees there may have had short needles because of poor mineral nutrition. But the ratio of needle length to its weight ranked the plantations: Newaygo highest,

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[3] Personal communication, Department of Forestry, Michigan State University, East Lansing, Michigan.

Russ intermediate, and Higgins Lake lowest. This ratio is a measure of the linear density and/or the thickness of the needles. The pronounced differences between the plantations in the ratio suggest that it may be an index to the drought resistance of the trees. Newaygo is subject to drought with its deep, coarse sand, its southern location, and an annual precipitation lower than the other two sites. Though Russ Forest is farther south than Newaygo, the finer textured soil can store more water and make it available to the trees during a longer portion of the water year. Higgins Lake is the northern most planting and receives more precipitation than Newaygo. It should also have a lower potential evaporation rate than either of the other plantings. Needles from trees grown at Higgins Lake were the thinnest and/or least dense.

Between Seedlot Differences

For the analysis of variance of the Main Study there were two degrees of freedom for plantation (p), 44 for between-seedlot (s) differences, and 88 for error.

The Error Term Study provided an estimate of the seedlot x plantation (s x p) interaction. Five seedlots were sampled at each of the three sites. The samples for each seedlot were composited over each of the halves of each planting so that there were 2 degrees of freedom for plantation, 3 for replication within plantation, 4 for seedlot, 8 for s x p interaction, 12 for error, making a total of 29 degrees of freedom.

The Error Term Study showed significant and highly significant s x p interactions for the foliar levels of magnesium, copper, and aluminum (Table11). Of these three elements only magnesium showed

Table 11. 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 541 [a]	.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

[a] - GERman, SPAin, SWEden, TURkey, URAl Mountains.

significant between-seedlot differences. Its s x p interaction will therefore be considered. In this connection the soil-test data for the magnesium levels at the plantings should be recalled. Russ was highest, Higgins Lake intermediate, and Newaygo low to the point of deficiency in soil magnesium. The seedlots from Germany, Turkey, and Spain interacted with site (Table 11). 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, this indicates that this fast growing seedlot has the ability to extract this nutrient from the soil when the element is present in only small quantities. But once the needs of this German seedlot for foliar magnesium are met, it does not accumulate the element any further (Table 11). 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 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. Wright and Bull (1963) reported that Spanish origins tend to be more tap-rooted than provenances from regions with more precipitation than Spain. If tap-rootedness also means that the trees have a larger root system, these Spanish origins can tap a larger volume of soil for its nutrients than shallow-rooted provenances. This may be of particular advantage when an element becomes limiting to growth.

Foliar magnesium levels were generally lowest in the northern seedlots, highest in the fast growing provenances from Belgium, Germany, and France, and intermediate in the southern seedlot which grew medium fast.

Percent foliar nitrogen decreased in general with a decrease in the latitude of the seedlot's collection area at Russ. Seedlot MSFG 222 from Sweden had the highest nitrogen content with 2.02 percent and MSFG 246 from Spain had the lowest with 1.65 percent. The standard deviations of the most northerly seedlots at all sites, however, were higher than those of the remaining seedlot-array. This indicates larger between-plantation fluctuations in nitrogen content of these northernmost seedlots than in the remaining ones.

Percent foliar phosphorus presented the same general picture as nitrogen. It decreased with latitude from a high of .228 percent in MSFG 229 from Finland to a low of .179 percent in MSFG 246 from Spain. The standard deviations and between-planting differences also paralleled the nitrogen differences.

The highly significant differences in the sodium content of the seedlots seem to be caused by high random variations between seedlots and do not show any regional trends. MSFG seedlots 245 and 238 from Spain and France, respectively, were exceptionally high with a content of about 100 parts per million (ppm) and MSFG 259 and 527 from Ural Mountains and Germany, respectively, were low with about 38 ppm.

Trees from the Siberian and Ural Mountain portion of the range of Scotch pine were low in boron. They averaged about 27 ppm as compared to an average foliar level of 32 ppm. The remaining variation between seedlots with regard to boron levels seemed to be randomly distributed.

The length of oven-dry needles showed a pronounced geographical trend. Trees in Wright and Bull's (1963) ecotypes F, G, and H, whose seed was collected in Poland, Germany, Belgium, Hungary, and northeastern France had the longest needles with an average of about 44 mm per needle. Those trees from Sweden, Finland, Norway, Latvia, the Urals, and Siberia had needles of intermediate length, averaging about 39 mm. Seedlots from southern France, Spain, Greece, and Turkey had the shortest needles, averaging about 31 mm. These trends correspond with the pattern described by King (1965b).

There were highly significant differences between the needle weights of different seedlots. Needle weight followed the same trends as needle length ($R = .952$). The average, oven-dry weight for a needle in the long needled group was .0143 g, for the group with medium long needles it was .0130 g, and in the short needled group the average leaf weighed .0094 g.

Highly significant differences between needle colors of the seedlots were observed. The pattern of the discoloration was identical with that described by King (1965b).

Table 12 makes the comparison of the F-values for the between-seedlot differences and the s x p interactions calculated from the data of the Main Study, the Error Term Study, and the Preliminary Investigation.

Table 12. Comparison of the F-values calculated from three experimental designs for the between seedlot differences and the s x p interactions in the tissue levels of Scotch pine seedlots.

Element	Between seedlot differences			s x p interaction	
	Main Study	Error Term Study	Prelim. Investigation	Error Term Study	Prelim. Investigation
			F-Values		
N	1.57*	7.74**	5.46**	1.34	1.28
K	1.30	3.83*	2.36	2.52	2.67**
P	1.78*	9.20**	5.09**	.37	7.70**
Na	2.40**	1.77	1.07	2.38	2.50**
Ca	.70	2.11	2.40	1.46	1.76
Mg	1.85*	1.50	3.45	3.20*	1.38
Mn	.68	.53	.36	1.10	.98
Fe	1.40	18.14**	4.33**	2.22	3.81**
Cu	.90	1.30	.42	4.79**	.74
B	2.18**	1.84	.60	.45	3.40**
Zn	.82	1.61	8.65**	.83	3.06**
Al	1.49	2.40	6.06**	3.24*	2.18*
			Degrees of Freedom		
Main factor	44	4	4	8	16
Error	88	12	80	12	80

*, ** - Indicate significance at the five and one percent level, respectively.

The F-values in that table are comparable in that all are based on error terms which include significant s x p interactions.

The data for the nitrogen, potash, and phosphorus levels for the between-seedlot differences agreed well in all three studies. Differences between the results of the studies occurred mainly in the F-values for the trace elements. These differences may be due to: (a) differences in the sites; (b) departures from randomness in the seedlots chosen for the Error Term Study and the Preliminary Investigation; and (c) an influence of the year of sampling on foliar mineral levels.

The influence of site on foliar mineral levels has been discussed. The F-values for between seedlot differences for both the Error Term Study and the Preliminary Investigation are based on the same five seedlots grown on different sites. Departures between the F-values of those two studies may therefore indicate either site or year influences. Such differences occur in the zinc and aluminum tissue levels. (Table 12).

Differences in the significance of F-values for between seedlot differences for the Main and Error Term Studies may indicate a departure from randomness in the seedlots selected for the Error Term Study. The Main Study represents an approximation of the entire population and seedlots selected at random from it should show the characteristics of the population. Strong departures from randomness are indicated in the tissue levels of sodium, iron, and boron, weaker ones in the potash and magnesium concentrations. On the whole, however, the five seedlots chosen to represent the population appeared to present an accurate picture.

The variations of tissue mineral concentrations in time are presented for selected elements in Table 13. These elements had low coefficients of variation (see Appendix), important in detecting yearly differences, which might be small and therefore hard to detect with the few samples which were comparable. Table 13 shows that yearly fluctuations do occur in some elements. The moisture regime for a particular year more than any other single factor probably accounts for these differences in nutrient accumulation.

Table 13. Estimates of changes in the foliar mineral element levels of five seedlots growing at Higgins Lake in 1962 and 1963.

Element	Error mean square	Between years mean square	F-value [a/]
N	.0007	.0010	1.42
K	.0060	.0144	24.00**
P	.000051	.000533	10.45*
Mg	.000061	.000185	3.05

*, ** Indicate significance at the five and one percent levels, respectively.

[a/] - There were 4 degrees of freedom for error and 1 for years.

Comparison of the Foliar Mineral Levels Expressed as Percent Oven-dry Weight and as Unit Weight per Needle

It has been traditional to report mineral contents on the basis of oven-dry weight. This mode of expression does not necessarily reflect the total mineral content of the foliage. For instance, a long needle can contain more of an element but still be lower in its percent content when compared to a shorter but relatively denser needle. The theory for reporting tissue levels as percentages is that the relative content of an element reflects its availability and possible limitations on yield. Furthermore, percent composition is the direct result of chemical analysis and it is convenient for the comparison of the results obtained for organisms for which the size of the sampling unit varies considerably. Its use avoids the problems associated with the determination of sampling units which accurately reflect the total content.

Scotch pine needle lengths differed both between plantations for the same origins and between origins at the same location. An analysis of variance for the total mineral content per needle was therefore calculated. It showed highly significant differences between plantings for all elements, just as the percent composition values had done. But only for sodium were the between-seedlot differences significant. The seedlots did not differ significantly from one another in the total needle content of any other mineral.

From the results presented up to this point it is not possible to decide which mode of expression of mineral levels best reflects the plant's nutritional status. Total needle content and percent composition will both be used in some instances for the regression analyses of the relationships between mineral tissue levels and physical characteristics.

Relationships Between the Physical and Chemical Characteristics

The following sections present relationships between physical characters -- internode growth in 1963, needle length, weight and color -- and the twelve mineral elements for which the foliage was analyzed. These measurements and analyses comprise more than 4,000 individual values which had to be evaluated statistically. Electronic computers have made possible the fast and accurate calculation of almost any desired statistic and relationship from a mass of data. With tedious hand calculations obsolete, it is now more than ever the researcher's task to evaluate the meaning of the results. Manipulation of the data can result in statistically significant relationships where physiologically none exist. I hope to have avoided obvious statistical pitfalls, but to which degree the regression equations presented in the subsequent sections are reflections of the mineral nutrition of the trees and not merely statistical artifacts, cannot be determined.

Simple Correlations with 1963 Internode Growth as the Dependent Variable

For 34 origins common to the three plantings of the Main Study for which internode measurements were possible (Higgins Lake was weeviled heavily, some whorls had been lost), Russ averaged 8.20 inches, Newaygo 4.53 inches, and Higgins Lake averaged 3.08 inches.

Table 14 shows the simple correlations of height growth with the foliar levels of the mineral elements and with needle length, weight, and color. Correlations which were significant at one planting and not at another may either be non-existent or may not be strong enough to be statistically significant at the second planting. Height growth data were available for 92 origins at Russ, 52 at Newaygo, and 34 at Higgins Lake.

The height - foliar nitrogen correlation at both Russ and Newaygo was significant but of opposite sign. The smaller the tree, the higher its nitrogen content held true at Russ. At Newaygo, the taller the tree, the higher was its nitrogen level. Available soil nitrogen probably accounts for this difference. It should be recalled that the total soil nitrogen levels at both plantings were very similar (Table 9), but that the available soil nitrogen at Newaygo was probably lower. The fast growing trees from the German-Belgian-Czechoslovakian region had higher nitrogen levels than the south- or north-European origins at Newaygo. But at Russ the slow growing origins from Scandinavia had the highest nitrogen content. A factor other than soil differences between plantings, probably a genetically controlled difference relating to the nitrogen metabolism, was at play here. Multiple regression analysis will provide some answers to this problem and the phenomenon is discussed more extensively in the next section.

Foliar magnesium levels were associated with growth rates at all three plantings. German foresters (Möller, 1904; Brüning, 1959) observed that 'Kalimagnesia' (a fertilizer containing both potash and magnesium) accelerated Scotch pine growth rates on infertile sites in eastern

Table 14. Simple, positive or negative (-) correlations of 1963 internode growth with chemical and physical characters of Scotch pine grown at three locations. [a]

Character	Significance at the one percent level			
	Russ Forest	Newaygo Forest	Higgins Lake	All Plantings
N	-**	**	NS	**
K	**	NS	NS	**
P	NS	NS	NS	NS
Na	NS	NS	NS	NS
Ca	-**	NS	NS	-**
Mg	**	**	**	NS
Mn	NS	NS	NS	**
Fe	NS	**	**	**
Cu	NS	NS	NS	**
B	NS	**	NS	**
Zn	NS	NS	NS	NS
Al	NS	NS	NS	-**
Needle length	**	**	NS	**
Needle weight	NS	**	NS	NS
Needle color	**	**	NS	**

[a] There were 90 degrees of freedom at Russ Forest, 50 at Newaygo Forest, 32 at Higgins Lake, and 176 for all plantings. Correlation coefficients greater than .267, .354, .430, and.197, respecitvely were needed for significance at the 1 percent level.

Germany. Brüning (1959) applied nitrogen, phosphorus, potash, and magnesium to Scotch pine plantations and reported that potash and magnesium always were most effective in increasing growth. He believes that the infertile sites with which he worked were depleted more severely in potash and magnesium than in nitrogen.

Soil magnesium levels at Newaygo were low to the point of deficiency (about 5.7 pounds per acre, Table 8). At that planting the nutrient may well have been one of the growth limiting elements. At both other plantings magnesium was also significantly correlated with growth rate. Differences in the ability to accumulate the nutrient may well be present between seedlots desipte the s x p interaction reported previously.

Needle length rather than needle weight was correlated with height growth. This must have been due to between origin differences in needle length rather than between plantation differences because Higgins Lake with the lowest growth rate had the longest average needle. Russ, where trees grew fastest, had intermediately long needles. If needle length can be taken as an indicator of photosynthetic capacity, its role in internode growth is decidedly secondary to that of mineral nutrition.

Needle color and internode growth were correlated at both Russ and Newaygo. This is to some degree a statistical rather than a biological result. Growth rate does increase as the needle color of the seedlot becomes increasingly green if one considers the Scandinavian and central European origins. The Spanish and Turkish ones, however, which remain blue-green in winter are not highest but only intermediate in growth rate. Of course, correlations do not imply cause and/or effect relationships, they only indicate to which degree changes in one character were paralleled by changes in the other.

Multiple Regression with 1963 Internode Growth as the Dependent Variable

Table 15 gives the coefficients for the regression equations which relate 1963 internode growth at the three plantings to the foliar levels of twelve mineral elements. These equations by themselves give no direct information as to the significance of the contributions made 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, and (4) divide the difference-mean-square by the complete-regression-mean-square. Table 15 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.

The relationships determined by simple correlation (Table 13) and by multiple regression (Table 15) agree well with each other for N, K, P, Na, Mg, Cu, Zn, and Al. There were some differences in the results

Table 15. 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	All Plantings
N	%	-5.045	4.572	.727	-.224
K	%	16.796	1.760	2.974	11.500
P	%	-5.966	25.582	-15.561	-7.064
Na	ppm	.011	-.003	-.006	.005
Ca	%	-4.107	-2.393	-2.008	-12.435
Mg	%	73.340	46.502	36.394	19.670
Mn	ppm	-.001	-.030	-.004	.024
Fe	ppm	-.003	.011	.042	.026
Cu	ppm	-.248	.094	-.107	-.186
B	ppm	.015	-.023	.010	.131
Zn	ppm	.040	.018	.006	.041
Al	ppm	-.006	.004	-.003	-.051
		Regression constant			
		6.303	-11.026	-1.566	1.463

for Ca, Mn, Fe, and B, probably indicating that these elements interacted with others which did make significant contributions to height growth. This interaction occurred between calcium and magnesium at Russ, and between iron and magnesium, and boron and nitrogen at Newaygo. The first element of each pair listed was the one which did not contribute to the regression equation but showed simple correlation with growth, and the second element was the one which contributed significantly to the regression equation and interacted with the first element.

At Russ, N, K, and Mg made significant contributions to the regression equation for internode growth. The nitrogen content was inversely related to internode growth. This might have been due to an excess of nitrogen in the trees or some other cause. Tissue nitrogen levels were higher than at the other two plantings (Table 8), but when Russ nitrogen levels are compared with concentrations reported by other investigators (Table 2), they do not appear to be sufficiently high to be detrimental to growth. Irmak (1958) reported higher levels than the ones found at Russ and did not indicate that height growth was retarded. The inverse relationship between nitrogen and internode growth does not appear to be due to nitrogen toxicity.

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 9) and the foliar levels were intermediate (Table 8), multiple regression analysis indicated that potassium made a highly significant, positive contribution to internode growth at Russ (Table 16). It appears that the level of nutrition

Table 16. 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	All Plantings
N	3.1*	3.7*	.2	.0
K	5.5**	.1	1.4	3.0**
P	.0	2.0	2.7	.1
Na	.6	.1	1.5	.1
Ca	.4	.2	.6	3.0**
Mg	14.8**	11.5**	17.0**	1.4*
Mn	.0	5.3*	.0	1.4*
Fe	.0	.5	14.8*	1.1*
Cu	1.6	.6	3.5	.8
B	.0	.2	.1	4.5**
Zn	1.7	.5	.4	1.4*
Al	.0	.1	.1	8.5**
Amount of total variance accounted for by regression [a/]				
	46.9%	69.7%	60.1%	58.3%

*, ** - 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, and 165 for all Plantings.

a/ - 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.

at Russ was so high that a foliar level of potash sufficient at the other plantings was deficient at Russ. This in turn 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 foragers 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. The nutrients are in balance in the native range. But at Russ, where the trees did not absorb sufficient potash and nitrogen was adequate, the relatively poor capacity of these origins to absorb potassium accentuated the increase in 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 to be 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 16), probably indicating that at that site this nutrient was one of the growth limiting factors. This also bears out an earlier speculation that most of the total nitrogen at Newaygo was unavailable to the trees.

The partial regression coefficient for phosphorus at the Newaygo planting was of opposite sign from those at the other plantings. But this element did not add significantly in the explanation of height growth at any planting. A test to determine whether the regression coefficient was significantly different from the other plantings at Newaygo was therefore performed. With this test the null hypothesis that the partial regression coefficient for phosphorus at Higgins Lake was equal to that of Newaygo was tested.

$$H_o\text{:}\ b(P)_{HL} = b(P)_N$$

$$t = \frac{b(P)_{HL} - b(P)_N}{\sqrt{\left(\text{Std. error } b(P)_{HL}\right)^2 + \left(\text{Std. error } b(P)_N\right)^2}}$$

where $b(P)_{HL}$ is the partial regression coefficient for phosphorus at Higgins Lake,

$b(P)_N$ is the partial regression coefficient for phosphorus at Newaygo,

and t is Student's t-test, with the sum of degrees of freedom for errors (39 + 21 = 60) degrees of freedom.

The resulting t (= 2.05) was significant at the five percent level. It appears that the significance of phosphorus to internode growth differed at the Newaygo planting from the other plantings.

As did the simple correlation, multiple regression indicated that magnesium tissue levels contributed significantly to internode growth at all three sites. Comparison of magnesium levels reported by other workers (Table 2), simple correlation, and multiple regression all indicated that magnesium was deficient at the three plantations analyzed in this study.

Foliar manganese levels were highest at Newaygo (Table 8) and the partial regression coefficient for this nutrient was ten times larger here than at the other sites (Table 15). These high levels of manganese were associated with a significant reduction of internode growth at Newaygo (Table 16).

Iron tissue levels were low at Higgins Lake. Regression analysis indicated that these low levels were associated with increased growth. The significant, positive, simple correlation between iron and phosphorus tissue concentrations seemed to have no particular influence on growth.

Table 16 contains examples of the statistical artifacts mentioned previously. Aluminum, a non-essential element, was not associated with internode growth at any planting. But when the combined data for all three plantings were analyzed by multiple regression, this element made by far the most significant contribution to the variance in internode growth explainable by mineral tissue content. This artifact was caused by the distribution of the foliar aluminum contents between plantings. Tissue levels at Russ, where trees grew fastest, were low and at the other, much slower growing plantations, the levels of aluminum were higher. There was no relationship between the element and internode growth within any planting, but a regression line which "explains" much of the regression could be fitted to the data.

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 were calculated. Tables 17 and 18 show the regression equations and the contributions of the individual elements to the regression. The transformation from a percent to a weight per needle concentration resulted in similar regression equations and no new relationships were discovered. Rather, seven of the sixteen significant contributions of elements shown in Table 16 (based on percent oven-dry weight content) do not appear in Table 18 (based on weight per needle). Significant contributions of sodium at Russ, manganese and iron at Newaygo, iron at Higgins Lake, and magnesium, manganese, iron, and zinc for all plantings 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 dependent variable.

Table 17. 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	All Plantings
N	mg	-40.48	34.22	-6.22	-1.64
K	mg	163.92	-60.41	33.72	88.42
P	mg	31.58	41.30	-155.16	-56.50
Na	10-4mg	.15	-.01	-.07	.07
Ca	mg	-19.80	31.26	-18.29	-119.20
Mg	mg	540.35	291.49	215.65	90.92
Mn	10-4mg	-.24	-.09	.14	.12
Fe	10-4mg	.05	-.06	.16	.16
Cu	10-4mg	-1.30	.70	-.32	-.66
B	10-4mg	.02	.57	.13	1.24
Zn	10-4mg	.02	-.16	.02	.14
Al	10-4mg	.05	-.19	.01	-.35
		Regression constant			
		4.00	.44	2.11	3.39

Table 18. The significance of the contributions 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	All Plantings
N	4.0**	1.8	.5	.0
K	16.3**	1.3	3.6	3.7**
P	.1	.1	4.6	.0
Na	2.1**	.0	5.1	.3
Ca	.2	.2	1.3	4.0**
Mg	12.3**	1.7	16.8**	.3
Mn	1.6	.3	.5	.5
Fe	.2	.1	5.7	.5
Cu	.8	.3	1.1	.1
B	.0	.9	.3	5.1**
Zn	.1	.3	.1	.2
Al	.1	2.5	.0	7.6**
Amount of total variance accounted for by regression [a/]				
	59.6%	72.8%	56.4%	60.4%

*, ** - 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, and 165 for all plantings.

a/ - 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.

The Association of Needle Color with Mineral Tissue Levels

The seasonal yellowing of Scotch pine resembles the deficiency symptoms of several nutrients. Attempts to prevent color changes through fertilization have been unsuccessful, however.

Because several trace elements, not previously investigated in Scotch pine, were included in this study, possible relationships between mineral element levels and needle color were investigated. Multiple regression equations relating tissue levels of mineral elements, expressed both as percent of oven-dry weight and as weight per needle, are given in Table 19. Table 20 shows the significance of the elements in contributing to the regression equations.

With both modes of tissue level expression, nitrogen and potassium were significantly associated with needle color at Russ. This was most likely not a cause and/or effect relationship. Northern seedlots which were high in nitrogen and low in potassium also happen to be very yellow in winter. The association of calcium with needle color occurred only at Russ and is not readily explainable. Magnesium was significantly correlated with needle color both at Newaygo and Higgins Lake, this is probably an indication of magnesium deficiency rather than a genetically controlled phenomenon. Magnesium, as will be recalled, also was significantly correlated with internode growth. None of the trace elements showed any consistent relationship between plantations with needle color.

These findings together with those of Gerhold (1959a) indicate that needle yellowing in winter is not associated with the nutrition of Scotch pine.

Table 19. Partial regression coefficients for the mineral element content, both on a percent and weight per needle basis, when needle color is the dependent variable.

	Partial regression coefficients					
	Percent in foliage			Weight per needle		
Element [a/]	Russ Forest	Newaygo Forest	Higgins Lake	Russ Forest	Newaygo Forest	Higgins Lake
N	-8.72	-5.53	3.58	-56.69	-13.50	-23.60
K	19.09	-25.88	33.10	201.21	-205.85	-6.40
P	-2.04	-14.17	-157.86	76.48	47.91	16.12
Na	.02	.01	.03	.17	.04	.16
Ca	-14.78	20.30	-7.13	-70.14	91.61	-118.12
Mg	-13.80	106.69	185.13	25.09	1638.51	631.91
Mn	-.03	-.08	-.10	-.21	-1.29	-1.25
Fe	.00	.02	.14	-.04	.24	1.07
Cu	-.06	.32	.01	-1.83	6.80	-.37
B	.05	.30	-.12	.02	2.33	-2.21
Zn	.01	-.21	.00	.32	-1.71	.13
Al	-.04	-.03	.00	-.14	.02	-.34
	Regression constant					
	29.20	31.44	-10.44	15.14	14.30	16.58

a/ - Units: N, K, P, Ca, Mg as percent oven-dry weight under 'Percent in foliage' heading, as mg per needle under 'Weight per needle.' All other elements as ppm or 10^{-4}mg per needle, respectively.

Table 20. The significance of the contributions of the mineral elements, both on a percent of oven-dry weight and weight per needle basis, to the regression equations for needle color.

	Percent of total variation accounted for by the element					
	Percent in foliage			Weight per needle		
Element elim. from regression	Russ Forest	Newaygo Forest	Higgins Lake	Russ Forest	Newaygo Forest	Higgins Lake
N	4.9**	.4	.2	4.0**	.0	.3
K	3.7**	2.4	6.7	12.6**	1.2	.1
P	.0	.0	10.6	.1	.0	.0
Na	1.2	.2	1.3	1.1	.0	1.1
Ca	2.7*	1.4	.3	1.0	.1	2.1
Mg	.2	5.3*	16.4*	.0	7.4**	5.5
Mn	1.2	3.6*	.5	.6	4.9*	1.7
Fe	.0	.0	6.3	.0	.1	9.3*
Cu	.0	.6	.0	.7	1.7	.1
B	.3	3.2*	.6	.0	1.2	3.9
Zn	.0	7.6**	.0	.8	2.6	.2
Al	1.7	.6	.0	.3	.0	2.0
Percent of total variance in color accounted for by regression [a]						
	64.3	70.0	47.3	65.5	63.6	59.2

*, ** - 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.

[a] - 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.

Evidence to date allows two alternatives which might explain the yellowing of Scotch pine in winter. Gerhold (1959b) and Wettstein and Grüll (1954) have demonstrated that light quality, light intensity, and length of photoperiod all have an important influence on Scotch pine discoloration. The first alternative is that chlorophyll synthesis is curtailed by a combination of these factors and the second possibility is that chlorophyll is broken down in the needles faster than it is synthesized. There are no reports of variations in chlorophyll synthesis among races. Pigment breakdown has not been studied extensively and surveys to determine which substances appear after discoloration of Scotch pine needles are necessary. Absorption spectra of needles are promising in this regard. The spectra of many substances in the leaves are known. By comparison of the pine needle spectra with those of the identified substances, clues to the identities of some of the substances appearing and/or disappearing during the course of discoloration might be obtained. Chlorophyll is destroyed by the action of acids and the reaction rates have been studied (Schanderl *et al.*, 1962). Schanderl [4/] proposes the following pathway for chlorophyll breakdown:

Chlorophyll minus magnesium ⟶ Pheophytin
Pheophytin minus phytol ⟶ Phyophorbite
Phyophorbite, break of isocyclic ring ⟶ Chlorin and rhodin

A comparison of the color scoring method used by King (1965b) and the one used in this study was possible. King scored colors directly

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[4/] Personal communication. S. H. Schanderl, Food Science Department, Michigan State University, East Lansing, Michigan.

in the field on the basis of ten grades. Differences in light conditions and changes in color perception while traveling from one planting to the next might have influenced his error term. In this study the needles were oven-dried, ground, and the color scored on the tissue homogenate on the basis of 18 grades. Lighting changes and differences in color perception were thus greatly reduced. But a treatment error -- oven-drying -- was introduced. The seedlot x plantation mean square used to represent King's method is one which he reported for five plantings which included the three scored in the Main Study. The methods were compared by the standard deviations, calculated with the following formula:

$$\sigma = \left(\sqrt{\frac{\text{s x p mean square}}{\text{No. of plantings sampled}}} \right) \text{x (Ratio of color grades)}$$

A standard deviation of 1.54 grade units resulted for King and one of .938 for this study. If it can be assumed that one of King's grades was equal to 1.8 of the present units, the error introduced by drying is smaller than changes in color perception between plantations. But scoring color on the homogenates is economically justifiable only when very precise measurements are desired, i.e. when glaucous surface phenomena are to be excluded, or when the homogenate is to be further analyzed regardless of color scoring.

Association of Needle Length and Needle Weight with Foliar Elements

Table 21 gives the regression equations for needle length and weight based on percent oven-dry weight mineral contents. Table 22

Table 21. Partial regression coefficients for the mineral element contents (percent oven-dry weight) for the regression equations of 1963 needle length and 1963 needle weight.

	Partial regression coefficients					
	Needle length			Needle weight		
Element [a/]	Russ Forest	Newaygo Forest	Higgins Lake	Russ Forest	Newaygo Forest	Higgins Lake
N	12.83	-4.65	14.98	.076	.017	-.094
K	71.00	64.26	-127.57	.223	.332	-1.886
P	28.18	281.81	760.40	.077	1.285	7.691
Na	-.04	-.07	.05	.000	.000	.000
Ca	11.56	-70.42	-39.37	.301	-.514	-5.125
Mg	242.54	283.60	-236.38	1.242	1.694	-4.378
Mn	.21	-.21	-.44	.002	-.002	-.006
Fe	-.15	.09	.45	-.001	.001	.004
Cu	-1.85	.62	-1.38	-.013	.000	-.007
B	-.28	-.75	-1.28	-.002	-.005	.012
Zn	.47	.53	.08	.004	.003	.001
Al	.03	.15	-3.69	.001	.001	-.004
	Regression constant					
	-19.73	-21.31	88.19	-.135	-.108	1.677

a/ - Units: N, K, P, Ca, Mg as percent oven-dry weight, all other elements as ppm.

Table 22. The significance of the contributions of the mineral elements (percent oven-dry weight) to the regression equations for needle length and needle weight.

Element elim. from regression	Percent of variation accounted for by the element					
	Needle length			Needle weight		
	Russ Forest	Newaygo Forest	Higgins Lake	Russ Forest	Newaygo Forest	Higgins Lake
N	.8	.1	.3	.4	.1	.1
K	4.0*	4.4*	6.4	.5	2.2	8.5*
P	.1	6.6**	15.7**	.0	2.6	15.5*
Na	.4	2.2	.4	.9	1.4	.1
Ca	.1	4.8*	.6	1.1	4.8*	1.0
Mg	6.4**	10.9**	1.7	2.1	7.2*	5.7
Mn	3.2*	6.7**	.6	3.9*	8.8**	1.3
Fe	2.2	.8	4.0	2.8	3.4	2.7
Cu	3.5*	.7	1.5	2.1	.1	.4
B	.9	5.9**	4.1	1.0	4.4*	3.4
Zn	9.3**	14.0**	.2	7.0**	10.5**	.7
Al	.1	4.3*	5.4	.5	4.3*	4.9
	Percent of the total variance explained by the regression [a]					
	42.6	69.1	59.3	44.0	61.0	56.1

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

[a] - 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.

shows the significance of the contributions to the regression equation for individual minerals.

Potassium was significantly associated with needle length at both Russ and Newaygo. Fast growing, long needled origins had higher potash levels than short needled ones. Even though this nutrient plays an important role in carbohydrate metabolism and translocation (Meyer and Anderson, 1952) it is doubtful that this association of potassium with needle length was a cause and/or effect relationship. Had it been, the needles of trees grown at Russ and Newaygo should have had significant increases in their needle weights as the potash level rose. Needle weights did not increase (Table 22). Russ seemed to be potassium deficient and soil tests at Newaygo for potassium averaged only 28 pounds per acre (Table 9). Limited amounts of potash in the tissue may have caused the element to be utilized only for more basic metabolic functions than carbohydrate storage. This would have obscured needle weight - high potassium relationships which might exist when potash is not limiting.

Phosphorus levels were significantly associated with needle length at Newaygo and Higgins Lake. This may reflect the low soil phosphorus levels at those two plantations, about 31 and 80 pounds of available phosphorus per acre, respectively. By comparison, Russ soil tests showed about 220 pounds of phosphorus per acre (Table 9). If this level was sufficient for the normal development of needle length and weight and there was no difference between seedlots in regard to phosphorus accumulation, no differences in needle length and weight would appear.

Calcium was significantly associated with needle length at Newaygo.

Soil tests for calcium at that site showed about 100 pounds per acre (Table 9), only about one-fourth to one-fifth as much as the other two sites. The negative association of calcium and needle length may mean that shorter-needled seedlots (southern European seedlots) were better calcium accumulators than the long needled ones when calcium becomes limiting in the soil.

The effects of the probable magnesium deficiency were evident for needle length at Russ and Newaygo. At both plantings longer needles were associated with higher magnesium contents.

Summary of Results

The main objectives of this study were: (1) To investigate the effect of site on nutrient accumulation of Scotch pine in general, (2) To explore the possibility that seedlots react differently to the same site, and (3) To relate nutrient contents to genetic differences. The order of the objectives above does not imply an order of their importance.

The foliar levels of all twelve minerals investigated in this study varied highly significantly between three plantations. This points up the high degree in 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 between-seedlot differences in the ability to accumulate nitrogen, phosphorus, sodium, magnesium, and boron.

The pronounced differences between seedlots in height growth, autumnal foliage color, and needle length of Scotch pine are under genetic control (Wright and Bull, 1963; King, 1965b). Multiple regressions between these gross-characters 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 between-site 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/or 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 results in organic nitrogen accumulation in the plants (Wall, 1940). The negative association was therefore 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 it and fast growing seedlots were associated with high foliar magnesium levels. Future studies should investigate whether this is a cause and effect relationship. The results of this study in regard to between-seedlot differences in the foraging ability for nitrogen and magnesium warrant the initiation of controlled experiments. The first series of such experiments should determine nutrient levels which permit trees to grow in the upper response regions of the Mitscherlich curve. In the second series the foliage of different seedlots grown at the estimated optimum nutritional levels should be analyzed. If the fast growing seedlots maintain their growth advantage over slower growing ones and there are no between-seedlot differences in their foliar nutrient concentrations, differences in metabolic efficiency are indicated. On the other hand, if between-seedlot differences in the foliar nutrient levels appear, the pathway from gene to growth expression has its seat in translocational or root system differences.

The results of this study together with those of Gerhold (1959a) indicate that the genetically controlled color differences between seedlots in winter are not caused by differences in the nutritional levels of the trees. Evidence to date suggests that both photoperiod and temperature affect winter color. Research along the lines which led to the discovery of phytochrome as the substance connected with the flowering stimulus in plants might be fruitful. Investigations should be directed towards finding a substance which either inhibits chlorophyll synthesis or accelerates its destruction.

Needle length was influenced by more foliar minerals than any other physical characteristic measured in this study. Here seems to be a sensitive indicator of the nutrient status of Scotch pine. Its major drawback, of course, is that it is influenced by so many minerals that it will be impossible to diagnose the deficiency of any specific element from needle length alone.

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APPENDIX

Table A. Units and ranges of Scotch pine characters at three locations.

Measurement	Unit	Range			
		Russ Forest	Newaygo Forest	Higgins Lake	All Plantings
N	%	1.68-2.22	1.62-2.08	1.54-1.92	1.54-2.22
K	%	.44- .62	.37- .54	.48- .64	.37- .64
P	%	.19- .27	.19- .24	.15- .22	.15- .27
Na	ppm	18-134	11-110	44-128	11-134
Ca	%	.27- .52	.22- .49	.32- .77	.22- .77
Mg	%	.04- .11	.02- .08	.08- .15	.02- .15
Mn	ppm	548-1202	608-1202	209-378	209-1202
Fe	ppm	72-143	53-118	41-88	41-143
Cu	ppm	6.0-13.7	3.5-13.7	4.3-14.7	3.5-14.7
B	ppm	23.6-52.4	26.8-47.0	14.6-29.5	14.6-52.4
Zn	ppm	36-99	24-87	38-99	24-99
Al	ppm	725-1329	1077-1659	825-1426	725-1659
Needle length (oven dry)	mm	24.7-53.5	22.0-37.5	32.0-55.6	22.0-55.6
Needle weight (oven dry)	g	.006-.020	.005-.011	.007-.023	.005-.023
Needle color	1-18	2-16	1-15	1-14	1-18
Internode growth (1963)	inches	2.0-14.7	2.3-6.7	1.0-4.3	1.0-14.7

Table B. Coefficients of variation of the measurements of Scotch pine at three locations.

Measurement	Coefficient of variation in percent [a]			
	Russ Forest	Newaygo Forest	Higgins Lake	All Plantings
N	6.1	4.6	4.7	7.4
K	7.2	7.7	7.3	11.7
P	7.4	6.2	7.2	8.7
Na	36.7	38.8	26.0	35.9
Ca	15.4	18.6	8.7	17.5
Mg	18.9	32.2	8.6	36.5
Mn	21.4	17.6	15.2	39.1
Fe	16.5	15.9	18.3	25.5
Cu	17.5	22.9	27.1	24.1
B	12.9	11.2	13.5	21.2
Zn	18.5	25.8	15.7	20.5
Al	15.1	10.6	13.5	19.5
Length 5 needles	16.0	14.5	17.7	21.9
Length 10 needles	15.3	14.8	16.4	21.2
Length 20 needles	15.1	14.3	16.6	32.2
Needle weight	22.2	19.0	23.7	42.3
Color I	32.7	48.9	52.7	49.7
Internode growth	30.3	30.6	23.3	32.7

[a] - These coefficients are based on the overall mean and standard deviations of 92 samples at Russ, 52 at Newaygo, 34 at Higgins Lake, and 178 for all plantings.

Table C. Analysis of Variance of 45 different Scotch pine provenances based on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Foliar Nitrogen Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	1.18137482	.59068741	64.59142 *
Provenances	44	.63136593	.01434923	1.56908 *
Error	88	.80475850	.00914498	
Total	134	2.61749924		

Foliar Potassium Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	.38929333	.19464667	135.25667 **
Provenances	44	.08216000	.00186727	1.29754
Error	88	.12664001	.00143909	
Total	134	.59809334		

Foliar Phosphorus Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	.02373160	.01186580	71.87894 *
Provenances	44	.01290307	.00029325	1.77642 *
Error	88	.01452707	.00016508	
Total	134	.05116174		

Table C. Analysis of Variance of 45 different Scotch pine Provenances based on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Foliar Sodium Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	7934.23703712	3967.11851856	11.26328
Provenances	44	37177.08148179	844.93367004	2.39890 **
Error	88	30995.09633903	352.21700385	
Total	134	76106.41485808		

Foliar Calcium Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	.34192593	.17096296	50.65443 *
Provenances	44	.10446370	.00237418	.70344
Error	88	.29700741	.00337508	
Total	134	.74339704		

Foliar Magnesium Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	.10285481	.05142741	376.76222 **
Provenances	44	.01112593	.00025286	1.85249 *
Error	88	.01201185	.00013650	
Total	134	.12599259		

Table C. Analysis of Variance of 45 different Scotch pine provenances based on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Foliar Manganese Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	140289.52592707	70144.76296317	256.30956**
Provenances	44	8244.19259283	187.36801347	.68464
Error	88	24083.14073582	273.67205382	
Total	134	172616.85925768		

Foliar Iron Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	27940.37037092	13970.18518546	94.31858 *
Provenances	44	9109.21481482	207.02760943	1.39773
Error	88	13034.29631553	148.11700359	
Total	134	50083.88150163		

Foliar Copper Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	102.38044444	51.19022222	14.64704
Provenances	44	138.57066667	3.14933333	.90112
Error	88	307.55288885	3.49491919	
Total	134	548.50399996		

Table C. Analysis of Variance of 45 different Scotch pine provenances baded on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Foliar Boron Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	6469.39259270	3234.69629635	252.51470 **
Provenances	44	1226.32592593	27.87104377	2.17574 **
Error	88	1127.27407339	12.80993265	
Total	134	8822.99259203		

Foliar Zinc Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	2008.90370372	1004.45185186	6.41306
Provenances	44	5660.54814830	128.64882155	.82138
Error	88	13783.09628099	156.62609420	
Total	134	21452.54814168		

Foliar Molybdenum Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	8.00370370	4.00185185	27.50636 *
Provenances	44	3.01703704	.06856902	.47130
Error	88	12.80296297	.14548822	
Total	134	23.82370371		

Table C. Analysis of Variance of 45 different Scotch pine provenances based on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Foliar Aluminum Content

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	35232,77037093	17616,38518546	87,43003*
Provenances	44	13238,77037066	300.88114479	1,49327
Error	88	17731,22964514	201.49124597	
Total	134	66202,77038746		

Needle Color I

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	STATISTIC
Plantings	2	339,60000001	169,80000000	64,85417 *
Provenances	44	1893,73333335	43,03939394	16,43866 **
Error	88	230,40000028	2.61818182	
Total	134	2463,73333361		

Needle Color II

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	313,91111112	156,95555556	39,45309 *
Provenances	44	2271.33333334	51,62121212	12,97575**
Error	88	350,08888907	3.97828283	
Total	134	2935,33333352		

Table C. Analysis of Variance of 45 different Scotch pine provenances based on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Needle length of 5 fascicles

Source	D.F.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	119307,21481621	59653,60740811	128,78422 **
Provenances	44	100606,37037167	2286,50841753	4,93627 **
Error	88	40762,11843203	463,20589127	
Total	134	260675,70361919		

Needle length of 10 fascicles

Source	D.F.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	486207,03704363	243103,51852181	184,99168**
Provenances	44	420780,77037876	9563,19932666	7,27720**
Error	88	115643,63009892	1314,13216022	
Total	134	1022631,43751763		

Needle length of 15 fascicles

Source	D.F.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	10862,85925940	5431,42962968	201,01115 **
Provenances	44	9137,21481484	207,66397306	7,68541 **
Error	88	2377,80741121	27,02053876	
Total	134	22377,88148523		

Table C. Analysis of Variance of 45 different Scotch pine provenances based on one composite sample from each of 3 experimental plantings (Russ, Newaygo, and Higgins Lake)

Needle length of 20 fascicles

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	19497.79259303	9748.89629637	200.59110**
Provenances	44	17623.65925970	400.53771044	8.24137**
Error	88	4276.87407595	48.60084177	
Total	134	41398.32592846		

O.D. weight of 40 needles

Source	d.f.	SUM OF SQUARES	MEAN SQUARE	F STATISTIC
Plantings	2	2.02296148	1.01148074	138.73786**
Provenances	44	1.28566370	.02921963	4.00786**
Error	88	.64157185	.00729059	
Total	134	3.95019704		

Table D. Three-plantation (Russ, Newaygo, Higgins Lake) means and standard deviations for the measurements of 45 Scotch pine seedlots.

	Nitrogen %		Potassium %		Phosphorus %		Sodium ppm	
	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
AFIN 229	1.913	.359	.506	.115	.2276	.026	62.3	15.6
BSWE 546	1.920	.242	.533	.092	.2153	.021	61.6	28.5
CSWE 222	2.020	.332	.520	.091	.2246	.030	49.3	12.2
CFIN 230	2.000	.294	.510	.098	.2280	.032	80.3	17.0
CNOR 273	1.960	.230	.546	.046	.2246	.021	59.0	8.8
CSWE 522	1.920	.240	.566	.050	.2123	.025	69.0	5.0
CSWE 543	1.920	.160	.546	.070	.2070	.012	52.3	31.2
CSWE 544	1.920	.170	.533	.061	.2156	.019	67.3	22.5
DLAT 223	1.873	.113	.513	.030	.2156	.012	48.3	17.7
DLAT 224	1.913	.185	.480	.115	.2183	.016	74.3	18.5
DSWE 541	1.926	.061	.540	.040	.2210	.024	52.0	8.0
DSWE 542	1.853	.170	.573	.083	.2183	.022	76.6	24.9
DSWE 550	1.866	.090	.503	.028	.2073	.017	65.6	24.0
ESIB 227	1.800	.140	.483	.047	.2156	.019	70.6	2.8
ESIB 255	1.893	.181	.510	.078	.2160	.026	73.3	25.0
ESIB 256	1.840	.105	.513	.090	.2183	.016	57.3	25.6
EURA 258	1.766	.070	.506	.061	.2043	.019	47.3	22.0
EURA 259	1.826	.144	.480	.020	.2183	.016	37.0	23.3
FPOL 211	1.953	.147	.490	.026	.2096	.014	60.0	32.9
FPOL 317	1.980	.173	.500	.052	.2216	.030	83.6	9.5
GGER 202	1.873	.110	.520	.052	.2130	.019	70.0	22.5
GGER 203	1.820	.111	.496	.085	.1983	.017	43.6	28.2
GGER 204	1.900	.091	.486	.057	.2126	.021	60.0	26.2
GGER 207	1.913	.057	.520	.069	.2100	.022	53.3	15.1
GGER 208	1.906	.080	.503	.063	.2216	.021	59.3	15.0
GGER 527	1.853	.110	.520	.040	.2100	.008	38.0	14.0
HFRA 241	1.920	.177	.523	.081	.2180	.029	88.6	9.5
HGER 251	1.940	.060	.553	.117	.2243	.018	86.0	26.1
HGER 253	1.926	.030	.503	.081	.2156	.012	60.3	28.5
HBEL 530	1.966	.050	.566	.070	.2180	.000	48.0	28.2
HHUN 553	1.793	.041	.530	.055	.2073	.009	79.3	20.3
JFRA 235	1.900	.052	.526	.075	.2183	.008	88.6	4.5
JYUG 242	1.900	.069	.506	.094	.2183	.022	75.6	12.5
KTUR 213	1.866	.080	.523	.086	.2156	.009	56.0	25.2
KTUR 220	1.800	.190	.533	.122	.2123	.025	65.0	29.5
KTUR 221	1.913	.061	.546	.113	.2216	.021	55.6	36.1
KGRE 243	1.840	.103	.516	.075	.2130	.030	88.6	4.5
KGRE 244	1.840	.091	.533	.080	.2156	.017	80.3	12.0
MFRA 238	1.833	.041	.510	.088	.2066	.019	103.3	17.0
MFRA 239	1.833	.100	.503	.066	.2043	.012	96.3	21.9
NSPA 218	1.853	.061	.506	.041	.1956	.018	74.0	10.0
NSPA 219	1.786	.100	.496	.077	.1956	.018	54.3	21.4
NSPA 245	1.793	.064	.513	.083	.1933	.022	101.0	17.4
NSPA 246	1.646	.094	.446	.057	.1790	.024	79.0	.0
NSPA 247	1.826	.070	.496	.075	.1983	.020	97.0	26.9
Overall Mean & S.D.	1.878	.139	.516	.066	.2128	.019	67.7	23.8

	Calcium		Magnesium		Manganese		Iron	
	%		%		%		%	
	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
AFIN229	.473	.136	.063	.040	89.0	46.1	91.6	31.6
BSWE546	.426	.115	.076	.025	81.6	42.1	69.0	26.2
CSWE222	.433	.046	.073	.035	70.3	43.5	71.0	16.3
CFIN230	.436	.098	.060	.034	77.6	39.0	71.0	20.5
CNOR273	.376	.073	.066	.035	78.0	47.7	86.3	37.0
CSWE522	.406	.073	.066	.040	87.6	50.8	74.6	40.1
CSWE543	.416	.070	.070	.040	74.0	48.1	69.0	20.6
CSWE544	.446	.063	.080	.036	85.3	50.8	73.3	22.8
DLAT223	.436	.144	.073	.041	73.6	46.5	69.6	9.2
DLAT224	.390	.141	.080	.030	71.6	46.1	85.6	21.5
DSWE541	.423	.011	.076	.035	80.0	52.1	78.6	21.7
DSWE542	.446	.063	.066	.035	81.3	52.3	65.6	17.7
DSWE550	.390	.017	.076	.035	88.0	45.4	74.6	24.1
ESIB227	.426	.161	.066	.040	81.0	50.4	70.0	11.5
ESIB255	.453	.058	.060	.040	74.3	47.6	68.3	30.1
ESIB256	.436	.132	.066	.041	75.0	40.1	78.0	38.4
EURA258	.423	.070	.063	.030	73.6	44.9	67.6	7.5
EURA259	.416	.070	.066	.045	74.3	42.9	71.6	8.5
FPOL211	.396	.085	.090	.034	67.0	36.5	83.0	15.1
FPOL317	.403	.030	.086	.025	81.3	44.8	79.6	15.9
GGER202	.406	.085	.083	.032	73.0	44.3	79.6	21.5
GGER203	.370	.087	.086	.025	69.3	47.8	78.6	14.8
GGER204	.420	.125	.086	.035	73.0	46.0	97.0	18.2
GGER207	.386	.058	.090	.036	69.3	44.0	92.6	19.6
GGER208	.423	.090	.096	.028	72.3	45.2	88.3	15.1
GGER527	.410	.000	.086	.041	64.0	30.8	88.3	28.4
HFRA241	.406	.025	.086	.020	64.0	32.9	81.6	6.5
HGER251	.426	.056	.084	.030	74.6	42.1	81.6	19.3
HGER253	.386	.040	.090	.036	81.3	43.6	84.0	21.0
HBEL530	.423	.090	.090	.020	77.0	36.3	89.3	19.8
HHUN553	.396	.041	.090	.030	74.0	38.9	89.3	12.7
JFRA235	.430	.000	.086	.037	59.3	24.7	78.0	22.5
JYUG242	.433	.025	.073	.032	64.6	35.9	71.0	15.7
KTUR213	.363	.135	.080	.043	74.3	44.0	84.0	13.1
KTUR220	.380	.098	.076	.030	73.0	48.5	77.3	13.6
KTUR221	.370	.132	.080	.040	70.3	46.0	79.3	15.3
KGRE243	.450	.034	.076	.035	61.3	36.2	81.6	24.1
KGRE244	.470	.045	.076	.037	61.3	34.0	84.0	21.0
MFRA238	.453	.040	.076	.035	61.0	34.0	79.6	12.6
MFRA239	.433	.115	.080	.043	58.6	28.3	79.6	24.7
NSPA218	.386	.070	.073	.032	71.6	48.5	81.6	19.7
NSPA219	.380	.098	.076	.037	70.0	47.2	63.6	11.9
NSPA245	.396	.080	.070	.036	60.0	29.5	70.0	24.9
NSPA246	.360	.045	.076	.047	64.0	36.0	61.6	17.8
NSPA247	.400	.017	.076	.037	66.0	34.6	70.3	25.5
	.413	.074	.077	.030	72.7	35.8	78.0	19.3

	Copper		Boron		Zinc		Molybdenum	
	ppm		ppm		ppm		ppm	
	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
AFIN229	9.06	1.96	32.3	6.0	61.6	10.6	2.13	.50
BSWE546	6.60	4.69	29.0	6.9	58.0	1.7	1.93	.41
CSWE222	9.00	1.77	35.3	8.1	70.0	5.5	2.10	.17
CFIN230	7.06	1.22	30.6	6.6	60.3	3.5	2.10	.43
CNOR273	7.03	2.15	31.6	7.0	50.3	6.5	1.83	.40
CSWE522	7.66	3.78	31.3	6.3	62.6	5.1	2.10	.43
CSWE543	7.26	1.96	31.6	10.6	65.0	8.6	1.96	.32
CSWE544	7.86	3.00	37.3	9.0	62.6	5.1	2.30	.26
DLAT223	8.80	2.42	29.6	8.5	61.0	17.3	2.06	.75
DLAT224	8.16	1.26	30.6	5.7	61.0	17.7	1.90	.90
DSWE541	8.20	2.42	33.3	14.1	62.6	2.3	2.06	.15
DSWE542	7.36	1.72	35.0	12.2	60.3	3.5	2.13	.40
DSWE550	7.26	1.96	31.6	9.2	59.6	9.8	1.73	.11
ESIB227	8.20	2.55	26.0	4.0	62.0	22.5	2.06	.92
ESIB255	7.06	.92	25.6	8.3	69.6	4.6	2.13	.25
ESIB256	7.40	2.42	26.6	8.7	67.3	3.5	2.03	.70
EURA258	7.06	.92	29.3	10.0	61.6	10.6	2.06	.57
EURA259	7.60	.80	27.3	7.5	67.6	9.4	2.00	.52
FPOL211	7.60	1.38	32.3	8.6	65.6	16.1	1.86	.49
FPOL317	8.70	.51	32.3	10.6	67.3	7.5	1.90	.50
GGER202	9.56	1.32	34.6	9.4	69.3	16.7	1.93	.65
GGER203	7.63	1.44	33.0	9.5	59.3	20.5	1.76	.51
GGER204	11.06	2.32	35.6	5.7	72.3	26.0	2.00	.75
GGER207	9.03	1.32	33.6	9.2	68.0	14.5	2.03	.20
GGER208	8.86	4.20	36.0	10.8	70.0	26.5	2.00	.52
GGER527	8.53	3.10	34.0	9.1	65.6	15.3	1.96	.11
HFRA241	7.86	.46	32.0	10.5	65.0	7.2	2.00	.17
HGER251	9.30	1.70	33.6	11.0	65.0	1.7	2.06	.28
HGER253	7.90	1.70	31.3	9.0	61.6	4.0	1.83	.25
HBEL530	9.30	.90	30.3	8.7	73.3	20.3	2.13	.64
HHUN553	9.30	.90	32.0	11.1	69.0	12.2	1.96	.20
JFRA235	8.43	.85	31.6	9.0	75.6	20.2	2.10	.00
JYUG242	7.60	1.38	28.6	12.0	63.6	3.5	2.00	.17
KTUR213	10.30	4.35	32.3	6.0	54.3	26.8	1.83	.80
KTUR220	7.86	.92	30.0	11.3	51.6	20.7	1.90	.62
KTUR221	7.33	.46	31.0	8.0	51.6	18.5	1.80	.72
KGRE243	9.00	1.03	33.0	10.4	62.3	4.0	2.20	.17
KGRE244	9.30	.90	34.0	9.6	70.0	7.9	2.40	.20
MFRA238	9.30	.90	35.0	7.9	62.6	7.5	2.30	.17
MFRA239	9.36	2.60	34.6	6.1	66.6	11.1	2.40	.60
NSPA218	9.93	3.49	41.0	14.9	58.0	1.7	1.90	.30
NSPA219	7.33	1.22	30.6	5.7	48.0	13.1	1.86	.70
NSPA245	7.33	.46	35.3	6.4	59.6	14.1	2.06	.46
NSPA246	7.00	1.77	27.6	10.1	48.0	3.4	1.93	.15
NSPA247	7.33	3.21	29.6	9.2	53.6	6.5	2.00	.17
	8.24	2.02	32.0	8.1	62.6	12.6	2.01	.42

	Aluminum ppm		Color I		Color II		Weight O.D. wt. of 40 needles in g	
	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
AFIN229	120.3	23.1	4.6	.5	5.0	3.0	.350	.121
BSWE546	120.0	39.3	2.6	1.1	2.6	1.1	.403	.125
CSWE222	117.0	12.0	4.3	2.0	4.0	1.0	.473	.150
CFIN230	129.3	21.3	4.3	1.5	2.6	2.0	.376	.058
CNOR273	99.0	7.5	5.0	2.6	4.3	2.0	.500	.147
CSWE522	121.6	27.0	3.6	2.0	4.6	3.0	.456	.185
CSWE543	123.6	19.3	4.0	1.7	3.3	2.3	.500	.141
CSWE544	128.0	28.3	6.0	2.0	4.6	1.5	.486	.180
DLAT223	112.3	19.0	4.3	2.3	3.3	1.5	.566	.200
DLAT224	107.3	27.7	4.3	1.5	3.6	2.0	.486	.111
DSWE541	130.0	16.3	7.3	1.5	6.6	2.0	.536	.196
DSWE542	109.3	35.9	6.0	1.7	4.0	1.7	.533	.280
DSWE550	142.6	7.0	6.6	4.0	7.6	3.7	.510	.151
ESIB227	123.0	33.9	5.3	2.0	5.3	3.2	.616	.213
ESIB255	133.0	10.5	3.3	2.5	1.6	1.1	.590	.187
ESIB256	108.0	12.5	4.0	3.4	3.6	2.0	.446	.116
EURA258	134.0	20.0	4.0	3.6	4.3	3.2	.623	.241
EURA259	125.6	15.1	4.3	2.5	5.3	3.2	.546	.200
FPOL211	118.6	26.8	6.0	4.3	5.6	3.2	.606	.181
FPOL317	106.6	20.1	8.6	.5	6.0	2.0	.570	.282
GGER202	109.0	30.4	10.6	4.1	10.6	2.3	.553	.240
GGER203	107.6	27.0	8.3	2.5	9.6	3.2	.453	.178
GGER204	120.3	34.2	8.0	5.2	7.3	3.0	.626	.258
GGER207	114.0	35.6	9.6	4.0	10.3	4.6	.600	.245
GGER208	116.3	38.9	10.6	2.3	9.6	1.1	.526	.215
GGER527	131.0	31.4	8.6	2.0	7.6	3.2	.530	.170
HFRA241	94.0	23.2	11.6	3.0	11.3	4.7	.616	.255
HGER251	120.3	14.6	10.6	1.5	11.0	2.0	.606	.172
HGER253	119.0	30.8	11.0	2.0	11.0	3.0	.583	.159
HBEL530	119.6	10.2	10.3	2.0	11.3	2.0	.536	.155
HHUN553	111.3	17.5	10.6	1.5	9.3	3.7	.580	.135
JFRA235	123.6	19.6	10.6	1.5	10.3	1.1	.420	.088
JYUG242	115.0	24.5	12.6	3.2	13.3	2.0	.426	.184
KTUR213	117.0	26.0	13.3	2.8	13.6	4.1	.356	.105
KTUR220	110.0	35.1	15.0	1.0	14.3	2.5	.393	.160
KTUR221	120.3	30.9	13.6	2.5	14.6	3.2	.326	.070
KGRE243	107.0	9.8	12.6	2.0	13.0	2.0	.413	.105
KGRE244	115.0	20.6	12.6	3.2	12.6	3.2	.460	.168
MFRA238	106.3	16.8	13.3	2.0	12.6	.5	.343	.119
MFRA239	101.6	25.7	13.3	2.0	14.0	2.6	.363	.120
NSPA218	115.0	10.3	13.6	1.5	13.3	3.2	.380	.122
NSPA219	112.3	25.0	13.0	2.0	14.3	2.8	.350	.095
NSPA245	99.6	14.5	12.3	1.5	13.3	3.7	.293	.087
NSPA246	111.0	10.5	13.0	1.7	13.3	.5	.326	.102
NSPA247	112.3	28.1	13.3	2.0	14.0	3.0	.346	.141
	116.4	22.2	8.71	4.2	8.5	4.6	.479	.171

Needle Length

	5 fasc.		10 fasc.		15 fasc.		20 fasc.	
	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.
AFIN229	157.3	37.4	301.6	50.5	45.6	7.2	61.0	11.2
BSWE546	168.6	24.0	327.3	57.4	48.6	7.5	66.6	11.3
CSWE222	181.0	27.6	353.3	64.2	53.6	11.0	72.0	13.8
CFIN230	166.6	27.5	341.6	56.1	50.3	7.3	65.6	10.1
CNOR273	207.3	41.4	405.0	79.3	58.3	11.5	78.3	16.7
CSWE522	191.6	38.1	369.0	77.6	54.3	11.5	72.6	16.6
CSWE543	194.6	36.6	383.6	71.7	57.6	10.1	77.3	15.0
CSWE544	190.3	48.6	378.0	96.1	56.6	14.4	76.6	20.5
DLAT223	198.3	43.6	387.0	90.1	58.3	14.2	78.0	17.4
DLAT224	166.6	23.0	360.3	66.0	54.0	9.1	71.3	11.7
DSWE541	197.6	55.8	401.6	87.5	61.0	15.0	81.6	17.8
DSWE542	195.0	68.7	409.3	140.4	63.0	19.9	82.0	24.8
DSWE550	198.3	42.5	385.6	71.5	57.3	9.5	76.6	13.5
ESIB227	206.6	45.3	420.0	88.4	64.0	13.5	86.3	18.1
ESIB255	198.0	35.6	403.3	72.3	61.0	11.3	83.3	17.0
ESIB256	184.6	18.5	369.6	41.3	56.6	7.7	76.0	12.5
EURA258	206.3	36.7	430.0	79.3	64.0	13.4	85.3	18.4
EURA259	197.6	36.5	402.3	79.7	60.0	11.1	80.6	16.0
FPOL211	227.6	56.0	453.0	113.9	66.6	16.2	91.0	21.9
FPOL317	215.0	59.0	421.0	104.7	62.6	15.2	83.3	23.5
GGER202	203.3	44.8	408.3	92.5	60.3	14.7	83.0	20.4
GGER203	175.3	47.2	348.6	97.2	55.3	13.0	72.0	16.5
GGER204	213.3	49.3	433.6	84.0	65.6	13.8	88.0	19.9
GGER207	228.3	48.5	458.3	118.1	66.6	18.2	89.6	22.1
GGER208	191.6	49.0	400.0	108.2	61.3	15.9	81.6	20.9
GGER527	203.6	45.9	417.6	76.4	61.3	10.0	82.0	14.1
HFRA241	225.0	40.9	441.6	115.3	67.0	18.0	90.3	25.3
HGER251	244.3	62.5	483.3	117.1	71.6	15.5	97.0	20.8
HGER253	226.3	64.7	446.0	94.1	66.3	14.0	90.6	16.0
HBEL530	223.3	40.7	444.6	86.9	67.3	13.0	88.6	12.0
HHUN553	200.0	32.0	426.6	61.1	64.6	10.0	87.3	12.0
JFRA235	183.3	20.8	352.3	46.1	53.3	6.4	70.3	8.3
JYUG242	186.6	62.9	365.0	115.3	55.0	16.5	73.0	21.5
KTUR213	151.6	43.6	309.3	66.6	47.0	9.5	60.6	12.6
KTUR220	165.0	37.7	326.6	87.3	50.6	13.3	67.0	16.8
KTUR221	160.0	40.9	310.6	61.3	47.0	7.5	61.6	10.6
KGRE243	166.6	38.8	311.6	50.0	47.6	8.7	64.6	11.8
KGRE244	183.6	40.6	355.0	76.9	54.6	10.2	73.6	14.8
MFRA238	141.0	25.9	288.3	41.6	42.3	6.1	55.3	8.5
MFRA239	147.0	29.8	280.0	47.6	41.6	7.2	56.0	10.3
NSPA218	163.0	37.5	313.3	63.5	47.0	8.6	63.3	12.5
NSPA219	150.0	22.9	293.3	48.5	44.3	8.6	60.3	10.9
NSPA245	127.3	20.5	269.3	49.0	41.0	7.5	52.3	11.1
NSPA246	139.0	31.0	278.3	61.7	41.3	8.6	54.6	10.0
NSPA247	144.6	33.2	295.0	67.2	44.0	9.1	59.3	13.3
	186.5	44.1	372.4	87.3	55.9	12.9	74.8	17.5