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Intraspecific Genetic Variation of *Quercus rubra* L., Northern Red Oak¹⁾

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(Received July 1980 / February 1981)

Summary

Growth and phenological characteristics of *Quercus rubra* L. indicated that intraspecific genetic variation is discontinuous with the exception of dormancy processes. Changes in growth rate likely reflects genetic differences among populations due to different site or climatic requirements. Variation in leaf flushing dates among populations may be due to different requirements in the prerequisite number of hours at cold temperatures to initiate spring growth.

Genetic controls of dormancy processes were selected for in response to photoperiod and temperature regimes. A high degree of winter leaf retention is prevalent in western populations. Rate of individual tree growth within a provenance can be predicted at an early age. Inherent growth potential is not associated with any of the phenological characteristics studied.

Key words: Northern red oak, *Quercus rubra*, genetic variation, provenance test, phenology.

Zusammenfassung

Wachstums- und phänologische Merkmale von Roteiche (*Quercus rubra* L.) zeigen, daß die intraspezifische genetische Variation, mit Ausnahme von Ruheprozessen, diskontinuierlich ist. Beschleunigung oder Unterdrückung des Wachstums spiegeln wahrscheinlich genetische Unterschiede zwischen Populationen infolge unterschiedlicher Standortansprüche wider. Variation zwischen Populationen in Blattaustriebsdaten mag auf unterschiedliche Voraussetzungen in der notwendigen Stundenzahl bei kühler Temperatur, die das Frühjahrswachstum initiieren zurückzuführen sein.

¹⁾ Published as Journal Paper No. 6039, Journal Series, Nebraska Agricultural Experiment Station. Research reported was conducted under Project 20–28.

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Eine genetische Kontrolle von Ruheprozessen als Reaktion auf photoperiodisches und Temperaturverhalten konnte durchgeführt werden. Ein hoher Grad an Beibehaltung der Winterbelaubung kann bei westlichen Populationen vorhergesehen werden. Die Wachstumsrate der Bäume kann bereits in einem frühen Alter vorausgesagt werden. Das inherente Wuchspotential steht mit keinem der untersuchten phänologischen Merkmale in Beziehung.

Introduction

Quercus rubra L., northern red oak, is native to North America with a range from the North Atlantic coast to the midwest prairies and slightly above the St. Lawrence River to near the Gulf Coast (Fig. 1). Northern red oak was classified into two subspecies, *Quercus borealis* (MICHX.) F. and *Quercus borealis maxima* (MARCH.) SARG., but these two forms are no longer recognized as separate taxa because of introgression and failure to breed true (LITTLE, 1953).

Little genetic research has been done with northern red oak because of the great number of years to reproductive

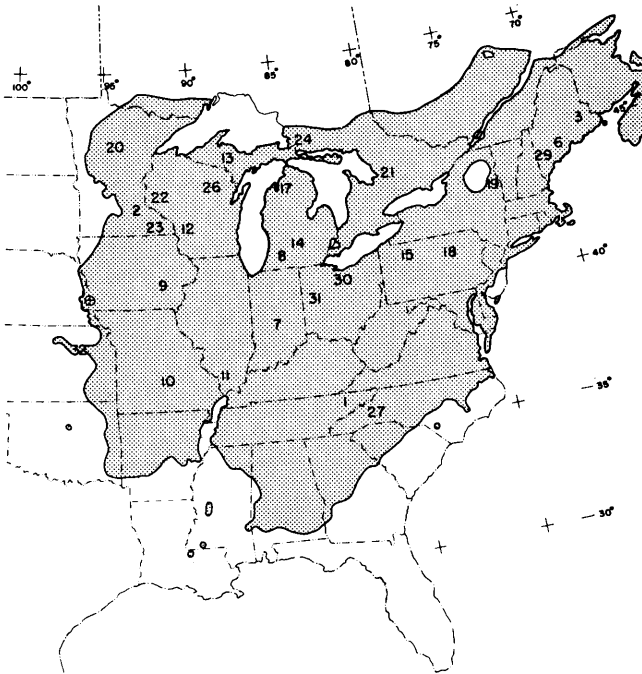


Figure 1. — Natural range of *Quercus rubra* L. with locations of provenances. The plantation location near Plattsmouth in eastern Nebraska is indicated by a circle

maturity and difficulties of vegetative propagation. Previous studies of *Quercus rubra* indicated that genetic variation is generally discontinuous (DENEKE, 1975; GALL and TAFT, 1973; KRAHL-URBAN, 1966; KRIEBEL, 1965; KRIEBEL *et al.*, 1976; SCHREINER and SANTAMOUR, 1961). There is evidence that trees from certain widespread geographic areas are genetically similar (KRIEBEL, *et al.*, 1976).

The objective of this study was to determine patterns of genetic variability by comparisons of growth and spring and fall phenological characteristics of various population samples.

Materials and Methods

This research was part of a regional tree improvement project of the North Central States Agricultural Experiment Stations (NC-99) under the leadership of Professor

HOWARD B. KRIEBEL, Ohio Agricultural Research and Development Center (KRIEBEL *et al.*, 1976). Each provenance collection consisted of open-pollinated progenies from up to ten mother trees (Fig. 1). All seed was collected from natural stands except provenance 31, a planting thought to consist of trees native to Ohio. One year old stock was planted over a three year period (1962—64) at Horning State Farm near Plattsmouth, Nebraska (41° 00' latitude, 95° 52' longitude, 305 meters elevation). KRIEBEL's design of 32 plots in seven randomized complete blocks was used. Each square plot consists of 16 trees spaced 2.75 by 2.75 meters. The Nebraska planting contains 28 provenances due to shortage of nursery stock. The four remaining plots were planted by direct seedlings of oak of unknown origin to avoid open spaces. Provenance 5 was not analyzed because of observed pin oak, *Quercus palustris* MUENCHH., characteristics in a majority of the trees.

Height, diameter (DBH), and spring and fall phenological observations were recorded and analyzed. Prior to analysis, it was observed that trees planted in 1964 were disproportionately smaller than trees planted in 1962 and 1963. To determine whether the 1964 trees, as a whole, were growing at a significantly lower rate than the 1962—3 trees, a split plot analysis of variance was conducted upon the pooled cumulative height and diameter growth means.

Growth data of populations planted in 1962 and 1963 were analyzed separately from 1964 populations. Height growth

Table 1. — Height growth between 1969-74.

a. Trees planted 1962-3

Year planted	Provenance	Growth (m)
1962	2	2.79
1963	12	2.71
1963	22	2.64
1963	23	2.55
1962	29	2.50
1962	1	2.48
1962	21	2.46
1963	9	2.44
1962	20	2.42
1962	11	2.34
1962	26	2.32
1963	10	2.21
1962	17	2.15
1962	19	2.11
1962	31	2.09
1962	3	1.95
1962	24	1.94
1962	13	1.90
1962	6	1.84
1962	7	1.81

b. Trees planted 1964

Provenance	Growth (m)
18	1.79
32	1.71
8	1.68
15	1.53
14	1.43
30	1.31
27	1.18

Lines connect means that are not significantly different according to the Student-Neuman-Keuls test, $\alpha = .05$.

during the period 1969—74 was calculated as a measure of tree growth during part of the plantation's life. Annual height and diameter growth were calculated by dividing the 1974 height and 1975 diameter by tree age.

Trees in four blocks were observed every two days in the spring of 1975 to determine date of leaf flush which was defined as the day when an estimated 50 percent of the buds had expanded to reveal small leaves. Phenological observations were made weekly from September 23 to November 18, 1975. Leaf fall color date was defined as the day when 25 percent or more of a tree's leaves changed from green color. When 75 percent or more of the leaves turned brown, they were recorded as dead. Leaf drop was scored as complete when a tree had lost 75 percent or more of its leaves. The tree was scored as having retained its leaves if 25 percent or more of the leaves were present on January 12, 1976. Comparisons among provenances were made of the periods measured in days between leaf flush and fall color for the 1975 season.

All variables were subjected to an analysis of variance conforming to the linear model for the randomized complete block design. The type I error level, $\alpha = .05$, was chosen for testing the significance of observed differences.

Student-Neuman-Keuls multiple range test (SNK) was utilized to separate the populations which were significantly different.

Simple correlation coefficients were calculated for cumulative growth measurements, growth rates, and spring and fall characteristics to show association among traits. Partial correlations involving provenance altitude were not calculated because elevations of sampled trees within a provenance varied as much as 238 meters.

Results and Discussion

Tables 1—8 illustrate variation patterns in growth and phenological characteristics.

Height of trees in the plantation in 1974 ranged from 2 to 9 meters with a mean plantation height of approximately 4.5 meters. Trees of provenances planted in 1962—63 grew significantly faster in height and diameter than trees of populations 8, 14, 15, 18, 27, 30, and 32 which were planted in 1964. Slow growth might have been caused by competing annuals which invaded after initial plantation preparation. However, it is possible that genetic factors could be respon-

Table 2. — Average annual height and diameter growth (DBH).

a. Trees planted 1962-3

<u>Height</u>			<u>Diameter</u>		
<u>Year planted</u>	<u>Provenance</u>	<u>Growth (m)</u>	<u>Year planted</u>	<u>Provenance</u>	<u>Growth (m)</u>
1962	2	.46	1962	2	.70
1963	22	.44	1962	31	.67
1962	1	.43	1962	7	.64
1963	12	.43	1962	19	.63
1962	11	.42	1962	1	.63
1963	9	.41	1963	22	.62
1962	31	.41	1962	21	.61
1963	10	.41	1962	29	.61
1962	19	.41	1962	11	.60
1962	7	.40	1963	9	.59
1962	21	.40	1962	3	.59
1962	29	.40	1963	12	.58
1962	20	.40	1962	20	.58
1962	26	.39	1963	23	.56
1963	23	.39	1962	26	.56
1962	17	.39	1962	6	.55
1962	3	.38	1963	10	.55
1962	6	.36	1962	17	.54
1962	24	.33	1962	24	.49
1962	13	.32	1962	13	.48

b. Trees planted 1964

<u>Height</u>		<u>Diameter</u>	
<u>Provenance</u>	<u>Growth (m)</u>	<u>Provenance</u>	<u>Growth (m)</u>
32	.31	32	.42
8	.30	18	.40
18	.29	8	.40
14	.29	14	.37
15	.27	15	.35
27	.25	27	.33
30	.23	30	.28

Lines connect means that are not significantly different according to the Student-Neuman-Keuls test, $\alpha .05$.

Table 3. — Elevations of provenances and leaf flush comparisons based on number of days between April 25, 1975 and date when 50 percent of leaf buds opened.

Elevation (m)	Provenance	Days
274	2	2.5
396	20	3.0
411-434	22	4.1
381-411	12	4.9
183-210	24	5.1
488	26	5.2
213-378	13	5.2
259-335	23	5.4
137-171	11	5.5
49-55	3	5.7
317-350	32	5.7
299-329	9	6.4
178-183	21	6.4
282-414	1	6.5
49-140	19	6.7
372-402	10	6.7
91	6	6.7
91	29	7.4
229-277	7	7.7
269	31	7.8
421	17	10.3
427	18	11.0
293	30	11.9
762-1006	27	12.4
253-265	8	13.7
354-396	15	14.2
265	14	14.8

Lines connect means that are not significantly different according to the Student-Neuman-Keuls test, $\alpha = .05$.

Table 5. — Percentage of trees retaining 25 percent or more leaves on January 12, 1975.

Provenance	Percent
2	55
23	53
12	51
32	47
9	29
18	12
3	11
22	10
19	10
8	5
20	5
29	5
6	5
17	4
30	3
14	3
24	2
27	2
11	2
31	2
21	2
10	2
15	0
1	0
13	0
26	0
7	0

Lines connect means that are not significantly different according to the Student-Neuman-Keuls test, $\alpha = .05$.

Table 4. — Comparison of fall leaf color, death, and drop based on number of days between September 23, 1975 and date of occurrence.

Color		Death		Drop	
Provenance	Days	Provenance	Days	Provenance	Days
20	10.2	20	18.4	20	24.7
13	13.0	13	23.3	13	28.8
26	13.6	26	24.3	26	29.4
24	14.9	24	27.1	24	34.7
32	15.4	22	29.2	22	35.8
3	17.3	2	29.4	3	39.5
30	17.4	32	30.8	29	41.0
2	17.4	23	31.0	6	41.1
27	17.6	3	31.2	32	41.9
22	17.6	9	33.4	30	42.0
14	17.8	6	34.4	23	42.1
15	18.1	12	34.7	9	42.2
9	18.4	29	34.9	15	42.7
23	18.5	27	36.6	14	43.0
6	19.3	8	36.8	17	43.1
11	20.0	30	36.8	2	43.2
8	20.3	19	37.1	8	43.4
29	20.5	14	37.1	27	43.7
19	20.9	21	37.5	21	44.5
18	21.1	17	37.7	12	44.8
17	21.9	31	38.8	31	44.8
12	22.1	15	38.8	19	45.8
10	22.4	11	38.8	11	46.1
31	22.5	18	41.1	10	47.1
21	22.6	10	41.7	18	47.3
7	28.7	7	43.3	7	50.0
1	29.5	1	47.4	1	51.5

Lines connect means that are not significantly different according to the Student-Neuman-Keuls test, $\alpha = .05$.

sible since all but two of the populations originated in a small area within the total range (Fig. 1).

The height growth between 1969—74 and average annual height and diameter growth rates were not associated with provenance latitude and longitude (Table 7). These non-significant correlations, coupled with the split plot analyses results and disjunctive patterns in the SNK tests (Tables 1—2), indicate that with respect to growth, *Q. rubra* is discontinuous in variation. This agrees with the conclusions of DENEKE (1975), GALL and TAFT (1975), KRIEBEL (1965), and KRIEBEL *et al.*, (1976).

High correlations of 1966 height with 1974 height ($r = 0.84$), 1975 DBH ($r = 0.87$), and average annual height and diameter growth ($r = 0.79$) and ($r = 0.84$), respectively, suggest that it might be possible to detect the fastest growing trees within a population at a very early age. Early detection of superior growing populations is not possible, however, as KRIEBEL *et al.*, (1976) found correlation coefficients were low for age comparisons of 1 versus 8 years and 1 versus 14 years. The correlations between cumulative growth measurements and diameter growth in 1975

Table 6. — Days between leaf flush and fall color for the 1975 growing season.

Provenance	Days
14	154.1
15	154.9
27	156.1
30	156.4
8	157.5
20	158.2
13	158.7
26	159.5
32	160.6
24	160.8
18	161.3
17	162.6
3	162.6
9	163.1
6	163.6
23	164.1
22	164.2
29	164.2
19	165.2
11	165.5
31	165.9
2	166.0
10	166.7
21	167.1
12	168.5
7	172.0
1	174.0

Lines connect means that are not significantly different according to the Student-Neuman-Keuls test, $\alpha = .05$.

(1975 DBH minus 1974 DBH) were low indicating that growth potential cannot be determined by growth in any one year.

Correlation of cumulative growth measurements with various growth rates generally showed progressively higher correlations as the trees grew older (Table 8). The correlation between 1966 height and 1969—74 height growth rate shows little association ($r = 0.38$), but the correlation 1974 height with 1969—74 height growth rate is relatively high, ($r = 0.74$). Inspection of Table 8 shows progressively higher

Table 7. — Partial correlation coefficients of tree characteristics and latitude and longitude.

Characteristic	Latitude	Longitude
Height growth between 1969-74 (1962-3 provenances)	.07	.33
Height growth between 1969-74 (1964 provenances)	.21	.21
Average annual height growth (1962-3 provenances)	-.39	.21
Average annual height growth (1964 provenances)	.67	.75
Average annual DBH growth (1962-3 provenances)	-.24	.20
Average annual DBH growth (1964 provenances)	.57	.64
Date of leaf flush	-.30	-.50*
Date of fall leaf color change	-.64*	-.15
Date of leaf death	-.81*	-.40
Date of leaf drop	-.78*	-.17
Percent of leaf retention on January 12	.09	.48*
Days between leaf flush and fall color	-.37	.24

* denotes significance at the $\alpha = .05$ error level

Table 8. — Correlation coefficients of characteristics studied. 1969-74 height and 1969-75 DBH are cumulative measurements. Height growth 1969-74 is the growth in height for that period.

	1966 ht.	1969 ht.	1972 ht.	1974 ht.	1969 DBH	1972 DBH	1975 DBH	Height growth 1969-74	Ave. annual height growth	Ave. annual DBH growth
1966 ht.	1.00	.97	.91	.84	.92	.90	.87	.38	.79	.84
1969 ht.	--	1.00	.93	.87	.92	.90	.88	.38	.82	.85
1972 ht.	--	--	1.00	.95	.84	.92	.92	.57	.93	.90
1974 ht.	--	--	--	1.00	.74	.87	.90	.74	.99	.88
1969 DBH	--	--	--	--	1.00	.93	.88	.17	.64	.82
1972 DBH	--	--	--	--	--	1.00	.97	.39	.83	.95
1975 DBH	--	--	--	--	--	--	1.00	.53	.87	.99
Ht. growth 1969-74	--	--	--	--	--	--	--	1.00	.89	.80
Ave. annual ht. growth	--	--	--	--	--	--	--	--	1.00	.95
Ave. annual DBH growth	--	--	--	--	--	--	--	--	--	1.00

correlations between 1969—74 height growth rate and cumulative height measurements. This progressive pattern and the lack of association between 1969—74 height growth rate and 1966 height indicate that the tallest trees, as of 1974, had begun rapid growth before 1969 and this rate continued into the 1969—74 period. Trees initially slow growing apparently began growing faster some time after 1969 accounting for progressively increasing correlation coefficients. Patterns of correlations between DBH cumulative measurements and 1969-74 height growth rate are also similar.

Trees of certain provenances grew fast during the early life of the plantation and then slowed while those of other provenances continued to grow at a constant or accelerated rate of height growth with increase in age (Figure 2). This type of growth behavior was previously reported in *Q. rubra* (GALL and TAFT, 1973) and also in *Pinus ponderosa* LAWS. (NAMKOONG and CONKLE, 1976).

A genetic basis for differences in initiation of rapid growth could reflect the degree of selection pressure applied by the type of plant community in each respective provenance to *Q. rubra* genotypes. In an area with heavy ground cover, selection pressures for initial fast growth

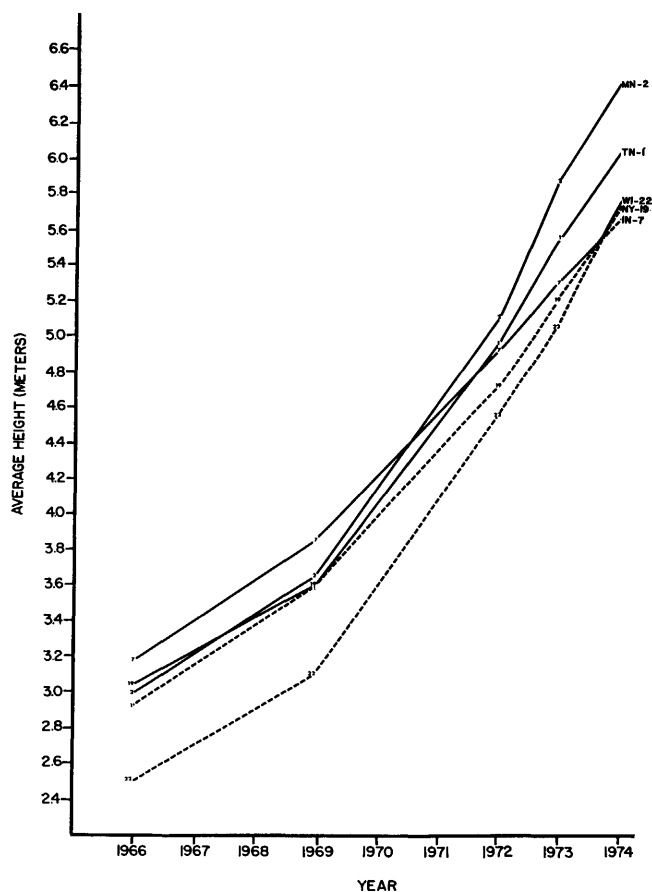


Figure 2. — Height growth of five provenances of red oak planted in 1962-3. The three fastest growing populations are depicted by solid lines. The line designating a population changes from solid to dashed or visa-versa as the ranking changes.

would be strong in species of intermediate tolerance such as *Q. rubra*.

Genetic variation among populations in recovery and effect from transplanting could determine early growth performance. Seedlings of a provenance might be able to recover from transplanting shock more quickly than those of another provenance because of size, vigor, or better root development, but might not be well enough adapted to a specific site to maintain rapid growth. Trees which establish themselves more slowly after planting could be better adapted to the site conditions and increase rate of growth during a later period of years. YING and BAGLEY (1976) suspected patterns in early growth of *Populus deltoides* BATH., eastern cottonwood, to be related more to field establishment ability of unrooted cuttings than with inherent growth potential.

Changes in environmental conditions from year to year, at the planting site, could cause growth rate differences reflecting genetic variation among populations. Periodic fluctuations in rainfall, temperature, or other factors could slow growth of trees of some provenances while favoring growth of other population samples.

The correlations of phenological data with growth data were low, implying little information about growth potential can be determined by observation of initiation of spring growth and all dormancy processes. The number of days between leaf flush and fall color probably has no association of diameter growth as shown by the low correlation with amount of diameter growth in 1975 ($r = 0.12$). This

result concurs with PERRY (1971) who states that in August trees still have functioning chloroplasts and are able to conduct photosynthesis but have ceased visible growth. All correlations of growth data with leaf flush were negative indicating that trees which flush earliest exhibit the best growth rates. GALL and TAFT (1973) observed similar behavior indicating that early flushing populations samples produced by the tallest trees.

Spring and fall phenological characteristics were observed in detail only in 1975. Phenological information over a period of several years is needed before reaching definite conclusions about association of phenology with growth. Observations in past years, however, indicate relative dates of spring leaf flush and fall leaf color change were consistent among populations.

Date of leaf flush was weakly associated with provenance longitude (Table 7) which is contrary to previous reports of leaf flush varying clinally with latitude provenance (GALL and TAFT, 1973) and elevation (MCGEE 1970, 1974). Lack of correlation between leaf flushing and provenance latitude is indicated by Table 7. Partial correlations with elevation were not calculated, however, examination of Table 3 reveals no association of leaf flushing date with provenance elevation. Though clinal variation of leaf flush with respect to longitude is indicated, inspection of Figure 1 and Table 3 shows the lack of a true east-west trend. Relative earliness of northwestern populations probably influenced the data enough to produce a significant coefficient with longitude. Therefore, in view of the diverse pattern found in this study and the different results found by GALL and TAFT (1973) and MCGEE (1970, 1974) it appears that the initial leaf flushing process(es) is (are) discontinuous in variation over the entire range of *Q. rubra*.

The lack of relationship of leaf flush with latitude indicates that photoperiod of provenance location is not primarily responsible for genetic variation present in initiation of *Q. rubra* leaf flushing processes. In this aspect, *Q. rubra* differs from other species of trees in which clinal north-south patterns of bud break have been recorded (NIENSTAEDT, 1974). Lack of clinal variation pattern was also indicated by FLINT (1972) who found that by early spring, considerable dehardening had taken place and differences among populations in winter hardening, which were correlated with provenance latitude, had disappeared. PERRY (1971) stated that after true dormancy had been achieved a tree must be exposed to a minimum number of hours at a certain temperature before growth resumes. The differences in leaf flush among populations could reflect differences among provenances in the minimum number of hours at a required temperature to initiate spring growth.

Fall phenological observations were found to be correlated with provenance latitude but not with longitude (Table 7). Differences among populations in fall phenological characteristics were also reported in other studies (DENEKE, 1975; KRAHL-URBAN, 1966; KRIEBEL, 1965; KRIEBEL *et al.*, 1976; SCHREINER and SANTAMOUR, 1961). Generally, mean dates of leaf fall color, death, and drop of upper latitude trees were significantly earlier than trees from lower latitudes (Table 4).

FLINT (1972) found the degree of cold hardiness of *Q. rubra* twigs to be strongly correlated with the latitude and to a lesser extent associated with annual temperatures of provenance location. This implies that temperature regimes of natural habitats are a secondary factor influencing

growth cessation processes. Photoperiod has been recognized as a primary factor in control of growth cessation processes in many tree species (NIENSTANDT, 1974). MORGENSTERN (1969) considered temperature to be an important secondary factor in growth cessation of *Picea mariana* (MILL.) B.S.P.. The lack of perfect correlation of fall phenology dates with latitude indicates that genetic differences in dormancy initiation among populations were probably selected for in response to a combination of photoperiod and temperature regimes endemic to individual provenance locations.

A high percentage of western populations retained leaves through the 1975–76 winter (Tables 5 and 7). The high degree of winter leaf retention could be a response to water limitations in the prairie environment. DENEKE (1975) found that trees from the more western populations survived better than trees of eastern populations in Kansas. Water availability is the most important factor limiting growth and survival (ZIMMERMAN and BROWN, 1971). Retention of leaves in the winter would allow snow trapping during the horizontal prairie snowstorms, providing additional moisture. Also, shading from the leaves would reduce the rate of snow melt and lower soil temperature around the tree thus reducing evaporation.

Trees were observed with various levels of leaf retention indicating that leaf drop is controlled by quantitative genes and/or different processes. Auxins are responsible for the formation of the abscission layer according to research reviewed by KRAMER and KOZLOWSKI (1960). Weather conditions and the strength of the vascular connections are also factors which determine rate of leaf fall. Potential for some degree of leaf retention is present in trees from most provenances. High leaf retention in western populations is probably due to natural selection within ancestral populations. The characteristics of the Sangamon paleosol suggest that prior to the Wisconsinan glaciation, eastern North American forests may have extended further west than present day boundaries (RUHE, 1965). Thus, the range of *Q. rubra* may have originally advanced as much as 100 miles west of its present distribution and selection favoring

leaf retention likely occurred in response to decreasing annual moisture.

The rankings in the multiple range test (Table 6) and partial correlation coefficients (Table 7) involving the days between leaf flush and fall color indicate the lack of clinal variation patterns within the species for this characteristic. The number of days between leaf flush and leaf color change appears to have no meaningful biological association with leaf flushing or dormancy processes.

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Summary of results on Scots pine (*Pinus sylvestris* L.) volume production in Ogievskij's pre-revolutionary Russian provenance experiments

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(Received August / December 1980)

Summary

On the basis of the available Russian literature data on volume per hectare was analysed from the provenance experiments on Scots pine (*Pinus sylvestris* L.) established in pre-revolutionary Russia in the years 1910–1916 by V. D. OGIEVSKIJ. Using the latest published data on volume/ha for each provenance the deviation from an experimental mean in units of standard deviation was calculated. These deviations are presented graphically for individual provenances on maps showing the location of the planting sites within a schematic outline of Imperial Russia. By

using this method it is possible to compare simultaneously the productivity and adaptability of the studied provenances. In general local provenances have had a relatively satisfactory growth. The analysis has generally confirmed the earlier reports made separately from various planting sites that pine provenances from the pre-revolutionary provinces Volynia, Minsk, Mogilev and Chernigov are of exceptional value. Also good are provenances from the Baltic region and from a narrow belt between latitudes 54° and 57° (provinces Moscow, Vladimir, Nizhni Novgorod, Kazan, Samara). The outlier provenances from