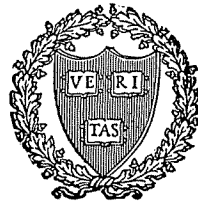


RED MAPLE STUMP SPROUTS:
DEVELOPMENT THE FIRST YEAR

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ABSTRACT

Stump sprouts in red maple (*Acer rubrum* L.) develop both from buried and external inhibited buds within two to six weeks after the stem is cut. The sprouts grow more rapidly than do long-shoots in seedling-origin trees and leaf and internode size is greater. Except in dense shade, sprouts grow for a longer period than do long-shoots. Stump vascular tissue formed after cutting the stem reorients toward active sprouts. Old stump tissue dies if not in living vascular connection to a sprout. The attachment of a sprout to the stump is often weak because the base of the sprout grows over the bark of the stump so that the vascular connection between stump and sprout is constricted.

Introduction

Most red maple (*Acer rubrum* L.) trees on the Harvard Forest are of stump sprout origin. The great number of stump sprouts is due both to the frequent incidence of red maple on most sites and to the high number of vigorous sprouts formed by red maple stumps, probably the most vigorous sprouter in the Northeast (Solomon and Blum, 1967). Thus, development of stump sprouts is an important part of the growth habit of red maple that influences the incidence of stems in the frequently-cut hardwood stands of New England.

This paper covers several aspects of the first year growth of red maple sprouts. Their origin, growth rate and inter-relationships with the parent stump are emphasized. During the first year sprout growth is, at least quantitatively, quite different from growth of stems of seedling origin. Eventually, the parent stump decays, its influence on sprout growth presumably disappears and then the sprout stems presumably grow as described in other papers in this series (Lyford and Wilson, 1964; Wilson, 1964, 1966).

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Materials

All stump sprouts came from a natural hardwood stand in compartment TS IV. The site is a series of large lobate solifluction terraces and has been described by Stout (1952). Part of the stand had been cut in the autumn and winter of 1966. In addition to observing stumps from this cutting, during the summer of 1967 in an uncut portion of the stand five trees were felled on May 31, five on June 14, five on June 30, five on July 28 and five on August 24, to investigate seasonal changes in sprout release and subsequent growth. Trees of seedling origin were sampled across the Tom Swamp road on a similar site where the 2-3 m high trees were growing in an old field.

Some stump sprouts and shoots on seedling origin trees were measured at weekly intervals for leaf and internode sizes. Other stumps were dug up with a bulldozer or backhoe and brought back to the lab where they were split and samples taken for sectioning. Sprouts were also cut out of stumps in the fall after growth had stopped.

Results and Discussion

Origin and Release of Inhibited Buds

There are two types of inhibited (dormant) buds in red maple that grow out to form stump sprouts. Both occur only on the stem or on the zone of rapid taper in the roots near the stem. The most common kind of inhibited bud is buried in the bark (Kormanik and Brown, 1966). These buds grow a little bit each year and keep from being overlaid by the wood. The buried buds are small and difficult to find, but if the bark is peeled off the base of a tree the location of each buried bud is marked by a conical projection of the wood where the bud has locally stimulated cambial activity (Fig. 1A). The other type of inhibited bud is a short-shoot that is external to the bark (Fig. 1B). These external buds appear to be exactly the same as those described by Church and Godman (1966) for sugar maple (*A. saccharum*). The external buds may be up to a centimeter long. There is virtually no internodal elongation and apparently one set of bud scales is produced each year.

Both types of buds are inhibited lateral buds that are derived from the original lateral buds on the main axis. All dormant buds have bud traces that can be followed through the wood to the pith. There was no indication that any buds arose on stumps *de novo* after cutting down the stem. The traces of buds buried in the bark branch frequently (Fig. 1D; Kormanik and Brown, 1966). Thus, the groups of 50 or more buds on the swollen knobby portions at the base (Fig. 1A) of the stump are all derived by branching of one original bud as are the horizontal lines of buried buds that occur further up the stem. External dormant buds are usually single and do not appear to branch.

Dormant buds on stumps cut during the winter start to grow in the spring at about the same time as do "normal" buds on intact trees, the middle of May in 1967. When trees are cut during the growing season, elongation of dormant buds occurs within two to five weeks (Table 1). Released external buds are usually visible before the buried buds have emerged through the bark. All stumps cut from May 31 to June 30 sprouted, four of five cut on July 28 sprouted, but only one of five cut on August 24 sprouted. On those stumps that sprout, new buds continue to emerge for four to five weeks after the first bud, but no new buds emerged after September 6 (Table 1). Even though new buds have stopped emerging, there are still more buried buds that appear to be inhibited by the growing sprouts.

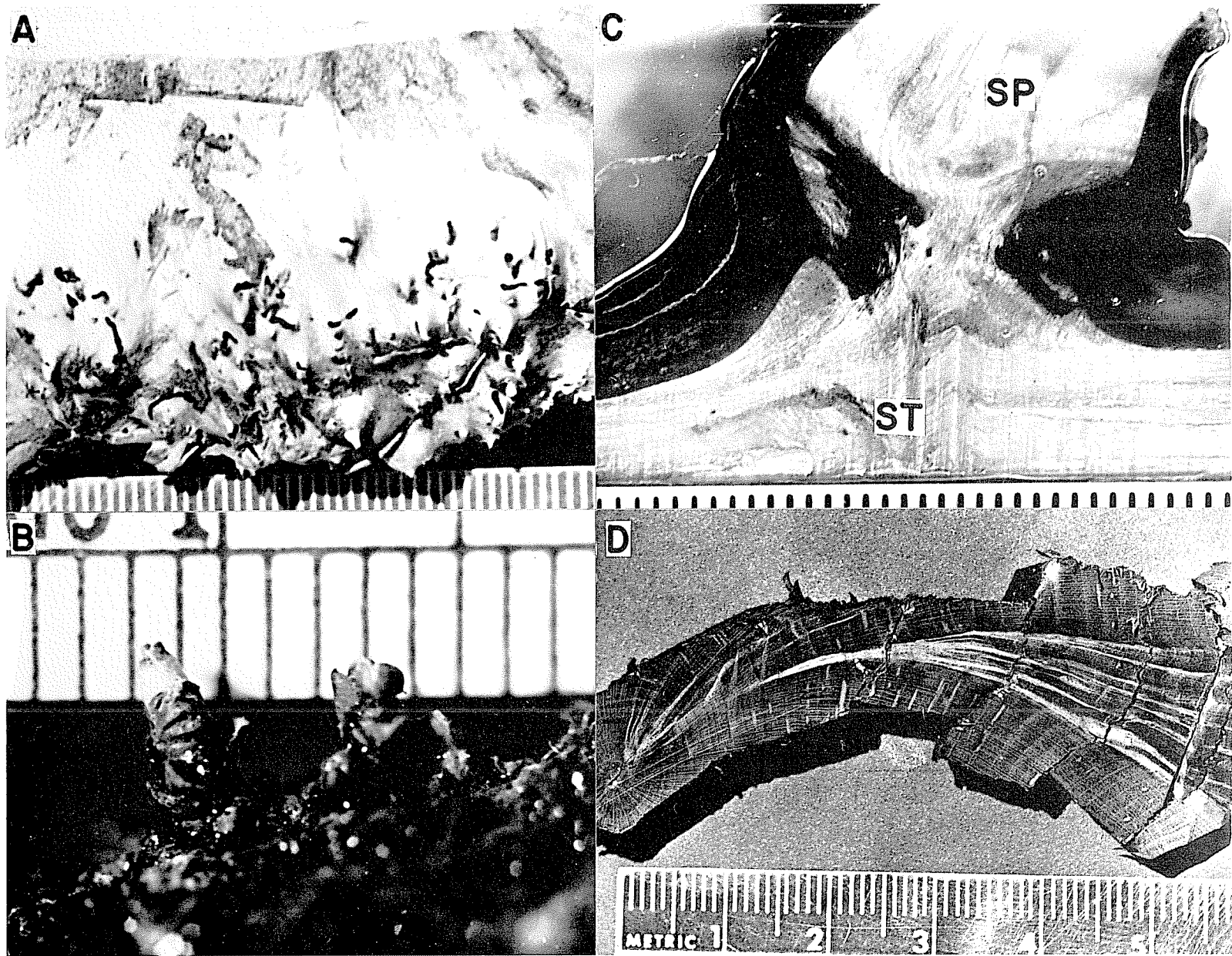


Figure 1. All scale divisions are in millimeters. A.—A “knobby” portion of a stump with the bark peeled off. The conical protrusions, 1-2 mm high, mark the bud traces of buried buds. The more than 60 buds on this knob all arose from one parent bud at the pith. B.—An external bud just starting to grow after the stem had been cut. C.— Longitudinal surface view of the point of attachment of a sprout. SP = sprout, ST = stump, dark tissue is the bark. Note the constriction of the vascular connection between stump and sprout. D.—Transverse surface of a segment from a stump showing the branching of a bud trace from the pith on the left to the external knob on the right.

Table 1. Time of bud release and growth cessation during summer 1967 and final length of annual increment in uncut control trees and in stump sprouts where the parent tree was cut at different times during the season.

Date Cut	First Bud Emergence	Last Bud Emergence	End of Leaf Growth	Final Length (mm)
Control	5/23	---	8/1-8/28	395- 630
Fall 1966	5/23-6/12	6/5-7/4	9/4-10/3	1065-2085
5/31/67	6/12-7/4	7/4-8/1	8/14-8/21	336- 977
6/14/67	7/4-7/24	8/1-8/14	8/14-8/26	125- 652
6/30/67	7/11-8/1	8/1-8/21	9/4-9/20	311- 522
7/28/67	8/21-9/4 ^a	8/26-9/10	9/10-9/20	1- 327
8/24/67	9/20 ^b	9/20	10/3	0- 6

^aOnly four of five stumps sprouted.

^bOnly one of five stumps sprouted, only one bud developed.

Table 2. Growth rates and leaf and internode sizes in controls (long shoots of uncut trees) and in stump sprouts where the parent tree was cut at different times during the season.

Date Cut	Leaf Pairs Produced Per Week	Leaf Length (mm)		Internode Length (mm)		Maximum Height Growth (mm/week)
		Maximum	Maximum Elongation Per Week	Maximum	Maximum Elongation Per Week	
Control	1.0-1.3	87-116	20-30	78- 86	25-40	79-126
Fall 1966	1.3-2.3	180-208	44-66	107-183	50-88	202-306
5/31/67	1.0-1.6	b				87-141
6/14/67	0.8-1.5					70-133
6/30/67	1.0-1.3					114-170
7/28/67	1.0-1.5					10- 86
8/24/67	1.0 ^a					3

^aOnly one stump sprouted, the one bud produced only one leaf pair.

^bFor stumps cut 5/31/67-8/24/67 data were taken only on rate of leaf pair production and rate of height growth.

An interesting point is that buried buds on four-foot lengths of cordwood will also sprout if the wood stays moist. These sprouts grew up to 10cm in height at the same rate as shaded sprouts and then apparently died from desiccation. Therefore, the stump root system is not required for sprout growth and the supply of nutrients to the growing sprout may be very local.

Growth

The rates of leaf production, leaf elongation and internode elongation, the final size of leaves and internodes, and the length of the season for leaf and internode elongation, were all greater in sprouts cut the previous winter than in long shoots (Table 2). The sprouts grew faster from the time they emerged, even before mature leaves had developed, and continued at about that rate until shortly before growth stopped in the fall.

Sprouts from stumps cut later in the season did not grow as fast or as tall (Table 2) as those cut in the winter. (In fact, they grew only slightly better than the control long shoots.) A major difference between these two sets of stumps, in addition to the time of cutting, was that those trees cut in the winter were cut during a cordwood cutting operation that greatly opened up the stand thus increasing light intensity, while those cut during the growing season were cut individually from a dense stand essentially without affecting light intensity. Thus, the first set grew under a far higher light intensity than the second. Although Solomon and Blum (1967) found that residual stand density had no effect on height of the two year old red maple sprouts, it seems likely that at ground level in this unthinned, dense stand light intensity was low enough to limit sprout growth.

In general, total height of sprouts in the unthinned stand was less in stumps cut progressively later in the season (Table 1). The growth rate did not decrease up to the end of June (Table 2) so this decline in final height was due primarily to a progressively shorter growing season.

The relationship between leaf and internode elongation is basically the same in sprouts as previously described for long shoots (Wilson, 1966). Each leaf pair starts elongating slightly before the internode just below it and leaf elongation continues one to two weeks longer.

Generally, final internode length in sprouts increases to a maximum of 150-200 mm at internodes two to six, then internode length may decrease slowly until the final internode (up to 23 internodes observed on sprouts in this study), or there may be up to 10 internodes that stay at 100-110 mm before a decrease at the end of the season. In long shoots the third or fourth internode is usually longest and the length of internodes decreases up to the final internode (maximum of 16 observed in this study). Average length of internodes in this study was 59-91 mm for five sprout trees and 34-39 mm for three control long shoots.

With the exception of the first two to three leaf pairs, which often appear to be modified bud scales, and the last three leaf pairs, which elongate during the period of overall reduced growth in the late fall, there is little or no correlation between leaf length and internode length. Internode length averaged about 95 mm for leaf lengths from 60 to 180 mm. Thus, it appears that growth of the leaf just above an internode is only partially responsible for internode growth because internode growth does not follow leaf growth in amount or duration.

Leaves on sprouts are about twice as big as leaves on long-shoots, but are essentially the same shape. Leaf shape is more variable in sprouts than in long-shoots. For instance, the range of the ratio blade length:blade width is 1.9-3.3 in different size sprout leaves, but only 2.1-2.9 in

sized long-shoot leaves, while the angle between the two main lateral veins was from 88-127° in sprout leaves and 99-114° in long-shoots. Thus, the shape of most sprout leaves is well within the range of shapes exhibited by the smaller long-shoot leaves. In general, sprout leaves appear to be extra large, but normal. In some other species such as the oaks, sprout leaves are both larger and abnormally shaped.

A survey of year-old sprouts showed that of 141, 46 had branched because the terminal bud had been injured, and of the 95 uninjured sprouts 30 had branched without injury. These laterals ranged in length from 1 to 50 cm, but most were 1-5 cm long. Most of the uninjured sprouts with branches had laterals at more than one node. Of the 30 sprouts, six branched at only one node, four at two nodes, six at three nodes, seven at four nodes and seven at 5-10 nodes. When a group of nodes produced laterals the only generalization about their distribution was that the bottom two to three nodes and the top six nodes usually had no laterals. There were often unbranched nodes within groups of branched nodes. Lateral buds on long-shoots normally do not elongate until the year after they are formed, but shoots characterized by rapid growth rates (like sprouts) often have laterals that develop during the same year (Champagnat, 1965).

The length of the growing season was somewhat extended in sprouts cut during the dormant season growing in the thinned stand. They started growing about the same time as normal long-shoots and kept growing a month or more longer (Table 2). The stumps cut in the unthinned stand on May 31 and June 14 started sprouting later than the start of long-shoot elongation, but stopped growing about the same time so that they grew from 10 to 11 weeks while long-shoots grew 13-15 weeks and sprouts in the thinned stand grew 17-23 weeks.

Relation of Sprouts to the Stump

Initial sprout growth is heavily dependent on materials supplied by the parent stump, yet the sprout often breaks off at the actual point of attachment to the stump. Obviously there is both a biological and mechanical relationship between the stump and the sprout. This section will treat the reorientation of vascular tissue in the stump to supply the sprouts, the death of cells inside the stump that are beyond the influence of the sprouts, and the structural aspects of the point of attachment of the sprout to the stump.

Within a short time after sprouts develop, new vessels produced by the stump reorient towards the growing sprouts. These vessels may grow at angles up to 45° from the vertical (Fig. 2A,3). The process is the same as vessel reorientation around wounds. The vessels become very irregular because connections between vessel elements are established laterally (Fig. 3A,C) as in experimentally induced vessel formation in the pith of *Coleus* stems (see Thompson, 1967). The result of this reorientation (presumably the sieve tubes in the phloem reorient the same way) is that even if there is only one sprout, it is in direct vascular connection with the whole of the stump and the whole of its root system, rather than just the portion directly below the sprout which was originally in direct vascular connection.

Just inside the stump, the tissue above a sprout, or above the ridge of reoriented tissue, all dies by the end of the first season. Further inside the stump the tissue is dead further down. As a result, when a stump is split there is a V or U-shaped portion of dead tissue with the living tissue extending at an angle down and into the center of the stump (Fig. 2B). The dead tissue is brown, the living tissue white, and the boundary between the two is usually marked by a green band presumed to be algae (Fig. 2B,3B).



Figure 2. A stump with one year-old sprouts. A.--External view, with the bark removed, showing reorientation of living "white" tissue toward growing sprouts. Dark horizontal marks are dye used to stain vessels (see Fig. 2A). B.--Internal view of split stump showing distribution of living (white) and dead (brown) tissue.

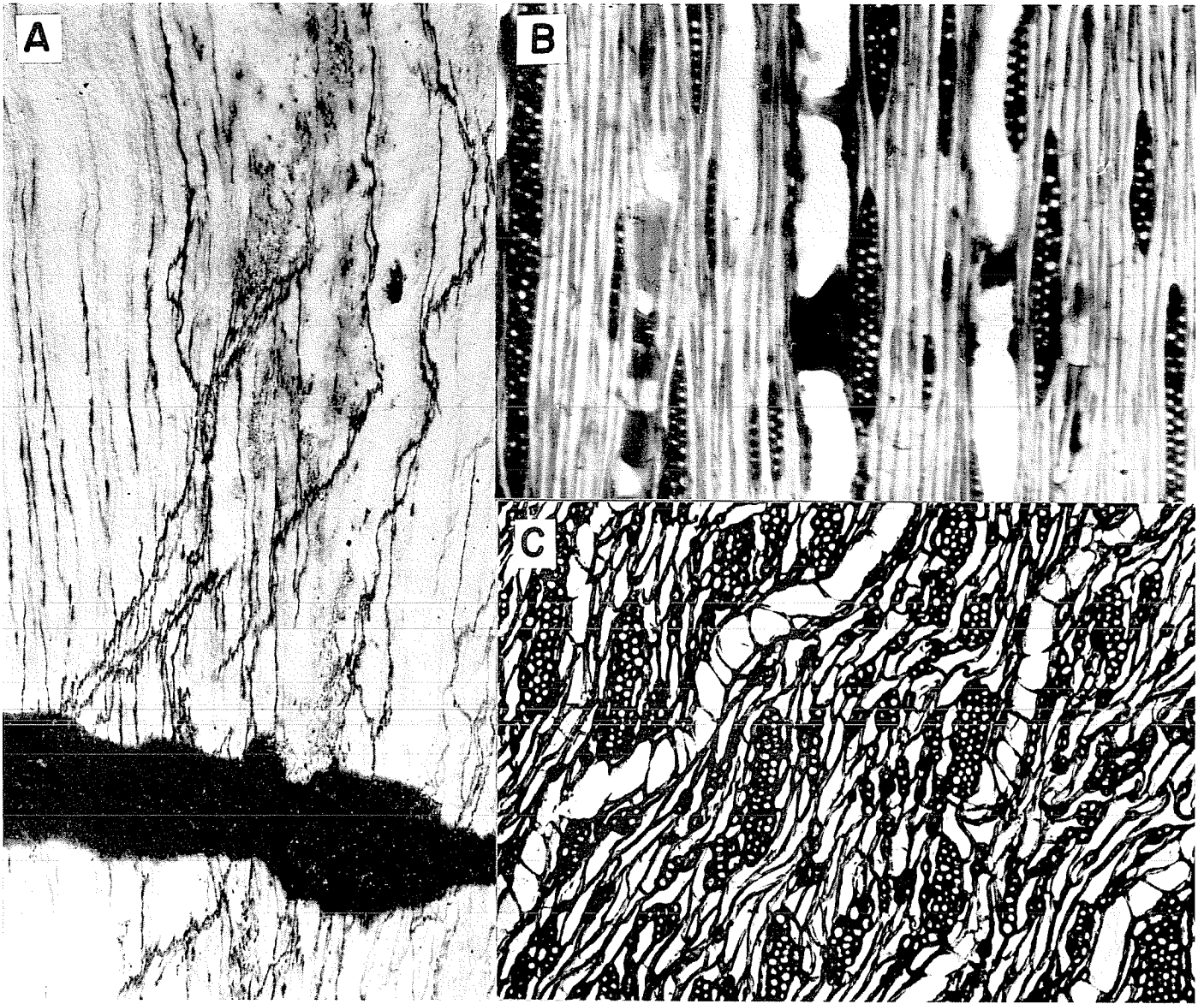


Figure 3. Details of vessel reorientation toward active sprouts. A.—Surface of living wood after the bark was peeled. Safranin dye was applied on the surface (dark horizontal stripe) and then the wood was scratched. The dye went into the vessels punctured by scratching, staining them dark red. The vessels in the wood before reorientation are shown by the regular vertical lines and the reoriented vessels, closest to the surface, are shown by the irregular, oblique lines (X 3.6). B.—Photomicrograph of a tangential section through wood of normal structure in the green strip between living and dead tissue in the stump (X 100). The dark mass in the vessel appears to be the material that produces the green color. C.—Structure of reoriented wood (X 100).

This pattern of death of cells in the stump is the first stage of the eventual decay of the stump. As in the reorientation of vessels, the growing sprout appears to influence the differentiation of cells in the stump. Actually, the maintenance of living cells inside the old stump may be merely associated with the existence of functional vascular tissue at the outside of the stump so that radial transport of materials can continue through the rays. This would be an indirect effect of the growing sprout rather than a direct effect of materials moving from the sprout to the cells inside the stump.

The point of attachment of the sprout to the stump is where the growth ring on the stump is widest and where the diameter of the sprout is greatest, so the area is considerably swollen. Yet, despite the apparent strength of this swollen attachment, many sprouts break off at that point either from their own weight or from the additional weight of ice or snow in the winter. This type of breakage occurs most frequently on sprouts placed high on a stump. Sections through the point of attachment show that the vascular connection is often severely constricted right next to the stump where it passes through the bark (Fig. 1C). In addition the base of the sprout often grows over the bark of the stump trapping segments of it, somewhat comparable to the trapping of bark in apple tree crotches (Eames and Macdaniels, 1947). Thus, although the attachment as a whole may swell and appear very strong, the actual vascular attachment may be quite small. Apparently the bark acts to girdle the growing sprout. The thinner bark low on the stump presumably offers less resistance to the lateral growth of the sprout and does not restrict the vascular connection. When the sprout is girdled, materials moving down the sprout tend to accumulate and cause an even more marked swollen base.

Conclusion

The results of this study suggest the following sequence of events during the first year of sprout development. Inhibited, dormant buds are always present at the base of the stem. They grow a bit each year and those buried in the bark branch occasionally, thus increasing the number of dormant buds. When the stem is cut the external buds start elongating almost immediately and some of the buried buds enlarge, split the bark and then elongate rapidly. The bark may restrict initial elongation and later may restrict increase in sprout diameter at the point of attachment. The sprout produces hormones in the growing leaves and acts as a sink for materials moving from the stump. New vascular tissue in the stump is oriented towards the sink represented by the sprouts. Therefore carbohydrates and water from the whole stump and root system can move readily into the sprout. Within about a month, production of growth regulators by growing sprouts appears to be high enough to inhibit all the remaining inhibited buds. These buds continue to grow slowly just as they did before the stem was cut. Tissue in the stump dies if it is not physiologically connected with the sprouts, either through axial vascular tissue or radial wood rays. The unusually high growth rate of the sprouts must be due to movement of materials from the stump to the sprout, but this movement is regulated by the sink represented by the sprout. Therefore, deep shade that restricts sprout growth presumably does so by restricting leaf growth and production of growth regulators.

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