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A provenance and progency test in northern red oak (quercus rubra L.)

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To the Graduate Council:

I am submitting herewith a thesis written by William R. Gall entitled "A provenance and progency test in northern red oak (quercus rubra L.)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Eyvind Thor, Major Professor

We have read this thesis and recommend its acceptance:

John Rennie, Otto Schwartz, Kingsley Taft Jr

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

November 15, 1973

To the Graduate Council:

I am submitting herewith a thesis written by William R. Gall entitled, "A Provenance and Progeny Test in Northern Red Oak (Quercus rubra L.)." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Eyvind Thor
Major Professor

We have read this thesis
and recommend its acceptance:

K. A. Taft

Otto J. Schwarz

Accepted for the Council:

Hilton A. Smith
Vice Chancellor for
Graduate Studies and Research

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A PROVENANCE AND PROGENY TEST
IN NORTHERN RED OAK
(*Quercus rubra* L.)

A Thesis
Presented to
the Graduate Council of
The University of Tennessee

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
William R. Gall
December 1973

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ABSTRACT

Seedlings of forty-nine open-pollinated families of northern red oak (Quercus rubra L.) from six geographic sources were evaluated for total height at two, three and four years from seed; for diameter a foot above ground and total height at six years from seed and for date of bud break and number of flushes at four, five and six years from seed.

The amount of heat required for bud break of northern red oak, as represented by a temperature summation, was not a constant. Total height was not related to latitude of the seed source and is thus probably not controlled by photoperiod. Date of bud break of the seedlings was associated with latitude and elevation of the seed source and is possibly related to length of frost-free period of the seed source. Seed source selection for date of bud break should prevent frost damage to planted northern red oak seedlings.

Seed source, among-family and within-family selection yield predicted gains in juvenile height of 28 to 55 percent in an open-pollinated seed orchard. These gains depend upon the inclusion of a single outstanding seed source in the test. Such gains should ameliorate the problem of poor juvenile height growth in planted northern red oak.

Heritability estimates for total height six years from seed range from .20 to .37.

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CHAPTER I

INTRODUCTION

Little genetic work has been done in northern red oak (Quercus rubra L.). Knowledge of the genetics of this species is important because it is a fast-growing and desirable member of both the central and Appalachian upland hardwood forests. It is an abundant member of the potential climax forest of most of the East.

This study has two objectives: to evaluate both geographic and additive genetic variation in an experimental population with regard to total height, diameter and bud break of northern red oak and to relate yearly variation in date of bud break to environmental variables at the planting site.

With regard to the first objective, it was desired to estimate the relative importance of variation due to seed source and that due to half-sib familial resemblance. A subordinate objective was to explain the variation associated with seed source in terms of environmental factors which vary from one source location to another. Another subordinate objective was to estimate heritabilities within the experimental population for the characteristics studied. Since the outplanting may be converted to a seed orchard by roguing, the heritabilities could be used to predict expected gains in a suitable selection program.

Considering the second objective, the goal was to examine as many environmental variables as possible which, under field conditions, might be related to the date of bud break and to determine that variable or that combination of variables which most consistently explains the variation in date of bud break from year to year. Attainment of this objective would aid in understanding the physiology of this species, could be used to predict dates of bud break for particular genotypes and would affect the successful selection of planting locations for northern red oak of different provenances.

CHAPTER II

LITERATURE REVIEW

Genetics of Height Growth in Open-pollinated Hardwood Families

Little information is available on genetics of height growth in hardwoods based on open-pollinated families. Even less has been published giving heritability estimates for height growth in hardwoods.

Farmer and Wilcox (1966) used the two-year-old open-pollinated progeny of selected mother trees of eastern cottonwood to obtain estimates of heritabilities for total height and diameter, among other characters. Heritability estimates of first-year height and diameter were 0.93 and 0.52, respectively. Those of second-year height and diameter were 0.35 and 0.16, respectively, considerably less than in the first year.

Estimates of genetic variance for height were low in open-pollinated eastern cottonwood progeny. The percent of variance due to differences among families was 10.0 for second-year height, 5.9 for third-year height and 12.8 for third-year diameter. No attempt was made to calculate heritabilities. However, estimates of variance components were provided; estimates of heritabilities computed from those estimates are 0.40 for second-year total height, 0.24 for third-year total height and 0.51 for third-year diameter (Farmer, 1970).

Forty open-pollinated families of sweetgum were used by Wilcox (1970) to estimate heritabilities of total height at each of two outplanting locations for each of three years. Heritability estimates were 0.67 for second-year height, 0.45 for third-year height, 0.40 for fourth-year height, 0.34 for third-year diameter and 0.32 for fourth-year diameter.

Heritability estimates were derived for total height and diameter of open-pollinated walnut seedlings from 17 mother trees from 6 sources (Bey, Hawker and Roth, 1971). Heritability estimates for height and diameter of four-year-old seedlings were 0.45 and 0.40, respectively.

In this study, genetically identical pairs were derived by longitudinally splitting the hypocotyl and epicotyl of germinating seeds.

Genetic variance components were estimated by Kriebel (1965) for total height of open-pollinated northern red oak families from 16 sources. However, these variance components were not published. Identity of the mother trees was retained, and ten mother trees from each source were used. Trees were one year old when the data were taken. Another analysis was done when the trees were three years old, using only six sources. The first analysis, which included northern provenances with very poor height growth, showed a larger effect due to provenances than to families. In the second analysis, which did not include any northern provenances, the situation was reversed.

Several generalities regarding estimates of narrow sense heritability may be formulated, based on these five articles as summarized in Table II-1: (1) There are few estimates for either height or diameter growth of hardwoods which are based on plots of more than one tree; (2) nursery estimates are high; (3) in some cases estimates decrease in size as the seedlings grow older; (4) several of the estimates for height of two- to four-year-old seedlings lie within the range from 0.40 to 0.45; (5) many of the estimates for diameter lie within the range from 0.32 to 0.52; (6) there are no published estimates of heritability of height growth for northern red oak.

Genetics of Flushing in Open-pollinated Families of Hardwoods and Conifers

Flushing dates of trees have been studied for many years; however, few estimates of narrow-sense heritability for this character have been reported.

Heritability of stage of bud break of Norway spruce was estimated by a parent-offspring regression. It was apparent that, even among the late-flushing variety, this character varied strongly at the individual tree level. The correlation coefficient had a value of 0.63. The heritability is said to be high, but no estimate was given, since it was not known if all the offspring were half-sibs and not full sibs (Lacaze, 1969).

Heritability of flushing in the open-pollinated progeny of one population of mother trees of white fir which were 130 to 140 years old was estimated at 0.40. Heritability of the same character in the offspring of the putative next generation, which was 40 years old, was much lower. Progenies of the second generation were more late flushing and more vigorous than those of the first. Vigor (height and diameter) and late flushing were positively correlated, phenotypically, in both populations and were positively correlated genetically in the first population (Arbez and Millier, 1970).

Table II-1. Heritabilities of height and diameter obtained or derived from four articles

Species and Author	1st Year Ht.	1st Year Diam.	2nd Year Ht.	2nd Year Diam.	3rd Year Ht.	3rd Year Diam.	4th Year Ht.	4th Year Diam.
Cottonwood (Farmer & Wilcox, 1966)	0.93	0.52	0.35	0.16				
Cottonwood (Farmer, 1970)			0.40		0.24	0.51		
Sweetgum (Wilcox, 1970)			0.67		0.45	0.34	0.40	0.32
Walnut (Bey, _et al._, 1971)							0.45	0.40

Farmer (1970) found a high genetic correlation between early foliation date and final diameter. Estimates of heritability of foliation date in open-pollinated eastern cottonwood progeny were not given by Farmer. However, heritability estimates computed from variance components, based on the design which was given, were 3.46 for third-year foliation date and 3.66 for fourth-year foliation date.

Heritability of flushing date based on forty open-pollinated families at two outplanting locations was estimated by Wilcox (1970).

Date of foliation differed significantly among families and between locations. For two years, family times location interactions were significant for foliation date. Heritability estimates were 1.11 for third-year foliation date and 1.27 for fourth-year foliation date at one location and 0.54 and 0.98 for the same variables at the other location.

Frost damage to the terminal bud of black walnut seedlings causes multiple-topped and/or crooked trees (Bey, 1971a). When 20-25 sources of black walnut were outplanted at three locations, and progeny from 82 open-pollinated trees were direct seeded at two locations, estimates of heritability for flushing date were 0.67 and 0.96 for the Jackson and Union County, Illinois, plantings, respectively. To eliminate seed source effects, flushing date means were adjusted to the latitude of the planting site before computing heritability.

Seed from 17 parent trees of black walnut from 6 sources was planted at one location. Estimates of heritability were 0.67 for leaf flush and 0.76 for leaf fall. Correlations indicate that selection for fast growing sources will mean concurrent selection for trees that have more branches and more crook (Bey, et al., 1971).

From the preceding discussion and Table II-2, one may conclude that, even when the heritability estimates for date of bud break are less than one, they are high and that one author has reported estimates which are greater than one. Another author has reported variance components from which heritability estimates greater than one have been calculated. No heritability estimates for date of bud break in northern red oak are available.

Genetic Variation in Chilling Requirement

Genetic variation in the chilling requirement has been investigated to some extent. Two publications will be reviewed which demonstrate that the extent of the chilling requirement varies according to seed source. Familial variation in chilling requirement has not been demonstrated.

Red maple progenies from sources with frost-free seasons ranging from 100 to 365 days were used by Perry and Wang (1960). They found that

Table II-2. Heritability estimates for date of bud break.

		Heritability Estimate	
Species and Author		1st Year	2nd Year
Norway Spruce (Lacaze, 1969)		0.63	
White Fir (Arbez and Millier, 1970)		0.40	
Cottonwood (Farmer, 1970)		3.46	3.66
Sweetgum	1st Location:	1.11	1.27
(Wilcox, 1970)	2nd Location:	0.54	0.98
Walnut	1st Location:	0.67	
(Bey, 1971a)	2nd Location:	0.96	
Walnut (Bey, *et al*., 1971)		0.67	

chilling treatment hastened the break of dormancy for plants from more northern latitudes but delayed the break of dormancy for plants from Florida. Date of break of dormancy was strongly correlated with frost-free period of the seed source.

In tests with seven chilling periods and four provenances of sugar maple, Kriebel and Wang (1962) concluded that the pattern of variation in date of bud break is not the direct result of variation in chilling requirement. In general, however, the longer the chilling period, the shorter was the period before flushing. Apparently, during the period from mid-February to outdoor bud break in late April, some other environmental factor replaced the requirement for additional chilling as the stimulus controlling onset of growth.

Physiology of Dormancy

Several authors are cited frequently in works dealing with dormancy. These four: Samish, Doorenbos, Wareing and Vegis have written outstanding literature reviews in the field of dormancy and have formulated the leading hypotheses and theories on the subject.

Doorenbos (1953) categorizes the different types of dormancy as imposed dormancy, summer dormancy and winter dormancy. The inhibitory system of summer dormancy in oak seems to be favored by light. Species of oak have been shown, he says, to have no or only a slight response to daylength. Furthermore, winter dormancy is difficult to break in *Quercus*, and continuous illumination does not break dormancy in the genus.

Dormancy is separated by Samish (1954) into quiescence, rest and correlated inhibition. He says that chilling terminates rest in deciduous plants but does not terminate growth suspension in evergreens. According to him, it has been demonstrated that inhibitors are synthesized in the bud scales of resting buds, that the individual bud is the seat of rest and that response to a stimulus is localized in the bud. There is a question, he maintains, as to whether the cambium starts independently to grow again or whether the cambium responds to a stimulus originating in the buds, although the connection between resumption of cell division in the cambium and the awakening of buds was already known.

Vegis (1955) postulates that "genetically determined unequal sensitivity" toward high temperature causes forest plants of different provenances cultured under the same conditions to initiate growth and form dormant terminal buds at different times and daylengths. In plants of Hydrocharis morsus ranae, he showed that high temperature inhibits growth and produces dormancy, whereas long days promote growth and prevent dormancy.

Vegis is one of the few researchers who have studied the effects of temperature and of the interaction of temperature and photoperiod on dormancy. Many aspects of Vegis' theories are not widely accepted. However, some of his work may be useful in explaining phenomena connected with dormancy. Wareing's work and theories have received much wider acceptance and are in the mainstream of research on dormancy.

The most generally held views are those put forward by Wareing. In one publication (Wareing, 1956), he says that dormancy is induced by short days in some species. After the chilling requirement has been satisfied, in those plants which have a chilling requirement, bud break is controlled primarily by temperature and will occur at any photoperiod, given the proper temperature conditions.

In another paper, he (Wareing, 1969) discusses the hormonal theory of dormancy and the theory, espoused by Vegis, that dormancy is regulated by temperature and restricted oxygen uptake. The hormonal theory is that dormancy is regulated by a balance between growth-promoting and growth-inhibiting hormones. Wareing says that phytochrome is apparently involved in photoperiodic dormancy responses, although "red/far red reversibility" has not been clearly demonstrated.

In a third publication (Wareing and Saunders, 1971), the authors present a comprehensive review of literature on research into the relationship between postulated hormones--endogenous and exogenous--and dormancy in various plant organs. The hypothesis is again put forward that a balance between inhibitors and promoters (i.e., abscissic acid and the gibberellins) controls dormancy. Hormonal effects on nucleic acid metabolism are postulated as a mechanism of control.

Many publications deal with photoperiodic control of the onset of dormancy, but few deal with temperature control of the release from dormancy, other than those on the chilling requirement, and even fewer on any interaction between photoperiod and temperature in the control of the onset of dormancy.

Red oak receiving long day treatment made no greater shoot growth than trees exposed to normal photoperiod and did not grow later in the autumn (Kramer, 1936). In the spring, there was no difference between the time at which dormancy was broken in the normal and in the long day series. Dormant seedlings of red oak were brought indoors in early January and subjected to long and short days. The trees receiving additional light resumed growth sooner than those with a short day.

Red, white and black oak, American chestnut and American beech failed to break dormancy in continuous darkness (Pauley, 1954b).

Exposure to ethylene chlorohydrin, clipping of all the terminal buds and exposure to low temperatures induced northern red oak (Q. borealis) and other oaks to break dormancy before controls (Fergus, 1955).

In an experiment by Zasada and Zahner (1969), variation in stage of vessel development among trees of northern red oak was not more than a few days, and was always associated with degree of shoot development.

In a study by Larson (1970), red oak seedlings were exposed to several soil temperature treatments. The number of buds that broke dormancy was not related to the soil temperature treatments.

According to the preceding publications, then, dormancy cannot be broken in northern red oak either by continuous illumination or continuous darkness. However, after the chilling requirement is satisfied, long days produce earlier bud break in red oak than short days under the same indoor temperature regime. Although soil temperature does not affect date of bud break in red oak, northern oak does have a chilling requirement for breaking of dormancy. Stage of vessel development is associated with the breaking of dormancy in red oak, so genetic and environmental control of date of bud break may affect the proportion of earlywood and thus the specific gravity.

Effect of Temperature on Growth of Trees

The best known work relating temperature to growth of trees is on fruit trees. Brown (1953) used the number of hours experienced during the first six weeks after full bloom in each of several temperature classes to determine the relative efficiencies of different temperatures in promoting development of the apricot. Satisfactory predictions of the time of apricot harvest can be made based on temperature data for the 42 days following bloom.

The use of heat sums, interaction of temperature and daylength in control of flowering in bulbous plants and biennials, annual and diurnal periodicity in deciduous trees and tomato plants, respectively, effects of soil temperature and the effect of temperature on width of tree rings were reviewed by Went (1953).

Short days induce dormancy in several tree species, and long days prolong growth (Downs and Borthwick, 1956). At higher temperatures it took a greater number of eight-hour days to induce dormancy, and at temperatures lower than 70° F. growth was inhibited even on 16-hour photoperiods.

A new temperature summation method was used by Lindsey and Newman (1956), based not on means but on the daily maximum and minimum and on the assumption of a linear growth curve, to determine meteorological thresholds and time periods which controlled date of first flower of 51 herbaceous and woody species over a thirty-year period.

In a study by Ahlgren (1958), initial spring activity in basswood, bur oak, large-toothed aspen and sugar maple seemed unrelated to any specific temperatures. In the species studied, no obvious correlation appeared between current temperature levels and the beginning of either flowering or leafing.

In a review of the 230-year history of the heat unit approach, Wang (1960) pointed out that growth rate is not always a linear function of temperature, that growth versus time is sometimes a near-linear function, that this function is similar to the summation of heat units versus time and that because of their linearity these two physiologically unrelated functions sometimes coincide.

In another study on the effect of soil temperature, Larson (1970) showed that red oak seedling growth was related to the daily degree-hours of soil heat received. Both tops and roots increased as the degree hours increased. Alternating daily soil temperatures provided no growth advantape over constant temperature.

Regression analysis was used to demonstrate a relationship between percent survival of yellow-poplar grafts and degree days. The equation $Y = 14.62 + 0.029X$ yielded a significant regression coefficient, where Y is percent survival and X is degree days. The coefficient of determination indicated that 43 percent of the variation in graft survival is associated with the variation in degree days (Evans and Thor, 1971).

A temperature summation explained 99 percent of the variation among 131 herbaceous and woody species in average date of first flower. The equation used was $Y = 20.74 + 0.61X - 0.0005X^2$, where Y is the average temperature summation for each species over ten years (Taylor, 1972).

It has been assumed in some of these studies that the amount of heat required for a particular growth response is a constant for a species and is represented by a temperature summation. It has also been assumed that the amount of heat is the primary factor controlling such a growth response in the time intervals investigated. The criticism levelled by Wang (1960) is the most serious one affecting investigations which are based on or attempt to demonstrate the validity of these assumptions.

It may be noted that no attempt has been made in the past to relate the date of bud break of trees to a temperature summation based on hourly temperatures.

Attempts to Relate Height Growth to Date of Bud Break

Several researchers have attempted to relate height growth to date of bud break, with varying success. Ching and Bever (1960), Ford and Sucoff (1961) and McGee[1] found little or no relationship between height growth and date of bud break in Douglas-fir, hybrid poplars and

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[1] In press.

northern red oak, respectively. Silen (1962) and Krahl-Urban (1966) found that clones of Douglas-fir and seedlings of northern red oak, respectively, which leafed out earlier grew taller. Efimov (1967) showed that, between the early- and late-flushing forms of Quercus robur, organic matter production was higher in the latter.

Relationships of Geographic Variables to Date of Bud Break and Height Growth

Seed source differences in date of bud break are usually explained by selection pressures at the source location due to one or more environmental variables. Most of the following results are explained in this way.

McGee (1970, 1973) found a relationship between date of bud break of red oak seedlings and the elevation of the mother trees. In addition, bud bursting of seedlings of Douglas-fir from high altitudes generally occurs later than in other stocks (Ching and Bever, 1960). In an experiment conducted by Pauley (1954) altitudinal ecotypes of Populus trichocarpa grown under uniform temperature and daylength conditions clearly indicated that low elevation types were significantly more precocious than high elevation types. Partial regression of date of bud break of sugar maple on both average July temperature and latitude of the seed source showed that latitude has a strong relation to the response but that warm season temperature seems to be less important, since the partial regression of date of bud break on latitude was significant at the one percent level and that of date of bud break on temperature was only significant at the five percent level (Kriebel, 1956).

Trees of cottonwood and sycamore growing in their native locations were used to show that the temperature associated with the end of the growing season was higher than that associated with the beginning of the season. No single temperature was critical or decisive in either the initiation or cessation of growth. The regression of temperature at the beginning or end of the growing season on photoperiod and photoperiod squared were computed, and statistically significant regressions were obtained for both species for the beginning of the growing season. In this study, data for only one year were used, and the effects of genetic variation were not examined (Kaszkurewicz and Fogg, 1968).

Walnut trees from southern sources flushed earlier than trees from northern sources (Bey 1971a). Trees from all sources had a shorter flushing time at northern locations. Winter chilling requirement and photoperiodic response seem to explain most reasonably why trees from southern sources flush earlier.

In another study on walnut (Bey, Hawker and Roth, 1971), after four years trees from southern sources were taller and larger in diameter, had greater branch length, flushed earlier and dropped their leaves later than trees from local and northern sources.

The date of bud break of sugar maple in Ohio field tests began in trees of extreme northern and northeastern provenances and progressed to trees of southeastern, southern and western provenances (Kriebel and Wang, 1962). These results are the reverse of those of Bey (1971a) for walnut and Ching and Bever (1960) for Douglas-fir.

Vegis (1955) says that when plants of a northern provenance are moved south, their maximum growth temperature is exceeded earlier in the summer, so that dormancy occurs earlier than in the place of origin, and that the reverse holds true for plants of southern provenance which are moved north. In contradiction to other theories, he says that the delayed flushing of fruit trees in regions with mild winters and high summer temperatures is not because of a great chilling requirement which is not satisfied, but to a deeper and longer rest into which the growing point enters due to its higher "genetically determined sensitivity" to the high summer temperature; that is, its low maximum growth temperature.

Physiological Variation Associated with Variation in Date of Bud Break

Physiological variation associated with variation in date of bud break between early- and late-flushing forms of *Q. robur* was investigated by Efimov (1967). He found that the rate of photosynthesis of the late-flushing form was higher than that of the early-flushing form. As mentioned earlier, organic matter production was higher for the late form. The two-year-old seedlings of the late form were larger, although the leaf area was the same. The chlorophyll content of leaves of fifteen-year-old oaks was higher for the late form than the early form.

Physiology and Dormancy of Trees: a Conceptual Framework

Literature on the genetics of chilling requirement and on the physiology of all stages of dormancy was included in this review as an aid to forming a conceptual framework for the understanding of the physiology and genetics of dormancy in trees. Results of the present research might be fitted into such a framework, and this framework might suggest some testable hypotheses for future investigation.

First, it appears that dormancy in trees is under the primary control of one environmental variable at certain times and that this variable, which is the primary controller of dormancy and growth, changes with the periodic annual cycle of time. In some trees, rest is induced by short days; in most, it may be hypothesized, afterrest is removed by a cumulative effect of higher temperatures, which might be called a warming requirement. In changing from control by one variable to control by another variable, there are probably interactions between the two variables. It is generally assumed to be true that photoperiod does not affect the removal of afterrest, although this assumption has been shown not to be true for red oak (Kramer, 1936). In red oak, too, dormancy is evidently not induced by short days. It may be that in red oak rest is induced by some other factor, such as high temperatures, as suggested by Vegis (1955), or there may be endogenous factors which induce dormancy in red oak without an environmental stimulus.

Since seed source variation in chilling requirement and date of bud break have been demonstrated, it may be that seed source variation in photoperiodic induction of rest and family variation in all three factors exist. It is here suggested that genetic variation at the seed source and family levels in onset of rest, chilling requirement and date of bud break represent a variation in "genetically determined sensitivity", to use Vegis' phrase, to the environmental stimuli which are in primary control of dormancy and growth at the time. There would thus be interactions, not only among the variables in their control of growth, but between the genotypes and the variables. This "genetically determined sensitivity" to environmental variables would mean, too, that in measuring genetic variation in growth response one is really measuring genetic variation in sensitivity to an environmental stimulus plus interactions between genotype and stimulus.

One problem arising in field studies of dormancy in temperate zones is that, at a given location, both photoperiod and temperature decrease in the fall and increase in the spring. Thus, in field studies the effects of the two are always confounded to some degree even when experiments are repeated from year to year. This situation leads one to suspect that temperature and photoperiod both interact in controlling onset of rest and possibly in removal of afterrest.

In the photoperiodic induction of rest, there is no critical daylength or dark period which must be attained, as in short-day induction of flowering. Photoperiodic effects on rest and afterrest, then, may be hypothesized to be effects of a change in daylength rather than effects of a critical daylength. The same may be true of temperature.

CHAPTER III

MATERIALS AND METHODS

Plant Materials, Outplanting Design and Data Collection

Selection of Parent Trees

It was originally intended that, at each source stand, one superior phenotype would be selected on the basis of the TVA hardwood grading system. Ten surrounding trees were then to be used to make up the stand collection, identity of each mother being retained. However, good acorn crops are infrequent, so only three stand collections were made according to the original criteria, those being the Norris Dam, the Norris Lake and the Cumberland Plateau stands. All mother trees for the remaining three stands had only to meet the single criterion of containing a good butt log. Mother trees within a given stand (source) were always from 200 feet to 1/4 mile from each other. Forty-nine open-pollinated families of northern red oak from six geographic locations (table III-1), ranging from northern Alabama to central Ohio (Figure III-1), made up the experimental population.

Acorn Collection and Nursery Experiment

Acorns were collected in the fall of 1966. Before planting in the nursery, the acorns in each family collection were weighed; the mean weight in grams per acorn was computed for each family, and the mean volume in cubic centimeters per acorn was determined for each family by water displacement.

Acorns were germinated in the nursery in three replications to minimize nursery effects, and germination percentage was estimated for each family. Seedlings were grown in the TVA nursery at Norris, Tennessee, during the 1967 growing season.

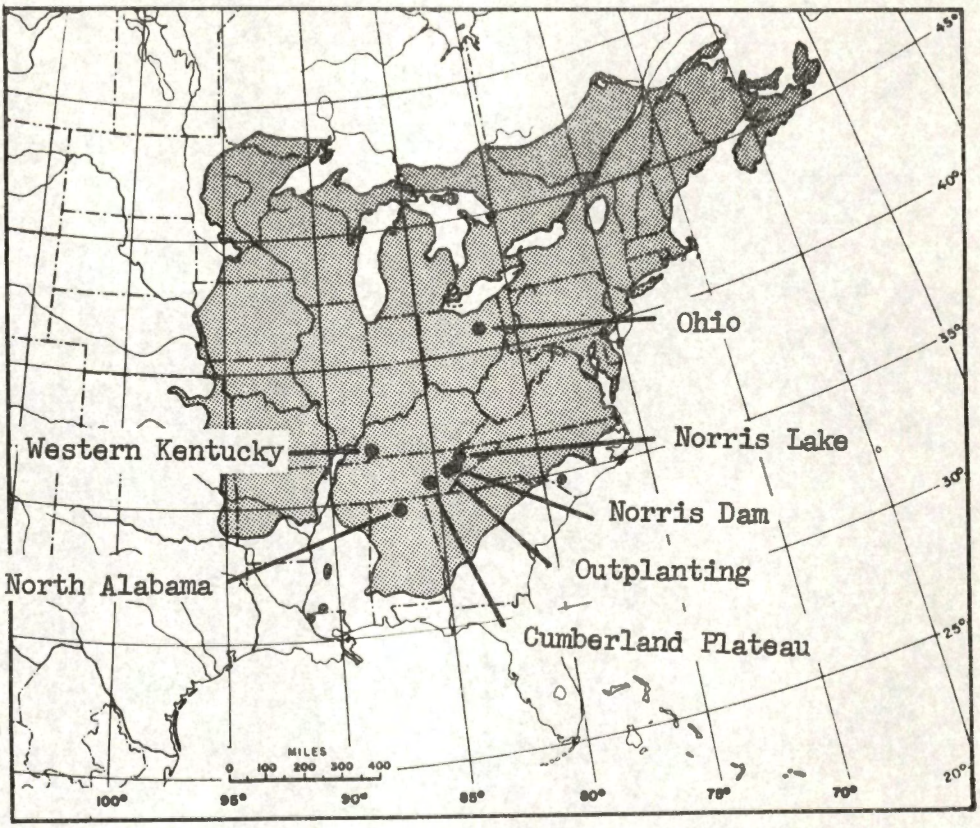


Figure III-1. Locations of seed sources and outplanting site within the range of northern red oak.

Map is taken from U.S. Forest Service.

Table III-1. Locations of seed sources, number of families from each, latitude, longitude and elevation in feet.

Source	No. of Families	Code Number	Latitude	Longitude	Elevation
Ohio	8	OH	40° 45'	81° 55'	960
Western Kentucky	5	99	36° 49'	88° 2'	500
Norris Lake	11	52	36° 20'	83° 57'	1300
Norris Dam	10	51	36° 12'	84° 5'	1100
Cumberland Plateau	10	00	35° 44'	85° 22'	1200
North Alabama	5	89	34° 31'	86° 57'	550

Outplanting Site and Cultural Treatments

Seedlings were outplanted in April, 1968, on Jones Island in the Clinch River below Melton Hill Dam. Jones Island lies at a latitude of 35° 54' N., a longitude of 84° 21' W. and is nearly flat, with an elevation of 760 feet above sea level. The soil is a Pope very fine sandy loam. No record of chemical analyses of the Pope series has been published, and there are no site index estimates for these soils. The 3.61 acres included in this test has a ground cover of Kentucky 31 Tall Fescue.

Site preparation consisted of plowing once and disking three times. Seedlings were planted by dibble, and a fertilizer pellet (18-8-3 analysis with 1% magnesium added and an additional 3% insoluble potash) was placed in each backhole. Simazine was applied once, in 1968, to control the fescue. After that, the fescue was mowed during each growing season.

Climatological Data

Mean annual precipitation of the area is 48 inches; mean annual evapotranspiration, 28 inches; mean freeze-free period, 220 days; mean daily January temperature, 40° F., and mean daily July temperature, 75° F. (Nelson and Zillgitt, 1969).

Outplanting Design

A split plot design was used, with the six stands randomized within each of seven blocks and the varying number of families within each stand randomized only within that stand and not throughout each block (Figure III-2). There were thus 49 families per block.

Fertilizer Treatments

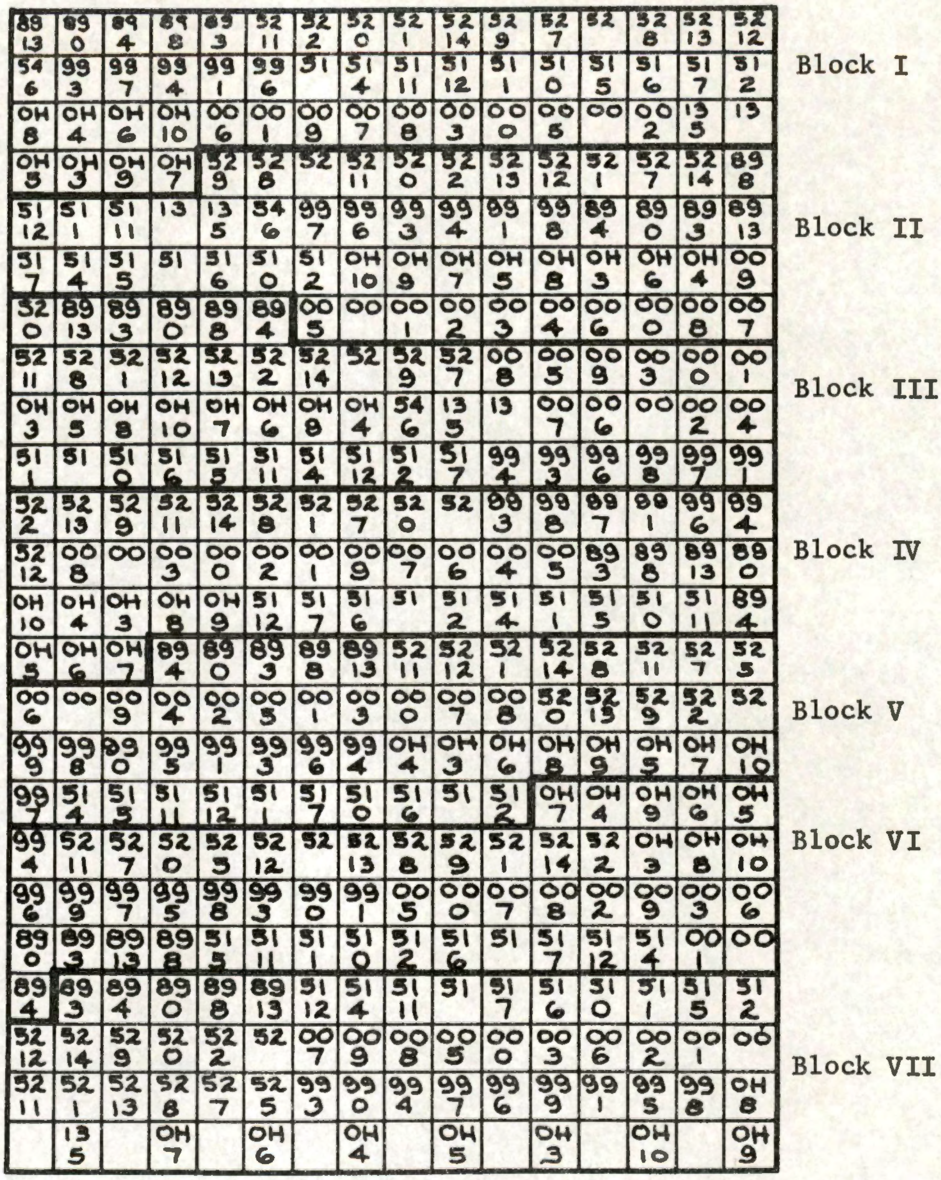
In May, 1971, six of the blocks were regrouped into three replications, each containing two blocks. One block in each of the three replications was selected at random and treated with 220 lbs. of nitrogen per acre by the application of 0.22 lbs. of ammonium nitrate per tree in a two-foot-diameter circle. Blocks receiving fertilizer were numbers 2, 3 and 6.

Data Collection

Meteorological data were obtained from the records of the National Oceanic and Atmospheric Administration Environmental Research Laboratories for station 30, located at Oak Ridge National Laboratory. Hourly temperatures and daily precipitation were obtained for February, March, April and May of 1970, 1971 and 1972. Station 30 is located at a latitude of 35° 56' N., a longitude of 84° 19' W. and an elevation of 886 feet above sea level, and is thus less than three miles away from the outplanting site with a difference in elevation of approximately 130 feet.

Total height of every tree, to the nearest tenth of a foot, was measured in October of 1968, 1969 and 1970 and in September, 1972. In September, 1972, diameter a foot above ground was measured to the nearest tenth of an inch on every tree.

Date of bud break was observed in April and May of 1970, 1971 and 1972 for the first, third and fifth trees, or the nearest substitutes, in each plot in five of the seven blocks. The trees were visited every three to five days during the leafing-out period and rated on a scale from one to three. On the day when a particular tree was judged to have reached a rating of three, the number of days after march 31 was recorded



89 13	89 0	89 4	89 8	89 3	52 11	52 2	52 0	52 1	52 14	52 9	52 7	52	52 8	52 13	52 12	
54 6	99 3	99 7	99 4	99 1	99 6	51	51 4	51 11	51 12	51 1	51 0	51 5	51 6	51 7	51 2	Block I
OH 8	OH 4	OH 6	OH 10	00 6	00 1	00 9	00 7	00 8	00 3	00 0	00 5	00	00 2	13 5	13	
OH 5	OH 3	OH 9	OH 7	52 9	52 8	52	52 11	52 0	52 2	52 13	52 12	52 1	52 7	52 14	89 8	
51 12	51 1	51 11	13	13 5	54 6	99 7	99 6	99 3	99 4	99 1	99 8	89 4	89 0	89 3	89 13	Block II
51 7	51 4	51 5	51	51 6	51 0	51 2	OH 10	OH 9	OH 7	OH 5	OH 8	OH 3	OH 6	OH 4	00 9	
52 0	89 13	89 3	89 0	89 8	89 4	00 5	00	00 1	00 2	00 3	00 4	00 6	00 0	00 8	00 7	
52 11	52 8	52 1	52 12	52 13	52 2	52 14	52	52 9	52 7	00 8	00 5	00 9	00 3	00 0	00 1	Block III
OH 3	OH 5	OH 8	OH 10	OH 7	OH 6	OH 8	OH 4	54 6	13 5	13	00 7	00 6	00	00 2	00 4	
51 1	51	51 0	51 6	51 5	51 11	51 4	51 12	51 2	51 7	99 4	99 3	99 6	99 8	99 7	99 1	
52 2	52 13	52 9	52 11	52 14	52 8	52 1	52 7	52 0	52	99 3	99 8	99 7	99 1	99 6	99 4	
52 12	00 8	00	00 3	00 0	00 2	00 1	00 9	00 7	00 6	00 4	00 5	89 3	89 8	89 13	89 0	Block IV
OH 10	OH 4	OH 3	OH 8	OH 9	51 12	51 7	51 6	51	51 2	51 4	51 1	51 5	51 0	51 11	89 4	
OH 5	OH 6	OH 7	89 4	89 0	89 3	89 8	89 13	52 11	52 12	52 1	52 14	52 8	52 11	52 7	52 5	
00 6	00	00 9	00 4	00 2	00 5	00 1	00 3	00 0	00 7	00 8	52 0	52 13	52 9	52 2	52	Block V
99 9	99 8	99 0	99 5	99 1	99 3	99 6	99 4	OH 4	OH 3	OH 6	OH 8	OH 9	OH 5	OH 7	OH 10	
99 7	51 4	51 5	51 11	51 12	51 1	51 7	51 0	51 6	51	51 2	OH 7	OH 4	OH 9	OH 6	OH 5	
99 4	52 11	52 7	52 0	52 5	52 12	52	52 13	52 8	52 9	52 1	52 14	52 2	OH 3	OH 8	OH 10	Block VI
99 6	99 9	99 7	99 5	99 8	99 3	99 0	99 1	00 5	00 0	00 7	00 8	00 2	00 9	00 3	00 6	
89 0	89 3	89 13	89 8	51 5	51 11	51 1	51 0	51 2	51 6	51	51 7	51 12	51 4	00 1	00	
89 4	89 3	89 4	89 0	89 8	89 13	51 12	51 4	51 11	51	51 7	51 6	51 0	51 1	51 5	51 2	
52 12	52 14	52 9	52 0	52 2	52	00 7	00 9	00 8	00 5	00 0	00 3	00 6	00 2	00 1	00	Block VII
52 11	52 1	52 13	52 8	52 7	52 5	99 3	99 0	99 4	99 7	99 6	99 9	99 1	99 5	99 8	OH 8	
	13 5		OH 7		OH 6		OH 4		OH 5		OH 3		OH 10		OH 9	

Figure III-2. Outplanting layout.

Each number represents a family plot of twelve seedlings planted in two rows of six. The top number in each box is the stand number; the bottom number represents the family.

as the date of bud break or leafing-out of that tree. The ratings are illustrated in Figures III-3 through III-8 and were defined as in Table III-2.

Oaks do not grow continuously in a growing season, but grow and set a bud, then flush and grow and set another bud. A tree may flush as many as four times in a single season. The number of flushes and the length of each flush were recorded in the growing seasons of 1970, 1971 and 1972 for the trees on which initial bud break observations were made.

To record the number of flushes and the length of each flush, the trees were visited about once a month after leafing-out was complete. Each of the three trees in each plot was measured and the total height compared with that at the end of the preceding season. The difference was taken to be the new growth. The number of flushes represented by the new growth was determined by observing bud scale scars and by noting the difference between old leaves and fresh, succulent leaves.

Table III-2. Definitions of ratings.

Rating	Description
1	Completely dormant.
1+	Buds beginning to swell and change color.
2-	Yellow color showing between bud scales.
2	Buds swollen, but not showing light between bud scales or leaves.
2+	Buds showing light between some, but not all, still-folded leaves.
3-	Leaves out, but not fully unfolded.
3	Leaves at tip of bud unfolded.

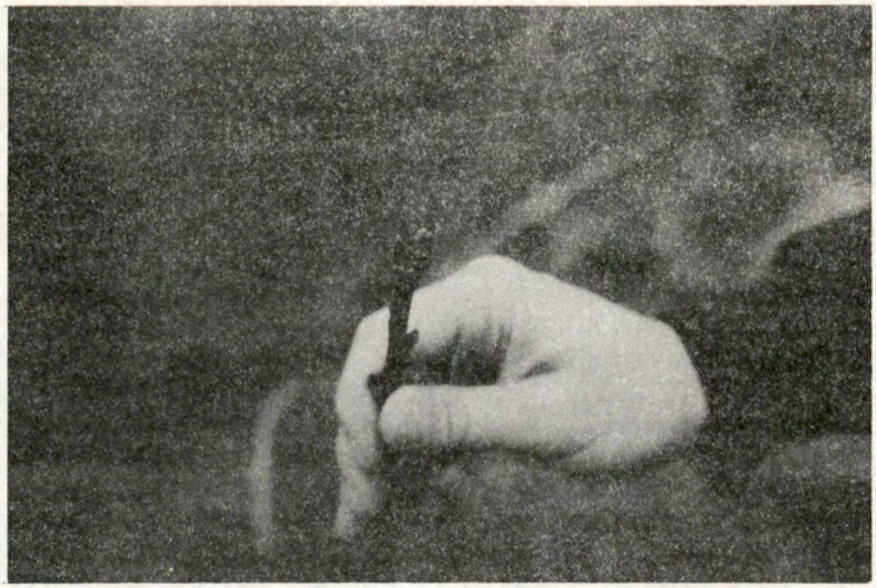


Figure III-3. Stage 1: completely dormant.

Figure III-4. Stage 2: buds swollen, but not showing light between bud scales or leaves.

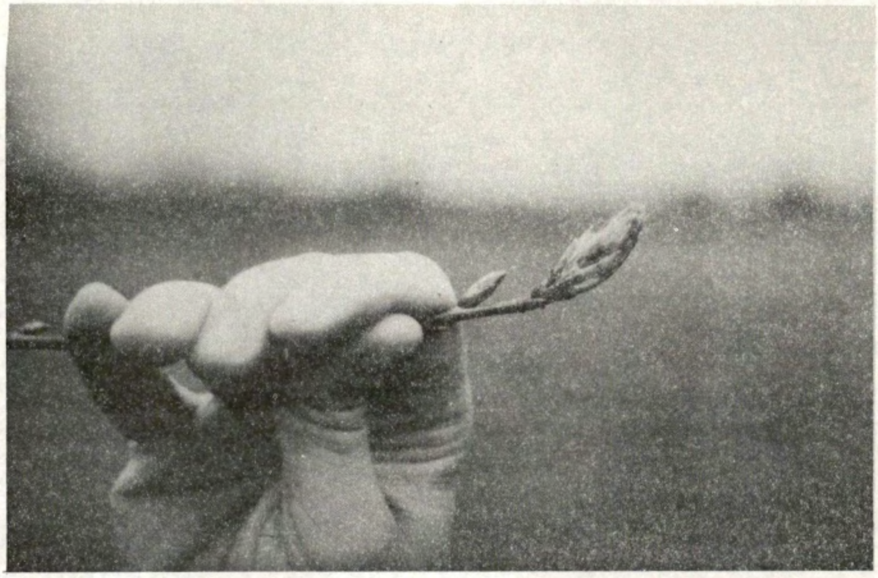


Figure III-5. Stage 2+: buds showing light between some, but not all, still-folded leaves.

Figure III-6. Stage 3: leaves at tip of bud unfolded.

Figure III-7. Stage 2-: yellow color showing between bud scales.

Figure III-8. Stage 3-: leaves out, but not fully unfolded.

Analysis

Analysis of Variance

Statistical analyses were performed using the Statistical Analysis System (Service, 1972). Two forms of analysis of variance were computed, using the PROC ANOVA routine of the SAS.

The first of the two forms of analysis of variance used was the compact family block (Panse and Sukhatme, 1954). In this type of analysis, one analysis of variance computation is done using stand means and omitting the family term. Another analysis of variance computation is completed, one for each stand, omitting the stand term and including the family term.

One reason for using the compact family block analysis was that there were unequal numbers of families in each stand. This meant that the PROC ANOVA routine would not give the correct value for the sum of squares of the families within stands term. In addition, the calculation of the coefficients of the variance components, if done correctly, can turn into a monumental task.

Another reason for using the compact family block design is that the error variances might differ significantly from stand to stand and consequently in taking a pooled estimate of error, the error may be overestimated with respect to some stands and underestimated with respect to others. As a result, it would not be appropriate to carry out an overall test of significance of differences among families within stands, as the differences might be significant in some and non-significant in other stands; and the latter might mask the former (Panse and Sukhatme, 1954). In other words, a false null hypothesis might be accepted for the family effect in some stands.

One of the principles of experimental design is that replicates be relatively homogeneous. When this cannot be, the replicate may be divided into sub-blocks which are relatively homogeneous, as in the compact family block design. Snyder (1966) says that a compact family block design is advantageous where genotypes divide themselves naturally into groups within which variation is smaller than between groups.

According to Federer (1955), the compact family block design is a form of incomplete block design known as a nonfactorial split plot. It is nonfactorial because the families in one stand are not equivalent to families in another stand.

Two forms of the compact family block analysis were used: one without fertilizer treatment and one with fertilizer treatment. In the first of these forms, two sets were used, one for 1968, 1969 and 1970 total heights and one for 1970, 1971 and 1972 dates of bud break (Table III-3). The model used for 1972 total height including fertilizer treatment is presented in Table III-4.

In the tables for compact family block analyses, the number of families in the degrees of freedom column is designated by an f, because a separate computation is done for each stand, and the number of families is different for each.

It is believed that the restriction on randomization of families does not preclude the use of a combined analysis, since a factorial split plot is a form of analysis in which the split plot treatments are randomized in just this way. Furthermore, in the combined form of analysis the family term is nested. Thus, the family within stand term involves sampling within each stand, and there is no reason, in this type of situation, that the randomization of families should not be restricted to the stand from which they are samples.

With the preceding considerations in mind, a combined analysis was carried out on each of the sets of data. Bartlett's Test was performed on the error variances of the family portions of the compact family block analyses, to determine whether the error variances were homogeneous so that it would be known whether the combined analysis overestimated or underestimated the error variance for some stands.

Three forms of the combined analysis were employed: one without fertilizer treatments or years, one with fertilizer treatment and without years and one without fertilizer but with years. Table III-5 presents the combined analysis used for the analysis of 1968, 1969 and 1970 total heights; 1970, 1971 and 1972 dates of bud break; 1970 number of flushes, and 1970 growth increment. The second combined analysis model (Table III-6) was used for 1972 height and diameter. The third

Table III-3. Compact Family Block Analysis I

n	Source	d.f.[a]	d.f.[b]	Components of Variance
6	Stand	5	5	$\sigma^2_{BS} + b\theta^2_S$
7	Block	6	4	$\sigma^2_{BS} + s\sigma^2_B$
	Block x Stand	30	20	σ^2_{BS}
f	Family	f-1	f-1	$\sigma^2_W + \sigma^2_{BF} + wb\theta^2_F$
7	Block	6	4	$\sigma^2_W + w\sigma^2_{BF} + wf\sigma^2_B$
	Block x Family	6(f-1)	4(f-1)	$\sigma^2_W + w\sigma^2_{BF}$
12	Within Plot	77f	10f	σ^2_W

[a] Used for analyzing 1968, 1969 and 1970 total heights.

[b] Used for analyzing 1970, 1971 and 1972 dates of bud break.

Table III-4. Compact Family Block Analysis II.[a]

n	Source	d.f.	Components of Variance
2	Fertilizer (N)	1	$s\sigma^2_{RN} + r\theta^2_N$
3	Replication	2	$n\sigma^2_R$
	Replication x Fertilizer	2	$s\sigma^2_{RN}$
6	Stand	5	$n\sigma^2_{RS} + rn\theta^2_S$
	Stand x Fertilizer	5	$\sigma^2_{RSN} + r\sigma^2_{NS}$
	Replication x Stand	10	$n\sigma^2_{RS}$
	Replication x Stand x Fertilizer	10	σ^2_{RSN}
2	Fertilizer	1	$\sigma^2_W + wf\sigma^2_{RN} + wfr\theta^2_N$
3	Replication	2	$\sigma^2_W + wfn\sigma^2_R$
	Replication x Fertilizer	2	$\sigma^2_W + wf\sigma^2_{RN}$
f	Family	f-1	$\sigma^2_W + wn\sigma^2_{RF} + wrn\theta^2_F$
	Family x fertilizer	f-1	$\sigma^2_W + w\sigma^2_{RFN} + wr\sigma^2_{NF}$
	Replication x Family	2(f-1)	$\sigma^2_W + wn\sigma^2_{RF}$
	Replication x Family x Fertilizer	2(f-1)	$\sigma^2_W + w\sigma^2_{RFN}$
12	Within Plot	66f	σ^2_W

[a] Used for analyzing 1972 total height.

Table III-5. Combined Analysis I.

n	Source	d.f.[a]	d.f.[b]	d.f.[c]	d.f.[d]	Components of Variance
3	Stand	2	2	5	5	$\sigma^2_W + wf\sigma^2_{BS} + wbf\theta^2_S$
7	Block	6	4	6	4	$\sigma^2_W + wf\sigma^2_{BS} + wfs\sigma^2_B$
	Block x Stand	12	8	30	20	$\sigma^2_W + wf\sigma^2_{BS}$
10	Family/Stand	27	27	24	24	$\sigma^2_W + w\sigma^2_{BF(S)} + wb\theta^2_{F(S)}$
	Block x Family/Stand	162	108	144	96	$\sigma^2_W + w\sigma^2_{BF(S)}$
12	Within Plot	2310	300	2310	300	σ^2_W

[a] Used for the analysis of 1968, 1969 and 1970 total heights, balanced with 3 stands.

[b] Used for the analysis of 1970, 1971 and 1972 dates of bud break, 1970 number of flushes and 1970 growth increment, balanced with 3 stands.

[c] Used for the analysis of 1968, 1969 and 1970 total heights, balanced with 6 stands.

[d] Used for the analysis of 1970, 1971 and 1972 dates of bud break, 1970 number of flushes and 1970 growth increment, balanced with 6 stands.

Table III-6. Combined Analysis II.

n	Source	d.f.[a]	d.f.[b]	Components of Variance
2	Fertilizer (N)	1	1	$\sigma_W^2 + wfs\sigma_{RN}^2 + wfsr\theta_N^2$
3	Replication	2	2	$\sigma_W^2 + wfsn\sigma_R^2$
	Replication x Fertilizer	2	2	$\sigma_W^2 + wfs\sigma_{RN}^2$
3	Stand	2	5	$\sigma_W^2 + sfn\sigma_{RS}^2 + wrfn\theta_S^2$
	Stand x Fertilizer	2	5	$\sigma_W^2 + wf\sigma_{RSN}^2 + wfr\sigma_{SN}^2$
	Replication x Stand	4	10	$\sigma_W^2 + wfn\sigma_{RS}^2$
	Replication x Stand x Fertilizer	4	10	$\sigma_W^2 + wf\sigma_{RSN}^2$
10	Family/Stand	27	24	$\sigma_W^2 + wr\sigma_{RF(S)}^2 + wrn\theta_{F(S)}^2$
	Fertilizer x Family/Stand	27	24	$\sigma_W^2 + w\sigma_{RNF(S)}^2 + wr\sigma_{NF(S)}^2$
	Replication x Family/Stand	54	48	$\sigma_W^2 + wn\sigma_{RF(S)}^2$

Table III-6 (continued)

n	Source	d.f.[a]	d.f.[b]	Components of Variance
	Replication x Fertilizer x Family/Stand	54	48	$\sigma^2_W + w\sigma^2_{RNF(S)}$
12	Within Plot	1980	1980	σ^2_W

[a] Used for the analysis of 1972 height and diameter, balanced with 3 stands.

[b] Used for the analysis of 1972 height and diameter, balanced with 6 stands.

model (Table III-7) was used for a temperature summation, to be explained later. For each combined analysis, there are two sets of degrees of freedom because the number of families in each stand was balanced in two ways. The first way of balancing the number of families was by deleting all families except ten families in each of three stands, leaving a total of thirty families. These three stands were selected because they were the only three stands which contained at least ten families each. The second way was by deleting all families except five in each of the six stands, leaving, again, a total of thirty families. The families to be deleted were selected with the use of a random number table.

The first reason for balancing the number of families in each stand was that the PROC ANOVA routine would not give the correct value for the sum of squares of all families within stand term if an unbalanced analysis were used. The second was that the calculation of the coefficients of the variance components would be a monumental task if an unbalanced analysis were used.

Aside from the legitimacy of using the combined analysis, there were other reasons for its use. It was thought that a single estimate of heritability would be more consistent, more reliable and more desirable than an estimate for each stand. Further, the relative sizes of the stand and family variances can be compared using the combined analysis but not with the compact family block analysis.

The components of variance were omitted from many of the analysis of variance tables because their inclusion would have been unduly repetitious.

Fertilizer effects were assumed to be fixed, since there were only two levels of this factor. Stand effects were assumed to be fixed; first, because the source locations are not representative of the species range and would not allow inferences to be made about the species population; and second, because, within the area from which the stands were selected, the choice of stand locations is discontinuous, with five stands widely separated from the sixth and with two of the stands located less than twenty miles from each other. Even though the effects due to stands were assumed to be fixed, however, the results might be

Table III-7. Combined Analysis III.

n	Source	d.f.[a]	d.f.[b]	Components of Variance
3	Year	2	2	$\sigma^2_W + wfs\sigma^2_{BY} + wbfs\sigma^2_Y$
5	Block	4	4	$\sigma^2_W + wfs\sigma^2_{BY} + wyfs\sigma^2_B$
	Block x Year	8	8	$\sigma^2_W + wfs\sigma^2_{BY}$
3	Stand	2	5	$\sigma^2_W + wf\sigma^2_{SBY} + wfy\sigma^2_{SB} + wfb\sigma^2_{SY} + wfby\theta^2_S$
	Stand x Year	4	10	$\sigma^2_W + wf\sigma^2_{SBY} + wfb\sigma^2_{SY}$
	Block x Stand	8	20	$\sigma^2_W + wf\sigma^2_{SBY} + wfy\sigma^2_{SB}$
	Block x Stand x Year	16	40	$\sigma^2_W + sf\sigma^2_{SBY}$
10	Family/Stand	27	24	$\sigma^2_W + w\sigma^2_{BYF(S)} + wy\sigma^2_{BF(S)} + wb\sigma^2_{YF(S)} + wby\theta^2_{F(S)}$
	Year x Family/Stand	54	48	$\sigma^2_W + w\sigma^2_{BYF(S)} + wb\sigma^2_{YF(S)}$
	Block x Family/Stand	108	96	$\sigma^2_W + w\sigma^2_{BYF(S)} + wy\sigma^2_{BF(S)}$

Table III-7. (continued)

n	Source	d.f.[a]	d.f.[b]	Components of Variance
	Block x Year x Family/Stand	216	192	$\sigma^2_W + w\sigma^2_{BYF(S)}$
3	Within Plot	900	900	σ^2_W

[a] Used for the 3-stand analysis of a temperature summation.

[b] Used for the 6-stand analysis of a temperature summation.

applied to the Tennessee Valley, since five of the stands are located along the course of the Tennessee River or its tributaries.

Family effects were assumed to be fixed because individual mother trees were not selected randomly. In three of the stands, one mother tree was a superior phenotype selection. All the other trees had to meet the single criterion, as stated before, of containing a good butt log. Furthermore, the mother trees in each stand were not widely separated to preclude many of the progenies' being full sibs.

Components of variance were derived using the method of Schultz (1955) and, for the third form of the combined analysis, which included a years term, the model **of Wilm** (1945). Duncan's New Multiple Range Test was used to distinguish between means.

Heritability Estimates

Heritability estimates were computed in a manner which was very nearly the same for all analysis of variance models. For the first compact family block analyses, the method of computation was:

$$h^2 = \frac{4\theta_F^2}{\sigma_W^2 + \sigma_{BF}^2 + \theta_F^2} .$$

For the second compact family block analysis, the method was:

$$h^2 = \frac{4\theta_F^2}{\sigma_W^2 + \sigma_{RF}^2 + \theta_F^2} .$$

For the first combined analysis, the formula was:

$$h^2 = \frac{4\theta_{F(S)}^2}{\sigma_W^2 + \sigma_{BF(S)}^2 + \theta_{F(S)}^2} .$$

And for the second combined analysis, the form was:

$$h^2 = \frac{4\theta_{F(S)}^2}{\sigma_W^2 + \sigma_{RF(S)}^2 + \theta_{F(S)}^2} .$$

Since only one location was used, the genetic component estimated was assumed, as in Namkoong et al., (1966) to represent $\sigma^2_A + \sigma^2_{AE}$, where σ^2_A is the causal component due to additive inheritance and σ^2_{AE} is that due to the interaction of additive inheritance with location.

Heritability estimates for 1972 total height were corrected for maternal effects according to the following model:

$$h^2 = \frac{4(1 - r^2)\theta^2_{F(S)}}{\sigma^2_W + \sigma^2_{RF(S)} + (1 - r^2)\theta^2_{F(S)}},$$

where r = correlation between acorn weight and 1972 total height.

Gains

The first method of calculating genetic gains is taken from Namkoong et al, (1966) and is illustrated as follows for the first combined analysis, using family and within family selection but no stand selection:

$$G = i_1 \frac{\sigma^2_{F(S)}}{\sigma_1} + i_2 \frac{3\sigma^2_{F(S)}}{\sigma_2},$$

where:

G = genetic gain

i_1 = family selection intensity

i_2 = within family selection intensity

$$\sigma^2_1 = \frac{\sigma^2_W}{wb} + \frac{\sigma^2_{BF(S)}}{b} + \sigma^2_{F(S)}$$

$$\sigma^2_2 = \sigma^2_W + \sigma^2_{BF(S)} + 3\sigma^2_{F(S)} .$$

The second way of computing gains was on the basis of stand and within plot selection. The stand gain was computed as the difference between the overall mean and that of the selected stand. This gain, a realized one, is a predicted gain as well, since it was assumed that the selected stand will reach the same equilibrium in the next generation that it has in the present one. The predicted gain for within plot selection was computed as in the first method.

A third way of computing gains was based on a new progeny test from a selected stand. It was proposed that one return to the source location of a selected stand, make an acorn collection of 30 open-pollinated families and outplant them in the present outplanting location. It was assumed that the realized and predicted stand gains would be the same as in the second method and that the variance components for the progeny test would be the same as in the first method. Gains were predicted for the offspring of the proposed progeny test on the basis of stand, family and within plot selection.

The fourth method of computing gains was the same as the first, except that a correction was made for maternal effects. A correlation was found between acorn weight and both total height and diameter six years from seed. The correlation coefficient, r, was used in the following way to make the correction:

$$G = i_1 \frac{(1 - r^2)\sigma^2_{F(S)}}{\sigma_1} + i_2 \frac{3(1 - r^2)\sigma^2_{F(S)}}{\sigma_2}$$

where:

$$\sigma_1 = \frac{\sigma^2_W}{wb} + \frac{\sigma^2_{RF(S)}}{b} + (1 - r^2)\sigma^2_{F(S)}$$

$$\sigma_2 = \sigma^2_W + \sigma^2_{RF(S)} + 3(1 - r^2)\sigma^2_{F(S)} .$$

The quantity $(1 - r^2)$ was multiplied by the family within stand component of variance because r^2 is the fraction of the linear variances of total height and diameter which can be attributed to their linear regressions on acorn weight, while $(1 - r^2)$ is the fraction free from the effect of acorn weight (Snedecor and Cochran, 1967). The family within stand component of variance was the only component multiplied by $(1 - r^2)$ because it is assumed that acorn weight is strongly inherited at the family level. Thus, most of the effect of acorn weight would be on the family within stand component. It is recognized, however, that these calculations yield only an approximation of that proportion of the predicted gain which is free from maternal effects.

Stand and Family Effects

The relative importance of stand and family effects was estimated by using the sum of all the components of variance in a given analysis of variance model as the phenotypic variance and taking the stand and the family components of variance as proportions of the phenotypic variance thus accounted for.

Correlation and Regression

PROC REGR with the CORR option was used to obtain correlations between acorn weight and 1968, 1969, 1970 and 1972 total heights. In addition, this procedure was used with the stated option to obtain all possible two-way correlations among the following variables: 1970, 1971 and 1972 total heights; 1970, 1971 and 1972 dates of bud break; 1970, 1971 and 1972 height increments; 1970, 1971 and 1972 numbers of flushes; latitude, longitude and elevation of the seed sources; a temperature summation for 1970, 1971 and 1972 at the outplanting site, and a moisture index for 1970, 1971 and 1972 at the outplanting site. These correlations were used to determine which independent variables in later regression analyses were truly independent of each other and to determine which sets of variables should be used in a PROC STEPWISE analysis.

PROC STEPWISE was used with the NOSTEP and MAXR options to find the regression equations, using different combinations of variables, which yield the largest coefficients of determination. In these analyses, 1970, 1971 and 1972 total heights and height increments were used as dependent variables; 1970, 1971 and 1972 dates of bud break and numbers of flushes were used at one time as dependent and at another time as independent variables; and latitude, longitude and elevation of the seed sources, a temperature summation, and a moisture index for 1970, 1971 and 1972 were used as independent variables.

PROC REGR was used to find the coefficients of determination and the regression coefficients for three regression equations, one for each year, in which number of days after March 31 served as the dependent variable and a temperature summation served as the independent variable. In addition, the corrected and uncorrected sums of squares and cross products and sums were obtained using the USSCPΣ SSCP and SIMPLE options of the REGR procedure. These statistics were then used in an analysis of covariance computation, as outlined by Snedecor and Cochran (1967), to determine whether the three regression lines were different.

The number of days after March 31 and temperature summations for the three years, which had been six variables (two variables x three years), were then combined to form two variables which were replicated by years. "Years" was thus a classification variable for each of the two observational variables. Next, a single regression equation was computed, using number of days after March 31 as the dependent variable and a temperature summation for each of the three years as the independent variable. Each number of days after March 31 and each temperature summation was thus replicated three times, once for each year. Furthermore, an additional regression equation was computed, in which number of days after March 31 for the three years was the dependent variable and the temperature summation plus the square of the temperature summation were the independent variables.

Calculation of Temperature Summation and Moisture Index

The temperature summation was computed from the hourly temperatures at the Oak Ridge National Laboratory station of the National Oceanic and Atmospheric Administration. The following formula was used:

$$TS_n = \sum_{i=1}^{n} HS_i$$

where:

$$HS_i = \frac{1}{24} \sum_{j=1}^{24} (T_j - 32)$$

T_j = temperature at hour j, degrees Fahrenheit

n = number of days from January 31 at which the accumulation of temperature ends

TS_n = cumulative temperature summation over n days.

In practice, n is the same as the date of bud break in number of days after January 31.

The moisture index was computed in the following manner[1]:

$$x_i = x_{i-1} + P_i - E_i$$

where:

x_i = moisture index for day i

x_{i-1} = moisture index for the previous day

P_i = precipitation on day i

E_i = evaporation on day i.

The evaporation data were from Weather Service records for Knoxville, Jefferson City and the Neptune 3S station, which is run by the Corps of Engineers in Cheatham County. Evaporation data for each month was taken from the station, among these three, which was nearest and from which data was available for that month in Weather Service Climatological Data for Tennessee.

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[1] Bell, F. F., unpublished class notes for Plant and Soil Science 2130.

CHAPTER IV

RESULTS AND DISCUSSION

Compact Family Block Analysis

The effect of fertilizer on total height is not presented because the determination of the effect of fertilizer was not a goal of this study. It was decided to exclude the determination of fertilizer effects from the study when it was learned that the genotype-fertilizer interactions were not significant at the five percent level and because it was necessary to place limits on the paper. In addition, it was thought that the discussion of the main effect of fertilizer on total height would be repetitive of results and discussion obtained and presented for northern red oak by other workers.

It was decided not to present the data for number of flushes because it seemed related to the fertilizer effect primarily and because it was necessary to limit the scope of the study. In addition, because the length of each flush was not entered on the computer card, inferences could not be made with regard to the relative importance of number of flushes and growth rate.

Total Height

The source effect was significant at the one percent level or better for 1968, 1969, 1970 and 1972 total heights, using the compact family block form of analysis. Mean heights for each of these years, by source, are presented in Table IV-1. As indicated in the table, the western Kentucky source was shown by Duncan's New Multiple Range Test to differe significantly at the 5 percent level from four other sources, but not from the Norris Dam source, with regard to total height in 1972. No other sources are significantly different from each other with regard to 1972 total height.

Table IV-1. Mean heights by source and year, in feet, based on all 49 families.

Source	1968 Ht.	1969 Ht.	1970 Ht.	1972 Ht.
Western Kentucky	1.68	2.43	3.31	5.22 [a]
Norris Dam	1.68	2.16	2.86	4.31
North Alabama	1.60	2.18	2.85	3.92
Ohio	1.27	1.72	2.38	3.36
Norris Lake	1.31	1.79	2.43	3.25
Cumberland Plateau	1.23	1.74	2.39	3.20

[a] The western Kentucky source is significantly different from four other sources at the 5 percent level of probability.

Table IV-2 presents estimates of components of variance and heritabilities, by source, for 1968, 1969, 1970 and 1972 total heights. As may be seen from the table, two of the estimates of heritability for 1968 total height are greater than one, and four of the estimates of heritability are based on estimates of the variance component for families which were not significantly different from zero at the five percent level.

Bartlett's Test for homogeneity of variance was performed on the error variances used to test the family effect, and the results indicate that variances were homogeneous at the five percent level for 1969, 1970 and 1972 total heights but were heterogeneous for 1968 total height.

Bud Break

The source effect was significant at the one percent level or better for 1970, 1971 and 1972 dates of bud break, based on the compact family block analysis. Mean dates of bud break for each of these years are presented by source in Table IV-3. By Duncan's New Multiple Range Test, the North Alabama, Norris Lake and Ohio sources were significantly different from each other and from the other three sources in all three

Table IV-2. Estimates of components of variance and heritabilities, by source, for 1968, 1969, 1970 and 1972 total heights.

Source	Variable	$\hat{\theta}^2_F$	σ^2_{RF}	σ^2_W	h^2
Ohio	1972 Ht.	46.3	25.1	300.4	.50
	1970 Ht.	11.0	9.5	92.1	.39
	1969 Ht.	7.0	4.2	49.6	.46
	1968 Ht.	2.3	0.0	14.1	.57
Cumberland Plateau	1972 Ht.	35.3	55.4	387.4	.30
	1970 Ht.	10.7	17.0	108.2	.31
	1969 Ht.	6.8	8.9	62.6	.35
	1968 Ht.	6.4	1.4	17.2	1.02
Norris Dam	1972 Ht.	33.4	14.0	365.1	.32
	1970 Ht.	2.9	15.0	96.0	.10 n.s.[a]
	1969 Ht.	1.9	6.6	54.4	.12
	1968 Ht.	1.5	1.7	17.7	.29
Norris Lake	1972 Ht.	-2.8	63.0	329.7	-.03 n.s.
	1970 Ht.	6.3	15.6	88.0	.23
	1969 Ht.	5.8	5.1	51.0	.37
	1968 Ht.	6.9	0.3	13.9	1.30
North Alabama	1972 Ht.	-2.3	8.1	380.9	-.02 n.s.
	1970 Ht.	1.7	7.7	112.3	.06 n.s.
	1969 Ht.	2.2	2.8	69.1	.12
	1968 Ht.	4.7	1.9	22.8	.64
Western Kentucky	1972 Ht.	59.4	16.1	318.7	.60
	1970 Ht.	14.3	18.0	99.3	.43
	1969 Ht.	7.9	9.7	62.5	.40
	1968 Ht.	4.6	1.2	16.8	.82

[a] n.s. indicates the family component in the analysis of variance was not significant at the 5 percent level of probability.

Table IV-3. Mean dates of bud break by source and year, in days after March 31, based on all 49 families.

Source	1970 Days	1971 Days	1972 Days
North Alabama	22.3	25.3	21.2
Cumberland Plateau	24.9 [a]	29.6	26.1
Western Kentucky	25.0	29.8	26.2
Norris Dam	25.7	30.9	27.4
Norris Lake	27.8	33.5	31.0
Ohio	34.2	40.8	38.3

[a] Three dates connected with line are not significantly different at the 5 percent level of probability.

years (five percent level). The Cumberland Plateau, western Kentucky and Norris Dam sources could not be separated from each other at the five percent level. All sources broke buds in exactly the same order each year, as may be seen from the table.

Estimates of components of variance and heritability for 1970, 1971 and 1972 dates of bud break are presented in Table IV-4. Four of the heritability estimates are greater than one. Six heritability estimates are based on estimates of the component of variance for the family effect which are not significantly different from zero at the five percent level.

The fertilizer effect on 1972 date of bud break was tested and found to be not significant at the five percent level by constructing artificially two replications containing four blocks, all of which had been observed for date of bud break and two of which had been fertilized. Since the fertilizer treatment was found not to affect date of bud break, this variable was omitted in further analysis, and the simpler form of both the compact family block and the combined analysis was used.

Bartlett's Test was performed on the error variances used to test for the family effect, and the results indicate that the variances were homogeneous at the five percent level for 1970 and 1972 dates of bud break, but were heterogeneous for 1971 date of bud break.

Combined Analysis

Total Height

Levels of significance of the source and family effects for combined analyses of 1968, 1969, 1970 and 1972 total heights and 1972 diameter, based on balancing with three stands and with six stands, are given in Table IV-5. It is evident from the table that the stand and family effects are significant at the five percent level or better for all these variables.

Estimates of components of variance and heritabilities for 1972 total height and diameter based on three stands and on six stands are presented in Table IV-6. The heritability estimates for these two

Table IV-4. Estimates of variance components and heritability for 1970, 1971 and 1972 dates of bud break, by source.

Source	Variable	θ^2_F	σ^2_{RF}	σ^2_W	h^2
Ohio	1970 Bud Break	2.38	0.00	22.7	.38
	1971 Bud Break	2.81	2.73	13.5	.59
	1972 Bud Break	1.49	3.00	20.0	.24 n.s.[a]
Cumberland Plateau	1970 Bud Break	0.41	1.59	6.9	.18 n.s.
	1971 Bud Break	0.72	11.10	14.8	.11 n.s.
	1972 Bud Break	1.52	10.22	19.0	.20 n.s.
Norris Dam	1970 Bud Break	1.55	1.54	6.4	.65
	1971 Bud Break	10.10	0.00	15.9	1.55
	1972 Bud Break	13.16	0.88	24.3	.82
Norris Lake	1970 Bud Break	1.02	1.16	10.5	.32
	1971 Bud Break	1.54	4.28	21.9	.22 n.s.
	1972 Bud Break	4.55	0.00	38.2	.43
North Alabama	1970 Bud Break	1.27	1.82	4.3	.68
	1971 Bud Break	5.32	2.03	8.2	1.37
	1972 Bud Break	7.72	1.80	7.7	1.80
Western Kentucky	1970 Bud Break	1.93	1.07	4.4	1.04
	1971 Bud Break	2.27	3.01	13.4	.49 n.s.
	1972 Bud Break	4.35	1.56	16.4	.78

[a] n.s. indicat-s the family component in the analysis of variance was not significant at the 5 percent level of probability.

Table IV-5. Levels of significance of the source and family effects for combined analyses of 1968, 1969, 1970 and 1972 total heights and 1972 diameter.

Variable	3 Stands	
	Significance of θ^2_S	Significance of $\theta^2_{F(S)}$
1972 Height	0.01	0.01
1972 Diameter	0.05	0.05
1970 Height	0.002	0.0001
1969 Height	0.0005	0.0001
1968 Height	0.0001	0.0001
	6 Stands	
	Significance of θ^2_S	Significance of $\theta^2_{F(S)}$
1972 Height	0.01	0.01
1972 Diameter	0.01	0.01
1970 Height	0.0001	0.0001
1969 Height	0.0002	0.0001
1968 Height	0.0001	0.0001

Table IV-6. Estimates of components of variance and heritabilities for 1972 total height and diameter.

Variable	3 Stands			
	$\theta^2_{F(S)}$	$\sigma^2_{RF(S)}$	σ^2_W	h^2
1972 Height	21.92	46.78	360.94	.20
1972 Diameter	0.4808	1.152	9.0095	.18
	6 Stands			
	$\theta^2_{F(S)}$	$\sigma^2_{RF(S)}$	σ^2_W	h^2
1972 Height	36.02	19.00	334.82	.37
1972 Diameter	0.9249	0.448	8.9856	.36

characters are higher and more nearly of the same size when the analysis is based on five families in each of six stands than when it is based on ten families in each of three stands, although each method includes 30 families. This is not to say, however, that the heritability estimates which are nearly the same size are necessarily better estimates simply for that reason.

Table IV-7 presents estimates of components of variance and heritabilities for 1968, 1969 and 1970 total heights, based on 30 families in three stands and in six stands. The heritability estimates for 1968 total height are disproportionately high, as may be seen in the table.

The relative sizes of the components of variance for 1968, 1970 and 1972 total heights and 1972 diameter, based on three and six sources and expressed as percentages of total phenotypic variance, are presented in Table IV-8.

Table IV-7. Estimates of components of variance and heritabilities for 1968, 1969 and 1970 total heights.

	3 Stands			
Variable	$\theta^2_{F(S)}$	$\sigma^2_{RF(S)}$	σ^2_W	h^2
1970 Height	6.96	15.92	96.88	.23
1969 Height	5.10	6.87	55.83	.30
1968 Height	5.18	1.17	16.06	.92
	6 Stands			
	$\theta^2_{F(S)}$	$\sigma^2_{RD(S)}$	σ^2_W	h^2
1970 Height	9.16	14.76	96.55	.30
1969 Height	5.82	6.34	56.85	.33
1968 Height	3.67	1.05	17.55	.66

When the analysis is balanced with three stands, the within plot component is larger than when the analysis is balanced with six stands. The within plot component is much greater than either the stand or the

Table IV-8. Relative sizes of components of variance for 1968, 1969, 1970 and 1972 total heights and 1972 diameter, expressed as percentages of total phenotypic variance.

Variable	θ^2_S	$\theta^2_{F(S)}$	σ^2_W	θ^2_N	σ^2_R	σ^2_{RN}	σ^2_{SN}	σ^2_{RS}	σ^2_{RSN}	$\sigma^2_{NF(S)}$	$\sigma^2_{RF(S)}$	$\sigma^2_{RNF(S)}$	σ^2_{Total} [a]
3 Stands													
1972 Height	5	3	55	3 n.s.	2	2	0 n.s.	1	5	1 n.s.[b]	7	16	100
1972 Diameter	4	3	53	4 n.s.	3	2	0 n.s.	1	9	1 n.s.	7	13	100
1970 Height	4	5	72		4			2			13		100
1969 Height	6	7	73		4			2			8		100
1968 Height	20	18	56		1			1			4		100
6 Stands													
1972 Height	9	5	47	6	3	1	0 n.s.	4	5	0 n.s.	3	17	100
1972 Diameter	10	5	47	8	3	0 n.s.	0 n.s.	4	5	1 n.s.	2	15	100
1970 Height	6	7	70		1 n.s.			5			11		100
1969 Height	7	7	72		1 n.s.			5			8		100
1968 Height	10	14	69		1			2			4		100

[a] Explanation of subscripts: S = stands; F(S) = families within stand; W = within plot; N = fertilizer (nitrogen); R = replications; RN = replications times fertilizer; SN = stands times fertilizer; RS = replications times stands; RSN = replications times stands times fertilizer; NF(S) = fertilizer times families within stand; RF(S) = replications times families within stand; RNF(S) = replications times fertilizer times families within stand.

[b] n.s. indicates the effect was not significant at the 5 percent level.

family component, no matter which way the analysis is balanced; but for height, it becomes relatively smaller as the trees grow older and taller.

Heritability estimates for 1972 total height, when corrected for maternal effects, were 0.18 based on the 3-stand analysis. In each case, the difference is only 0.02, so the effect of acorn weight on heritability of total height at six years from seed is not great.

Gains

When only the 49 families used in the analysis are considered, the total area of the outplanting is 3.40 acres, containing 4116 trees. The number of trees per acre is thus 1210. If half of the families are rogued and if 11 trees in every remaining 12-tree plot are rogued, the resulting density would be 50.4 trees per acre, a reasonable density for a seed orchard. There is, however, no guarantee that if the families and individuals thus rogued are chosen on the basis of inferiority in 1972 height or diameter the remaining trees will be evenly spaced or situated so as to avoid inbreeding. However, if, as the first method of selection, an open-pollinated seed orchard is created on this site by these intensities of among-family and within-family selection, the mean height and diameter of the progenies should be larger than that of the original experimental population by the percentages given in Table IV-9. These percentages are the gains predicted using the formula on page 37 and the components of variance obtained by balancing the analysis of variance with ten families in each of three stands and with five families in each of six stands. Predicted gains are generally higher for the analyses based on six stands than for those based on three stands.

If, as the second selection method, the western Kentucky stand and four trees in each twelve-tree plot within that stand are selected, there should be an increase in the mean height of the open-pollinated progeny on a similar site of 27 percent due to stand selection and 12 percent due to within-plot selection--a total of 39 percent. The gains are taken as a percentage of the mean of the original experimental population and are based on the analysis of variance balanced with five families in each of six stands.

Table IV-9. Predicted gains in height and diameter at six years from seed, as percentages of the population means.

	Height	Diameter
3 Stands	22	20
6 Stands	31	33

If 50 open-pollinated families of acorns are collected from the western Kentucky location and outplanted on the same experimental site, it is assumed that the mean of the new experimental population will be the same as that of the western Kentucky stand in the present experiment and that the components of variance will be the same. Furthermore, if half the families and one tree in each twelve-tree plot within those families are selected, the open-pollinated progenies which would result, if planted on a similar site, should have a gain in mean total height due to stand selection which, as in the preceding case, would be 27 percent of the mean of the original population, a gain due to among-family plus within-family selection which would be 21 percent, a total of 58 percent. This is the third method of selection and is also based on an analysis of variance balanced with five families in each of six stands.

When the first selection method is corrected for maternal effects, as shown in Table IV-9, the predicted gain in total height after five years in the field, based on balancing with six stands, is 28 percent, as opposed to 31 percent without the correction. When the third method is corrected for maternal effects, the predicted gain is 55 percent, as opposed to 58 percent without correction.

Means for 1972 total height and diameter, based on the three-stand balanced analysis, are shown in Table IV-10. Duncan's New Multiple Range Test shows the Norris Dam source to be significantly different from the Cumberland Plateau and Norris Lake sources with regard to both characters at the five percent level. Means for the same two variables, based on the six-stand balanced analysis are given

Table IV-10. 1972 mean heights, in feet, and diameter, in inches, by source, based on ten families in each of three sources.

Source	1972 Height	1972 Diameter
Norris Dam	4.31	0.64
Cumberland Plateau	3.38[a]	0.52
Norris Lake	3.35	0.51

[a] Two sources connected by lines are not significantly different at the 5 percent level of probability.

in Table IV-11. Duncan's Test shows the western Kentucky source to be significantly different from all other sources with regard to both characters at the five percent level. In addition, the Norris Lake source is significantly different from the Norris Dam and North Alabama sources.

Table IV-11. 1972 mean heights, in feet, and diameters, in inches, by source, based on 5 families in each of 6 sources.

Source	1972 Height	1972 Diameter
Western Kentucky	5.64	0.88
Norris Dam	4.40[a]	0.66
North Alabama	4.33	0.64
Ohio	4.04	0.56
Cumberland Plateau	3.55	0.54
Norris Lake	3.15	0.46

<u>Bud Break</u>

Both the stand and the family effects were found to be significant at the one percent level or better in the combined form of analysis for 1970, 1971 and 1972 dates of bud break with the analyses balanced in both of the ways mentioned previously.

Estimates of components of variance and heritabilities for 1970, 1971 and 1972 dates of bud break using both methods of balancing are presented in Table IV-12. All but one of the estimates of heritability are rather high, but all are less than one.

Table IV-12. Estimates of components of variance and heritabilities for 1970, 1971 and 1972 dates of bud break.

	3 Stands			
Variable	$\theta^2_{F(S)}$	$\sigma^2_{RF(S)}$	σ^2_W	h^2
1970 Bud Break	0.97	1.50	8.02	.37
1971 Bud Break	4.21	5.14	17.51	.63
1972 Bud Break	6.63	3.14	26.24	.74
	6 Stands			
	$\theta^2_{F(S)}$	$\sigma^2_{RF(S)}$	σ^2_W	h^2
1970 Bud Break	1.56	1.34	8.61	.54
1971 Bud Break	4.83	3.94	13.29	.88
1972 Bud Break	4.30	4.30	19.07	.70

Relative sizes of variance component estimates are presented in Table IV-13 as percentages of total phenotypic variance. From the table, it may be seen that the stand component accounts for a greater proportion of the total phenotypic variation than the family component and a somewhat greater proportion than the within plot component when the analysis is balanced with six stands. The within plot component is several times greater, however, than either the stand or the family component when the analysis is balanced with three stands. Differences among years are not appreciable.

Table IV-13. Relative sizes of variance component estimates as percentages of total phenotypic variance for 1970, 1971 and 1972 dates of bud break.

Variable	θ^2_S	$\theta^2_{F(S)}$	σ^2_W	σ^2_R	σ^2_{RS}	$\sigma^2_{RF(S)}$	σ^2_{Total}
3 Stands							
1970 Bud Break	18	7	60	2 n.s.[a]	2	11	100
1971 Bud Break	10	13	55	2 n.s.	4	16	100
1972 Bud Break	14	15	60	2 n.s.	2 n.s.	7	100
6 Stands							
1970 Bud Break	56	6	30	0 n.s.	3	5	100
1971 Bud Break	52	10	28	0 n.s.	2	8	100
1972 Bud Break	49	8	34	0 n.s.	1 n.s.	8	100

[a] n.s. indicates the effect was not significant at the five percent level.

Mean dates of bud break for 1970, 1971 and 1972 based on an analysis using three stands are presented in Table IV-14. Duncan's Test indicates that the Norris Lake source is significantly different in all three years from the Norris Dam and the Cumberland Plateau sources (five percent level). In Table IV-15 means are presented for the same three variables based on an analysis using six stands. Sources broke buds in the same order in all three years. In Table IV-15, it is apparent that better mean separation is obtained for 1970 and 1972 dates of bud break by this form of the combined analysis than by the compact family block analysis.

Correlation and Regression

In the discussion which follows, correlation coefficients are reported only for correlations which were significant at the five percent

Table IV-14. Mean dates of bud break by source and year, in days after March 31, based on 10 families in each of 3 stands.

Source	1970 Bud Break	1971 Bud Break	1972 Bud Break
Norris Lake	28.0	33.4	31.0
Norris Dam	25.8[a]	30.9	27.4
Cumberland Plateau	24.9	29.6	26.0

[a] Sources connected by the same line are not significantly different at the 5 percent level of probability.

Table IV-15. Mean dates of bud break by source and year, in days after March 31, based on 5 families in each of 6 stands.

Source	1970 Bud Break	1971 Bud Break	1972 Bud Break
Ohio	33.9	40.2	37.3
Norris Lake	27.7	33.1	30.8
Norris Dam	25.7	30.7	27.2
Cumberland Plateau	24.7[a]	29.8	26.4
Western Kentucky	24.7	29.2	25.4
North Alabama	22.3	25.3	21.2

[a] Sources connected by the same line are not significantly different at the 5 percent level.

level. Coefficients of determination are reported only for regressions which were significant at the five percent level and in which the sequention effect of each variable was significant at the five percent level.

Statistical Models for Temperature Summation and Moisture Index

As shown in Table IV-16, the temperature summation and date of

Table IV-16. Values of r for correlations[a] among dates of bud break and temperature summations for three years.

	1970 B.B.	1971 B.B.	1972 B.B.	1970 T.S.	1971 T.S.	1972 T.S.
1970 Bud Break		.83	.76	.99	.84	.77
1971 Bud Break			.86	.83	.99	.86
1972 Bud Break				.76	.86	.99
1970 Temperature Summation					.84	.77
1971 Temperature Summation						.86
1972 Temperature Summation						

[a] Significant at the five percent level.

bud break were highly correlated with each other, and each variable was highly correlated with itself and with the other in different years. Correlations between the moisture index and date of bud break are presented in Table IV-17. In reality, these are correlations between number of days after March 31 and the temperature summation and moisture index. The temperature summation and moisture index are associated with the number of days after March 31. Neither the date of bud break nor the environmental variables is associated with the same day each year. The question, then, is whether the date of bud break is associated with the same values of the environmental variables in different years.

Table IV-18 presents coefficients of determination for multiple regression equations associating number of days after March 31 with several forms of the environmental variables (the temperature summation and moisture index). It appears that the temperature summation alone is the best predictor of days after March 31, but that the square of the moisture index is related to the number of days after March 31 in each of the years studied. Figure IV-1, page 58, presents the statistical

Table IV-18. Variables in multiple regression equations for number of days after March 31 and their coefficients of determination.

Dependent Variables	Independent Variables	R^2
1970 Days	1970 Temperature summation	.9875
1970 Days	1970 Temperature summation and (temperature summation)^2	.9884
1971 Days	1971 Temperature summation	.9944
1971 Days	1971 Temperature summation and moisture index	.9965
1971 Days	1971 Temperature summation, (moisture index) (temperature summation) and (moisture index)^2	.9972
1971 Days	1971 Temperature summation, (moisture index) (temperature summation), (moisture index)^2 and (temperature summation)^2	.9973
1971 Days	1971 Temperature summation, (moisture index) (temperature summation), (moisture index)^2, (temperature summation)^2 and moisture index	.9973
1972 Days	1972 Temperature summation	.9966
1972 Days	1972 Temperature summation and (moisture index)^2	.9976
1972 Days	1972 Temperature summation, (moisture index)^2 and (moisture index) (temperature summation)	.9976

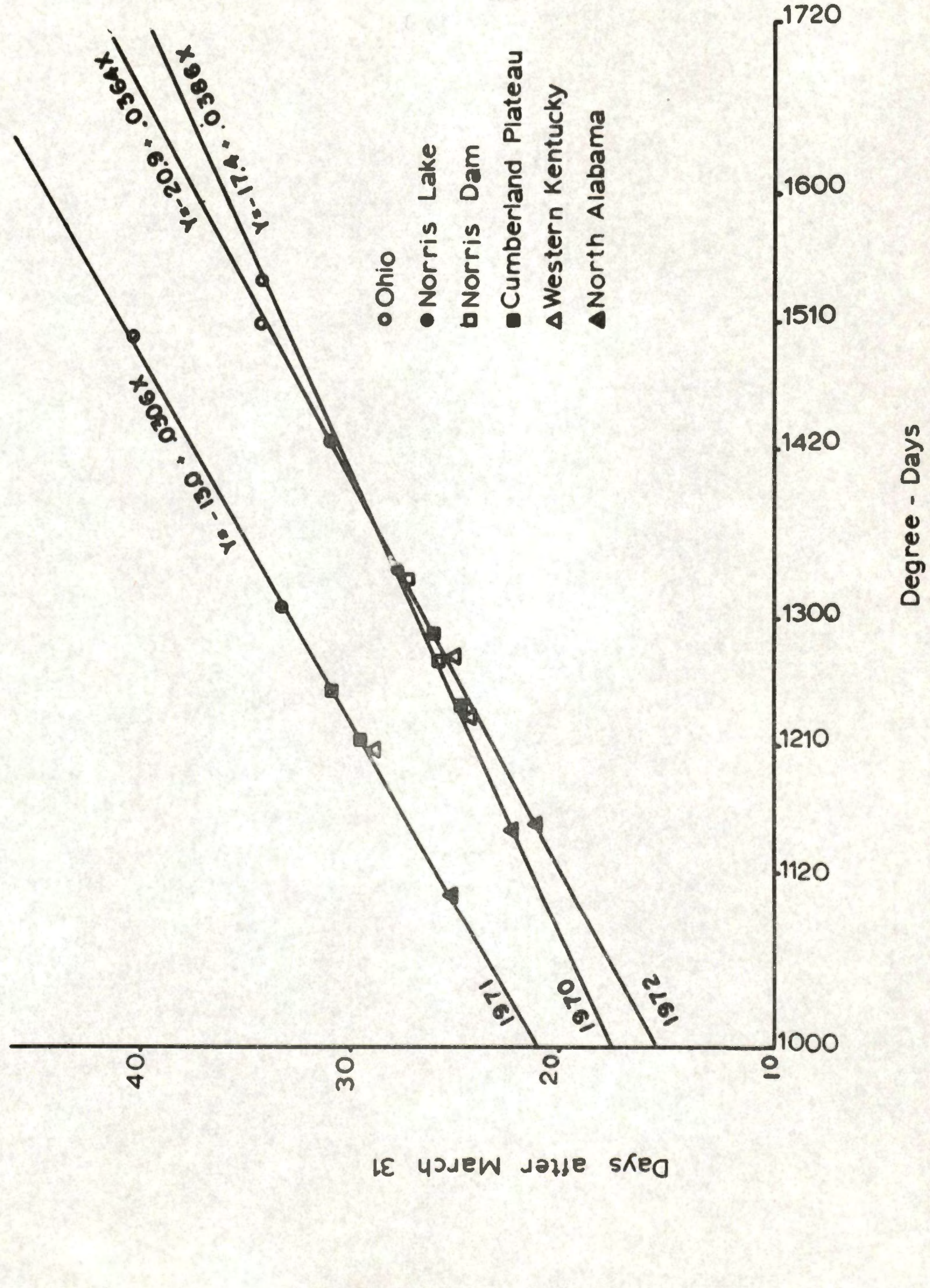

Figure IV-1. Regression lines for the association between number of days after March 31 and the temperature summation. Stand means are plotted along each line.

Table IV-17. Values of r for correlations between date of bud break and the moisture index.

	1970 Moisture Index	1971 Moisture Index	1972 Moisture Index
1970 Bud Break	.47	.65	n.s.[a]
1971 Bud Break	.49	.66	n.s.
1972 Bud Break	.43	.57	-.09

[a] n.s. indicates the correlation was not significant at the five percent level.

models for the association between the temperature summation and the number of days after March 31 in three different years. Stand means are plotted along each line. An analysis of covariance was used to compare these three regression lines, but Bartlett's Test, performed on the residual mean squares, indicated that the variances were heterogeneous, so the results of the comparisons of slopes and intercepts, as they assume homogeneity of variances, will not be presented.

An analysis of variance computed on the temperature summation indicated that the year effect was significant at the five percent level.

All computations in this section were based on 702 observations.

Seed Source Level

An interesting thing happened with regard to the associations between date of bud break and latitude and elevation of the seed source. As may be seen in Table IV-19, the correlations between date of bud break and latitude of the seed source were high in all three years, but those between date of bud break and elevation of the seed source were not significant (five percent level) for any of the three years studied. However, the multiple regression expressing date of bud break as a

Table IV-19. Values of r for correlations involving latitude, longitude and elevation of the seed source and height growth and bud break of seedlings.

	1970 Bud Break	1971 Bud Break	1972 Bud Break	1970 Ht.	1971 Ht.	1972 Ht.
Latitude	.95	.94	.92	n.s.	n.s.	n.s.[a]
Longitude	-.85	-.86	-.87	.94	.89	.90
Elevation	n.s.	n.s.	n.s.	-.80	n.s.	-.83

[a] n.s. indicates the correlation was not significant at the five percent level.

function of latitude and elevation of the seed source was significant (five percent level) in 1971 and 1972, and the sequential effect of each variable was significant (five percent level) in both years. The coefficients of determination of these two regressions were high (Table IV-20). The simple regressions between date of bud break and elevation of the seed source were not significant in any of the three years investigated, so only the regression lines predicted for the association between date of bud break and latitude and that between date of bud break and longitude in 1970, 1971 and 1972 are presented in Figures IV-2 and IV-3, respectively.

The only regressions between total height and seed source variables which were significant (five percent level) were those between total height and longitude of the seed source in 1970, 1971 and 1972 (Table IV-21), although the correlations between total height and elevation of the seed source were significant (five percent level) in 1970 and 1972 (Table IV-18, page 57).

All computations in this section were based on six stand means.

Family Level

The outstanding results at the family level were the correlations

Table IV-20. Variables in multiple regression equations relating date of bud break to latitude, longitude and elevation of the seed source and their coefficients of determination.

Dependent Variable	Independent Variables	R^2
1970 Bud Break	Latitude of the seed source	.90
1970 Bud Break	Latitutde and longitude of the seed source	.98
1971 Bud Break	Latitude of the seed source	.88
1971 Bud Break	Latitude and elevation of the seed source	.98
1972 Bud Break	Latitude of the seed source	.84
1972 Bud Break	Latitude and elevation of the seed source	.97

Table IV-21. Coefficients of determination for regressions of total height on longitude.

Dependent Variables	Independent Variable	R^2
1970 Height	Longitude of the seed source	.89
1971 Height	Longitude of the seed source	.80
1972 Height	Longitude of the seed source	.83

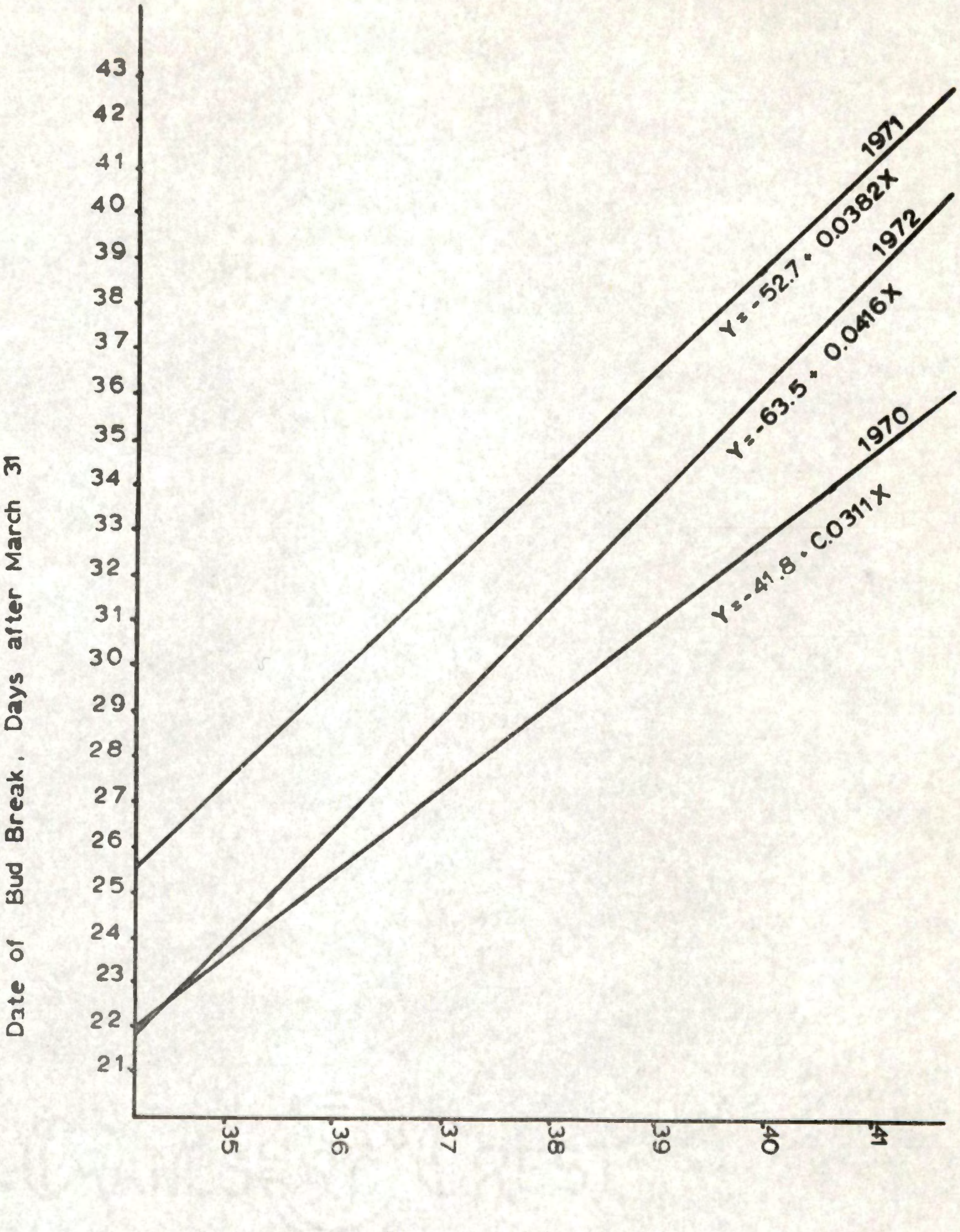

Figure IV-2. Regression lines predicted for date of bud break as a funtion of latitude of the seed source.

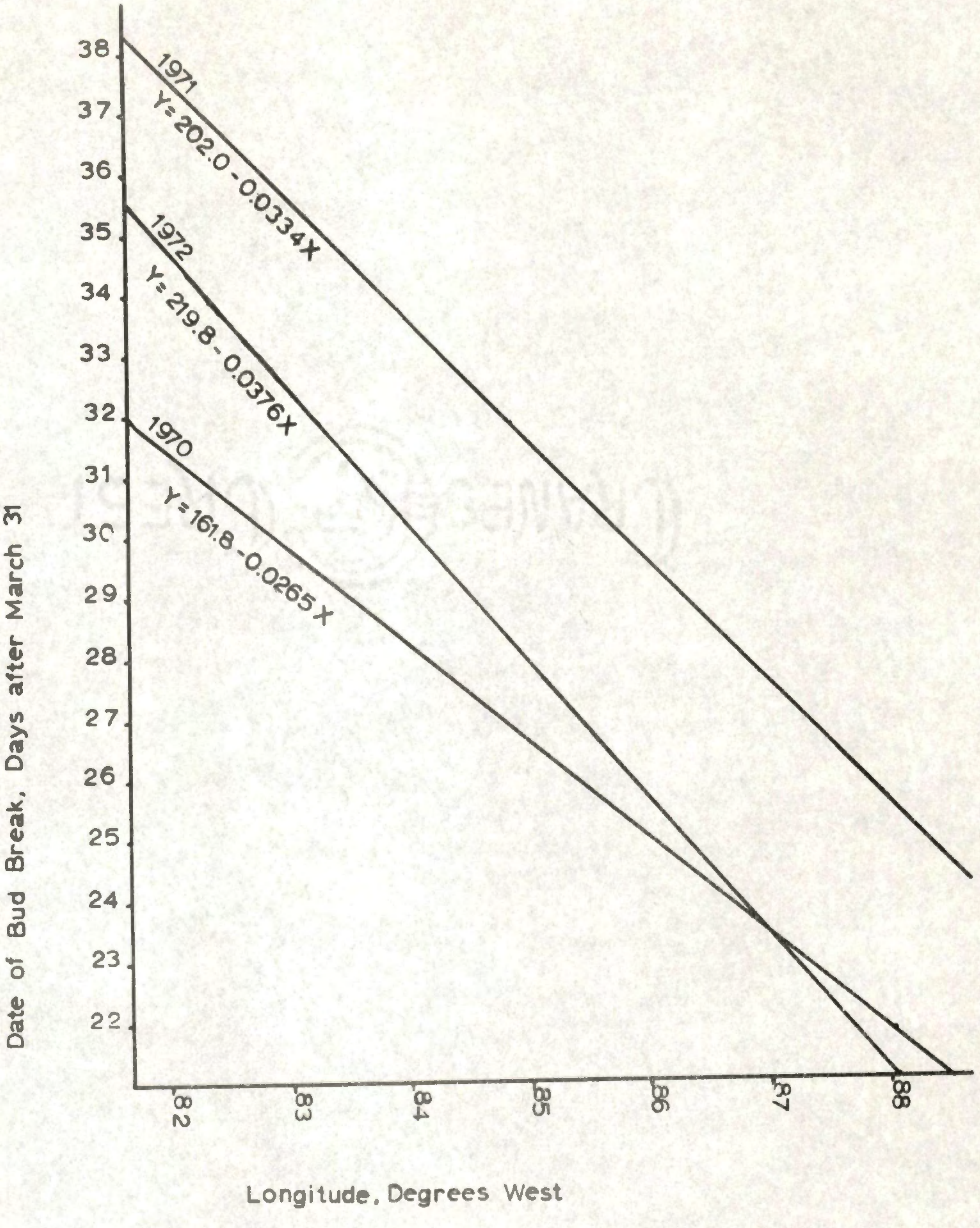

Figure IV-3. Regression lines predicted for date of bud break as a function of longitude of the seed source.

between total height and acorn weight and between diameter and acorn weight (Table IV-22). These correlations are based on 49 family means and were significant (five percent level) in each year in which measurements were taken. The correlation between total height and acorn weight decreased with age of the seedlings.

Table IV-22. Values of r for correlations among acorn weight, acorn volume, percent germination and 1968, 1969, 1970 and 1972 total height.

	1972 Diam.	Acorn Wt.	Acorn Vol.	% Germ.	'68 Ht.	'69 Ht.	'70 Ht.	'72 Ht.
1972 Diameter		.29	.33	n.s.[a]	.32	.69	.78	.89
Acorn Weight			.92	n.s.	.61	.51	.44	.31
Acorn Volume				n.s.	.57	.51	.44	.32
Percent Germination					.28	.30	.35	.35

[a] n.s. indicates the correlation was not significant at the five percent level.

Individual Trees

All the computations in this section were based on 702 individual tree observations for each variable. The results indicate to what degree different observations on the same tree are associated with each other. 1972 diameter was significantly correlated with total height (five percent level), and the size of the correlation decreased as the difference increased between 1972 and the year in which total height was measured (Table IV-23). Both 1972 diameter and total height in all three years were significantly negatively correlated (five percent level) with date of bud break in 1970, 1971 and 1972 (Tables IV-23 and IV-24).

Growth increment was significantly negatively correlated with date of bud break in only 1971 and 1972 (Table IV-25). The correlations between growth increment and total height were not as strong as would be expected (Table IV-25). The correlation between date of bud break and number of flushes was significant (five percent level) only in 1972 (Table IV-24). Thus, date of bud break and number of flushes may be considered independent variables except in 1972.

Table IV-23. Values of r for correlations between 1972 diameter and date of bud break in 1970, 1971 and 1972 as well as total height in 1968, 1969, 1970 and 1972.[a]

	'68 Ht.	'69 Ht.	'70 Ht.	'72 Ht.	'70 B.B.	'71 B.B.	'72 B.B.
1972 Diameter	.32	.69	.78	.89	-.13	-.25	-.29

[a] Significant at the five percent level.

Table IV-24. Values of r for correlations among date of bud break, total height and number of flushes in three years.

	1970 Ht.	1971 Ht.	1972 Ht.	F0	F1	F2[a]
B0	-.14	-.13	-.12	n.s.[b]	n.s.	-.11
B1	-.26	-.26	-.25	n.s.	n.s.	-.12
B2	-.33	-.27	-.28	n.s.	.11	-.14

[a] Explanation of symbols: B0 = 1970 bud break, etc.; F0 = 1970 number of flushes, etc.; Ht. = total height.

[b] n.s. indicates the correlation was not significant at the five percent level.

Table IV-25. Values of r for correlations among growth increment, total height, number of flushes and date of bud break.

	B1	B2	Ht71	Ht72	F2[a]
G1	-.12	n.s.[b]	.72	.66	-.11
G2	-.17	-.18	.31	.63	.38

[a] Explanation of symbols: G1 = 1971 growth increment, etc.; B1 = 1971 bud break, etc.; Ht71 = 1971 total height, etc.; F2 = 1972 number of flushes, etc.

[b] n.s. indicates the correlation was not significant at the five percent level.

A curious situation existed with regard to the regressions expressing total height and height increment as functions of date of bud break and number of flushes. When total height was the dependent variable, date of bud break yielded the highest coefficient of determination in a one-variable regression equation (Table IV-26). Yet when height increment (height growth) was the dependent variable, number of flushes was the independent variable which yielded the highest coefficient of determination in a one-varia-le regression (Table IV-27). In Tables IV-26 and IV-27, the use of 1972 date of bud break and 1972 number of flushes as independent variables in the same regression equation must be considered not valid, since these two variables were significantly correlated (five percent level). The coefficients of determination for the multiple regressions of 1971 height growth on 1971 number of flushes and date of bud break are much larger than those for 1970 and 1972. The explanation for this phenomenon may lie in the fact that 1971 was the year in which fertilizer was applied to three of the seven blocks. The regressions were computed on the basis of 702 observations from five of the seven blocks, including two which had been fertilized. Mean heights in 1972 for the fertilized and unfertilized blocks were 4.6 and 3.7 feet respectively, so the fertilizer treatment appeared to increase total

Table IV-26. Variables in multiple regression equations for total height and their coefficients of determination.

Dependent Variables	Independent Variables	R^2
1970 Height	1970 Bud Break	.02
1970 Height	1970 Bud Break and Number of Flushes	.04
1971 Height	1971 Number of Flushes	.10
1971 Height	1971 Number of Flushes and Bud Break	.16
1972 Height	1972 Bud Break	.08
1972 Height	1972 Bud Break and Number of Flushes	.09

Table IV-27. Variables in multiple regression equations for height growth and their coefficients of determination.

Dependent Variables	Independent Variables	R^2
1970 Height Growth	1970 Number of flushes	.14
1971 Height Growth	1971 Number of flushes	.41
1971 Height Growth	1971 Number of flushes and bud break	.42
1972 Height Growth	1972 Number of flushes	.14
1972 Height Growth	1972 Number of flushes and bud break	.16

height. Mean numbers of flushes in the fertilized blocks were 1.24 in 1970, 2.04 in 1971 and 1.19 in 1972, whereas in the unfertilized blocks they were 1.31, 1.31 and 1.43, respectively. Thus, in 1972, the year after fertilizer application, the mean number of flushes was larger in the unfertilized than in the fertilized blocks, as had been the case before fertilizer was applied. Fertilizer application, then, appeared to increase the number of flushes only during the year in which it was applied. With both height growth and number of flushes increased, the range of each over which the regression was computed is extended, and the chances of a stronger relationship being discovered are increased.

CHAPTER V

CONCLUSIONS

Environmental Effects

Hypotheses

The hypotheses on which the study of environmental effects on bud break was based were that: (1) the amount of heat required for bud break of a particular genotype of northern red oak is a constant; (2) the amount of heat required for bud break of a particular genotype is represented by a temperature summation; and (3) the amount of heat received by the seedlings is the primary factor controlling bud break.

Wang's (1960) criticisms of the temperature summation approach were that: (1) growth rate is not always a linear function of temperature; (2) growth is sometimes a near-linear function of time; (3) a temperature summation is a near-linear function of time; and (4) because of their linearity, these two functions sometimes coincide but are physiologically unrelated.

Conclusions

Conclusions based on the results of this study are that: (1) the temperature summation is a near-linear function of time; (2) the amount of heat required for bud break of a particular genotype of northern red oak, as represented by the temperature summation, is not a constant; (3) the temperature summation may not represent the amount of heat required for bud break of a particular genotype of northern red oak; and (4) the amount of heat, if represented by the temperature summation, is not the only factor controlling bud break of a particular genotype. Some factor or factors other than the amount of heat received apparently cause considerable year-to-year variation in date of bud break.

Seed Source Effects

Hypotheses

Hypotheses which served as the basis for the investigation of seed source relationships were that: (1) seed source variation in total height is large enough to make seed source selection feasible; (2) selection by seed source for date of bud break is the primary way in which frost damage can be avoided; (3) date of bud break and/or date of cessation of growth are associated with photoperiod; (4) duration of active growth is associated with photoperiod; (5) total height is associated with duration of active growth and thus with both date of bud break and/or date of cessation of growth; (6) since photoperiod of the seed source is associated with latitude of the seed source, date of bud break and/or date of cessation of growth and total height are also associated with latitude of the seed source. Alternative hypotheses to numbers 3, 4 and 6 were that: (7) date of bud break and/or date of cessation of growth are associated with length of frost-free period of the seed source; (8) duration of active growth is associated with length of frost-free period of the seed source; (9) length of frost-free period of the seed source is associated with latitude and elevation of the seed source; and (10) date of bud break and/or total height are associated with latitude and elevation of the seed source.

Conclusions

It is concluded that selection for total height of only the western Kentucky source is warranted and that seed source variation in date of bud break is overridingly larger than familial variation in this character. Therefore, seed source selection for date of bud break, using the regressions of date of bud break on latitude and elevation of the seed source as guides, is the primary way in which frost damage to northern red oak can be avoided.

The analysis indicates that date of bud break is associated with latitude of the seed source, but total height is not. Total height is only weakly associated with date of bud break. Dates of cessation of growth were not recorded, so hypotheses regarding this variable were not tested. From a review of the literature, it is concluded that in northern red oak, neither date of bud break nor date of cessation of growth is strongly controlled by photoperiod (Doorenbos, 1953; Kramer, 1936; Wareing, 1956). As a consequence of this line of reasoning, it is concluded that total height is probably not controlled by photoperiod in northern red oak.

Hypothesis number 9 is assumed to be true. This hypothesis could not be tested, nor could an hypothesis relating date of bud break to length of frost-free period of the seed source; data on frost-free period of the seed source could not be obtained which was local or site-specific enough to distinguish among the seed sources. Date of bud break is associated with latitude and elevation of the seed source; therefore, date of bud break is probably associated with length of frost-free season of the seed source. Variation in chilling requirement is probably related to this association, but is not the only temperature factor involved (Kriebel and Wang, 1962; Perry and Wang, 1960).

Total height is associated with longitude and elevation of the seed source, but not with latitude. This supports the conclusion that total height is not related to photoperiod of the seed source.

Mother Tree Effects

Hypotheses

It was hypothesized that the heritability of total height of northern red oak seedlings six years from seed in this experiment is sufficiently large to justify selection among families and within families. There was a question as to whether selection will help to alleviate the problem of poor juvenile height growth reported by Olson and Hooper (1968).

It was further hypothesized that: (2) a maternal effect of acorn weight on total height affects the size of the heritability estimate and the predicted gains in total height; (3) a location by family within stand interaction affects the size of the heritability estimate for total height; and (4) selection for total height is the primary way in which genetic improvement can be made in northern red oak.

Hypotheses regarding date of bud break were that: (5) the heritability of date of bud break is large; (6) a year by family within stand and a location by family within stand interaction affect the size of the heritability estimate for date of bud break; and (7) gains in total height can be made by selecting for early bud break.

Conclusions

It is concluded that heritability estimates for 1968 total height and 1971 date of bud break in this experiment are not valid because the family error variances in the compact family block analysis were heterogeneous. However, heritability estimates for total height six years from seed are valid, and the heritability of this character lies within the range from 0.20 to 0.37. The 0.37 value was obtained when the western Kentucky source, the outstanding one, was included. These heritability estimates apply only to trees from the same sources as those in this experiment, selected and grown on the same or a similar site and with the same cultural methods as in the Jones Island plantation.

Predicted gains in total height six years from seed range from 22 to 31 percent when only among-family and within-family selection at proportions of 50 and 8 percent, respectively, are practiced with the idea of turning the test into an open-pollinated seed orchard. If the test is turned into an open-pollinated seed orchard by selecting only the western Kentucky source and 33 percent of the trees within each family with no among-family selection, a gain of 39 percent is predicted. These gains were obtained when the western Kentucky source was included in the analysis.

If a new progeny test is created by returning to the western Kentucky seed source location and collecting acorns, and is then turned into an open-pollinated seed orchard by selecting 50 percent of the families and 8 percent of the trees within each family, a gain of 58 percent over the present unselected population on Jones Island is predicted.

Maternal effects are present through the sixth year from seed, and the size of both the heritability estimate and the correlation between acorn weight and total height decrease with age of the seedlings. The way in which the maternal effect affects the size of the heritability estimate is by their inclusion in the formula for estimating heritability as follows:

$$h^2 = \frac{4(\theta^2_{F(S)} + \sigma^2_{\text{Maternal}})}{\sigma^2_W + \sigma^2_{RF(S)} + \theta^2_{F(S)} + \sigma^2_{\text{Maternal}}} .$$

When the first method of computing gains is corrected for maternal effects, predicted gains range from 20 percent to 28 percent. The 28 percent gain is obtained when the western Kentucky source is included in the analysis. When the third method is corrected for maternal effects, the predicted gain is 55 percent. Thus, even when a correction is made for maternal effects, gains of 28 to 55 percent may be obtained by including and/or capitalizing upon the superiority of the western Kentucky source and by capitalizing upon the large number of trees in each plot. These gains will go far toward alleviating the problem of slow juvenile height growth in northern red oak.

Marquis (1973) made calculations of financial returns from planting genetically improved seed of northern red oak on site index 65 with average stand diameter 18 inches at harvest based on 10 and 20 percent reductions in rotation age. These calculations indicated that with a 20 percent reduction in rotation age, $0.60/acre/year would be lost. The reasons for the loss were the estimated $64/acre tree-improvement costs and the low value of the product relative to black cherry and paper birch. Annual profit with natural regeneration was estimated at $0.07/acre/year. With a 10 percent reduction in rotation age, the loss was $1.85/acre/year. Considering this information, it is possible that with a 30 percent reduction in rotation age, a tree-improvement program in northern red oak would pay for itself. However, a 30 percent reduction in rotation age is not the same as a 30 percent gain in total height, or even volume; and gains of 28 to 55 percent in juvenile height do not necessarily imply that similar gains in height of mature trees are possible.

It may be recalled that diameter gains were comparable to those predicted for height (p. 51). When the western Kentucky stand was included in the analysis, a gain in diameter of 33 percent was predicted in the first selection program. With a gain in diameter of 33 percent, a basal area of 77 percent would be expected. As shown on page 64, the correlation between total height and diameter in 1972 was 0.89, based on 702 observations. If this relationship holds true in the general population, gains in volume at six years from seed in the same selection scheme should be much greater than 77 percent. Unfortunately, these relationships cannot be extrapolated to mature trees; so it is not known how great the gain in volume of mature trees might be expected to be.

It is concluded that selection for total height is a major way in which improvement can be made in northern red oak, but research by Bey, <u>et</u> <u>al</u>. (1971) and Krahl-Urban (1966) indicates that improvement in hardwoods can be achieved by selecting for form and branching habit and that crook is related to frost damage.

Heritability of date of bud break is large, but the estimates probably include strong location by family within stand and year by family within stand interactions in the following way:

$$h^2 = \frac{4[\theta^2_{F(S)} + \sigma^2_{LF(S)} + \sigma^2_{YF(S)}]}{\sigma^2_{W} + \sigma^2_{RF(S)} + \theta^2_{F(S)} + \sigma^2_{LF(S)} + \sigma^2_{YF(S)}} .$$

The size of the location by family within stand interaction could be estimated; there was only one outplanting location, but the existence of such an interaction is indicated in sweetgum (Wilcox, 1970). Heritability estimates greater than 1.0 were also obtained in this experiment for some sources when the compact family block analysis was used. The size of the year by family within stand interaction was not estimated because such an estimation would necessitate an assumption that date of bud break is not affected by age. However, its existence is indicated by the variation from year to year in size of the heritability estimate obtained by the compact family block and combined analyses for this character and also by the heritability estimates obtained from the compact block analyses which were greater than 1.0 for some sources in some years.

Although the correlations between date of bud break are rather strong, ranging from -0.12 to -0.33, the coefficients of determination of the regressions of total height on date of bud break, which range from 0.02 to 0.10, indicate that the amount of variation in total height which is accounted for by variation in date of bud break is relatively small. Therefore, it is concluded that gains in total height obtained by selecting for early bud break will not be large compared to those which can be obtained by selecting on the basis of total height itself.

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