DUFFIELD placed it in the *Lariciones*. The karyological data for this species are not so easily interpreted as are the others, because the average value of the short-arm : long-arm ratios for the eleventh chromosome is slightly greater (0.754) than the upper limit of the submedian category; four of the ratios are just below 0.750 and six are slightly above. However, karyotypes for 20 species from seven other Groups have been determined, and only two of these species have a ratio below 0.800 for the eleventh chromosome (*Table* 4). The value for P. pinaster is so close to the arbitrary limit of the submedian category that it resembles the species of Lariciones more than those in any of the other Groups studied, including Insignes.

Summary

Karyotypes are described for 19 species of pine of the Group Lariciones. All species had a similar but distinct karyotype characteristic of the Group. The haploid *Lariciones* karyotype differs from those of other Groups by containing two heterobrachial chromosomes instead 04 one.

Karyological evidence supports the inclusion of Pinus halepensis, P. brutia, P. pityusa, and P. pinaster in the Group Lariciones. The karyotypes of these species are very similar to those of the generally accepted species of *Lariciones*, because they possess the heterobrachial eleventh chromosome characteristic of this group.

Résumé

Titre de l'article: Analyse des karyotypes des pins du groupe Lariciones.

L'auteur décrit les karyotypes de 19 especes de pin du groupe Lariciones. Toutes les especes présentent le karyotype caracteristique du groupe; chaque karyotype est cependant distinct. Le karyotype haploide des Lariciones differe de ceux des autres groupes: il comporte deux chromosomes hétérobrachiaux au lieu d'un.

L'analyse karyologique permet d'inclure dans le groupe Lariciones les especes suivantes: Pinus halepensis, P. *brutia*, P. pityusa et P. pinaster. Ces especes sont tres semblaMes a ceux des especes generalement considérées comme Lariciones, parce qu'elles ont le onzième chromosome hétérobrachial.

Zusammenfassung

Titel der Arbeit: Karyotypen-Analyse der *Kiefern-Gruppe* der Lariciones.

Für 19 Kiefernarten der Gruppe der Lariciones sind die Karyotypen beschrieben worden. Sie waren alle ähnlich, aber characteristisch für diese Gruppe. Der haploide Lariciones-Karyotyp unterscheidet sich durch das Vorkommen von 2 heterobrachialen Chromosomen, anstatt einem solchen bei anderen Kiefern-Gruppen.

Der karyologische Befund verlangt die Zuordnung von Pinus halepensis, P. brutia, P. pityusa und P. pinaster zur Gruppe der Lariciones. Die Karyotypen dieser Arten sind denen der bisherigen Lariciones sehr ähnlich, weil sie das für diese Gruppe charakteristische heterobrachiale 11. Chromosom besitzen.

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Effects of Inbreeding in Red Pine, Pinus resinosa Ait.[1])

By D. P. FOWLER[2])

(Received for publication May 1, 1964)

Introduction

"It would seem unwise to conclude that red pine has existed as a specific entity since the Cretaceous, for its Tertiary record is unknown, but the morphological evidence is temptingly suggestive." (PIERCE, 1957.)

Deposits assigned to the early Upper Cretaceous Dakota series have yielded cones and needles (CHANEY, 1954) and pollen (PIERCE, 1957) which are almost identical to those of contemporary Pinus resinosa. If these Cretaceous species (Pinus clementsii CHANEY and/or Pinus resinosipites PIERCE) are in fact red pine or close relatives of red pine, then the ancestry of this species extends back at least a hundred million years.

Red pine is the only North American species of the Lariciones group. Pinus tropicalis MOR., which occupies a limited range in Cuba and on the Isle of Pines, is the only other American representative of this group which is largely confined to Europe and Asia (SHAW, 1914).

Attempts to hybridize red pine with other species in the Lariciones group have, until recently, been unsuccessful. DUFFIELD and SNYDER (1958) reported a successful cross of Pinus nigra ARN. X Pinus resinosa, but thus far, attempts to repeat this cross have been unsuccessful.

The natural range of red pine is presented in Figure I and is based primarily on the map of RUDOLF (1957), with a few changes for Ontario and Manitoba. The range map is somewhat deceiving in that it indicates a relatively continuous distribution. Along the range limits, the distribution of red pine is actually disjunct and, in some cases, distances of 100 miles or more may separate individual locations. Outlying populations are found in West Virginia and northern Illinois (RUDOLF, 1957) as well as in northern Ontario (HADDOW, 1948), and Manitoba (VAARTAJA, 1962).

Cool to warm summers, cold winters, moderate rainfall, sandy soils and undulating topography are characteristic of the red pine habitat. This species occurs in areas of acid

[1]) Contribution 64 — 5. Ontario Department of Lands and Forests. This paper is the first of a series of papers based on a dissertation submitted to the Graduate School of Yale University as partial fulfillment of the requirements of the PhD degree in 1963.

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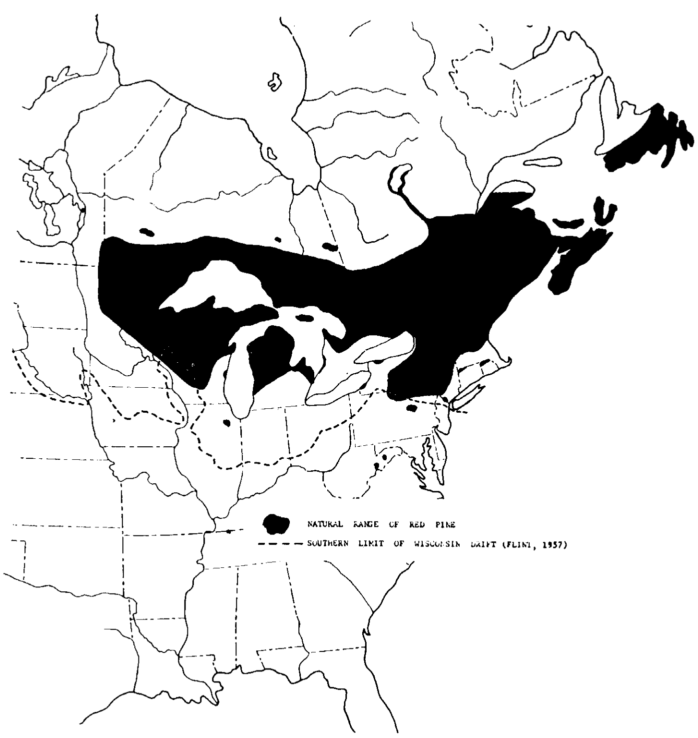

Figure I: — Map of eastern North America showing the natural range of red pine and the southern limit of the Wisconsin drift.

soil which have good drainage and aeration and where competition with other species is not severe.

The habitat of the species has a frost free period which averages from 80 to 160 days but may be as low as 40 days. Minimum temperatures of -60^0 F (-50^0 C) have been recorded in the coldest parts of its range. Annual precipitation ranges from 20 to 40 inches (50 to 100 cm.) but may exceed 50 inches (125 cm.) in eastern localities (Rudolf, 1957.) Haddow (1948) stated that the northern limit of red pine is related to the length of the frost free period and closely parallels the 35^0 F (1.7^0 C) mean annual isotherm. Red pine stands examined in northern Ontario appear to be much more restricted by the limited number of sites available than by low temperatures. Healthy, vigorous red pines, quite unlike those of species growing at the climatic limit of its range, were examined by the writer in the area north of Cochrane and Hearst, Ontario (latitude 49^0 N). Trees 70 to 80 feet (21 to 24 m.) in height at less than 100 years of age were measured.

Normally red pine is confined to well-drained podzolized soils, but the species does well on a variety of sites. It has been occasionally reported growing on quite moist sites (Rudolf, 1957) and the writer has observed it, in association with black spruce, *Picea mariana* (Mill.) B. S. P., and tamarack, *Larix laricina* (Duroi) K. Koch, on wet soils near Windsor, Nova Scotia. Red pine is generally found growing on soils somewhat richer than those required by *Pinus banksiana* Lamb., and somewhat poorer than those required by *Pinus strobus* L.

Over most of its natural range, the species occurs at elevations of 800 to 1400 feet (240 to 425 m.) above sea level but in New England it may reach elevations of 2000 feet (610 m.). In the outlying stands in West Virginia, it is found at over 4000 feet (1220 m.) elevation (Rudolf, 1957).

Of the many factors that determine the genetic constitution of an organism, origin and dispersal are most important. The recent glaciation had a great effect on the distribution of the *Pinus* species of North America and there is a strong possibility that it had an influence on their present genetic composition. The most recent extensive glaciation of eastern North America was characterized by the Cary advance of the Wisconsin ice sheet, which reached its southernmost limits about 18,000 before present (Flint, 1957). Two major re-advances of the ice sheet, the Mankato (12—13,000 B. P.) and the Valders (10,600 B. P.) are generally recognized. The southern limits of the Wisconsin ice sheet are shown in *Figure I.*

It is generally agreed that the northern pine species retreated southward before the advancing ice sheet and returned as the ice receded. The question as to where red pine survived the last glacial period is largely unresolved. It has been suggested that many northern tree species survived this period in refuges located just south of the ice sheet (Braun, 1950). The present distribution of red pine offers no evidence of survival in specific refuges. On the contrary, the present wide distribution of the species and the occurrence of southern outliers in Illinois, Pennsylvania, New Jersey and Connecticut support the hypothesis that this species survived in several areas or in one almost continuous area south of the glacial limit. Further support of this hypothesis is obtained from pollen analysis. *Pinus* pollen is found in the lower levels of virtually all the pollen sequences made within the glaciated area. This indicates that pines were present over a wide longitudinal range in the southern parts of the glaciated area. Although most workers have not attempted to distinguish the various pine pollens that occur in their pollen sequences, the few who have (Cain and Cain, 1948; Davis, 1958; and Ogden, 1959) reported red pine pollen to be present along with that of white pine and jack pine. It would appear that the existence of refuges is not required to account for the present distribution of red pine.

The presence of isolated stands of red pine well north of its general range may be the result of chance recent dispersal of seeds into these areas or they may be the remnants of a more northern range for this species during the hypsithermal period (Devey and Flint, 1597).

Haddow (1948) considered the distribution of red pine in northern Ontario to be suggestive of "decadence and retreat". He suggested that these trees were "almost certainly self-fertilized" and that this resulted in a reduction in the amount of seed set (as shown by Johnson, 1945) and in turn the failure of red pine in competition with other species. This view is based on the old age of the trees and the lack of adequate regeneration. The writer, although not disagreeing with the suggestion that these stands are remnants, does not agree with the reasons upon which it is based. Observations indicate that this species regenerates well wherever suitable conditions are present.

Experimental Program

A red pine breeding program was initiated in 1956 by the Research Branch of the Ontario Department of Lands and Forests. The objectives of this program were to develop a red pine or "red pine-like" tree resistant to the European pine shoot moth, *Rhyacionia buoliana* Schiff. and suitable for planting in southern Ontario.

The first steps of this program were to obtain breeding materials representing the available genetic variation of this species and to establish a basis for the selection of superior types. Breeding materials in the form of scions and seeds were obtained from many areas in Canada and the United States, and established at the Southern Research Station, Maple, Ontario. During the course of this acquisition, it became evident that any criterion for selection, based on the available genetic knowledge of red pine, would be of limited value.

Red pine, regardless of its origin, was observed to be morphologically uniform. With few exceptions, the variation observed could be attributed more easily to environmental than to genetic differences. A survey of the literature revealed that, although genetic differences undoubtedly do occur among red pines from different origins, the magnitude of these differences is not great.

Controlled pollination experiments with members of the genus *Pinus* have shown that all the species tested were heterozygous for a large number of alleles. It was thus believed that self-pollination (if selfing was in fact possible) would reveal the type of genetic variation that existed in an individual tree by producing seed and seedlings homozygous for a number of alleles. To this end, self- and cross-pollinations were made on a number of trees. Data obtained from these crosses revealed that the trees were rather uniform genetically (Fowler, 1962).

A working hypothesis was established that red pine, unlike other species of the genus *Pinus*, is homozygous for a large number of alleles, self-fertile, self-compatible and that seedlings, resulting from self-pollination, suffer little inbreeding depression. Section I presents the findings of studies to determine if differences in morphological characters exist among trees of different origins when grown in a relatively uniform environment. In Section II, all data obtained from controlled pollination studies are presented. Section III reports on a number of studies of factors that may influence self-pollination under natural conditions. In Section IV, data comparing the findings of Section II with a similar, but less extensive study with *Pinus banksiana* and *Pinus strobus* are presented.

I. Natural Variation in Red Pine

Introduction

C. G. Bates (1927) deplored the then current forest nursery practice of purchasing red pine seed on a basis of cost with no regard to seed origin. He estimated that 25—50 percent of all forest plantings in the United States were wasted efforts because of the use of poorly adapted species and races of trees. It was not until 1939 that the U. S. Department of Agriculture developed a forest tree seed policy (Rudolf, 1957).

In 1928 the first serious attempt to study racial and individual tree variation in red pine was initiated by the U. S. Forest Service (Hough, 1952 a). In 1931 red pine from 37 seed sources were planted out at three National Forests in the Lake States (Superior, Chippewa and Huron) and, by 1933, additional plantings in these three locations brought the number of provenances being tested to 144. In 1937 further seed source plantings were made at the Chippewa National Forest and at the Kane Experimental Forest, Kane, Pennsylvania. The Huron National Forest plantings and the 1931—33 Chippewa National Forest plantings either failed or were destroyed by fire (Hough, 1952 a).

The surviving 1931—1937 provenance tests supply most of the information that is available on natural variation in red pine, although some less extensive studies have also made a contribution. The seed sources represented in these early studies are mostly of the Lake States area. Samples from other parts of the red pine range in the U. S. are rather sparse, and those from Canada almost non-existent.

In recent years the Canada Department of Forestry has established red pine provenance tests which cover the entire range of the species (Holst, 1957, 1960), and the Ontario Department of Lands and Forests has established studies which cover the species over its range in Ontario (Carmichael, 1962). Only preliminary results are available from these tests.

The seed sources tested in the 1931—1937 Lake States and Pennsylvania studies represent seed from individual tree collections, collections from small groups, limited locality collections, and general and mixed collections. The range from which these seeds were collected was first divided into seed collection centres by Bates (1930). Rudolf (1947, 1957) modified these centres into contiguous zones characterized by climate. These zones, eight in the Lake States and one called Eastern United States, have been utilized for the analysis of many of the data obtained from the Lake States and Pennsylvania studies.

Morphology: Red pine is an extremely uniform species (Bates, 1930; Rudolf, 1957; Holst, 1962). Attempts to find morphological characteristics separating different geographic origins have been unsuccessful (Rudolf, 1951, 1954). Rudolf (1947) found no consistent relationship between origin and seed characteristics, such as size, germination or chemical composition. Working with 28 seed sources representing eight seed zones, he reported that there was a general tendency for northern seed sources to produce smaller seed than southern sources, but that this was of little diagnostic value. He found no differences between seeds of different origins in respect to laboratory germination, nursery germination, tree percent of 1—0 stock and average weight of 1—0 seedlings. Hough (1952 b) found correlations between seed source and weight of red pine seed, and between seed weight and seedling size.

Eliason (1953) noted that red pine from Massey, Ontario, differed from other Ontario strains grown near Saratoga, N. Y., in that it had better growth, greener foliage, longer needles and one-year-old needles that were more perpendicular to the stem. Holst (1962) reported that, with the exception of a few minor localized variations, *e. g.* fastigiate forms from Wisconsin and "Tassel pine" from Bancroft, Ontario, red pine is remarkably uniform.

Survival: Rudolf (1947) observed that there was a tendency for seedlings from northern Minnesota, northern Wisconsin and adjacent Upper Michigan to survive better than seedlings from central Wisconsin, Michigan and New England in plantings at the Superior National Forest in northern Minnesota. This tendency was not very strong because some of the seedlings showing the poorest survival had their origin in northern Minnesota. Hough (1957) found no significant differences in survival of provenances in the Pennsylvania plantings. Significant differences in survival between trees of three origins planted at the Ottawa National Forest in Upper Michigan were reported by Benzie (1958). Trees from the local source survived better than those from the Upper Michigan National Forest which, in turn, had better survival than those from the Chippewa National Forest, northern Minnesota. It would appear from Benzie's data that mortality was related to incidence of dead tops and to a canker which had not been identified.

Frost Resistance: The results of tests of differences in frost hardiness of seedlings of different origins were reported by BATES (1930). He studied the effects of freezing temperatures on seven-month-old seedlings after they had been subjected to a short hardening period. Despite serious losses due to a variety of causes and the low number of seedlings used in the tests (a total of 149 seedlings representing 28 seed lots), a general trend was evident in the data. Northern sources, in general, were more frost resistant than southern ones. RUDOLF (1949) studied damage resulting during the winter of 1947—48 on 37 provenances of red pine at the Superior National Forest. Frost damage, which was least noticeable on local sources, tended to increase as latitude of the source decreased.

Red pines from northwestern Ontario were less severely damaged by a late spring frost (early June) than local red pine near Chalk River, Ontario (HOLST, 1962).

Photoperiodic response: Red Pine from 51° N latitude ceased growing and formed terminal buds slightly earlier than seedlings from 45° N when raised in an environment characterized by a short photoperiod — nine hours dark period (VAARTAJA, 1962). The interaction between provenance and photoperiods was small in comparison with results obtained from *Picea* species (VAARTAJA, 1962). RUDOLF (1954) studied earliness of shoot growth in over 160 seed lots from eight regions (see *Figure I — 1*). In general, he found that the southern provenances begin shoot growth earlier, but there were fast and slow starters from all but the northeastern Minnesota region. These differences may have been in response to temperature rather than photoperiod.

Wood Characteristics: The relationship between wood density and provenance was studied by REES and BROWN (1954). Cross sections from ten trees of each of 19 provenances grown at the Chippewa National Forest were obtained from 17-year-old trees.

No significant differences were found for percentage summer wood, average diameter inside bark, diameter growth for the last five years, height growth for the last eight years, volume index times total height, or age at the cross section (82" above ground). Analysis of variance revealed that the specific gravity of trees from the Bay City, Michigan seed source (S. G. .341) differed significantly from that of the other 18 provenances (S. G. range .310 to .326). SCHUMANN (1960), in a study of all 50 provenances represented in the Kane, Pennsylvania test plantings, reported significant differences in wood specific gravity between trees representing different climatic regions as well as between trees representing different provenances within these regions. The averages of all 50 provenances ranged from .303 to .341 while the range of averages for the nine regions was .319 to .329 (see *Figure I — 1*).

The writer has combined some of the seed source information presented by HOUGH (1952 a) and the specific gravity data given by SCHMUANN (1960) in *Table I — 1*. It is interesting to note that the range of the variation sampled from the 22 half-sib progenies differs so little from the range measured for the other kind of collections. The average spread of measurements for the one-parent progenies is 88 percent of that of the general or mixed collections.

Growth: Most of the information available on the relationship between growth and seed origin in red pine is presented in a series of papers by P. O. RUDOLF reporting on the 1931—1937 Lake States plantings and by A. F. HOUGH for the 1937 Pennsylvania planting. Many of the provenances are common to both the Lake States and to

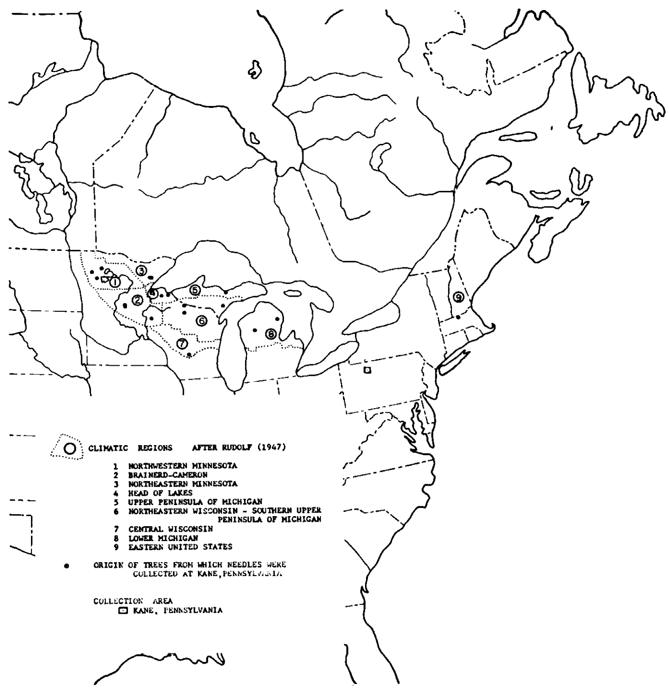

Figure I — 1: — Map of eastern North America showing location of collection area and origins of trees from which needles were collected at Kane, Pennsylvania.

Table I — 1: — Total range, average range and average difference between highest and lowest specific gravity for different kinds of seed collections.*)

Collection Type	Number of Provenances	Total Sample Range	Average Range	Average Difference
Individual tree	22	.212 to .491	.259 to .416	.157
Small groups	12	.230 to .482	.260 to .417	.157
Limited locality	8	.183 to .522	.250 to .442	.192
General and Mixed	8	.207 to .491	.251 to .429	.178

*) Information from HOUGH (1952) and SCHUMANN (1960).

the Pennsylvania plantings, and the climatic regions of the provenances, upon which the analyses are based, are the same.

RUDOLF (1947) reported on 37 provenances planted in the Superior National Forest in 1931. When the trees were ranked on a combined basis of good position in the stand, crown vigor, soundness (free of damage or disease), and form, most of the provenances were satisfactory. Out of the nine best lots (best 25 percent) the best three were from northern Minnesota and the remainder from northwestern Minnesota (1), northern upper Michigan (1), northeastern Wisconsin (3) and southern upper Michigan (1). Provenances from New England, lower Michigan, central Wisconsin and northwestern Wisconsin generally did not compare as well. Large differences between provenances in the same region were evident in respect to all characters examined in this study, *e. g.* some provenances with low rank in all characters studied were from northern Minnesota which, as a region, ranked high.

Fifty-one provenances planted in the Chippewa National Forest in 1937 revealed no striking differences in height at 14 years of age, while they revealed distinct differences when planted in Pennsylvania (RUDOLF, 1953).

BUCKMAN and BUCKMAN (1962) reported that, at 27 years of age, there were no significant regional differences in tree height for one Ontario and 48 Lake States provenances planted near Cass Lake, Minnesota. The mean height of provenances from the eight regions was 39.8 feet and the regional averages were all within 0.7 feet of this mean. Significant differences were found between provenances within two of the regional groups. The greatest difference between provenance and its regional averages was 2.5 feet.

Hough (1952 b) found a significant correlation between the green weight of seedlings and subsequent five-year height growth in the plantation of 50 provenances planted at Kane, Pennsylvania in 1937. This tendency of the heavier seedlings to grow faster increased during the second five-year growing period. Highly significant differences in ten-year height growth between provenances and between climatic regions were recorded (Hough, 1952 a). The range of mean heights of the 50 provenances at ten years was 8.5 to 11.4 feet. The differences between provenances within regions approached, but did not reach, significance at the five percent level. Seeds from origins in Upper Michigan, eastern and central Wisconsin and Lower Michigan produced significantly taller trees than those from the most northern sources.

Ten-year height measurements of 12 Ontario provenances representing five geographic regions, planted in three localities in Ontario failed to show any significant differences between provenances or between provenances representing the five regions (Carmichael, 1962).

Materials and Methods

In the spring of 1961 a study was initiated to determine if differences exist between red pine of different origins when the trees are grown in the same environment. In this study needle, cone, seed, germination, and seedling characters were examined on provenance materials raised under similar conditions.

Needle Characters

Kane, Pennsylvania: In June, 1961, one-year-old needles were collected from four trees of each of nine climatic regions in the Kane, Pennsylvania, provenance test plantations (Hough, 1952 a). The climatic regions and origins of the trees used in this study are presented in *Figure I — 1.* All needle collections were made from the central portion of vigorous first-order shoots growing in the upper exposed portions of the tree crowns. The trees from which the needle samples were collected, had previously been selected for controlled pollination studies on the basis of abundance of ovulate strobili. Measurements were made on six needles from each tree. Needle length was recorded and then a one-centimeter section cut from the central portion of the needle. Number of rows of stomata, number of stomata per centimeter and number of serrations per centimeter were counted. The number of resin canals per needle was determined on hand sections made from the central portion of the needle.

Maple, Ontario: In August, 1962, needles were collected from grafted red pine trees established at the Southern Research Station, Maple, Ontariao. All grafting had been done on Scots pine, *Pinus silvestris* L., stock at least three years prior to this study. The origins of the scions are shown in *Figure I — 2.* Five clones from each of eight origins, representing most of the longitudinal range of red pine in Canada, were utilized in this study. One needle was collected from each of five ramets of each clone. Needle collections and needle measurements were made in the same manner as for the Kane provenance test material.

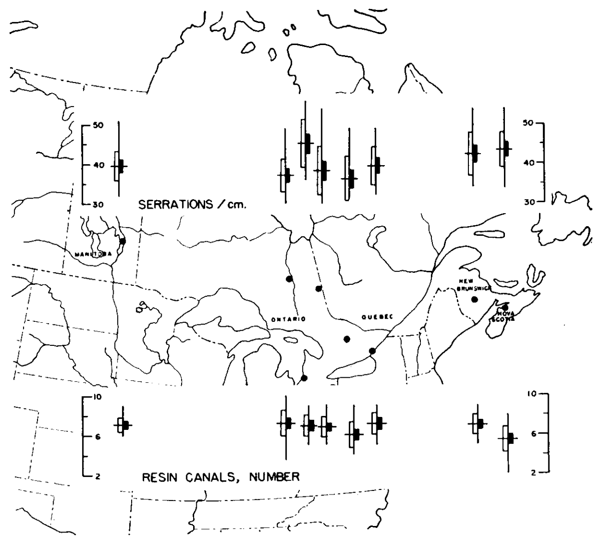

Figure I — 2: — Map of eastern Canada showing origins of clones from which needles were collected. Statistics pertaining to number of serrations (above) and number of resin canals (below) are presented in relation to the sample origins. The long vertical line represents the range; the short horizontal line, the sample mean; the rectangle to the left of the range line, one standard deviation above and below the mean; and the blackened rectangle to the right of the range line represents two standard errors above and below the mean.

Cone, Seed, Germination and Seedling Characters

In the fall of 1962, cones were collected from 34 of 36 trees which had been control-pollinated at Kane, Pennsylvania in 1961. Data were obtained for the following variables: cone length, number of seeds per cone, percent full seed, seed weight, percent germination, number of days to germinate, number of cotyledons and length of hypocotyls. The methods used to obtain these data are described in Section II (Fowler, 1964).

Results

Needle Characters

Kane, Pennsylvania: The summarized results are presented in *Table I — 2.* The following abbreviations are used in the Tables: d. f. = degrees of freedom; NS = non-significant; ** = significant at one percent level. No significant differences were found between the nine climatic seed source regions in respect to any of the five needle characters examined.

Maple, Ontario: The summarized results are presented in *Table I — 3.* Two of the five variables examined, namely number of serrations per centimeter and number of resin canals, were found to differ significantly at the one percent level in respect to regions of origin. *Figure I — 2* shows some of the statistics of these variables in relation to the region of origin. No definite longitudinal or latitudinal relationship was evident from the data.

Cone, Seed, Germination and Seedling Characters

The summarized results are presented in *Table I — 4.* Linear regression was used to test the relationship between latitude of origin and each of the eight variables examined. Only the regression of cotyledon numbers on latitude was significant at the five percent level ($F = 5.05$; $F_{.05} = 4.15$). Seedlings produced by trees from the northern latitudes had fewer cotyledons than seedlings of trees from southern latitudes *(Figure I — 3).*

Table I — 2: — Needle Characters, Kane, Pennsylvania. Averages of six needles per tree.

Climatic Region (Rudolf, 1947)	Tree Number	Needle Length, cm.	Stomata Rows Number	Serrations Number/cm.	Stomata Number/cm.	Resin Canals Number
1. North western Minnesota	4	13.5	6.3	39.0	113	4.7
	5	12.7	7.3	40.7	118	3.2
	12	10.9	6.3	39.5	119	5.2
	24	13.2	5.5	42.5	126	3.5
2. Brainerd-Cameron	23	13.5	6.3	39.8	122	2.0
	15	11.2	6.7	39.8	118	5.5
	27	13.0	6.5	38.2	110	5.3
	36	11.2	6.3	37.5	120	4.0
3. North-eastern Minnesota	13	13.5	7.5	36.2	120	2.3
	14	15.7	6.2	36.7	122	5.2
	16	11.4	5.3	41.7	115	2.3
	19	12.7	6.2	42.3	112	4.3
4. Head of Lakes	7	13.2	7.2	37.8	121	4.0
	8	12.4	7.5	35.3	124	4.0
	32	11.4	7.0	39.5	123	2.8
	35	13.0	6.2	39.8	108	3.5
5. Northern Upper Pen-insula of Michigan	20	14.7	6.0	40.0	109	5.2
	28	14.0	5.8	39.2	118	2.8
	30	12.2	5.8	41.2	120	3.7
	31	11.9	6.3	39.5	118	3.5
6. North-eastern Wisconsin Southern Upper Peninsula of Michigan	6	13.7	6.7	35.5	112	5.2
	18	11.6	7.0	42.0	115	5.3
	21	13.7	5.5	38.3	109	2.5
	22	11.6	5.8	39.7	117	2.8
7. Central Wisconsin	9	13.5	6.3	38.2	118	4.0
	10	15.0	7.5	38.7	112	4.3
	11	15.7	8.3	39.8	114	5.8
	17	13.7	7.5	38.5	116	3.2
8. Lower Michigan	33	11.9	7.3	43.7	126	5.0
	34	12.4	6.5	39.5	124	5.2
	—	11.7	7.2	39.8	120	4.5
	—	12.4	6.0	40.0	125	5.0
9. Eastern United States	1	16.5	6.7	39.2	125	6.8
	2	14.2	7.0	45.3	118	2.7
	3	13.2	5.5	36.3	117	4.7
	29	12.4	6.3	39.8	120	2.0
Analysis of Variance						
Source of Variation	d. f.					
Regions	8	NS	NS	NS	NS	NS
Trees in Regions	27					

Table I — 3: — Needle Characters, Maple, Ontario. Averages of five needles per tree.

Region of Origin	Clone No.	Needle Length, cm	Stomata No. Rows	Serrations No./cm.	Stomata No./cm.	Resin Canals No.
Nova Scotia	127	8.2	7.4	43.0	130	5.4
	128	9.7	7.2	48.4	136	5.8
	154	12.7	8.2	41.4	125	4.4
	135	12.3	10.0	40.2	121	5.2
	136	13.4	10.4	44.6	132	6.8
New Brunswick	137	9.9	8.0	44.8	144	6.6
	138	9.8	8.8	43.8	129	6.6
	140	12.4	9.6	37.8	122	7.0
	141	11.8	10.0	42.0	126	7.0
	142	12.8	10.0	43.6	123	7.6
S. E. Ontario	98	12.2	8.4	40.6	132	8.2
	99	13.2	9.8	41.2	126	6.2
	100	10.3	9.2	43.2	133	7.0
	101	13.7	9.2	38.2	119	7.4
	102	11.0	6.2	34.4	122	6.8
S. W. Ontario	96	10.4	9.2	45.5	127	7.0
	120	12.2	10.8	42.2	128	8.2
	121	5.9	5.2	47.8	131	5.8
	123	11.6	9.0	43.4	125	6.4
	124	11.8	10.0	47.2	125	7.0
Central Ontario	2	5.7	6.6	44.6	132	5.0
	5	12.3	8.8	33.6	125	6.8
	368	11.2	10.2	33.4	131	6.0
	369	9.5	9.0	31.6	128	5.6
	370	10.6	11.0	39.0	127	6.6
Northern Ontario	174	12.9	9.0	37.6	126	7.2
	175	11.6	9.0	42.0	124	7.0
	177	11.7	8.6	33.8	126	7.6
	178	10.6	7.4	33.8	138	6.2
	199	9.5	8.4	44.8	120	5.0
N. Central Ontario	201	13.2	8.6	40.0	123	7.8
	202	11.8	8.8	34.4	125	8.2
	203	11.7	10.8	36.0	121	7.6
	204	11.7	8.2	37.6	123	7.4
	205	9.9	6.0	37.6	127	5.2
Manitoba	144	14.3	7.8	40.2	126	7.2
	145	13.2	8.6	39.8	119	7.4
	147	12.8	8.2	36.4	120	7.0
	149	14.7	8.4	37.8	126	6.8
	151	12.8	8.4	43.8	131	7.2
Analysis of Variance						
Source of Variation	d. f.					
Regions	7	NS	NS	**	NS	**
Clones in Regions	32					

Hough (1952 b) presented the weight per thousand seeds of each of the seed lots comprising the Kane provenance test plantation. The relationship of these original seed weights and the weight of seed produced by the trees of corresponding origins at Kane was examined. The regression of progeny seed weights (Kane) on original seed weights was found to be non-significant ($F = .396$, $F_{.05} = .415$). The data are presented graphically in *Figure I — 4.*

Discussion and Conclusions

It is evident from the review of the literature on natural variation in red pine, as well as from the data obtained in this study that genetic variation is present in red pine among trees of different geographic origins. It is also evident that the magnitude of this genetic variation is low. None of the characters examined in this study, nor in other studies, revealed differences that could be used to distinguish trees of different origins.

It is likely that the differences found in number of serrations and number of resin canals between the needles of trees of different origins represent differences in the genetic components of these trees. The differences do not appear to be related to latitude, longitude or any obvious climatic factor of the place of origin. They are random in regard to geographic origin and may result from a chance distribution of different genes in these populations.

Hough (1952 b) found a significant correlation between seed source and seed weight in red pine. Rudolf (1947) reported a general tendency of northern provenances to produce smaller seed than southern ones. In both studies, the seed was collected from trees growing in their natural environment and the seed weight was probably influenced by these environments. In this study, the original latitude of the provenances and seed weight were not found to be significantly correlated. These seeds were obtained from trees of different origins growing in a relatively similar environment. The parent-progeny seed weight correlation

Table I — 4: — Cone, Seed, Germination and Seedling Characters, Kane, Penna. Table of Averages.

Latitude of Origin	Tree number	Region	Cone Length, cm.	Seeds/Cone Number	Full seed percent	Seed Weight, mg.	Germination percent	Number days to Germinate	Cotyledon number	Hypocotyl Length
42.7	1	9	3.4	22.0	73.6	9.8	95.6	21.0	6.5	31.9
42.7	2	9	3.4	25.8	86.0	8.2	89.9	23.1	6.5	29.9
42.7	3	9	2.8	5.9	58.5	9.8	91.3	30.2	6.6	31.5
42.7	29	9	4.4	62.7	73.4	9.8	96.7	18.9	6.4	32.3
43.6	9	7	3.7	15.9	69.2	10.1	90.6	27.7	6.4	29.8
43.6	10	7	4.1	21.0	81.0	8.7	93.5	20.1	6.4	29.2
43.6	11	7	3.6	10.3	82.9	10.1	97.4	22.7	6.8	31.1
43.6	17	7	4.3	12.4	89.2	12.3	94.4	22.7	7.0	33.3
44.3	33	8	3.9	20.1	68.3	10.5	84.3	25.6	6.4	33.1
44.6	34	8	3.9	21.8	60.5	9.6	96.7	26.1	6 5	31.8
45.4	23	2	3.1	20.0	64.0	8.1	91.5	25.0	6.4	28.1
45.4	36	2	3.1	21.4	71.9	6.6	91.7	26.4	6 0	27.3
45.5	22	6	4.3	24.3	82.5	11.7	87.7	24.5	6.8	36.0
45.9	25	6	3.7	20.3	82.0	11.5	90.0	22.9	6.4	34.5
45.9	26	6	3.4	23.0	84.8	8.9	73.7	29.0	6 3	32.3
46.0	6	6	4.3	20.0	80.0	10.6	87.5	24.7	6.3	33.6
46.0	18	6	4.1	25.0	73.6	9.8	89.2	27.1	6.5	32.4
46.1	27	2	4.4	31.0	92.3	10.2	95.9	20.5	6.4	33.1
46.4	20	5	3.9	13 0	76.9	10.2	80.0	32.3	6.6	30.0
46.4	28	5	3.8	30.0	89 3	9.3	94.4	26.6	6.3	31.6
46.4	30	5	3.5	25.2	81.9	9.1	93.6	23.3	6.2	30.0
46.4	31	5	2.1	15.0	73.3	8.1	81.8	28.2	7.0	27.5
46.4	21	6	3.3	13.1	61.9	8.9	95.1	23.1	6.5	27.7
46.5	7	4	3.9	20.0	60 0	9.1	87.5	27.2	6.4	32.9
46.5	8	4	3.4	8.0	56.3	9.1	88.9	24.8	6.3	29 0
46 5	32	4	4.2	14.6	81.2	9.8	82.8	26.7	6.4	33.2
46.5	35	4	3.2	12.2	70.5	8.5	90.3	21.9	6.5	31.6
47.2	4	1	3.4	14.5	70.0	8.2	100.0	21.8	6 2	28.6
47.5	24	1	2.9	13.7	65.0	7.6	95.8	26.1	6.2	28.5
47.5	13	3	3.7	4 0	75.0	8.3	33.3	26.0	6 0	35.0
47.5	14	3	4.2	31.0	22.6	8.9	85.7	34 6	6.2	30.6
47.5	16	3	3.6	25 9	55.1	8.7	76.3	20.9	6 2	32.5
47.5	19	3	3.6	22.0	28.4	9.8	87.5	27.4	6 3	31.6
47.6	12	1	2.9	6.0	83.3	9.2	100.0	21.4	6.4	29.4

was also found to be non-significant. It is evident then that the correlation reported by Hough (1952 b) resulted largely from environmental causes rather than from genetic ones and that the heritability of seed weight in red pine is low.

Of the eight cone, seed, germination and seedling characters examined in this study, only the number of cotyledons was found to be correlated with the original latitude of the provenances. Seedlings of northern provenances had fewer cotyledons than those of southern provenances. It is probable that red pine seedlings have an optimum number of cotyledons and that this number is smaller in the northern than in the southern part of the species range. The reason for this difference is obscure.

It is concluded that genetic difference between trees of different origins exist in red pine, but that the magnitude of these differences is small. The species is extremely uniform throughout its entire range, and there is no evidence of sub-species, varieties, or forms having developed.

Acknowledgements

The writer wishes to acknowledge the counsel of Dr. F. Mergen of the Yale School of Forestry and Dr. C. Heimburger of the Ontario Department of Lands and Forests. Assistance in analysing portions of the data was rendered by Mr. T. W. Dwight of the Ontario Department of Lands and Forests.

Grateful acknowledgment is made to Mrs. E. Creed, Miss. J. Robinson, Mr. N. McLeod, Mr. G. H. Saul and Miss. S. Hewitt for assistance with various aspects of this study. Thanks are also due to Mr. A. F. Hough, Mr. T. C. Grisez and Mr. H. Huntzinger of the U. S. Forest Service for making the Kane Provenance Test Plantation available to the writer.

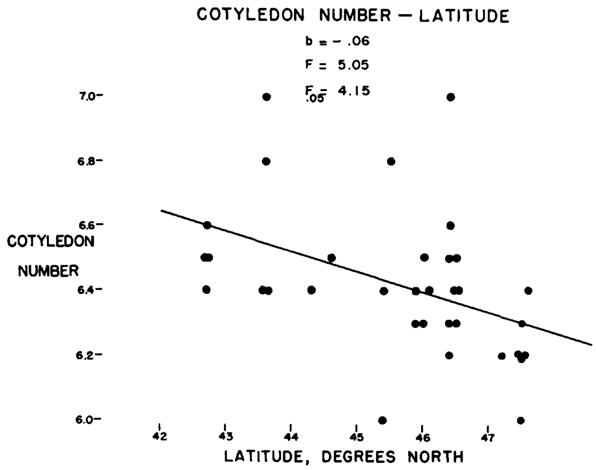

Figure I — 3: — Regression of cotyledon numbers on latitude of origins.

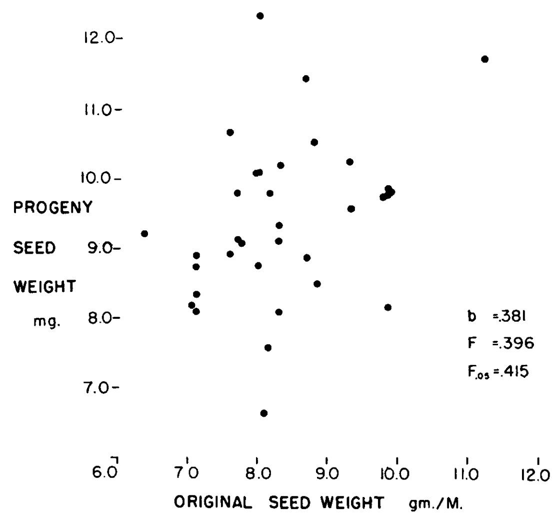

Figure I — 4: — Regression of progeny seed weight on original seed weight.

Summary

Needles from 36 red pine trees grown in a provenance test at Kane, Pennsylvania and representing nine climatic regions were examined. Needles were also examined from 40 grafted clones of red pine growing at Maple, Ontario and representing eight different geographic regions. Five needle characters were studied: needle length, number of rows of stomata, number of stomata per centimeter, number of serrations per centimeter and number of resin canals. In the clonal materials, serrations per centimeter and number of resin canals differed significantly between regions.

Cone length, number of seeds per cone, percent full seed, seed weight, percent germination, number of days to germinate, cotyledon number and hypocotyl length were examined on cones, seeds and seedlings from 34 trees grown in a provenance test at Kane, Pennsylvania and representing nine climatic regions. Of the eight characters examined, only cotyledon number was found to be significantly related to original latitude of the provenances. Trees of southern origins produced seedlings with more numerous cotyledons than trees of northern origins.

The parent-progeny seed weight correlation of the 34 trees at Kane, Pennsylvania was found to be non-significant and it was concluded that the heritability of seed weight in red pine is low.

Résumé

Titre de l'article: *Effets de la consanguinité chez Pinus resinosa Ait.*

L'Auteur a examiné les aiguilles de 36 *Pinus resinosa* poussant dans une plantation comparative de provenances à Kane, Pennsylvanie, et représentant neuf régions climatiques. On a également étudié les aiguilles de 40 clones greffés poussant à Maple, Ontario, et représentant huit régions géographiques différentes. Cinq caractères de l'aiguille ont été étudiés: longueur, nombre de rangées de stomates, nombre de stomates par centimètre, nombre de dents par centimètre et nombre de canaux résinifères. Dans les clones, les dents par centimètre et le nombre de canaux résinifères diffèrent de façon significative suivant les régions.

Sur les cônes, les graines et les semis provenant de 34 arbres poussant dans la plantation comparative de Kane, on a étudié les caractères suivants: longueur du cône, nombre de graines par cône, pourcentage de graines pleines, poids des graines, pourcentage de germination, nombre de jours nécessaires à la germination, nombre de cotylédons et longueur de l'hypocotyle. Sur les huit caractères étudiés, seul le nombre de cotylédons est lié de façon significative à la latitude d'origine des provenances. Les arbres des origines méridionales produisent des semis comportant plus de cotylédons que les arbres des origines septentrionales.

La corrélation parent-descendant pour le poids des graines sur les 34 arbres de Kane s'est révélée non significative et l'on conclut que l'héritabilité du poids des graines pour cette espèce est faible.

Zusammenfassung

Titel der Arbeit: *Effekte von Inzüchtung bei Pinus resinosa.*

Die Nadeln von 36 Bäumen aus einem Provenienzversuch in Kane, Pennsylvanien, die 9 Klima-Regionen repräsentierten, wurden untersucht. Ebenso wurden auch die Nadeln von 40 Pfropfklonen dieser Kiefer von Maple, Ontario, untersucht, die aus 8 verschiedenen geographischen Regionen stammten. 5 Nadelmerkmale waren geprüft worden: Nadellänge, Anzahl der Stomata-Reihen, Anzahl der Stomata je cm, Anzahl der Zähne je cm und Anzahl der Harzkanäle. Die Klone der verschiedenen Regionen unterschieden sich signifikant in der Anzahl der Zähne je cm und der Anzahl der Harzkanäle.

Zapfenlänge, Samenzahl je Zapfen, Vollkornprozent, Samengewicht, Keimprozent, Anzahl Tage bis zur Keimung, Kotyledonenzahl und Hypokotyllänge wurden bei den Zapfen, Samen bzw. Sämlingen von 34 Bäumen aus dem Provenienzversuch von Kane, Pennsylvanien, geprüft, die ihrerseits wieder 9 Klima-Regionen repräsentiert haben. Von diesen 8 Merkmalen stand nur die Kotyledonenzahl mit den Breitegraden der Provenienzen in Beziehung. Die Bäume südlicher Herkünfte produzierten Sämlinge mit zahlreicheren Kotyledonen als die der nördlichen.

Die Elter-Nachkommenschafts-Korrelation beim Samengewicht von 34 Bäumen von Kane war nicht signifikant, und es wurde daraus geschlossen, daß die Heritabilität des Samengewichtes bei *Pinus resinosa* gering ist.

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