IS VARIATION IN BUDBREAK OF RED OAK THE RESULT OF HEREDITY OR ENVIRONMENT?

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Abstract.--When outplanted over a wide range of elevations in the Southern Appalachians, northern red oak seedlings from sources at low elevations broke dormancy 11 days sooner than those from higher elevations. Variation within the three-tree sources averaged 3 days at a given outplanting site. This pattern in budbreak appears to persist for 8 or more years. Such variation greatly affects the ability of outplanted seedlings to withstand unseasonable cold weather and to compete with surrounding vegetation. At this time, it is difficult to tell whether the variation results from genetic differences or from environmental preconditioning of the sources.

Additional keywords: Quercus rubra, phenology, provenance.

In past years, many sound studies have been carried out that document the effect of provenance on seedling performance. As a result of these studies, few tree planters are willing to use seedlings from distant sources, until those sources are thoroughly tested. Usually, however, little thought is given to a source of seed if it is from reasonably close to the planting site. Such complacency may, in certain cases, be unwarranted.

I propose to discuss some of the implications of a study of the effect of seed-source elevation on the phenology of northern red oak (Quercus rubra L.). Early results of the study show that the time of budbreak varies considerably between seedlings from sources at different elevations. The overall importance of this finding to tree planters is not yet clear. But it is obvious that if seedlings from low-elevation sources are planted at higher elevations and break dormancy as if they are at a low elevation, the new vegetation will be exposed to the adverse weather normally associated with high elevations. Conversely, planted seedlings from a high-elevation source would have difficulty competing with the surrounding vegetation at lower sites if budbreak persistently lagged. In assessing the importance of this work to tree planters, answers to several questions are needed. First, what is the magnitude of the variation in budbreak? Second, how long does the variation persist? Third and most important, what is the cause of the variation? I wish to answer the question of magnitude, partially answer the question of persistence, and explore with you some of the possible causes of the observed variation in budbreak.

The study design and layout are as follows: Acorns were collected from three parent trees at each of four elevations-1,400, 2,700, 3,800, and 4,600 feet above sea level. The three parent trees at each elevation were located

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within a few hundred feet of each other; the four collection sites, which were within 100 miles of each other, were near the cities of Morganton, Asheville, Franklin, and Canton, North Carolina. Acorns from the 12 parent trees were then planted in March 1971 at four elevations--1,500, 2,200, 3,500, and 5,500 feet above sea level.

By late April and early May, most of the acorns had germinated. In spring 1972, one year after the acorns were planted, we began keeping records of budbreak. The first bud broke on April 10, and we made regular checks thereafter until May 18 when the last bud broke. For the purposes of this study, a bud was considered broken when green could be seen by the naked eye on any part of the terminal or lateral buds.

By April 20, about half of the seedlings in the study had broken their buds, and a definite pattern of budbreak was beginning to develop. A few of the seedlings from the lower elevations had fully developed leaves, while most of the seedlings from higher elevations had not yet broken their buds. The effects of a frost or hard freeze would have been quite discriminatory, with the seedlings from the lower-elevation sources bearing the worst of it.

The percentage of budbreak on April 20 and the average date of budbreak by elevation of the seed sources are shown in table 1. These figures are averages for all four planting sites. The table indicates that, by April 20, almost all of the seedlings from the 1,400-foot elevation had begun budbreak while only a third or *less* of the seedlings from the 3,800- and 4,600-foot sources had broken dormancy. There was an 11-day difference between average dates of budbreak for the 1,400- and 4,600-foot sources.

Table 1.--The effect of elevation of seed source on the time of budbreak of red oak seedlings

Elevation of seed source (feet)	Budbreak by April 20	Average date of budbreak
	Percent	
1,400	80	April 19
2,700	65	April 21
3,800	30	April 26
4,60o	15	April 30

A more complete breakdown of the data appears in table 2. It shows the average date of budbreak for each parent tree and each source by planting site. These data indicate relatively close agreement between the average dates of budbreak for parent trees from a given source at a given outplanting site. At the 1,500-foot outplanting site, for example, 17.8, 20.0, and 20.6 days elapsed

Table 2.--Average time of budbreak by elevation of seed source and outplanting site

Elevation of outplanting site (feet)	Seed source at elevation of--															
	1,400 feet				2,700 feet				3,800 feet				4,600 feet			
	Tree 1	Tree 2	Tree 3	Avg.	Tree 1	Tree 2	Tree 3	Avg.	Tree 1	Tree 2	Tree 3	Avg.	Tree 1	Tree 2	Tree 3	Avg.
	Days elapsed after April 1															
1,500	17.8	20.0	20.6	19.5	23.0	20.4	22.3	21.9	29.9	27.0	28.1	28.3	30.8	30.3	30.3	30.5
2,200	17.0	17.3	16.9	17.1	20.1	18.1	19.3	19.2	24.8	22.5	--	23.7	26.0	26.2	32.3	28.2
3,500	16.8	14.8	14.3	15.3	17.5	14.8	14.8	15.7	18.3	21.3	--	19.8	25.7	25.4	29.0	26.7
5,500	24.4	23.7	23.8	24.0	24.1	26.5	26.0	25.5	27.7	30.4	36.7	31.6	37.1	36.1	34.5	35.9

after April 1 before budbreak occurred in the seedlings from the three parent trees at the 1,400-foot elevation. At each outplanting site, the average spread of dates for budbreak between each of the four sources was 3 days.

There were also differences between the average dates of budbreak for the outplanting locations, with dates ranging from April 19 to April 29. The outstanding observation concerning the four locations is the consistent effect of seed source and parent tree. There was about an 11-day difference between dates of budbreak for low and high sources at each of the outplanting sites.

The data presented thus far show that we can expect differences in dates of budbreak to be associated with elevation of the seed source and also that budbreak will vary by outplanting site. What about persistance? How long will this effect last?

We have just completed taking the third-year data on budbreak and they have not been completely analyzed. The trends are about the same as the second year results. However, there does appear to be more variation within the three-tree sources.

Additional information on the longevity of the budbreak effect can be derived from observation of 8-year-old seedlings from three parent trees. The parent trees are located at elevations of 2,700, 3,500, and 4,800 feet above sea level, and the outplanting site is located at 2,200 feet. In each of the 8 years, budbreak for seedlings from the 4,800-foot source has lagged, ranging from 1 to 3 weeks behind the other two sources.

Thus, the effect of seed-source elevation on budbreak appears to be enduring. The longer the effect continues to be in evidence, the more important these study findings become, and the greater the need to determine the cause of the phenomenon.

One way to explore the cause and effect relationship between budbreak and seed source is to return to the classical choice between the effects of the environment and of heredity. Let us try to make a case for each possible cause.

First, we might attempt to prove that the environment is the primary cause for the observed differences in budbreak. Everyone is aware that the microclimate varies considerably between elevations. Light, temperature, humidity, rainfall, and winds will often be different at different altitudes. We expect colder temperatures and shorter growing seasons at the higher elevations. We can argue that the acorns are subjected to a different environment at each of these locales and that the environment preconditions the acorns to perform in certain ways. As proof of this argument, we can point out the generally close agreement between dates of budbreak for the seedlings from each set of three parent trees at the various outplanting sites (table 2). We could argue that it is not likely that the three parent trees in each set have the same parentage and that, consequently, the association must be due to effects of the environment at the source.

On the other hand, we can present an argument favoring heredity over environment. So far as we know, the four areas sampled have supported northern red oak for a long time--at least several generations. During this period, seedlings best adapted to the site would have the best chance of long-term survival. Thus, we should not be too surprised if the entire population of red oak trees on a mountaintop was proven to have a late-budding characteristic. Theoretically, this characteristic should be passed on through the offspring. In support of this theory, we can cite the same data that were used in the previous argument that environment is the primary cause of the observed differences in budbreak: the close agreement between dates of budbreak for the seedlings from each set of three parent trees at the various outplanting sites (table 2). Additional evidence tending to discredit the theory that environmental preconditioning determines budbreak is the effect of vernalization on red oak. Northern red oak acorns that have been exposed to cold treatment or stratified do germinate earlier and more uniformly than unstratified ones. Thus, those acorns collected at the higher elevation would have undergone considerable cold treatment prior to collection in October. Consequently, the environmental effect would tend to hasten budbreak, not retard it. It also seems that time would diminish any effect of the original environment after the acorns were outplanted elsewhere. Yet, seedlings 3 and 8 years old are continuing to manifest an association between elevation of the parent tree and time of budbreak.

After considering both arguments, I am unable to reach a decision as to the cause of the observed variation in budbreak of northern red oak. Perhaps the best course at this time is merely to accept the fact that there is an association between elevation of seed source and the time of budbreak and to reemphisize the practical implication of such an effect with the following example:

On April 25, 1972, a medium frost and a temperature of 26° F. occurred at the 1,500-foot outplanting site. On that date, many of the seedlings from the 1,400- and 2,700-foot sources had fully developed leaves and were visably damaged by the frost. On the other hand, seedlings from the two higher sources were not nearly so well developed and they sustained no visible damage. If this combination of budbreak plus frost is repeated for several years, then the cumulative impact on the growth, and ultimately on the survival, of these seedlings will be considerable.