Epicormic Branching: A Real Problem in Plus Tree Selection

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It is easier to describe those characteristics a tree must possess for incorporation in a tree improvement program if the final product is known. Selection criteria for trees destined for pulp differ in some ways from those for trees destined to become veneer. Epicormic branches would be of no consequence in selecting for rapid juvenile growth when trees will be coppiced at very short rotations, as suggested by McAlpine and Brown (1967). Unless otherwise stated, the remarks here will be confined to tree selection where the final product is assumed to be quality lumber for use in furniture or other products where a premium is placed on freedom from defect.

Epicormic branches have been a problem as long as foresters have been managing hardwoods. Many generalities have been made concerning why they arise and what can be done to minimize their occurrence. The fact remains, however, that we still do not understand the basic causes of their eruption. Many silvicultural manipulations intended to control epicormic branches at an acceptable level in natural stands are of limited value. These methods will become less valuable in the future. Why is this so? Simply because if we plan to raise genetically improved trees in the time permissible under prevailing economic conditions, we will have to utilize plantations where intensive practices are applied. Conditions in these plantings seem to be ideal for the eruption of epicormic branches.

Currently, one of the many criteria for selecting hardwood plus trees is that they have no epicormic branches. Even if the only criterion for plus tree selection wes resistance to epicormic branching, we would still have difficulty selecting for this trait. This is true for three rather diverse reasons. First, we do not understand the mode of inheritance of epicormic branche s. Second, we do not understand the mode of development of epicormics. Third, we are sampling at a given period in time when the selection is made, and this presupposes a status quo pattern for epicormic branch development. Evidence, however, points instead to a dynamic or constantly changing pattern which seems to be strongly influenced by tree age and size and by the effect of environmental factors that may partially or completely mask the individual tree's genetic constitution.

Epicormic branches come in two distinct sizes--long shoots and short shoots. All foresters know that the typical epicormic branches we learned about in hardwood silviculture occur as long shoots. These may occur on the boles after tree damage or stand disturbance. However, in many species the more typical expression of epicormic branching in closed stands is the occurrence of short shoots (fig. 1). Size alone is not the important

Figure 1. -- Short shoots are the typical morphological expression of epicormic branches in undisturbed sweetgum stands. Longer short shoots on left side of bole illustrate environmental effect on short shoot growth habit.

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criterion for classification. The primary consideration is the amount of internodal elongation and short shoots may exist for a number of years as a stalk several inches long or be almost stalkless. In either case, they are transient in nature.

On sweetgum trees, it is not at all uncommon to find a single leaf protruding from the bark with the stalk and bud of the short shoot completely covered. In this species, it is frequently difficult to detect the presence of short shoots during the dormant season because the shoot may not be long enough at this time to extend beyond the bark crevices.

In sweetgum, it is tempting to select a "short-shootless" tree as a desirable plus tree candidate. This is especially true with the emphasis placed on a clear butt log; yet, it is this species that best exemplifies the error that can be made when we attempt to make selections at such a point in time. Sweetgum is therefore a good choice of species to discuss when presenting the problem of epicormic branching in plus tree selection.

A close look at the terminal leader of any sweetgum will reveal the ultimate source of epicormic branches in this species. At each node there is one axillary bud accompanied by two collateral accessory buds (fig. 2). These collateral accessory buds

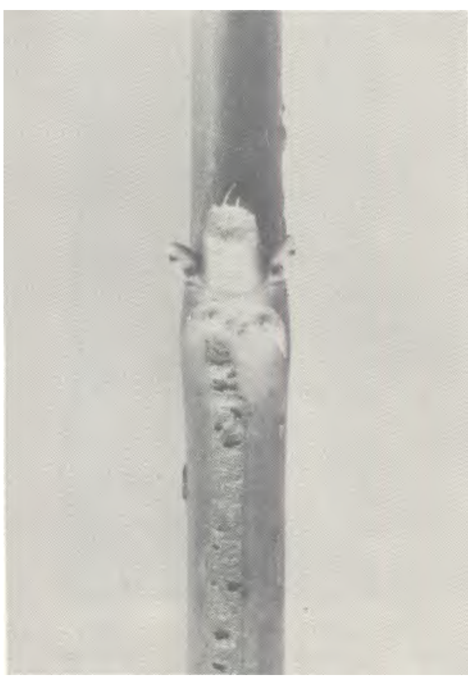

Figure 2.-- Each node on the current year's leader of sweetgum characteristically develops two collateral buds which eventually become suppressed trace buds.

are potential producers of epicormic branches. At some nodes, buds of this type are not readily visible. However, histological examination of these nodes always reveals the presence of the axillary bud and the two bud primordia (fig. 3). The axillary

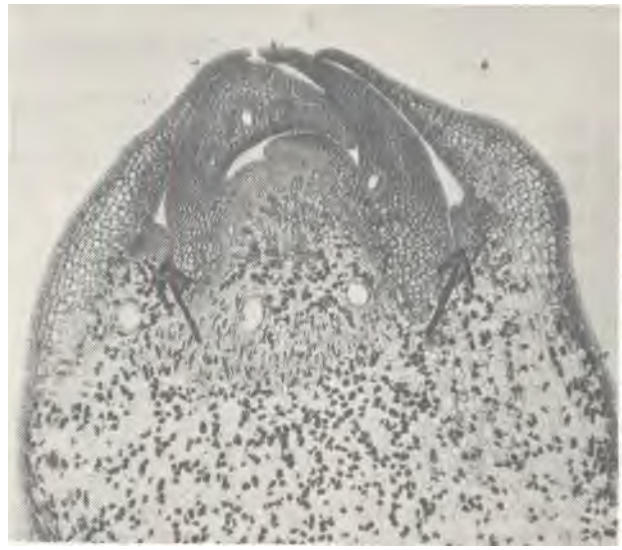

Figure 3.-- Even though axillary buds are barely visible at the base of the current year's growth, accessory bud primordia (arrows) are characteristically present. X 100

buds at one time or another give rise to branches whose longevity may vary considerably. While these axillary branches functi on, they inhibit the two associated acces so r y buds. Removal of these branches results in release and growth of the accessory buds. However, natural senescence and death of the branch does not cause a similar release of bud inhibition.

As the stem increases in diameter during the early life of the tree or shoot, the two accessory buds gradually become embedded in the bark. This usually occurs from three to five years after the buds are initiated. Externally, the accessory buds seem to have aborted, but histological examination reveals that the two well-developed buds are in a transitional stage and only the external scales are being sloughed off (fig. 4). With subsequent radial growth, these buds become completely embedded in the bark. They are now referred to as dormant or suppressed trace buds (fig. 5). The number of potential suppressed buds initiated on the new terminal shoot varies. It is evident, however, that the number is related directly to the number of nodes.

Figure 4.-- Accessory buds seem to abort a few years following initiation; however, only the outer bud scales are lost and the bud itself appears to be morphologically unaffected. X 125

The final envelopment of the bud by the bark does not cause complete cessation of growth, as the name suppressed trace bud might imply. On the contrary, these suppressed buds remain physiologically active. It is well known that suppressed buds grow enough to remain outside the expanding ring of wood. But of greater importance to us is that a single suppressed bud can be the progenitor of numerous others (Kormanik and Brown, 1964). This latter phenomenon results in suppressed buds being present in increasingly large numbers as the tree matures. At various times during the life of the tree, suppressed buds are partially released from inhibition and appear as short shoots. This occurs in seemingly random fashion on the bole of the tree, even though the tree has not been damaged or otherwise disturbed. Fortunately, under these conditions the short shoots are short lived, and once established, do not usually develop into long epicormic branches. The point here is that under natural, undisturbed conditions, short shoots rather than long shoots develop. What, then, would happen if the same tree were grown in a plantation at a wider spacing so that short shoots received more sunlight? If all such short shoots elongated as much as four inches and lived for five years, the search for clear lumber would be an extremely difficult undertaking. Depending perhaps on both internal as well as external factors, a poor tree in 1960 may be classified as an excellent tree at present.

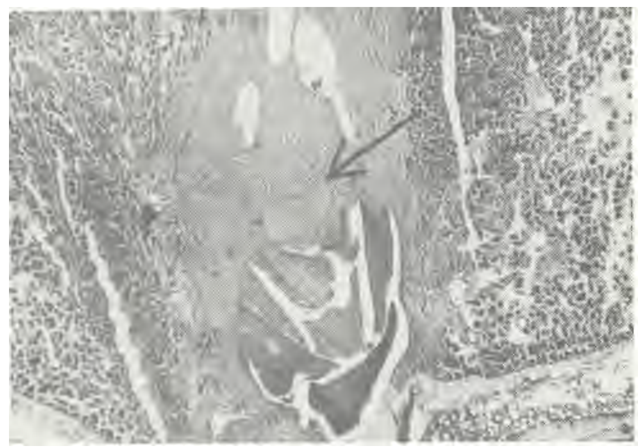

Figure 5.-- Suppressed buds such as this one (arrow) are found embedded in the bark of sweetgum of all ages. X 90

Although we have not made long-term observations of short shoot development on individual trees, we have made close examinations of many individual trees over a shorter period of time. A considerable number of mature trees have been cut and the entire boles, from stump to crown, have been sectioned into ½-inch discs to ascertain the presence of suppressed buds. These observations show, first of all, that there may be a period in the tree's development when suppressed buds are prone to multiply. This seems to occur most frequently in the center 8- to 10-inch core. When a stem is within this diameter range, the eruption of a short shoot may be associated with the appearance of additional suppressed buds at the base of each short shoot (fig. 6). We are slowly gathering evidence that this bole area of maximum suppressed bud activity gradually shifts upward as the tree grows, and in time, a clear butt log is evident. Although suppressed buds are present in the butt log, the number of short shoots is greatly reduced. The physiological processes that regulate this apparent change in suppressed bud activity, or degree of inhibition, are

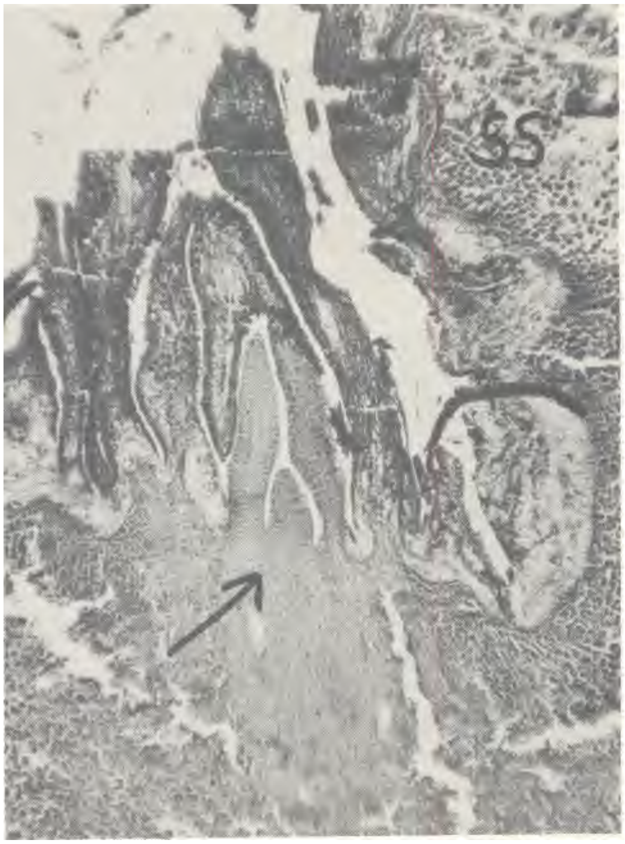

Figure 6.--The development of short shoots (SS) from suppressed buds may result in the proliferation of additional suppressed buds (arrow) that might produce additional short shoots or e p i co rm i c branches later in the life of the tree. X 120

poorly understood, as is the role that environment plays in these internal biological processes.

On the terminal leader and for some distance below it as mentioned earlier, the accessory buds, which can become suppressed buds, are inhibited by the action of the associated axillary buds, or, more correctly, by the branches that develop from the axillary. But what factors are involved in inhibition of suppressed buds on older trees after natural pruning has removed the branches low on the bole? Here, apparently, one or more inhibitory processes may be involved. The inhibition can be removed by different stimuli. The mechanisms of inhibition are not known, and in fact may vary among species. Even though our efforts have been concentrated on sweetgum, we feel that we still do not have sufficient developmental information on suppressed buds to search for differences among selected individuals. Furthermore, when one considers the magnitude of the progeny testing job and time involved to do the work, one can reasonably question the value of such an undertaking if it were based on our present knowledge.

During the past several years, we have been placing partial or complete girdles on the boles of trees of several species to determine gross patterns of suppressed bud inhibition. Results have convinced us that suppressed buds are more numerous on most trees than we originally thought. It is not unusual to count 250 epicormic branches and suppressed buds on the first 16-foot log after girdles are placed two or three feet apart along the bole of the tree. Usually, only long shoots are formed as a result of these girdles. Apparently, the girdle completely disrupts the inhibitory process.

Although these studies have shown that suppressed buds are numerous, they have also reinforced our conviction that tree improvement by judicious selection may be possible and indeed practical, for not all individuals of a species produce epicormic branches to the same degree as a result of the girdles. In fact, tree improvement of yellow-poplar may be a relatively simple task. Within this species, about 20 percent of the treated trees fail to produce epicormic branches of any consequence. If after a tree is girdled and released it still produces no epicormic branches, it is unlikely that they will develop at a later time. In fact, when we cut the first log of several such trees into thin discs, we found as few as 5 or 10 suppressed buds, and these had not been stimulated by girdling. However, when we cut several other trees which had sprouted profusely following treatment, we found up to 200 suppressed buds and epicormic branches on the first log.

An extremely interesting pattern of suppressed bud stimulation is becoming apparent through these girdling studies. That is, diffuse-porous species seem to have a different expression in the mechanism of suppressed bud inhibition than do some ring-porous species. However, we will have to treat more ring-porous species before we are certain of this. With diffuse-porous species, a single complete or partial girdle tends to stimulate epicormic branch eruption in a spirally oriented pattern that is quite similar to the tree's natural phyllotaxy. The pattern is, of course, not precise because of -the phenomenon of suppressed bud multiplication. The affected area of the bole extends about two feet below the girdle (fig. 7). Usually, below this spiral no additional

Figure 7.-- Eruption of numerous suppressed buds into long epicormic branches following girdling of sweetgum. The epicormic branches show a fairly definite phyllotaxic arrangement, even on old stems.

epicormic branches develop nor are short shoots on the bole visibly stimulated.

With ring-porous oaks, more special problems concerning response to girdling have become glaring. With water oak, on which epicormic branches are frequently found, regardless of stand density, a single girdle results in suppressed bud stimulation from the girdle to the ground. All water oaks girdled exhibited this response, regardless of age or size. White oak sometimes showed the same response as water oak, but frequently failed to respond at all. When we determined the origin of epicormic branches on responsive oaks, we found that at least 30 percent of the epicormics did not have a vascular connection with the pith (Kormanik and Brown, in press 1967). When suppressed white oaks were sectioned, this percentage was much higher. Very few large dominant white oaks produced more than two or three epicormic branches, whereas the suppressed and intermediates produced 30 or more.

In sectioning several large treated white oaks, we found surprisingly few suppressed buds. We have not studied the development of suppressed buds in the oaks and know nothing about any possible developmental patterns. White oak has a reputation for developing epicormic branches; therefore, several things may be happening. Either our three stands of white oaks are completely atypical, or white oak must have a tremendous potential for developing adventitious buds when growing under adverse conditions. Also, suppressed trace buds under these adverse conditions may become quite prolific.

If we cannot look at a tree and determine its tendency towards suppressed bud inhibition, and if we do not as yet have biological procedures for determining physiological differences, what can we do? With our limited knowledge we can only suggest selection criteria for those species which we have studied. For instance, at this stage of the game, the best we can recommend for white oak is to pick strong dominants and give the progeny adequate growing space. For yellow-poplar, response to partial girdling may be an adequate test for resistance to epicormics. Although we are not prepared to set epicormic branch selection guides even for sweetgum, we are convinced that for a rotation of 45 to 50 years, trees between 20 and 30 years of age should be selected, and these should be given complete release before the final determination is made. If selection of trees, based on our present knowledge, is made for sweetgum over age 60, one might be better off to ignore epicormic branching entirely. With this species, it can be emphasized that the lack of short shoots on older trees, even two logs up, should not be construed to mean lack of suppressed buds or superiority in maintaining them in a suppressed condition.

When one considers the fundamental development of epicormic branches, without considering the possibility of inherent differences of suppressed bud inhibition, the possibilities for selective improvement seem bleak. But in reality, inherent differences do exist. It is left to us only to determine methods of ascertaining these differences. Of the species we have examined, green ash perhaps offers us the greatest reason for hope. It is only under most adverse conditions that any but the suppressed and a few intermediate trees develop epicormic branches. The dominants and codominants remain clear. Yet, partial girdles put on dominant and codominant trees produce the most vigorous epicormic branches we have ever stimulated. It is difficult to believe the ability to keep suppressed buds inhibited evolved only in green ash.

LITERATURE CITED

Kormanik, Paul P. and Claud L. Brown.
1964. Origin of secondary dormant buds in sweetgum. USDA, Forest Service, Res. Note SE-36. October 1964.

Kormanik, Paul *P. and Claud L. Brown.*
1967. Adventitious buds on mature trees. USDA Forest Service, Res. Note., In press.

McAlpine, Robert G. and Claud L. Brown.
1967. Outlook for fiber from short-term coppice rotations. APA Quart. Paper 66-49: (2.11). April 1967.