Genecology of Larix laricina (Du Roi) K. Koch in Wisconsin

I. Patterns of Natural Variation[1]

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(Received for publication April 18, 1968)

Introduction

Genecology was originally defined by Turesson (1923) as the study of the natural variation of plants in relation to the environment. Turesson's early publications clearly indicated that genecological studies required a synthesis of genetic, ecologic, and taxonomic approaches (Heslop-Harrison, 1964). Heslop-Harrison stated that genecology can merge into taxonomy when primary aims are to classify patterns of intraspecific variation, into physiology when physical responses of an organism to the environment are of interest, and into genetics when the mechanisms of variation and selection are objectives of study. It is primarily the latter of these genecological approaches that concerns the present study, the general objective of which was to elucidate the patterns of natural variation of tamarack (Larix laricina [Dc Roi] K. Koch) in Wisconsin.

The distribution of tamarack in Wisconsin and the environmental features of the state combine to present rather unique posibilities for genetic differentiation among populations. Even though the southern boundary of the transcontinental range of tamarack occurs in southern Wisconsin (Roe, 1957), the distribution in Wisconsin, as shown in *Figure 1,* is marked by two patterns. Tamarack is ubiquitous in the north, but as the southern limits of distribution are reached, tamarack stands become sporadic geographically and occur as rather small, semi-isolated populations. It should be noted that the distribution of tamarack shown in Figure 1 for northern Wisconsin does not represent an intensive survey. General patterns of distribution were taken from Curtis (1959) who presented only extensive areas of occupancy. The ubiquity of tamarack in northern Wisconsin thus is much greater than indicated in the figure. By contrast, distributional patterns in southern Wisconsin represent an intensive survey conducted by Hansen (1933) and supplemented by the present author.

Glaciation and steep climatic gradients have a profound effect on environmental features of Wisconsin. The state is divided into two floristic provinces, the southern prairie-forest province and the northern cunifer-hardwood province, by a tension zone (Figure 1) which bisects Wisconsin from the northwest to the southeast (Curtis, 1959). This zone, corresponding to the average southern limit of the cool northern air mass, is from 10 to 30 miles wide, and across it nine precipitation and temperature factors vary significantly (Curtis, 1959). On the basis of microfossil evidence, Curtis believed that the tension zone has existed for about 10,000 years, although its exact position has varied.

Glacial action resulted in the subdivision of Wisconsin into two geologic provinces, delimited by topography and age. The southwestern quarter of the state, the Driftless Area (Figure *1),* was glaciated at least 15,000 years earlier than the remainder of the state (Frye, et *al.,* 1965). Whereas relatively rugged topography survived light glacial action in the Driftless Area, the rest of the state was planed by severe and repeated glaciations and was last entirely covered by the Cary ice sheet, 14,000 to 16,000 years ago (Frye, et *al.,* 1965).

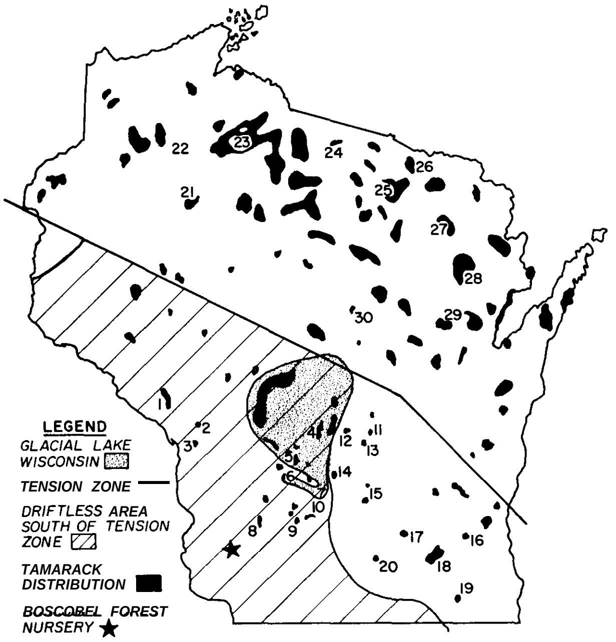

Figure 1. — Map of Wisconsin illustrating the general distribution of tamarack, geographic subdivisions, and stands (numbers) represented in open-pollinated collections. Scale: 1 inch = approximately 110 miles.

Despite differences in age between geologic provinces, the swamp or bog habitats for which tamarack is suited were established at approximately the same time in both provinces. Meltwaters from the Cary ice drained, in part, through the Driftless Area and resulted in deposition of approximately 100 feet of till in major river beds (Martin, 1932). Tributary rivers were thus dammed at their mouths and were forced to aggrade their beds and rapidly fill their valleys; the result was swamp habitats of two types; headwater lakes and oxbow lakes of the newly meandering streams (Hansbn, 1933). In the rest of Wisconsin, swamps arose in the numerous depressions and flood plains associated with severe glacial action (Martin, 1932). Therefore, the maximal age of swamps in the Driftless Area is mid-Cary, whereas that of swamps in southeastern Wisconsin is early post-Cary.

Environmentally, Wisconsin is divided into three geographic areas (Figure *1):* drifted northern Wisconsin above the tension zone, drifted southeastern Wisconsin below the tension zone, and the Driftless Area of southwestern Wisconsin which is also below the tension zone. In the remainder of this paper these three areas will be referred to as the north, southeast, and Driftless Area. The different climatic conditions north and south of the tension zone and

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[1] This paper is part of a Ph. D. dissertation prepared at the University of Wisconsin under the direction of D. T. Lester and O. L. Loucks. Approved for publication by the Director of the Wisconsin Agricultural Experiment Station. Financial support by the University of Wisconsin is gratefully acknowledged.

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between glaciated and relatively unglaciated terrain might be associated with greatly different selective pressures, from which genetic differentiation of populations among geographic areas might have resulted. Moreover, southern populations of typically boreal species, such as tamarack, might represent relics of early postglacial forests (CURTIS, 1959). Thus, the maximum possible time span of existence of outlying tamarack populations in southern Wisconsin makes possible genetic differentiation through either long exposure to rather constant selective forces associated with a given site or random genetic drift. Genetic drift might be of particular importance in the relatively small populations of the Driftless Area.

The objective of the present study was to explore the possibilities of genetic differentiation within the gene pool of tamarack in Wisconsin. Additional emphasis was given the possibilities of selective differentiation and random genetic drift in populations of the Driftless Area. In a subsequent paper the ecological relationships between tamarack communities in Wisconsin and the implications of genetic and ecological data on the paleoecological status of tamarack in southern Wisconsin will be considered.

Materials and Methods

Genetic diversity was studied in seedlings from open and controlled pollinations. Open-pollinated collections were used to assess the structure of the gene pool of tamarack in Wisconsin. Controlled pollinations were made to determine the degree of genetic differentiation between several outlying populations in southern Wisconsin.

Open-pollinated Materials

Open-pollinated cones were collected in 1964 from 30 tamarack populations *(Figure 1)*. Ten of the sample stands were located in northern Wisconsin, 12 stands were in southeastern Wisconsin, and eight stands were in the Driftless Area. Although stands 4 and 5 are located within the boundaries of the Driftless Area, they are also located in the basin of glacial Lake Wisconsin, which was in existence in post-Cary times. In terms of environment and age, these populations resemble stands located on Cary drift, and, therefore, they were included with the southeastern populations. Stands 6 and 7 are within the Baraboo River Basin, which was part of glacial Lake Wisconsin. Although the sites on which these stands are located cannot differ in age from those of southeastern Wisconsin, in terms of the surrounding topography and origin (oxbow lakes), these sites have a greater environmental similarity to those of the Driftless Area than to sites of the southeast. Therefore, these stands were considered as representatives of the Driftless Area. It will be seen later that the geographical classification of these stands had no effect on the results and interpretation of analyses.

Cones were collected from five to ten trees in each seed source. In order to obtain an unbiased but representative sample, trees were chosen at random within different parts of each stand. Seeds were sown in a randomized complete block design with five replicates in both northern and southern forest nurseries. Seed sources were nested within geographic areas; geographic areas and seed sources within areas were randomized in each replicate.

The entire northern planting and much of the southern planting (located at the Boscobel State Forest Nursery, *Figure 1)* were lost to fungal attacks, presumably damping off. In order to obtain a balanced design in the southern planting, seedlings were transplanted between replicates early in the first growing season. Transplanting necessitated elimination of one replicate. Minor additional losses of seedlings occurred as a result of frost heaving and root rot. After two seasons of growth, there remained in the southern nursery four replicates of each of the 30 stands; each stand was represented by approximately seven seedlings in each replicate, although three plots contained no seedlings.

For each seedling, first- and second-year height were measured, and the date of bud set and pattern of root development were scored. Seedling heights were measured to the nearest half-centimeter after internodal elongation had ceased. Date of bud set was defined as the date when bud scales were first observed. These data were scored semiweekly in the second growing season. The pattern of root development was scored after the seedlings were lifted from the nursery, and scoring was based on a scale of one to ten for increasingly horizontal patterns of root development.

Statistical analyses included an analysis of variance for date of bud set and pattern of root development and an analysis of covariance of total height on first-year height. The covariance analysis was used to adjust total height for non-genetic influences such as differential transplanting shock, severity of fungal attacks, and seed weight. For all analyses, the method of unweighted means for unequal subclass numbers was used after missing data were estimated (SNEDECOR, 1959).

Correlation analyses were also made to determine the relationship between the date of bud set and the frost-free period of the seed origin. Data on approximate frost-free period were obtained from longterm averages of weather stations (ANONYMOUS, 1956).

Control-pollinated Materials

Controlled pollinations were made in 1964 and 1966. The 1964 pollinations consisted of reciprocal population crosses, and the 1966 pollinations included intra-population crosses.

1964 Reciprocal Population Crosses: —

Reciprocal pollinations were made between five populations (numbers 51 to 55, *Figure 2)*, four of which were in the Driftless Area. The Driftless Area populations are located within three drainage systems. Stand 55 is on an oxbow lake of the Pine River; stand 51 is in a headwater lake of the north branch of Honey Creek; and populations 52 and 53 are located along tributary streams in the upper Baraboo River System. Stand 52 is in an oxbow lake-headwater lake complex, and stand 53 is located in a spring-fed upper watershed of the Baraboo System. Although population 53 is now represented by only five trees, inhabitants of that area relate the existence of additional trees in the immediate area. Population 54 is located in the basin of Lake Wisconsin. This stand is considered genetically representative of the contemporary tamarack gene pool of Wisconsin because tamarack is common in the area today and the earliest time at which the site was available for occupancy by tamarack corresponds more closely to sites of the southeast than to sites of the Driftless Area.

Pollen mixtures representative of each population were applied to strobili of 5, 2, 4, 5, and 3 trees in populations 51 to 55, respectively. Each pollen mixture contained pollen from 5 to 15 non-maternal trees. In addition to progeny from one intra-population and four inter-population crosses, selfed progeny were also obtained from each maternal

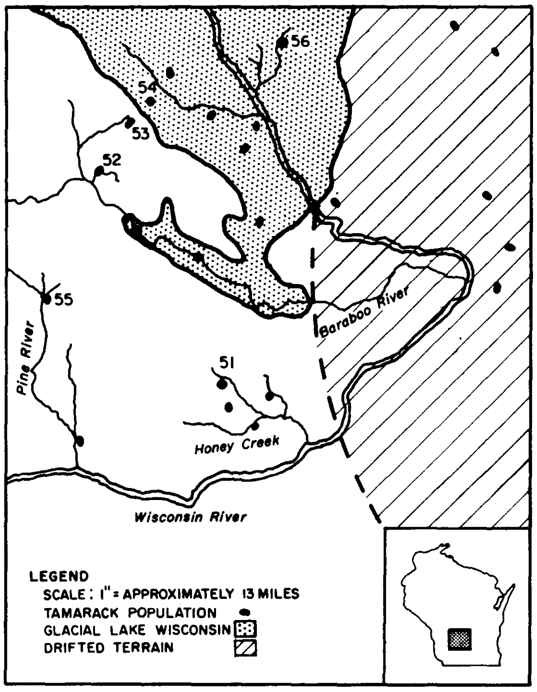

Figure 2. — Map of a portion of south-central Wisconsin showing drainage patterns, tamarack distribution, and maternal populations used in the control pollinations.

tree. In stand 53, three of the five trees were separated by about 30 yards from the two other trees, and to prevent selfing, intra-population crosses consisted of reciprocal crosses between the two groups. Pollen from the two groups was mixed for use in other populations.

Cones were collected in August, and seeds were extracted and stratified for about four months. In April, 1955, seeds were sown in pots which were arranged in a randomized complete block design with four replicates in a greenhouse. Although each cross was represented by a substantial number of seeds, fungal attacks severely reduced the number of seedlings. At the end of two years of growth, most population crosses were represented by 12 seedlings. Not all maternal trees were represented by progeny from each pollination in all replicates.

In November, after the first season of growth, pots were placed outdoors for the duration of the winter. They were returned to the greenhouse in the spring. Due to lack of greenhouse space, one replicate was placed in an adjoining greenhouse in which temperatures were not under control, and high temperature occurred early in the growing season. Seedlings in this replicate ceased growth early. After being transferred to a cooler greenhouse, seedlings of this replicate produced lammas shoots.

For each seedling, first- and second-year heights were measured, and the date of terminal bud set was scored. Date of bud set for seedlings in the replicate which was exposed to the high temperatures was not recorded because inequalities in the time of initiation and cessation of lammas growth precluded estimates of the termination of growth. Similarly, the 14 seedlings with lammas growth in other replicates were not scored.

Analyses of covariance of total height on first-year height and analyses of variance for date of bud set were used. For both height and date of bud set, analyses were performed to determine differentiation between pollen mixtures, maternal populations, and trees within populations; separate analyses were required because each tree was not represented by progeny from each pollen mixture in all replicates. The method of unweighted means for unequal subclass numbers (SNEDECOR, 1959) was used for all analyses.

1966 Intra-population Crosses: —

Of the selfed families obtained from the 1964 crosses, only population 55 was represented by an adequate number of seedlings for statistical treatment. Additional crossing was required for comparing progeny of self, inter-population, and intra-population pollinations. In 1966 three trees were pollinated within populations 51, 55 and 56 *(Figure 2)*; the latter population, similar to stand 54, is located in the basin of Lake Wisconsin. Self, intra-population, and inter-population crosses were made on each tree. Pollen for the inter-population crosses of trees in stands 51 and 55 was representative of stands 56; that used on trees of stand 56 came from stand 54. Rainy weather and low production of strobili reduced the effectiveness of pollinations. Lack of seed necessitated disregarding progenies of one tree in each stand.

Individual seed weights were obtained after the seeds had been brought to an equilibrium moisture content. In November, 1966, seeds were sown in pots which were placed at random on a greenhouse bench. Seedlings were grown under a 14-hour photoperiod. Although seeds had been stratified nearly 45 days, germination occurred over a 5-week period. To compensate for non-uniform germination, seedling heights were measured over a corresponding 5-week period, starting in mid-March, 1967. Each seedling, therefore, was measured approximately four months after emergence. At this time each maternal tree was represented by approximately nine seedlings for the pollinations from which adequate seeds were available. A hierarchial design of populations, maternal trees within populations, and pollinations within maternal trees was used. The method of unweighted means (SNEDECOR, 1959) was used in an analysis of covariance of first-year height on seed weight.

Results

Open-pollinated Materials

Results of the analyses of variance for date of bud set and pattern of root development and the analysis of covariance of total height on first-year height are given in *Table 1*. The means and DUNCAN's multiple range tests for geographic areas and seed sources within areas are presented in *Table 2*.

The analysis of variance for date of bud set indicates highly significant differences for all sources of variation. In addition to a continuous pattern of variation among seed sources within each geographic area, the multiple range tests indicate that, on the average, seed sources from northern Wisconsin set buds approximately one week earlier than those of the Driftless Area and southeastern Wisconsin, while no differences exist between mean dates for the latter two areas. The relationship between the mean date of bud set and the frost-free period of the seed origin is highly significant (r = .65) and is shown in *Figure 3*.

The analysis of the pattern of root development indicates a lack of differences among geographic areas, but highly significant differences among seed sources within areas. The latter, as shown by the multiple range tests, can be ascribed almost entirely to differences among seed sources

Table 1. — Summaries of analyses of variance for date of bud set and pattern of root development and the analysis of covariance of seedling height for open-pollinated progenies. Geographic areas are assumed to be fixed variates while replicates and seed sources within geographic areas are random. Means differing at a probability of .01 are indicated by **.

A. General form of the analyses

Source of Variation		Mean Square Code	Unweighted Components Expected in Each Mean Square	Coded Mean Square used for testing
Replication	(R)	1	$\sigma^2_E + \sigma^2_{RS,A} + \quad\quad + \sigma^2_R$	5
Geographic Areas	(A)	2	$\sigma^2_E + \sigma^2_{RS,A} + \sigma^2_{RA} + \sigma^2_{S,A} + \sigma^2_A$	4 + 3 — 5
Seed Sources within areas	(S,A)	3	$\sigma^2_E + \sigma^2_{RS,A} \quad\quad + \sigma^2_{S,A}$	5
R × A	(RA)	4	$\sigma^2_E + \sigma^2_{RS,A} + \sigma^2_{RA}$	5
R × S,A	(RS,A)	5	$\sigma^2_E + \sigma^2_{RS,A}$	6
Within	(E)	6	σ^2_E	

B. Results of analyses

Source of Variation	Analyses of Variance				Analysis of Covariance Total Height	
	Date of Bud Set		Root Pattern			
	d. f.	F	d. f.	F	d. f.	F
Replication	3	9.07**	3	1.22	3	1.51
Geographic Areas	2	8.44**	2	<1	2	<1
Seed Sources, A	27	2.79**	25	2.14**	27	3.34**
R × A	6	3.21**	6	1.76	6	1.33
R × S,A	81	1.90**	75	1.74**	81	1.23
Within	812		624		811	

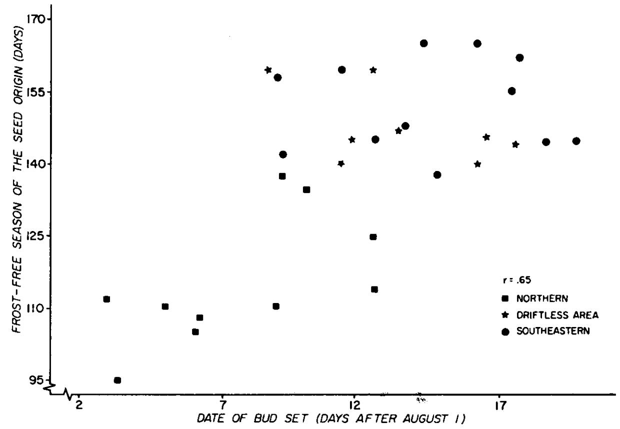

Figure 3. — Relationship between the frost-free period of the seed origin and the date of bud set of open-pollinated materials from the three geographic areas.

from southeastern Wisconsin. Variations in the pattern of root development for two seed sources are shown in *Figure 4*.

In the analysis of seedling height, the covariate, first-year height, accounted for 49 percent (r = .70) of the variation in total height. Highly significant differences among seed sources within geographic areas were indicated, but no differences were detected among geographic areas. As shown by the multiple range tests, the differences among seed sources are continuous between and within geographic areas.

Control-pollinated Materials

1964 Reciprocal Population Crosses: —

Since each maternal tree was not represented by progeny from each pollen mixture in all replicates, each statistical analysis required grouping of progenies in which at least one source of variation was disregarded. Three types of analyses were made for total height and date of bud set: (1) for assessing gross differences among pollen mixtures, maternal populations, and the various interactions involving these variables and replication; (2) for assessing differences among maternal trees within each population and the interaction with replication; and (3) for determining differences among types of pollinations (intra-population- inter-population and self for stand 55) for each population. In each

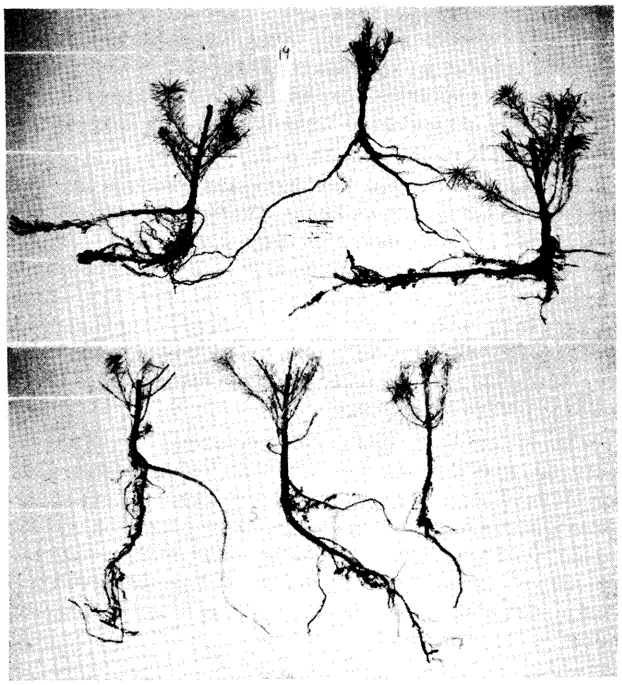

Figure 4. — Range of variation in pattern of root development within two seed sources, identified by numbers on stakes. Seedlings from source 19 had the shallowest mean pattern, whereas those from source 5 had the deepest. The markers are 7 inches long.

Table 2. — Duncan's multiple range tests of means of seedling height, date of bud set, and pattern of root development for geographic areas and seed sources within areas from the open-pollinated collections. Means not connected by the same line are significantly different with a probability of .05.

Pattern of root development (scores)		Date of bud set (days after August 1)		Adjusted total height (cm)	
A. Geographic Areas					
North	3.9	Southeast	14.1	North	31.2
Southeast	3.6	Driftless	13.1	Southeast	30.7
Driftless	3.5	North	7.5	Driftless	30.1
B. Seed Sources Within Areas					
		Driftless Area			
source	mean	source	mean	source	mean
2	4.3	10	17.2	1	33.4
1	4.1	7	16.0	7	31.9
6	3.9	6	15.7	6	30.6
7	3.8	1	13.0	3	30.2
8	3.4	2	12.1	10	30.1
3	3.1	9	11.4	2	29.6
10	3.0	8	11.0	8	28.9
9	2.9	3	8.4	9	27.9
		Southeast			
5	5.4	13	19.2	11	35.1
20	4.2	12	18.1	14	34.6
14	4.0	16	17.1	15	33.0
11	3.9	15	16.8	13	32.3
16	3.5	18	15.7	20	32.2
12	3.4	5	14.3	19	32.0
13	3.2	20	13.8	5	31.2
4	2.9	14	13.1	16	30.7
15	2.7	11	12.1	12	28.5
19	2.2	19	11.0	18	28.3
		4	9.0	4	27.0
		17	8.7	17	24.1
		North			
30	5.1	21	12.2	30	34.7
23	4.3	28	12.2	25	32.4
22	4.2	30	9.8	26	32.2
27	4.1	29	9.1	28	31.5
29	3.8	22	8.7	24	30.9
25	3.7	23	6.2	22	30.5
26	3.6	24	6.0	21	29.7
21	3.5	25	5.0	23	29.2
28	3.5	26	3.4	27	29.1
24	3.1	27	3.0	29	27.2

of these groups of analyses, the source of variation which was disregarded was that which either had no influence on the proposed tests or was shown to be insignificant in preceding analyses.

An outstanding feature of the statistical analyses of seedling height was the rather consistent effects of replication in nearly all analyses. This resulted from the poor performance of seedlings from the replicate which had been placed in the warm greenhouse; reduction in height of seedlings in this replicate averaged nearly 10 cm. A lack of significant effects of replication was noted in analyses for differences among progenies of maternal trees within three populations. However, it is uncertain whether the lack of replication effect was real or may have been a function of reduced degrees of freedom for the within-plot variance which resulted from the necessity of grouping progenies.

A second feature of the results of statistical analyses was nearly complete absence of significant differences for those sources of variation which pertain to natural variation. Only two differences of this nature were indicated: selfed progenies were significantly smaller than progenies of inter- and intra-population pollinations in population 55, and the date of bud set differed significantly between progenies of the two maternal trees from population 52. In addition, Duncan's multiple range test indicated minor differences in the height of seedlings from two maternal trees in stand 54. Yet, as illustrated in *Figure 5*, the range of variation in height within progenies was large, and mean differences between progenies within populations were substantial (maximum of 12 cm, in height and 16 days for bud set).

1966 Intra-population Crosses: —

In the analysis of covariance of first-year height on seed weight, the independent variable accounted for about 1 percent ($r = .08$) of the variability in seedling height. Statistical analyses indicated no differences among maternal populations, maternal parents within populations, or pollinations (self, intra-population, and inter-population) within maternal trees. Although the latter source of variation was statistically insignificant, comparisons of progeny means showed that selfed progenies were smaller than mean heights of progenies from inter- and intra-population crosses on the same parental tree. Average reduction in height of selfed progenies was small, being a maximum of 5 cm.

Three types of chlorophyll deficiencies were noted. These deficiencies included eight seedlings with mottled, pale-green cotyledons and green shoots, three seedlings with mottled, pale-green cotyledons and white shoots mottled with green, and one seedling with white cotyledons and a green shoot. These seedlings were dispersed among progenies of nine maternal parents and were represented in each type of pollination. In all but one case, seedlings deficient in chlorophyll in either cytoledons or shoots were smaller than the average normal seedlings from the corresponding cross. In the exceptional case, little difference in height was observed. Particularly noteworthy is the origin of the three seedlings with chlorophyll deficient shoots and two of the seedlings with pale-green cotyledons and green shoots. These resulted from intra-population crosses on individual trees in populations 55 and 51, respectively, and they indicate that at least two individuals in these stands carry alleles for the traits.

Discussion

The mode of origin and the age of the present tamarack populations in southern Wisconsin are relevant to interpretations of the present results. The infrequency of vegetative propagation by layering in the southern part of the range of tamarack (Duncan, 1954; Bannan, 1942) indicates that its reproduction is largely sexual. If, however, the present stands are descendents of individuals which occupied southern sites in mid- or early post-Cary times, asexual reproduction may have been common in the glacial climate. If layering occurred, it was either of limited extent or the resulting uniformity was negated by pollen or seed migration. The present results indicate no abrupt genetic differentiation between populations.

Increment borings indicated tree ages of about 65 years in population 55 and 50 years in stand 51. At approximately two feet in diameter, these trees are among the largest of this species in the state. Yet, their ages correspond to the

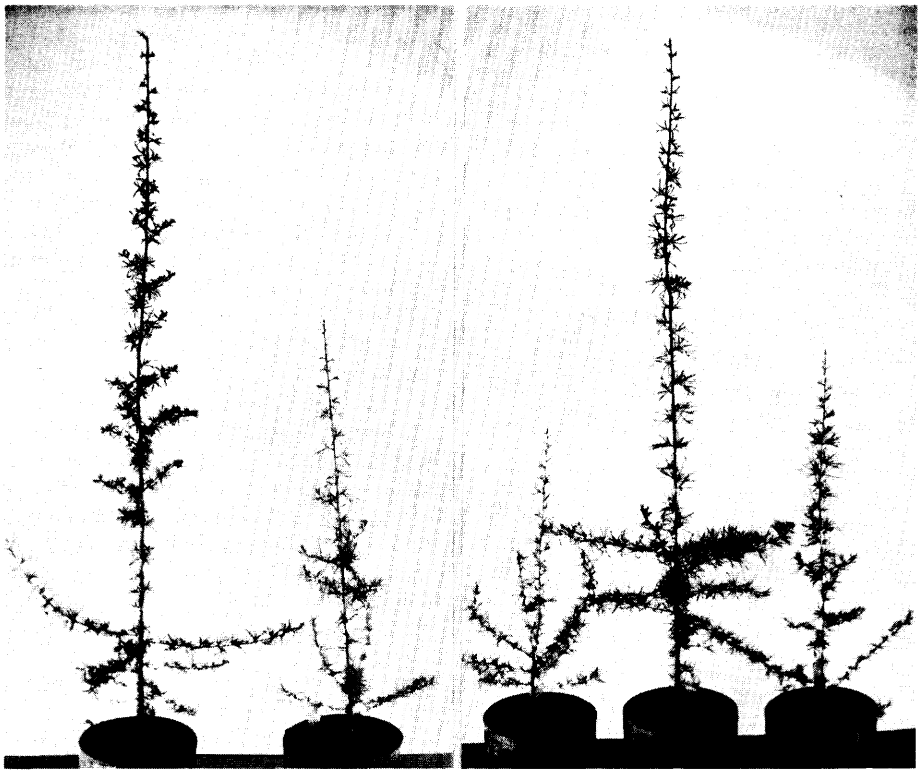

Figure 5. — Range of variation in seedling height within two control-pollinated progenies after two years of growth. None of these seedlings were in the replicate characterized by a reduction in elongation. — *Left:* progeny of 51-2 × 55; heights are 82 and 50 cm. — *Right:* The two seedlings on the right are progeny of 55-2 × 53. The seedlings on the left is a self from the same maternal tree. Heights are 36, 82, and 46 cm.

epidemic of the larch sawfly *(Pristiphora erichsonii* Hartig.) which occurred near the turn of the Twentieth Century and caused widespread destruction to tamarack in Wisconsin (Curtis, 1959). The present stands may have originated after stand destruction by the sawfly. However, since complete defoliation and stand demise require about seven years (Roe, 1957), it is probable that the present stands represent progenies from the previous stand rather than migrants from uninfested areas.

Open-pollinated Materials

The data *(Table 2)* indicated that a clinal pattern of variation exists among seed sources within geographic areas for total height, date of bud set, and pattern of root development. Although no differences among geographic areas were indicated for height and root pattern, statistically significant differences among geographic areas were found for date of bud set; northern seed sources appeared to be separated genetically from southeastern and Driftless Area sources. A discontinuous pattern of variation, however, cannot be deduced from data on date of bud set. *Figure 3* shows an unmistakably continuous relationship between the date of bud set and the frost-free period of the seed origin. Thus, differences between geographic areas in date of bud set result from geographic subdivisions which are perpendicular to the pattern of clinal response. Therefore, a clinal pattern of variation is evident for all three characteristics within and among geographic areas; the tamarack of Wisconsin is characterized by a single, heterogeneous gene pool, and differences between populations result from differential but overlapping heterozygosity.

The statistically significant effects of replication in the analysis of date of bud set and the significant interactions involving replication for both date of bud set and pattern of root development suggest that these variables are subject to modifications associated with microenvironmental differences at the planting site. Consequently, somewhat more objective measures of these variables appear desirable. Perhaps a quantitative measure of root depth with seedling height as a covariate would be appropriate for pattern of root development. Date of bud set, or termination of growth, could be best defined as a percentage of total elongation. Nevertheless, the consistency of differences between seed sources is pronounced with the present data.

A significant relationship ($r = .65$) was found between the date of bud set and the frost-free period of the seed origin. It is probable that an even better association would have been obtained with actual weather data from the bogs, instead of data from weather stations. Data from upland weather stations only approximate bog conditions (Rigg, 1947; Curtis, 1959). Furthermore, cold air drainage becomes more prominent with increasingly abrupt topography, and this could be responsible for a high proportion of the deviations from regression associated with sites of the Driftless Area *(Figure 3)*. Nevertheless, a wide range of frost-free periods (70 days) occurs in Wisconsin, and the associated variation in date of bud set is evident. Similar relationships across much broader geographic ranges have also been found for *Pinus sylvestris* L. (Langlet, 1936) and *Populus* species (Pauley and Perry, 1954).

Control-pollinated Materials

Statistical analyses of the 1964 reciprocal population crosses indicated no differences between maternal populations.

pollen mixtures, or trees within populations (except for date of bud set on progenies from maternal trees in stand 52). The apparent absence of differences among and within populations is further elucidated by data other than the statistical analyses. The range of variation within progenies of intra- and inter-population crosses *(Figure 5)* cannot be ascribed solely to environment. Moreover, neither intra- nor inter-population crosses produced uniform progeny. The inferior performance of selfed progeny as compared to progeny of intra- and inter-population crosses in stand 55 indicates an inbreeding depression, and combined with a lack of differences between progeny of inter- and intra-population crosses, genetic heterogeneity of each population is suggested. The conclusion is reached that individual trees and populations are highly variable genetically. Heterogeneous populations must contain individual trees which differ genetically. Differences between populations, as were observed with the open-pollinated materials, would then result from differential but overlapping heterozygosity.

Results of the 1966 intra-population crosses are also interpretable in terms of genetic heterogeneity. The occurrence of chlorophyll deficient seedlings from both intra- and inter-population crosses suggests genetic heterogeneity within and among populations. Anomalous results, however, stem from the failure to demonstrate an inbreeding depression for 1966 materials after one growing season. Homozygosity of these populations is incompatible with the previous results. That dominant gene action is lacking is plausible, for Dieckert (1964) found no inbreeding depression with European larch *(Larix decidua* Mill). However, this conclusion would also be incompatible with previous observations. Population 55 was used in both assessment of inbreeding, and an inbreeding depression was evident for this population in the 1964 materials after two years of growth. It is therefore most probable that the mean reduction in height of inbred progenies from 1966 materials was real, but it was statistically undetectable after one season of growth.

The failure of statistical analyses to detect differences among progenies in both 1964 and 1966 materials is probably due to the location of substantial genetic variation in the within-plot variance. This is explainable through the use of pollen mixtures. Since the individual trees are heterogeneous, mixtures of pollen from 5 to 15 trees from each population evidently represented an extremely variable mixture. The application of this mixture to heterozygous trees apparently resulted in a highly variable range of progeny from each tree. Since subclass numbers were small, it is not surprising that differences among maternal trees and among populations could not be detected. Only in population 52 were differences between progenies from different maternal trees indicated. Since only two maternal trees within this stand were control-pollinated, progeny sizes for these parental trees were larger than those for maternal trees in other populations. Thus, it is probable that genetic differences exist between trees in other populations and possibly between populations.

The heterogeneous state of several Driftless Area populations has a significant bearing on the possibilities of selective differentiation and random genetic drift in the small, semi-isolated and possibly very old tamarack populations in southern Wisconsin. Present tamarack sites in southern Wisconsin may have supported this species for 15,000 years. Since maturity of tamarack commonly occurs near 150 years (Roe, 1957), and since the intolerance of this species necessitates even-aged reproduction after initial site occupancy, 15,000 years of existence implies 100 to 150 discrete generations. Consequently, differentiation could have resulted from genetic drift and/or long exposure to rather constant selective pressure associated with a given site.

Genetic drift involves genetic differentiation resulting from chance segregation in small populations. Wright (1940) has shown that the combined effects of population size (N), selection coefficient (s), and migration rate (m) can result in chance fixation in a high proportion of subpopulations if the products of 4Ns and 4Nm are small (about 1); if, however, these products are large (100) random variability is negligible. If it is assumed that $s = .01$, as suggested for quantitative traits by Wright (1931), and $m = .025$, as suggested by Wright (1962) for isolation distances of about 10 miles, then genetic drift could have been significant if the effective population size was about 100 individuals. This is not unreasonable for population 55, for it is located on a small oxbow lake and contains less than 300 individuals today.

Although homozygosity by means of selection and genetic drift is thus theoretically plausible for southern populations, the results of this study indicate a highly variable tamarack gene pool within which populations are connected by overlapping heterozygosity. Discontinuous patterns of variation and homozygosity were not apparent in either the control- and open-pollinated materials. Genetic continuity between populations and geographic areas was indicated. The potential genetic consequences that stem from long existence on the southern sites have not occurred.

There is the possibility that southern populations have been relatively isolated throughout postglacial times, but that differentiation and fixation have been negated by selection for heterozygosity. Because the size of founder populations was probably limited, 150 generations of selection for heterozygotes could result in locally coadapted gene pools (see Dobzhansky, 1955; Lerner, 1958). To defect differential coadaptation, progenies must be grown in highly contrasting environments. The experimental design prevented this test.

Heterozygosity might also have been maintained throughout postglacial times by variable selection pressures or migration by seed and pollen. Seeds may be carried over the Driftless Area escarpment from the central plain and deposited in streams which feed the oxbow lakes. Furthermore, the tamarack populations of Wisconsin are continuous geographically *(Figure 1)*, and only population 55 is apparently isolated by more than 10 miles. Pollen exchange between populations may be common. Moreover, pollen might be carried long distances in thermal shells (Lanner, 1965) and might induce massive hybridization which would greatly enrich local germplasms. Regardless of the alternatives, heterozygosity is evident in southern populations.

In addition to their relevance to patterns of natural variation, data from the 1966 intra-population crosses provide information of a physiologic nature. The lack of association between seed weight and first-year height was striking. In contrast to tamarack, associations between these variables have been found in *Pinus monticola* Dougl. (Hanover and Barnes, 1962) and *P. strobus* L. (Pauley, *et al.*, 1955). Seedlings of these pine species, however, are characterized by an endogenous pattern of first-year shoot growth (Watt and McGregor, 1963), whereas shoot growth of tamarack is more exogenous. Tamarack seeds are smaller and lighter, but first-year seedling growth is generally greater than in the pines. The smaller proportion of the variability in first-year height of tamarack which was attributable to seed weight thus may be a consequence of the pattern and extent of first-year elongation.

The height of seedlings with the various classes of chlorophyll deficiencies was shown to be slightly smaller than the mean height of normal progeny of the corresponding cross. Since mean heights of the normal seedlings included individual trees of smaller height than the deficient seedlings, the consistency of the results could be coincidental. It is also possible that cotyledons are quite active photosynthetically, and even if shoots are normal, slight chlorophyll deficiencies of cotyledons may permanently retard shoot elongation in the first growing season.

Acknowledgements

The author gratefully acknowledges critical review of the manuscript by R. T. Bingham, U. S. Forest Service, Moscow, Idaho; E. I. Roe, U. S. Forest Service, St. Paul, Minnesota; and H. Nienstaedt, U. S. Forest Service, Rhinelander, Wisconsin.

Summary

The genecology of tamarack *(Larix laricina* [Du Roi] K. Koch) in Wisconsin was studied from a genetic viewpoint, with interest in patterns of natural variation and selective forces acting on the gene pool. The possibilities for genetic differentiation within species found throughout Wisconsin stem from two sources. Since the state is subdivided into three natural geographic areas by climatic factors and glacial boundaries, differential selective pressures associated with environmental differences could be responsible for ecotypic differentiation among geographic areas. Moreover, in southern Wisconsin tamarack reaches its southern limit of distribution and occurs in rather small, semi-isolated stands; differentiation among these stands, which, due to glacial history, may be approximately 15,000 years of age, is possible through random genetic drift, with or without variable migration and/or selection.

Genetic diversity was studied in seedlings from open and controlled pollinations. Open-pollinated progenies from 30 stands located throughout the state demonstrated clinal patterns of variation for 2-year height, date of bud set, and patterns of root development. Although significant differences between northern and southern seed sources were indicated for the date of bud set, these differences resulted from geographic subdivisions which were perpendicular to the north-south axis of clinal variation. The clinal nature for this variable was indicated from the significant correlation between the date of bud set and frost-free period of the seed origin.

Reciprocal controlled pollinations were made among four Driftless Area and one central Wisconsin stand, and intrapopulation crosses were made in three populations. Statistical analyses of progenies indicated no differences among pollens, maternal populations and maternal trees within populations. The occurrence of chlorophyll deficient seedlings from inter- and intra-population crosses, the high degree of variability within progenies, and the inferior performance of selfed progeny as compared to progenies of intra- and inter-population crosses indicated genetic heterogeneity. The failure of statistical analyses to detect differences was traced to the use of pollen mixtures; pollen from five to 15 trees was combined for each population and evidently represented a highly heterogeneous mixture.

The results of these studies indicated that the gene pool for tamarack in Wisconsin is highly variable and unsegmented.

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