

HARVARD UNIVERSITY
MARIA MOORS CABOT FOUNDATION
FOR BOTANICAL RESEARCH

Vascular Connections Between Roots
and Shoots of Acer rubrum
Coppice Growth and Implications for
Management

Ann Marie Lewis

Vascular Connections Between Roots and Shoots of Acer rubrum
Coppice Growth and Implications for Management

Ann Marie Lewis

Submitted in partial fulfillment
of the requirements
for the degree of
Master of Forest Science
to
Harvard Forest
Petersham MA
May 1982

TABLE OF CONTENTS

Abstract	iv
List of Illustrations	v
List of Tables	v
Acknowledgments	vi
I. Introduction	
A. Coppice management	1
B. Research on red maple stump sprouts	3
C. Related research	4
II. Materials and Methods	
A. Study sites	5
B. Dye application	
1. Tracing dye paths	6
2. Application of dye through sprout stubs	6
3. Application of dye through root stubs	11
C. Estimation of root ages	15
D. Vessel continuity between stems and roots	17
E. Diameter growth of sprouts	17
III. Results	
A. Description of the sprout clumps	20
B. Dye distribution in sprout clumps	
1. General observations	21
2. Application of dye through sprout stubs	22
3. Application of dye through root stubs	26
4. Reorientation of vascular tissue	34
C. Root ages	37

D. Continuity of vessels between stems and roots	40
E. Comparison of diameter growth	40
IV. Discussion	
A. Sprouts' use of root system	42
B. Vascular reorientation	45
C. Management implications	48
D. Remaining questions	49
Literature Cited	52

ABSTRACT

The vascular connections between stems and roots of 45 year old red maple (Acer rubrum L.) stump sprouts were investigated to determine the effect on diameter growth of removing all but one sprout per clump. Dye applications through the sprouts and the roots helped reveal the connections. It was determined that, in general, the remaining stem could use all or almost all of the clump's root system, but gypsy moth caterpillar damage prevented a comparison of increment growth rates between stems which were only crown released and those which also had more root area available. The effect of pressure gradients on xylem sap flow as it relates to this study is discussed, as is cambial reorientation. The ages of the roots of one sprout clump were estimated in order to compare them with root growth habits and with sprout ages. Management implications are outlined.

LIST OF ILLUSTRATIONS

Figure 1.	Application of dye through a sprout stub	8
Figure 2.	Application of dye through a root stub	13
Figure 3.	Air infusion technique for determining vessel continuity	18
Figure 4.	Uneven dye distribution in woody tissue	23
Figure 5.	Dye distribution within individual roots	25
Figure 6.	Crossover of methyl green in Tree Q	27
Figure 7.	Dye ascent in a root stub application control	29
Figure 8.	Movement of dye from the root of application into the remote sprout	30
Figure 9.	High concentration of dye in the stump of Tree N	31
Figure 10.	Third generation sprouts containing dye	33
Figure 11.	Reoriented vascular tissue in Tree 10	35
Figure 12.	Yearly diameter growth in root released trees and in trees which were only crown released	41
Figure 13.	Presumed pressure gradients in an intact sprout clump	43
Figure 14.	Presumed pressure gradients in a root released tree	44
Figure 15.	A view of Tree 10 showing vascular reorientation and the root through which growth hormones may have been transferred	47

LIST OF TABLES

Table 1.	Details of trees with sprout stub application of dye	9
Table 2.	Details of trees with root stub application of dye	14
Table 3.	Average ages of the roots of Tree D	38

ACKNOWLEDGMENTS

I extend my thanks to the community at the Harvard Forest for each individual's kind support. The help of Dr. Martin Zimmermann, Dr. Stefan Zajaczkowski, Monica Mattmuller, Dr. Ernest Gould, and Emery Boose was essential to this project's successful completion. I offer them my special thanks. Thanks also to Julio for his words of encouragement and to Harvey for his patient help with the manuscript.

I. INTRODUCTION

A. Coppice management

Because of the effort to maximize hardwood timber production, the management of coppice stands in eastern North America has come under increased scrutiny in the last several years (see, for example, Lamson, 1976; Lees, 1981; Tattar, 1973; Trimble, 1974; and Wendel, 1975). Red maple (Acer rubrum L.) stump sprouts constitute a significant portion of the regeneration on heavily cut sites in the eastern United States, and red maple coppice is common in New England woodlots where fuelwood harvest has increased dramatically in the last few years. Lees (1981) determined that at least three successive generations of red maple stump sprouts can produce useful wood, so it is important to understand the best management techniques for species such as red maple if production is to be maximized.

Among the first to investigate the management of red maple coppice, Campbell (1938) and Campbell and Spaulding (1942) conducted research on and made management recommendations for northern hardwoods including red maple stump sprouts. Their final guidelines did not differ significantly from other early management suggestions. However, before the 1970s, most of the management recommendations, especially with respect to thinning and selection of potential crop trees, were based on studies of oak coppice growth (Hepting and Fowler, 1962; Jemison and Hepting, 1949; Roth and Hepting, 1943 and 1969; and Roth and Sleeth, 1939). When the goal was to produce high yield in a few trees, it was recommended that coppice stands be thinned while the sprouts were still young (i.e. less than 20 years old). This helped to prevent competition among sprouts and improved

growth form. The amount of butt rot in the stand was reduced by removing all but one or two sprouts per stump, thus eliminating weakened sprouts and lessening the chances of decay entering through wounds caused by the death of suppressed sprouts. The basic recommendations for eastern hardwood coppice management were to select for sprouts of good form that originated at or near ground level on a small stump and to avoid cutting sprouts which formed a V-shaped union with other sprouts. These recommendations included the types of cuts that would best promote rapid healing of the thinning wound. Butt rot in oaks enters sprouts through the heartwood union with the stump and/or the other sprouts (Roth and Sleeth, 1939). These practices were applied to red maple as well as other species, although it was frequently recommended that red maple be selected against because of its poor wood quality. The suggested techniques, especially those based on the size of the stump or the sprouts, are difficult to follow because much of today's coppice growth exceeds the prescribed size limits for management. According to Tattar (1973), who based his conclusions on the work of Shigo (1965), the method for selecting future crop trees from red maple coppice growth differs from that for oaks. Because Shigo found more evidence of infection entering red maple stump sprouts through branch stubs than through the stump, Tattar concluded that red maple sprouts should be selected primarily by checking for well healed branch stubs. He minimized the importance of defects in the sprout base which are so important in coppice oak management.

These management strategies raise the question: Does thinning a sprout clump by leaving only one or two stems per stump significantly increase the increment growth above that obtained by crown release? This

study looks at the vascular connections and increment growth in red maple stump sprouts in order to determine how much of the clump's root system is available to the remaining sprout after removing the other sprouts. (This technique will be referred to as "root release".) An effort is made to determine whether a root-released tree has a significant diameter growth advantage over a tree which was only crown released.

B. Research on red maple stump sprouts

Relatively little research has dealt with the anatomy, physiology, and morphology of red maple stump sprouts. When a single red maple stem from seed (the parent stem) is cut, sprouts arise on the stump from dormant buds buried in the bark and from short-shoots external to the bark (Wilson, 1968). These begin elongation after the parent stem is cut. The sprouts not only make use of some of the preexisting roots, but also produce new roots (Lees, 1981). At least during the first year, vascular tissue entering those sprouts which are high on the stump is constricted where it passes through the bark, and the sprout frequently traps portions of the bark by growing over it. This causes a weak joint where the sprout and the stem meet and is often the site of breakage (Wilson, 1968). Wilson's work also indicates that within the first year, the stump tissue not in direct physiological connection with the sprout begins to die, leaving an inverted cone-shaped region of dead material in the stump. New vascular tissue is oriented towards the sprouts to yield more direct connections between the sprout and larger portions of the root system.

C. Related research

Some other research is applicable to coppice red maple, even though tree species other than red maple were investigated. In general, any given portion of a stem has a special connection to a certain part of the root system; i.e. it has more direct physiological connections with that part than does any other portion of the stem. For example, water transported via horizontal roots is transferred to the outer growth rings of the stem, while water from the tap root continues its ascent through the innermost rings (Riedl, 1937). Riedl also found that in some trees, (specifically ash) some of the vessels are continuous from root to stem; in others, he found no continuity (specifically birch). Some vessels in beech continued from one root in a graft into the other. Vessels rarely end in isolation; they usually taper out and end along one or more continuing vessels (Zimmermann, 1971). Vascular tissue in the xylem does not run straight up the stem; rather the tissue spirals in slightly different directions from growth ring to growth ring. This provides any part of the crown with resources from various parts of the root system over the years. Theoretically, the spiralling and vessel to vessel connections should give any part of the crown access to any part of the root system (Zimmermann and Brown, 1971). Because individual vessels weave in and out among other vessels, any part of the vascular system theoretically should be in connection with any other part. Thus one might suspect that the sprout remaining after root release has access to the materials transported by any part of the root system.

II. MATERIALS AND METHODS

A. Study sites

In the late summer and fall of 1981, trees for study were selected from two sites at the Harvard Forest. The first site is in Compartment VIII of the Prospect Hill Tract, and the soil is a Whitman very stoney silt loam. The site bears mostly red maple with red oak and other hardwood species. The stand was clearcut in the winter of 1936-37. In November 1979, fuelwood was removed in a high thinning. Since most of the trees were multiple stump sprouts, the guidelines suggested by Hepting and Fowler (1962) were followed during thinning to reduce the likelihood of butt rot in the remaining stems. The red maple sprout stems left after thinning which were used in this study had diameters ranging from 15 to 21 cm measured just above the basal taper. One of the original stumps measured 25 cm in diameter. At the time of the thinning, most clumps contained three or more sprouts and were thinned to one or two sprouts. The other site is in Compartment I of the Prospect Hill Tract and stands on a Gloucester stoney loam. It is a mixed hardwoods stand, and was also clearcut in the winter of 1936-37. At the time of this study, many of the red maples were multiple stump sprouts and were much smaller than the trees at Site I. The sprouts used from this site had diameters ranging from 3.0 to 10.5 cm; the original stumps had diameters on the order of 2.0 to 8.0 cm. Most of the trees used in the study were from the second site and were double sprouts.

B. Dye application

1. Tracing dye paths

In an effort to determine whether physiological connections actually exist between a sprout and various parts of the root system where there are no obvious direct vascular connections, dyes were introduced into the vascular tissue. After dye application (described below), most of the stumps were excavated and brought into the lab where photographs were taken of the roots, the points of attachment of the sprouts, and any above ground vascular connections between sprouts. The bark of some stumps was peeled to check the wood surface for dye distribution. Cross and longitudinal sections from the roots, the stumps, and the sprout stubs were checked by eye and with a microscope. The stumps were dissected indoors with an electric chain saw and a variety of handsaws. Dried wood was softened with a 5 to 10% solution of glycerin in 95% ethanol before smoothing or sectioning with a sliding microtome. This solution minimized the amount of dye dispersion during softening.

2. Application of dye through sprout stubs

Two methods of dye application were tried. In both methods, aqueous safranin and methyl green solutions (diluted to 1% w/v in tap water) were used. Both of these are basic stains which travel slowly in the vessels, but are more permanent than acid stains. An acid stain, fast green, dispersed so quickly that it was barely discernible in cross section when applied under field conditions. Where safranin and methyl green mix, vessels appear violet, which eases the task of determining which vessels

contain both colors.

In the first method, stain was gravity-fed into stumps through the cut surface of sprout stubs (Figure 1). Before sawing off a sprout between 5 and 25 cm above the junction with the stump, enough of the outer bark was removed with a drawknife to make a smooth surface. This surface extended 5 to 10 cm below the level of the cut to give a surface against which a watertight seal could be formed. After cutting, silicone rubber bathtub caulk from a caulking gun was beaded beneath the cut on the smooth surface and spread just enough to ensure a seal with the bark. A preformed slab of plasticine was molded into a collar around the stub, and the lower edge of the collar was pressed to the stub with the upper edge extending above the cut enough to form a 3 to 10 cm deep container to hold the dye solution. The silicone rubber, which is not water soluble before or after curing, created a watertight seal between the collar and the branch stub. A foil tent formed to fit over the plasticine kept evaporation down and precipitation out.

Dye was applied to Tree 10 (Table 1) using this method. This sprout clump was root released in the 1979 thinning, leaving a single stem. During this study, the stem was cut and dye was introduced through the resulting stub. Trees from Site II were double sprouts; safranin was applied to one sprout of the pair and methyl green to the other (Trees B through H in Table 1). These double sprouts were treated in two ways. Two of the clumps (i.e. Trees D and H) acted as controls and had both sprouts removed, and the dyes were applied to each sprout stub of the pair simultaneously. The dye applications were maintained for several days. Others (i.e. Trees B, C, and E) had one sprout cut from each stump and dye applied to that sprout stub for 2.5 to 8.5 days before the remaining

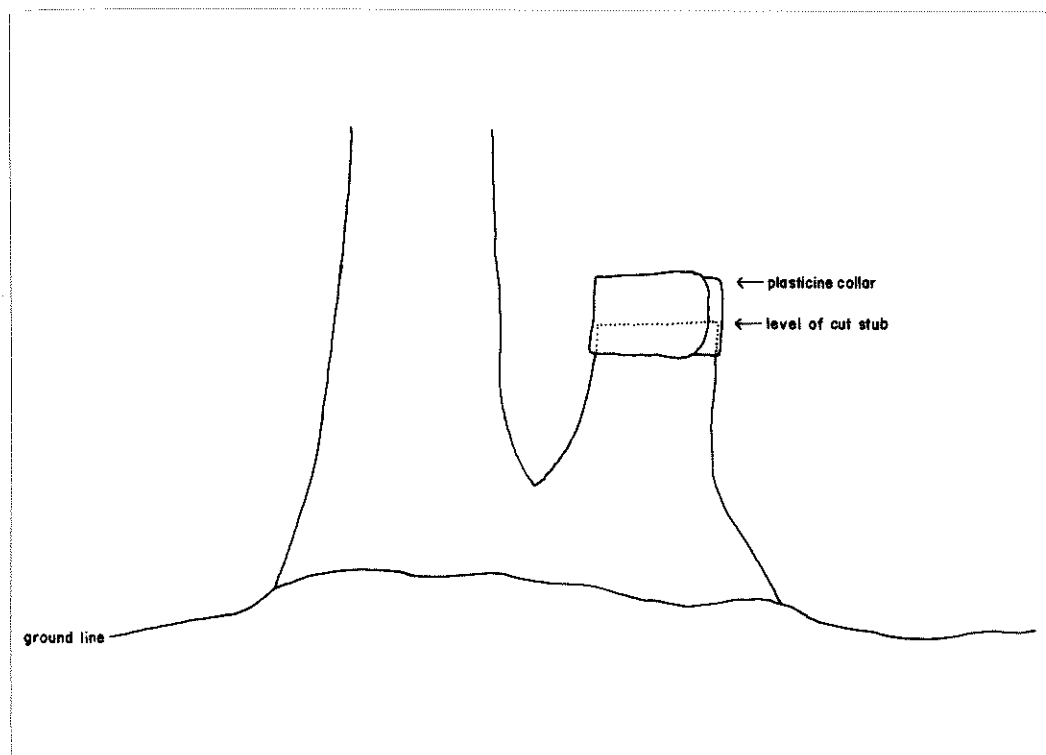


FIG. 1. Application of dye through a sprout stub. The diagram shows a cut sprout stub with a plasticine collar. The dye solution is contained by the collar and enters the stump through the cut surface of the sprout even when both sprouts are cut. Dye enters because of the pressure difference between the dye container and the tissue in the stump. At the surface of the dye solution the pressure is +1 atm; within the stump pressures are lower than 1 atm during periods of transpiration. The dye solution is carried along the gradient of decreasing pressures. A remaining sprout which is transpiring will maintain lower than atmospheric pressures within the stump. It is assumed that when both sprouts are cut, the pressures do not equalize for some time after cutting.

TABLE 1. Details of trees with sprout stub application of dye

Tree	Site*	Diameter original stump (cm)	Treatment [#]	Diameter of sprout (cm) [†] and type of dye applied		
				1	2	3
10	I	25.0	R	15.0 S	17.0	18.5
B	II	2.0	T	3.0 S	6.0 M	-
C	II	2.5	T	3.5 S	4.5 M	-
D	II	4.5	C	4.5 S	7.0 M	-
E	II	8.0	T	7.5 M	13.0 S	-
H	II	8.0	C	10.0 M	10.5 S	-

* See p. 5 for a description of the two sites.

[#] Each tree was treated in one of the following three ways:

R = Root released, i.e. all sprouts except Sprout 1 were removed in 1979. Sprout 1 was cut during study and dye was applied.

C = Control, i.e. Sprouts 1 and 2 were cut at the same time and dye was applied to both stubs simultaneously.

T = Test, i.e. Sprout 1 was cut and dye was applied; after several days Sprout 2 was cut and dye was applied.

[†] Sprouts were measured when dry. The following two dyes were used:

S = Safranin.

M = Methyl green.

sprout was cut and dyed. On two occasions, a period of days elapsed between the end of the first application and the start of the second. This had no apparent effect on the results of the experiment. The length of time that an application continued depended primarily on soil moisture conditions. When the soil was dry, dye uptake was rapid, and the treatments were of a shorter duration than they were under wetter conditions. Although an effort was made not to begin dye applications when significant rainfall was forecast within the next four days, rain could not be entirely avoided. Sometimes when the soil was very wet, absorption of the dye stopped; commonly the stumps exuded so that the volume of the dye solution in the container increased. In these cases, the applications were maintained for longer periods so that uptake could resume, unless it was determined that enough dye had already been absorbed. The total amount of dye that a stump was given was determined fairly subjectively and depended on the size of the stump and the speed of absorption. The goal was to have enough dye absorbed to stain a significant cross section of root for a distance of 10 to 20 cm from the root collar. Generally, the roots in which stain appeared were stained over a distance of at least 30 to 40 cm. Total dye absorption for a sprout ranged from 1 to 18 ml/cm² of cut surface. Dye solutions were replenished when they ran low, but occasionally a container ran dry overnight or during especially dry conditions; there was no apparent effect on the rate of dye uptake when the containers were refilled under these circumstances.

This method of applying stain to the cut surface of the sprout stub gave some interesting results which are discussed in the Results section; yet the technique left apparently healthy sections of the stumps and roots

unstained, even when adjacent tissue contained high concentrations of dye. In only one instance did a dye reach the roots attached to the sprout clump farthest from the point of application.

3. Application of dye through root stubs

With the above method, dye solution was introduced against the normal direction of transport in the xylem. It is not surprising that the dye entered a limited amount of tissue. According to Zimmermann and Brown (1971), during transpiration, xylem pressures are below atmospheric pressure and decrease on the order of 0.15 to 0.2 atm/m as the height increases up the tree. One would expect dye to take the path of least resistance and follow the gradient of decreasing pressures. If there are vascular connections between sprouts on a stump, and if one sprout continues to transpire while dye is applied to another sprout's stub, dye might be expected to appear in the xylem of the transpiring sprout, having followed the pressure gradient (+1 atm at entry to pressures increasingly below 1 atm as the stain ascends the transpiring sprout). In fact, dye was found in the stems of sprouts cut after their cohorts had been cut and stained. If the roots were pumping water, giving pressures above atmospheric, dye entering the stump at 1 atm could not be expected to displace this water. Also, it is likely that dye did not enter all tissue which was at a favorable pressure because it was diverted by strong pressure gradients in other tissue. This could account for unstained tissue adjacent to heavily stained tissue.

To work with the prevailing pressure gradients and to achieve a situation more closely approaching a natural one, a second method for

introducing the dye was tried. This technique promised to give a better idea of the extent to which a sprout could use the root system before and after root release. Trees from both sites were excavated around the root collar, disturbing the root system as little as possible, to find one or more appropriate roots. A suitable root was selected, which was easily accessible and was not too eccentric in cross section so that rubber tubing could be easily attached. Its junction with the stump was without obvious vascular connection to any sprout other than the one to which it was immediately attached (Figure 2). These requirements limited the root diameter to less than 2 cm. The roots fitted the description of Lyford and Wilson's (1964) rope-like roots which arise directly from the root collar without a zone of rapid taper. The roots were cut 2 to 10 cm from the stump and the cut surface was trimmed with a jackknife; a container of dye was attached with surgical tubing to the root stub. The joint between the root and the tubing was sealed with silicone rubber and fastened with a hose clamp to prevent leakage. The container, suspended on a ring stand, was covered with a foil tent to prevent evaporation. If dye uptake slowed significantly, the hose was temporarily removed, and the end of the root stub was retrimmed to remove accumulations of large dye particles.

The two trees from Site I treated with this method (Table 2, Trees 1 and 11) each had a root near the surface which appeared to have direct vascular connections to sprouts removed in 1979 and no direct connections with the remaining sprout. In both cases, the root looked alive and healthy. A dye container was applied to each of these roots. Tree N from Site II was excavated and removed from the soil, leaving the sprouts intact and ca. 20 cm of stub on each major root. A plastic bag protected the roots from drying during transport to the lab. The smaller

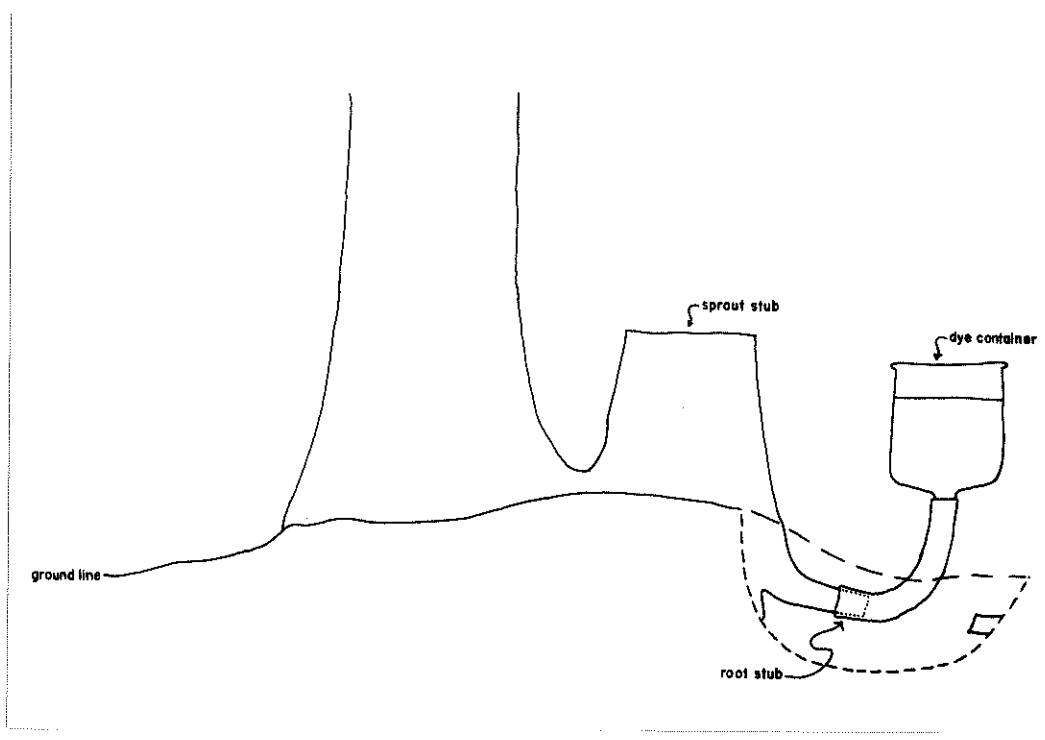


FIG. 2. Application of dye through a root stub. The diagram shows a dye solution being introduced into a cut root stub via tubing attached to a dye container. The associated sprout has been cut. Dye enters the stump because of the pressure difference between the dye container and the stump. The pressures created by transpiration within the stump are lower than the pressure in the container (+1 atm). These low pressures are maintained by continuing transpiration of the remaining sprout.

TABLE 2. Details of trees with root stub application of dye

Tree	Site*	Diameter original stump# (cm)	Treat- ment†	Diameter of § sprout (cm)			Diameter of root (cm) and type** of dye applied	
				1	2	3	1	2
1	I	U	R	16.0	9.0	9.5 ^{##}	-	1.3 S
11	I	U	R	20.5	10.5	14.0	-	1.7 S
O	II	4.5	T	6.5	4.5	-	-	1.4 S
P	II	3.5	C	6.5	6.0	-	1.2 M	1.3 S
Q	II	U	C	6.5	6.5	-	1.1 M	2.0 S
R	II	U	T	10.5	7.0	-	-	0.5 S 0.5 S
T	II	U	T	10.0	8.5	-	-	1.8 S
U	II	U	C	11.0	12.0	-	0.8 S	0.5 M 0.5 M
N	II	3.5	T ^{††}	4.5	3.5	-	-	1.0 S 0.4 S

* See p. 5 for a description of the two sites.

U = diameter of original stump was undetermined.

† Each tree was treated in one of the following three ways:

R = Root released, i.e. all sprouts except Sprout 1 were removed in 1979. Dye was applied to Root 2 (a root not directly associated with Sprout 1).

C = Control, i.e. both sprouts were left intact. Dye was applied to Root 1 (a root associated with Sprout 1) and to Root 2 (a root or closely associated pair of roots associated with Sprout 2).

T = Test, i.e. Sprout 2 was cut and dye was applied to Root 2 (a root or closely associated pair of roots associated with Sprout 2).

§ Sprouts were measured when dry.

** Roots were measured at the cut. The following two dyes were used:

S = Safranin.

M = Methyl green.

Tree 1 had seven sprouts in all; the remaining four sprouts had diameters of 12.0, 13.0, 13.0, and 14.5 cm.

†† Tree N was removed from the ground before Treatment T was applied.

sprout was removed above the crotch, and safranin was applied to a root associated with this sprout. Plastic tubing supplied water to 3 major roots associated with the larger sprout, and silicone rubber sealed the ends of all other large roots to increase the pressure gradient caused by transpiration. Dye application continued until the leaves wilted and yellowed (i.e. 3 days). Other trees from Site II were treated in two ways (Table 2). One group (i.e. Trees O, R, and T) had one sprout of each of the double sprouts removed a few centimeters above the junction with the stump. Dye was applied to a root or a closely related pair of roots which was associated with the cut sprout. The control group (i.e. Trees P, Q, and U) had one root, or one closely related pair of roots, associated with each of the two sprouts on a clump. Neither sprout was cut. One sprout of the clump had methyl green applied to its root(s), and the other sprout had safranin applied to the root(s) associated with it. These puddles were maintained for 2 to 15 days. For the other trees at Sites I and II, the dye containers were refilled for 7 to 16 days, until an increment core taken from the remaining sprout within 20 cm of the junction was stained. Total dye uptake through a root ranged from approximately 30 to 970 ml or from 50 to 750 ml/cm² of cut root surface. Tree I did not show staining in the remaining stem for 24 days. This container was removed after most of the leaves had senesced and fallen in the autumn. If the dye containers ran dry, no effect was noticed on the rate of uptake after refilling.

C. Estimation of root ages

In order to estimate the ages of the roots of one sprout clump,

Tree D, roots with a diameter of 1 cm or more were removed as close to the stump as conveniently possible with a handsaw. The dried roots were softened in an especially effective solution, 4% v/v ethylenediamine; sectioned with a sliding microtome; stained for starch with Lugol (i.e. 0.3 g KI and 0.1 g iodine dissolved in 45 ml of distilled water); and mounted in Permount. A light microscope made the earlier and more tightly spaced increments more distinguishable than they were by eye or with a dissecting microscope. Incomplete or tightly spaced growth rings; circumaxial, but not terminal, bands of parenchyma; and numerous pith flecks made determination of age difficult. Widely spaced growth rings, visible with the unaided eye, could be distinguished with magnification by means of the following characters: a terminal band of parenchyma containing starch stained by the Lugol; a band of cells having much less radial expansion than other cells in that growth ring or the next and/or having a distinctly regular outer edge; rays having discontinuous cells with tangential swelling at the growth ring border; and, frequently, a relatively wide initial band of fibers containing a band of evenly spaced vessels. Under low magnification, the terminal band of cells usually appeared amber colored, especially in the densely spaced inner growth rings. In counting, the amber band was considered the end of a year's increment. The other characters aided in determining questionable cases. Wilson (1964) found age determination in roots of red maple to be difficult because of cylindrically and longitudinally discontinuous growth rings. It was hoped that counting as close to the root collar as possible would reduce the complications of longitudinally discontinuous rings by counting in an area under strong influence of the stem where the rings had not yet tapered out. Counts were made towards the widest part of the root

in any given year, which helped to avoid missing cylindrically discontinuous rings. For each root, the average for several counts was taken. This method yielded satisfactory results, even for the oldest roots whose ages were the most difficult to determine.

D. Vessel continuity between stems and roots

Air infusion was used to investigate the continuity of vessels between a stem and the roots of a double sprout (Figure 3). The sprouts had basal diameters of 6.0 and 7.0 cm. In the field, the sprouts were cut leaving a ca. 75 cm stub on each. The clump was excavated, and the larger roots were cut no closer than 10 cm from the root collar. In the lab, the larger sprout stub was removed with a cut which angled from the crotch down to just above the root collar. The surface was trimmed with a razor blade, and a cork borer (1.6 cm dia.) was gently hammered into the cut surface just above a large root (7.0 by 3.5 cm). The root was sawed to give a smooth transverse surface before submerging the root system in water. Slight air pressure, ca. 5 psi, applied to cut ends of vessels via the cork borer should produce bubbles at the far end of those vessels which were also cut open at the root.

E. Diameter growth of sprouts

Increment growth comparisons were made on 3 red maples from Site I which were root released in the 1979 thinning and 2 red maples from the same site which had their crowns released but which were not root released. Two trees from an adjacent site which were root released the following year were also sampled. Samples were taken with an increment

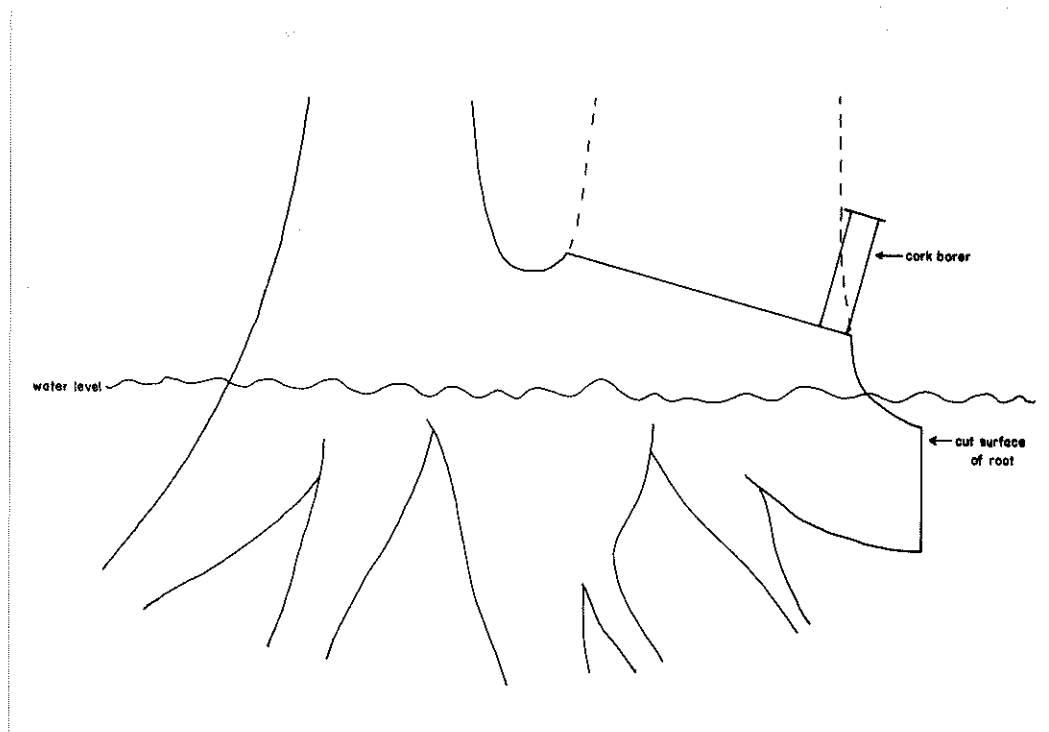


FIG. 3. Air infusion technique for determining vessel continuity. A cork borer is hammered into the outer growth rings of the cut surface of a sprout stub just above a major root. With application of slight air pressure through the cork borer, bubbles will appear on the cut surface of the root if any functional vessels are continuous between the cut surface of the sprout and the cut root surface.

hammer and shaved with a razor blade for measuring relative growth rates under a dissecting microscope. Samples whose growth rings were difficult to identify were sectioned with a sliding microtome, and the sections were mounted in Permount. Growth rates were determined under a light microscope.

III. RESULTS

A. Description of the sprout clumps

A general description of the sprout clumps will aid in understanding the results. All of the trees studied had gypsy moth damage in the early summer of 1981. Some had a large portion (greater than 75%) of their total leaf area eaten by the caterpillars; others had less than 25% of their leaf area removed. Typically the defoliation was ca. 50%. No new leaf growth was noticed on red maples after partial defoliation. In all but 2 of the dissected clumps, the sprouts had grown to surround the original stump, so that it was near the center of the clump. In Tree O, the sprouts developed to one side of the cut stump, leaving the open stump wound at the base of a sprout. A sprout of Tree N developed immediately on top of the original stump. In most cases, the clumps had closed the stump wound, but in a few cases the wound was still open.

The trend towards larger diameter sprouts was associated with a larger diameter original stump (Tables 1 and 2). Growth ring counts on a small sized clump and a large sized clump from Site II confirmed that the trees were within a year of each other's age, as one would expect in coppice growth from a clearcut. The two larger clumps from Site II had fewer roots emanating from their root collars than did the smaller clumps. Most of these roots had pronounced zones of rapid taper. Some of the larger roots had multiple centers indicating that they resulted from the fusion of two or more closely associated smaller roots. The smaller clumps from Site II had many roots, some of which had zones of rapid taper, but many originating at the root collar did not. The large roots of the larger stumps may have resulted from the fusion of either of these types of

roots, but were more likely to be the combination of roots with zones of rapid taper since these tended to be the type of root found in the lower part of the root collar where most of the fused roots originated. Of the two at least partially excavated trees from Site I, the one growing in the wetter soil on a buried rock pile (Tree 10) had many more relatively small roots lacking zones of rapid taper than did Tree 1. A small sampling of the roots indicated that few, if any, of these arose since the trees were root released in 1979. Most of the roots on the two stumps had marked zones of rapid taper. Little evidence of rotten root wood was found either in the soil or incorporated into any of the stumps.

The potential for transfer of xylem sap between parts of the clump was increased by abutting and fused xylem tissue above and below ground. Above ground the tissue of the sprouts abutted, and dissection frequently showed close physiological connections indicated by the dye transfer through the tissue. In the deep humus layer that accumulated in the center of the multiple sprout junction on trees from Site I, roots originating above the root collar and penetrating the humus often grafted with roots from other sprouts of the same clump. Such roots may actually become incorporated into sprout stems other than their own as the sprouts continue to grow. Root grafts were common in the soil, sometimes joining roots in a complex pattern. Dye traces were continuous through many of the grafts.

B. Dye distribution in sprout clumps

1. General observations

Although there were differences in dye distribution in the two methods

used (i.e. root and sprout applications), several similarities did exist. At the point of application, the dye stained all of the transverse area including vessel walls, fiber walls, and parenchyma. In areas at least slightly removed from the application point, the dye concentrated in certain areas rather than distributing evenly throughout the wood (Figure 4). Much of the unstained tissue appeared functional; it was not discolored, and the vessels showed no plugging with gums or tyloses under the microscope. It is possible that some of this tissue was nonfunctional, but that tyloses and gum deposits had not yet formed or were not common enough to be obvious under the microscope. In addition, the dye paths displayed a strong preference for the outer growth rings in the stems, roots, and stumps. If the dye was following decreasing pressure gradients, as expected, those places which did not stain and were not plugged probably did not have gradients favorable for the conduction of the dye solution.

2. Application of dye through sprout stubs

Dye application through the sprout stubs resulted in several interesting findings. As mentioned previously, dye did not penetrate into roots on the opposite side of the sprout clump from the application point, but dye did penetrate to some extent into all major roots on the side of the clump near its application. During excavation, it was clear that some roots contained high dye concentrations ca. 1 m from the stump, while the concentrations in others dwindled to very little within a few centimeters of the root collar. More careful investigation in the lab indicated that roots which appeared to have high concentrations of dye had larger areas

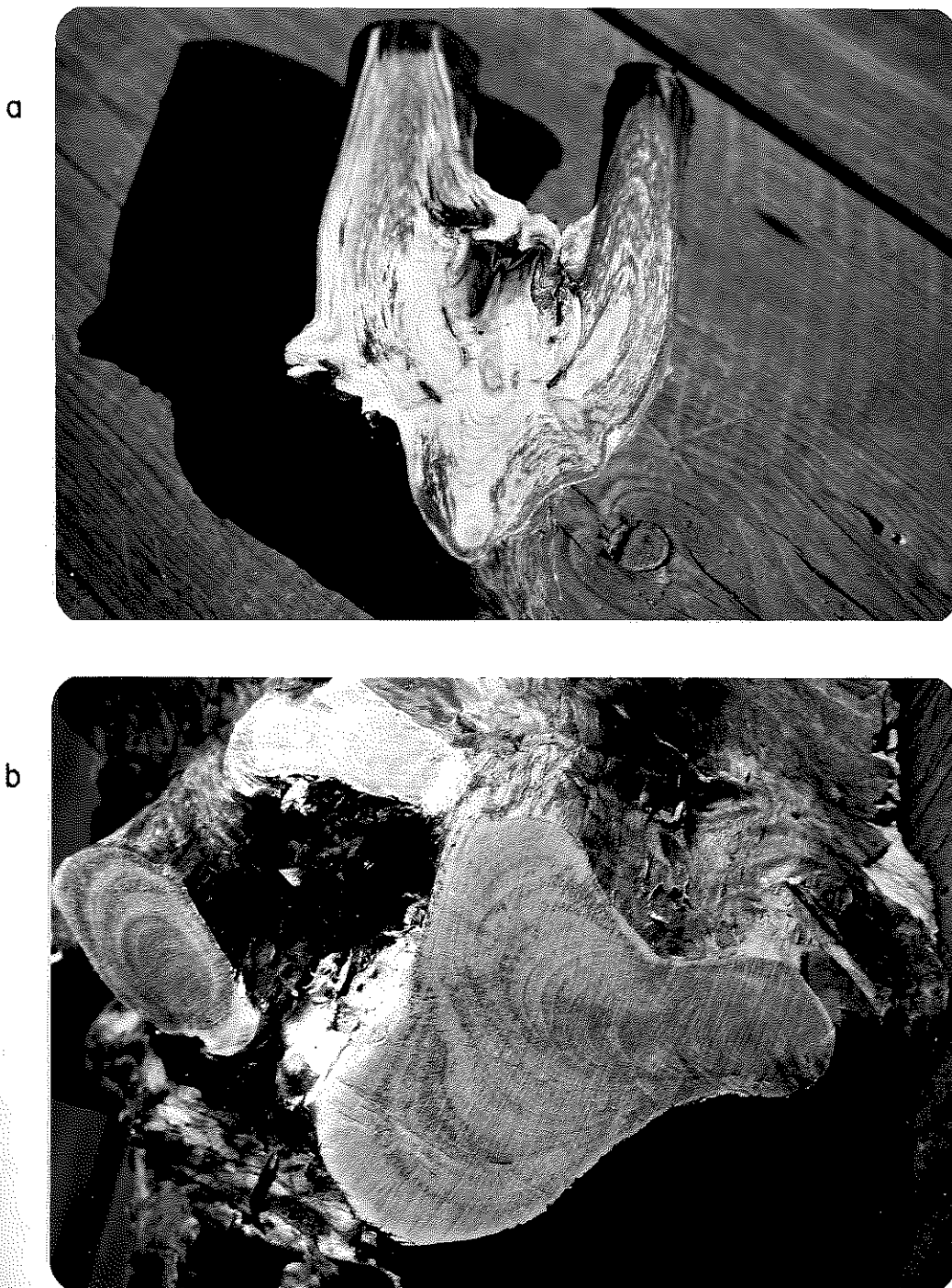


FIG. 4. Uneven dye distribution in woody tissue. (a) Longitudinal section through both sprouts of Tree C. Note the areas of unstained tissue at the centers of the stump and stems and the unstained areas which are intermingled with darkly stained tissue. (b) Transverse surfaces of some roots of Tree D. Here one can clearly see unstained discolored tissue in the central portions of the roots and unstained tissue which is not discolored in the outer portions of the roots. Tyloses were often not visible under the microscope in the latter type of unstained tissue.

in which the tissue was more darkly stained than did other roots. Not all roots had large dyed areas adjacent to the root collar, but most did, indicating that most of the root system was functional.

The variation between clumps was so extreme that it was impossible to determine differences in root dye patterns between test clumps (i.e. clumps with one sprout cut for dye application a few days before cutting the other sprout and introducing dye into the second sprout) and control clumps (i.e. clumps in which dye was introduced simultaneously into both sprouts). There were areas of overlap of the two dyes in the stumps of both cases, and some roots in both control and test clumps contained the two colors. In general, roots showing both colors originated at or near the junction of the two sprouts on the root collar, so that a clump with most of its major roots originating near the sprout junction had more roots with overlap than did others. In transverse section, dye colors extended towards each other with little or no overlap in some roots and with significant overlap in others (Figure 5). Areas of overlap looked violet to the eye. Magnification showed that overlap occurred in each of three configurations: neighboring vessels each stained with its respective dye; each vessel stained with an appropriate balance of both dyes to appear violet; and each vessel stained with both colors, but with one color predominating. There was probably a continuum among the three. In the last configuration, safranin was the strongly staining dye against a background of methyl green. Methyl green must disperse throughout the tissue more easily than safranin, because methyl green became the background color regardless of the order of application.

When the second sprout was cut for dye application in the test cases, the first dye was always found in the cut surface of the second sprout.

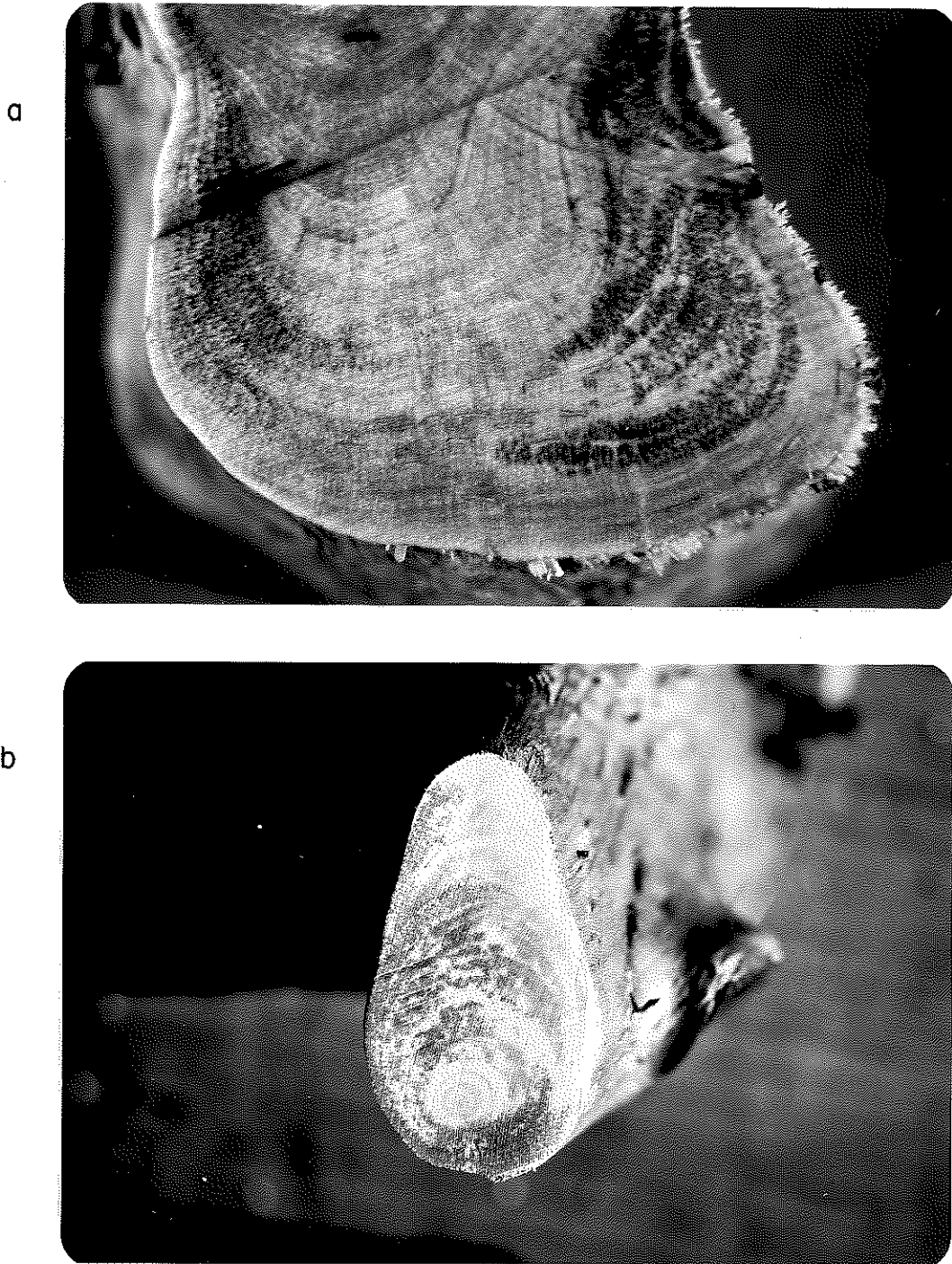


FIG. 5. Dye distribution within individual roots. (a) Transverse section of a root from Tree D in which dyed areas approach each other, but do not overlap. (b) Transverse section of a root from Tree C in which areas dyed with different colors overlap. The areas in which both dyes traveled appear violet. Note the greater dispersal of methyl green dye.

This was the only situation in which dye was consistently found predominantly in the innermost growth rings of the sprouts. Up to 40% of the transverse surface of the second sprout was colored with dye from the first application. After introduction of the second dye, that dye was sometimes found in the other sprout stub. It is likely to have been forced there by the slightly higher pressure caused by the elevation of the dye container above the height of the other stub. Even considering the greater tendency of methyl green to disperse, dye from the second application found in the other sprout stub was in less well defined areas than the dye from the first application found in the second sprout. Distribution of dye in the clumps with simultaneous applications also indicated that dye entering the clump without the strong pressure gradients induced by transpiration disperses more easily. Dye taken up through the transpiration stream in the test clumps was found in more distinct areas. The distribution of dye in the stumps of clumps receiving dye with a time lag between applications and those receiving dye simultaneously in both sprouts reflected the greater dispersal of dye moving without strong pressure gradients.

3. Application of dye through root stubs

Dye application via the root stub yielded the most important information concerning an individual sprout's ability to use the root system of the sprout clump. In one control (i.e. Tree Q), dye applied to a root crossed to the sprout not directly associated with that root (Figure 6); it was estimated that the crossover stained less than 0.1% of the transverse surface of that sprout at 2 cm above the crotch. The

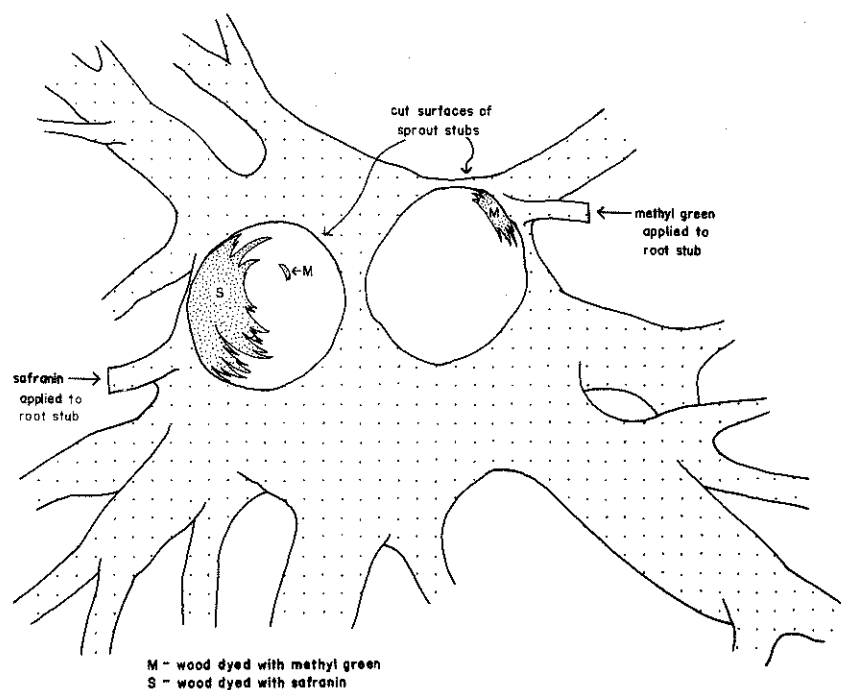


FIG. 6. Crossover of methyl green in Tree Q. This is an approximate representation of Tree Q in which methyl green dye passed from the root through which it was applied into its associated sprout and into the remote sprout. Tree Q was a control application (i.e., both sprouts were intact and transpiring). Concurrently with the application of methyl green, safranin was applied to a root associated with the sprout farthest from the methyl green application. This is the only root application control in which crossover occurred.

directly associated dye colored ca. 2% of the surface of the same sprout, and the dye which crossed over colored ca. 33% of its directly associated sprout. The crossover dye was not visible 20 cm above the crotch. The other controls exhibited no transfer of dye from one sprout to the other. Tree P, a control, was dissected, and aside from some movement into adjacent roots the dyes ascended the stems of their respective sprouts with comparatively little lateral and radial spread (Figure 7).

In 5 of 6 test clumps, including trees from Site I, dye applied to the roots associated with cut sprouts was incorporated into the transpiration stream of the remaining sprout. Dye was visible on the cut surface of the sprout associated with the root stub through which dye was applied in all three of the clumps from Site II and in Tree N. In the field, this dye did not appear until the surface of the cut was wet with rainfall. The dye on the surface of Tree N appeared almost immediately; the dye container was initially suspended above the height of the sprout stub. Tree O was dissected. More dye was visible in the sprout stub and in the roots than in the control, but much of the dye followed a direct and well defined path through the lower half of the stump and into the sprout that was transpiring at the time of dye application (Figure 8). Tree N, which was removed from the ground before dye application, also showed dye in the transpiration stream, but exhibited much more puddling of dye in the stump and roots than did Tree O (Figure 9). This may be attributed to a smaller pressure gradient from top to bottom of the transpiring stem than was found in the test clumps with intact root systems in the field. A smaller pressure gradient would pull less of the entering dye solution towards the apex, allowing more dye to settle in the roots and stump. At least two causes may account for the lessened pressure gradient. Evaporation of

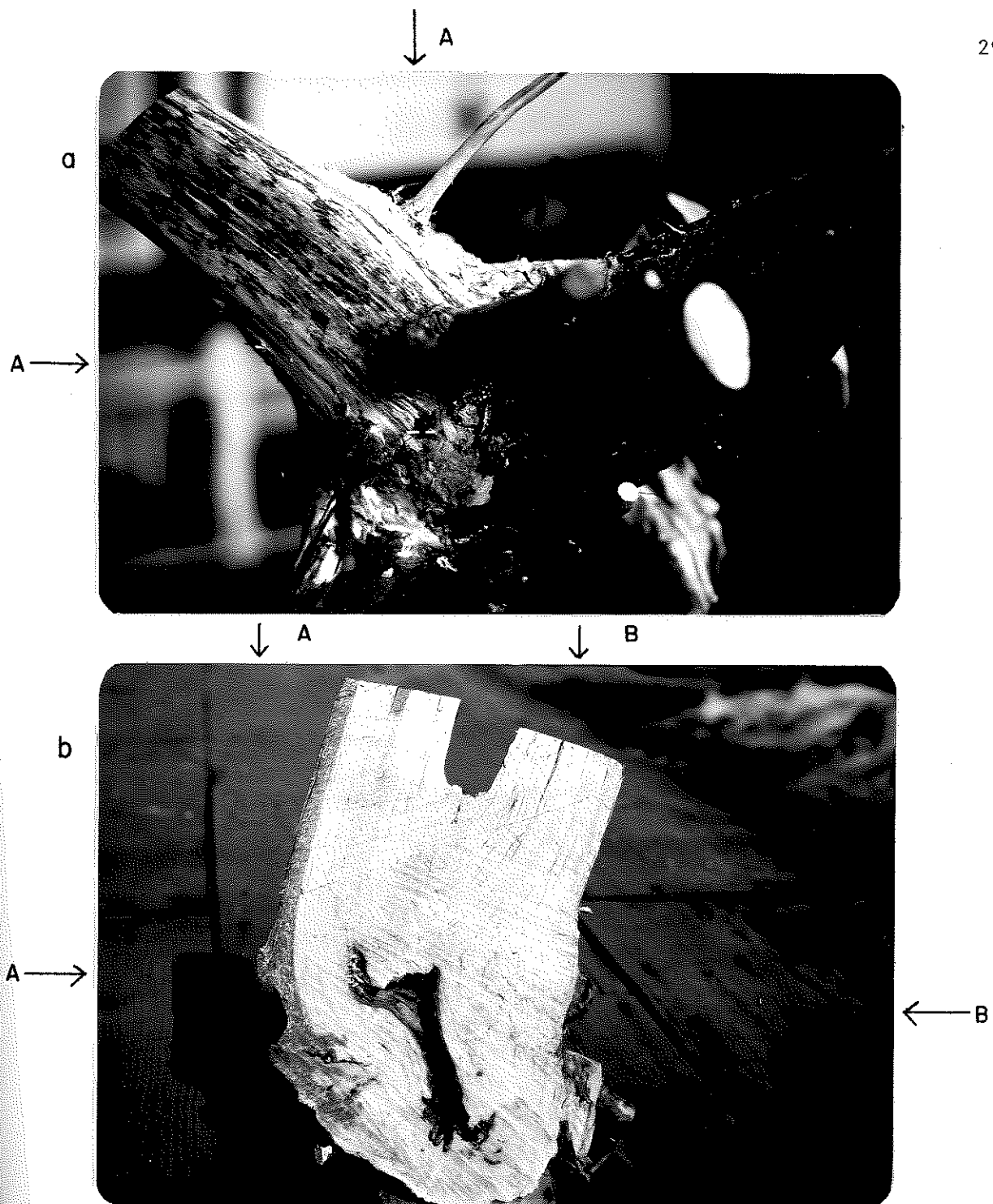


FIG. 7. Dye ascent in a root stub application control. These views of Tree P, (a) an end view from the root through which safranin was applied and (b) a longitudinal section through both sprouts, show that there was little lateral movement of dye in an application in which dye was introduced into roots with both sprouts intact and transpiring. The root through which safranin was applied is indicated at A, and the root through which methyl green was applied is indicated at B.

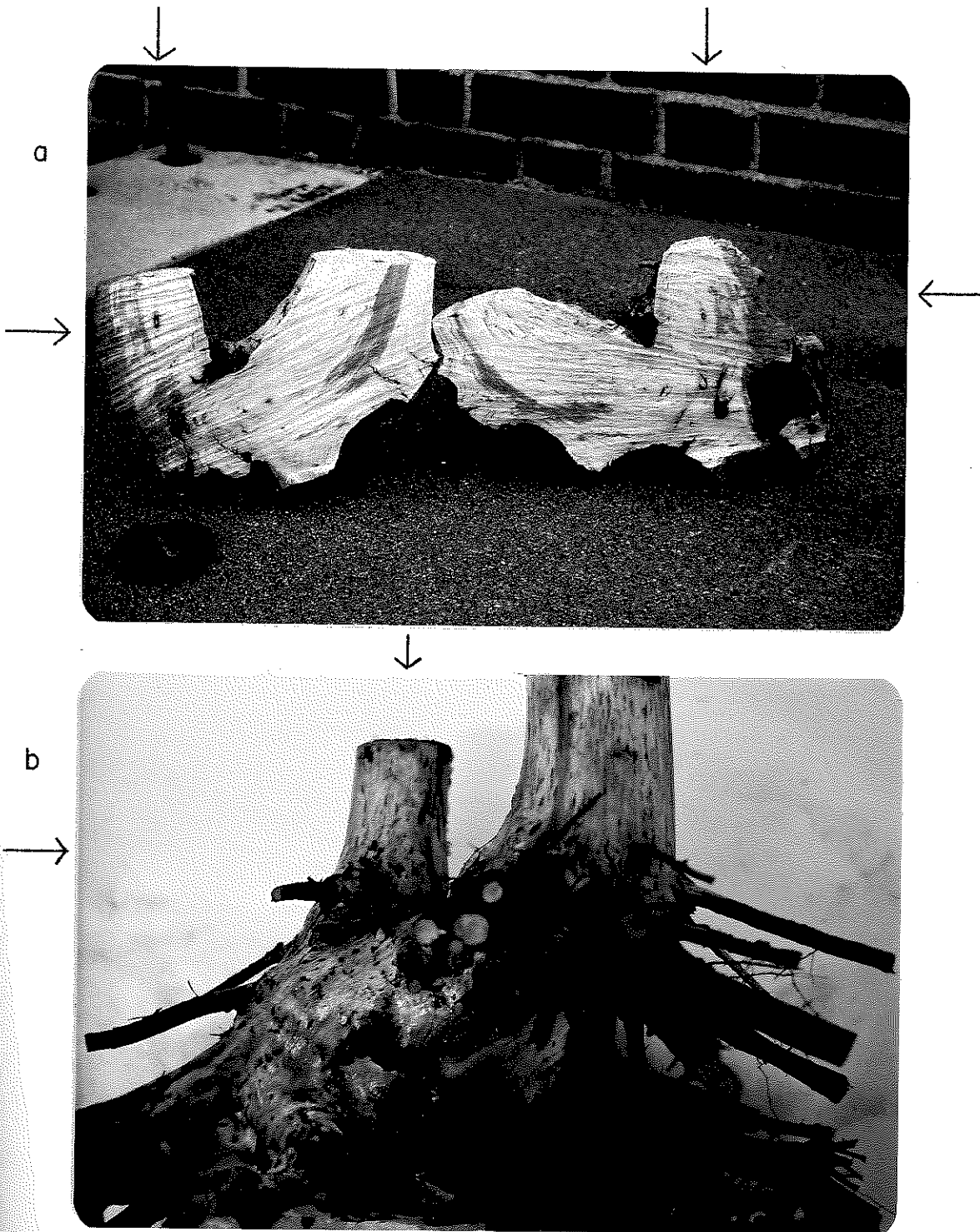


FIG. 8. Movement of dye from the root of application into the remote sprout. The sprout associated with the root through which dye was applied is indicated by arrows. This sprout was cut at the time of application; the remote sprout was uncut and transpiring. (a) Longitudinal section through both sprouts of Tree 0. (b) External view of the dye movement.

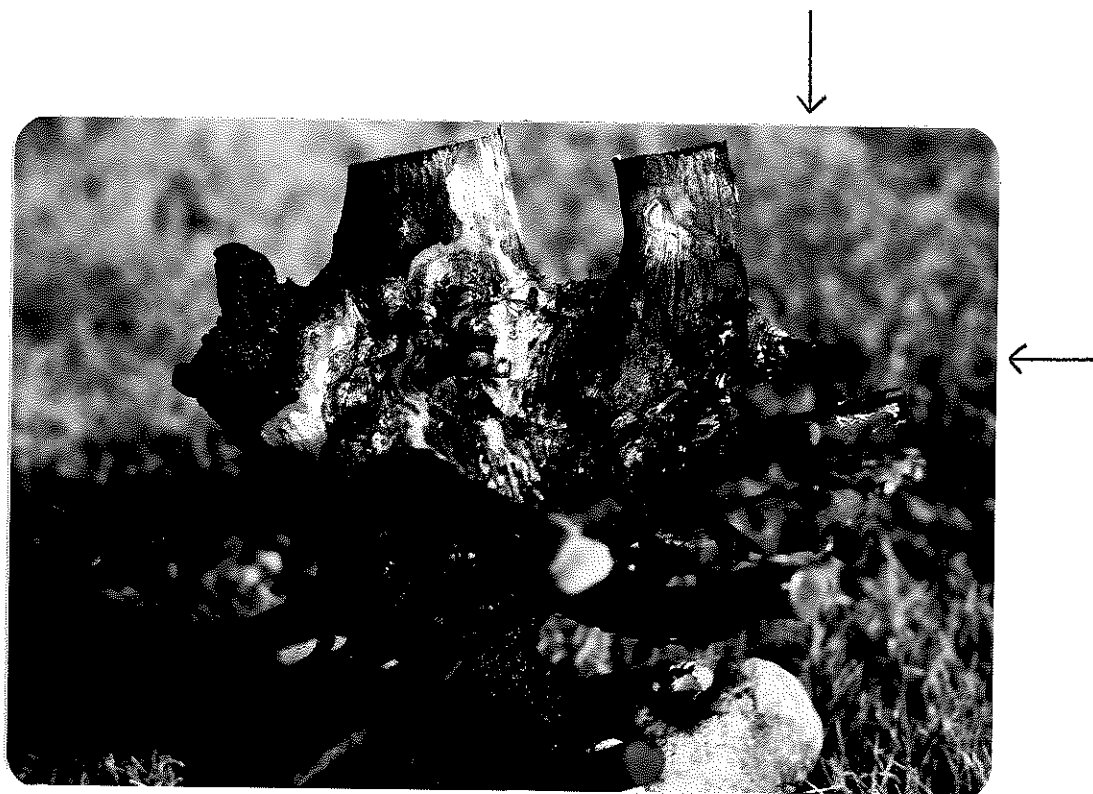


FIG. 9. High concentration of dye in the stump of Tree N. Tree N, which was removed from the ground before having one of its sprouts cut and dye applied through a root (indicated by arrows) associated with that sprout, had a high concentration of dye in the outer growth rings of the roots and stump.

water from the exposed roots and stump may have lowered the pressures within the stump during the dye application, and/or the puddling may have occurred towards the end of the application period as the leaves wilted and transpiration slowed.

The case in which the dye did not cross to the remaining sprout was Tree 1 at Site I. This clump had several sprouts with diameters less than 1.2 cm that had developed since the thinning. Even though the root through which dye was applied angled away from a group of these sprouts, and they were separated from the root by at least 16 cm, the group contained a high concentration of safranin (Figure 10). Many of the major roots at or below ground level on the side of the stump towards the root of application contained dye, but no dye was visible in the stem left after thinning. This tree was badly damaged by gypsy moths (50 to 70% of the leaf area was removed) and was starting to show color change in mid-September. However, other test trees which did take up dye had almost as much leaf area removed and had turned or were turning color. If the rate of transpiration of the third generation sprouts was especially high, the dye may have been diverted to them; but with the amount of dye present in the root system, it is not likely that the pressure gradient between the third generation sprouts and the application point diverted significant quantities of dye. It is much more plausible that the vascular connections between second generation sprouts in this clump were not very effective. Wood and bark samples taken from this stump showed the results of vascular reorientation after the thinning, presumably showing that there was at least some communication between parts of the clump after root release. It is also possible that the transpiration rate of the remaining second generation sprout was low for unknown reasons.

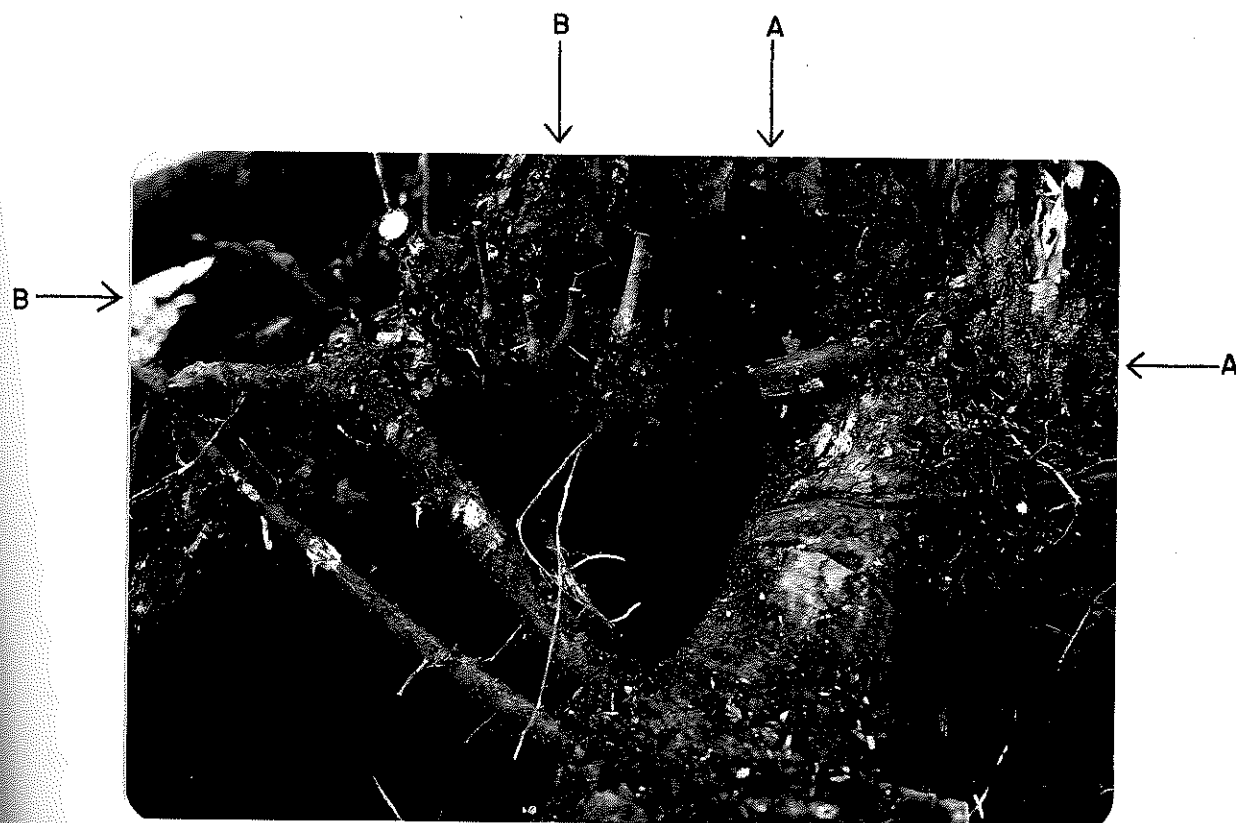


FIG. 10. Third generation sprouts containing dye. Dye introduced into Tree 1 through the root (A) moved into some of the sprouts which elongated after root release (B) in addition to traveling into some of the roots.

4. Reorientation of vascular tissue

Wood samples from several places on Tree 1 and from one place on Tree 10 (both root-released clumps) revealed vessels in the superficial layers of wood oriented at angles to the vessels in deeper layers. In some samples, the difference in orientation was much more noticeable in the phloem than in the xylem because the phloem layers were more easily separated by hand to show their orientation. The angling of the newer tissue connected second or third generation sprouts with roots that were not directly beneath the sprouts. In Tree 10, some vessels were oriented at angles of more than 45° from the orientation of the underlying layers (Figure 11a). Viewed under the microscope in transverse section, the new tissue was distinct from the older wood (Figure 11c). In this sample were two growth rings of distinct tissue, the outer ring being very narrow, irregular, and apparently containing no stained vessels. The cell walls were darker, and the cells, including the vessels, had a more rectangular outline and were not as radially expanded as were those in the older tissue. The radial files were more evident, the vessels were less distinguishable, and the parenchyma represented a larger percentage of the total number of cells. This section of the clump changed its cambial orientation and laid down the new vessels after being root released in 1979. The vessels shown in Figure 11a radiate from the root indicated in Figure 11b. Dissection proved the root to have originated from the sprout which shows the reorientation (B). The sprout was removed with others in the 1979 thinning, but the root abutted the remaining sprout (A) and had already fused with several roots associated with the remaining sprout. Dye travelled from A through the root to B and into the older, normally

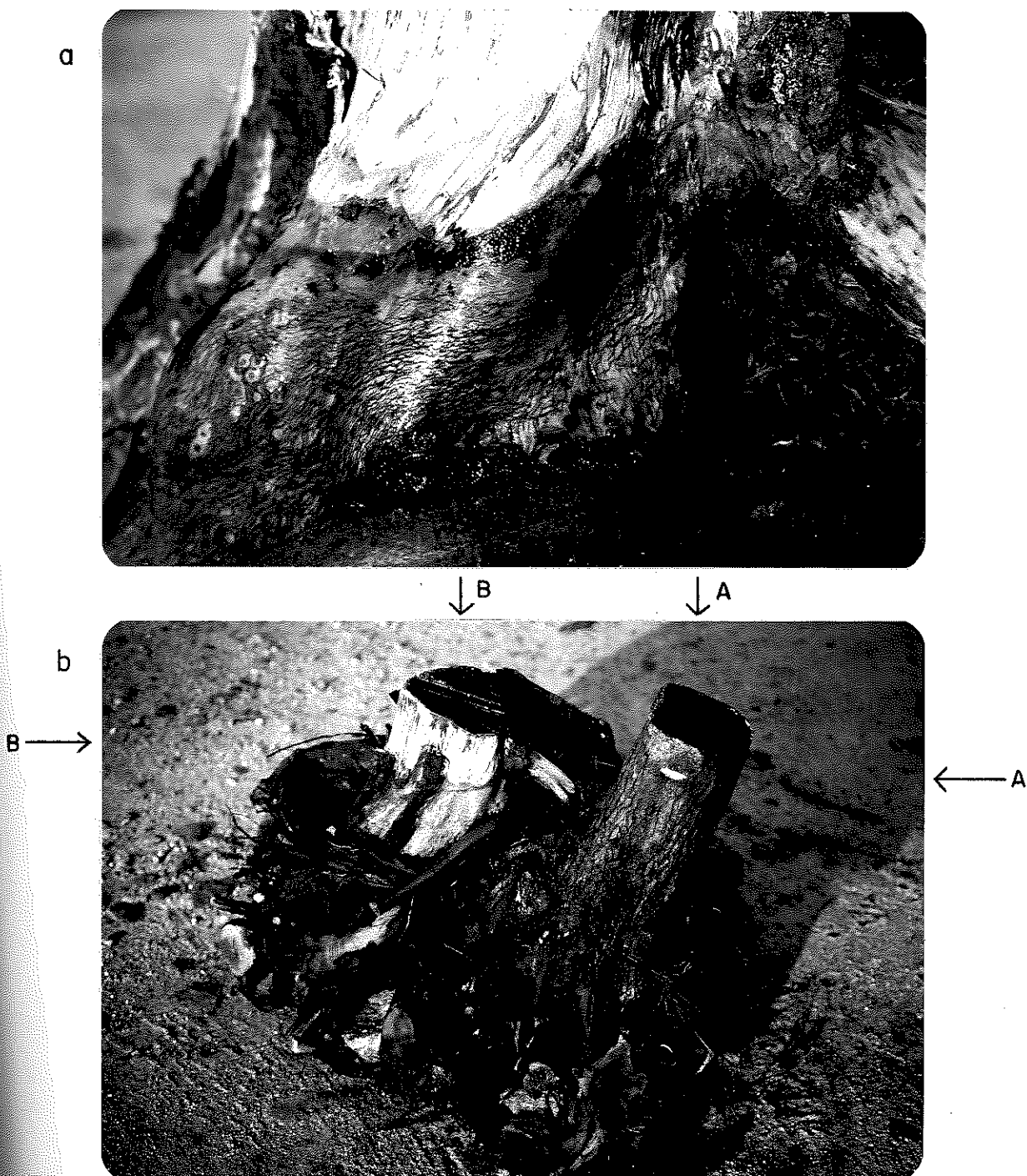


FIG. 11. Reoriented vascular tissue in Tree 10. (a) A close view of the reoriented vessels after peeling the bark to expose the surface of the reoriented tissue. Note the angles of orientation. (b) Overall view of the sprout clump. The sprout remaining after thinning is indicated at A. The sprout showing vascular reorientation is indicated at B; this sprout was cut during the 1979 thinning. Note the root which traverses between these two sprouts. Some of the bark has been peeled from the stump. (Continued on the next page.)

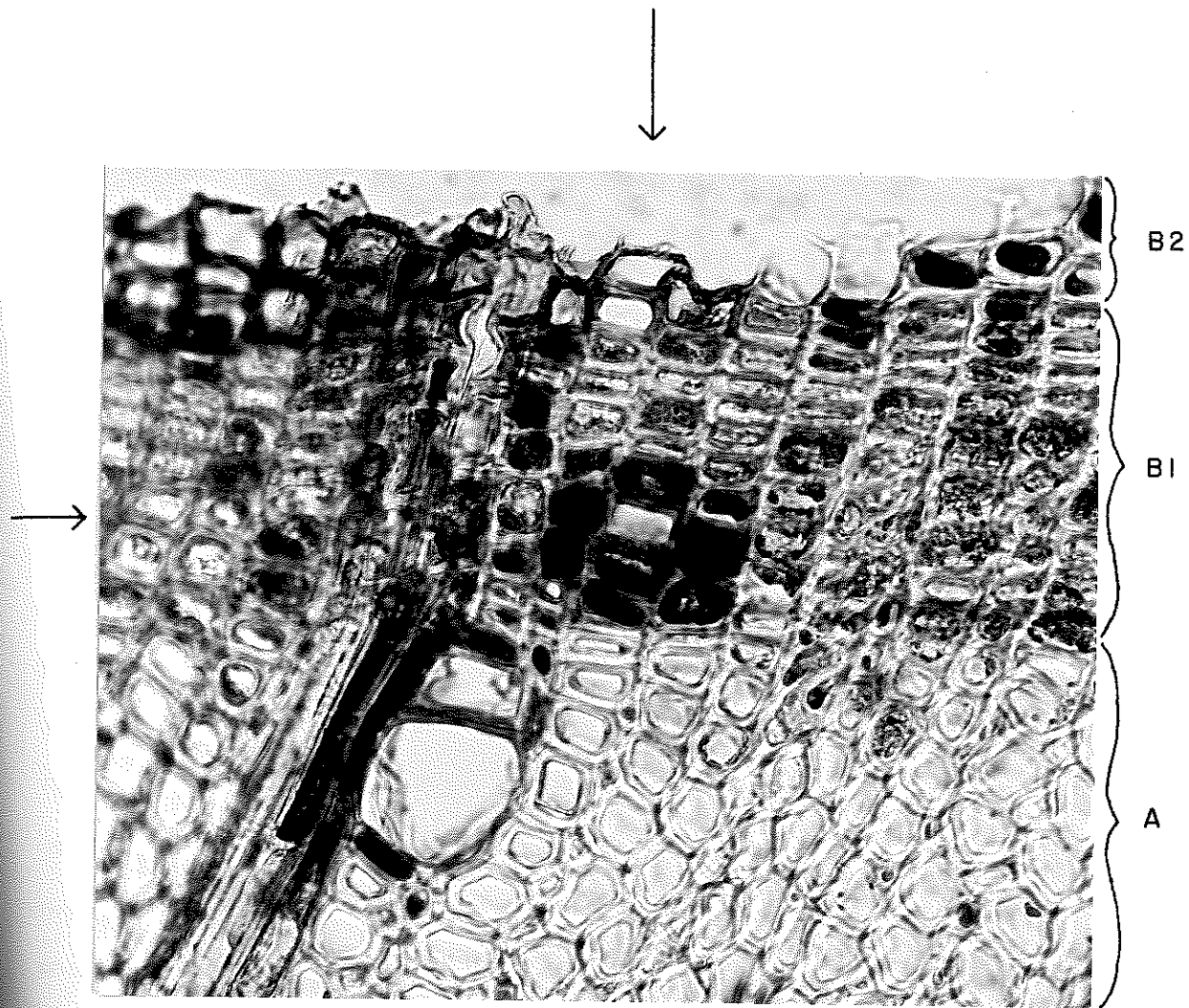


FIG. 11. (Continued from the previous page.) (c) A transverse section through reoriented tissue shows the differences between normal tissue (A) and two growth rings of reoriented tissue (B1 and B2). The arrows indicate a dye stained vessel in the reoriented tissue.

oriented vessels at the same time that it entered the more recent reoriented ones.

C. Root ages

Each excavated stump bore small roots originating at the root collar which displayed the characters of Lyford and Wilson's (1964) rope-like roots originating at the root collar without a zone of rapid taper. Lyford and Wilson described such roots as adventitious roots arising from proto-xylem poles. They found that these roots were positioned high on the root collar in wet soils, but developed on well drained soils after the larger roots were diseased or injured, or when the growth rate and physiological activity of the older roots slowed. In almost all examples of this type of root occurring in the current study, the roots were less than 1 cm and frequently only a few millimeters in diameter and originated at the base of a much larger root or in knobby areas which Wilson (1968) described as containing buried buds. After superficial examination of some of the sprout clumps in the current study, it was hypothesized that the roots showing zones of rapid taper were roots that originated with the parent tree before cutting, and that those roots lacking a zone of rapid taper were of adventitious origin, beginning elongation with the second generation sprouts or afterwards.

Increment counts of roots in Tree D showed that only 5 of the 16 roots were likely to have originated at or before the time the parent tree was cut (Table 3). Of these, 3 had sufficient numbers of growth rings to associate them with the original stem. The other two roots had growth ring counts of approximately the age of the sprouts, 45 years. The error

TABLE 3. Average ages of the roots of Tree D

	Root																
	1	2	3 [#]	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Growth form*	R2	R	-	R2	R	R	R	R	R2	T	R	T	R	T	T	R	T
Average age (years)	23	21	-	15	10	32	33	10	22	45	9	61	34	61	52	10	47
	27			24					15								

*Growth form is described as:

R = Ropelike roots originating at the root collar.

R2 = Ropelike roots with two centers originating at the root collar and appearing to have distinct zones of rapid taper.

T = Roots with marked zones of rapid taper.

Externally, Root 3 appeared to be a separate root but in fact was an integral part of Root 15 and did not have a separate center.

in counting was large enough so that it was impossible to determine whether these sprouts were originally associated with the parent stem or elongated with or soon after the sprouts. These 5 roots were the largest roots at the root collar, and each had a pronounced zone of rapid taper. They were more irregular in cross section and originated lower on the root collar than did the other roots. Although these characters distinguished the 5 roots from the other roots which were younger, the potential for confusion of root age classes based on morphological features existed. Some of the younger roots with zones of rapid taper appeared larger because they were fused with other young roots. Careful observation could distinguish between older large roots and younger fused roots in this clump. None of the roots originating as rope-like from the root collar had a ring count that dated it to the cutting of the parent stem. It is possible that some growth rings were overlooked during counting or that rings were discontinuous at the counting location, but it is unlikely that such a large number of rings were missed or lacking near the root collar.

The age of each root of other stumps' root systems was not estimated, but it might have been more difficult to determine relative root age by growth form on the other stumps, especially those with a higher incidence of root fusion. It is likely that roots lacking a zone of rapid taper on red maple stump sprouts are adventitious roots arising since the cutting of the parent stem. If these small roots are more vigorous than larger ones, a root-released sprout may use them to advantage. Third generation sprouts, elongating after root release of a second generation sprout, sometimes took advantage of the existing root system without producing new roots and sometimes produced very small diameter (1 to 2 mm) new roots.

D. Continuity of vessels between stems and roots

Vessels are continuous between sprout stems and roots. The air infusion method produced bubbles rising from several distinct places in the upper quarter of the root's transversely cut surface. Each place where bubbles formed must pinpoint the lower end of a vessel which was also cut open at the cork borer, since air cannot pass from one vessel to another or into intercellular spaces at the applied pressure. Tensions at the air/water interface are too large to allow bubbles to pass through pores in the vessel to vessel pits or through pores into intercellular spaces. The vessels which were cut at both ends traversed a distance of at least 10 to 12 cm between cuts.

E. Comparison of diameter growth

The increment samples confirmed the damage caused by gypsy moth caterpillars during the summer of 1981; all but one of the sampled trees experienced a decrease in growth during that year. Figure 12 shows a sampling of the growth curves for the last five years. Partial defoliation of selected trees may be reflected in the decreasing growth of those trees in the years preceding 1981. Although some root-released and some crown released trees showed an increase in growth during the year following release, others showed a decrease. Because of the erratic growth figures caused by the gypsy moth caterpillars, analysis of the data for comparisons of increment growth rates between crown released trees and trees which were also root released was impossible.

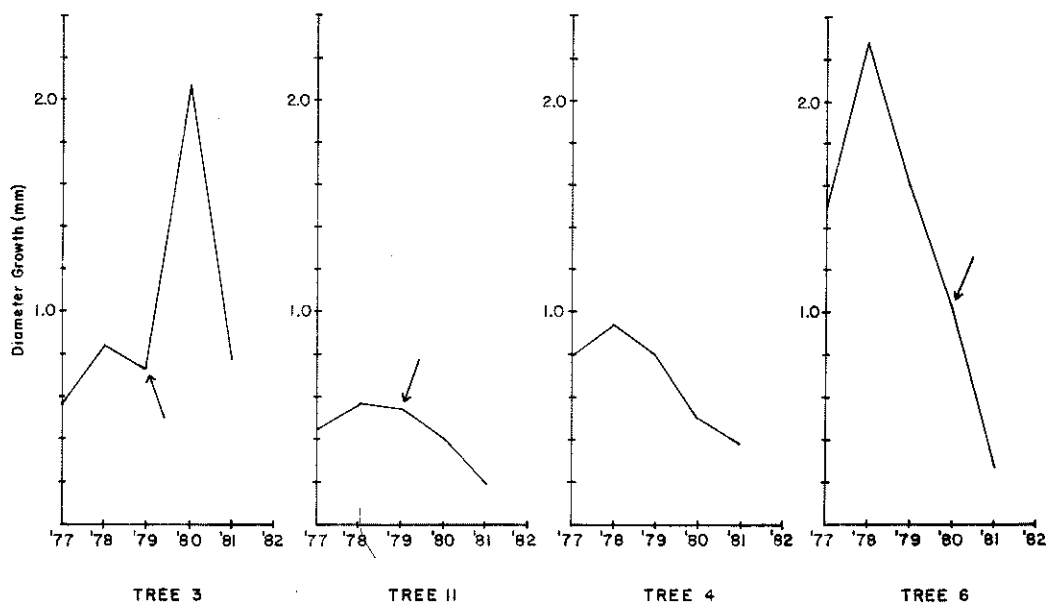


FIG. 12. Yearly diameter growth in root-released trees and in trees which were only crown released. This is a sampling of the trees which were measured for the last 5 years' diameter growth. The arrows indicate the year of root release (1979 for Trees 3 and 11; 1980 for Tree 6 which was neither root nor crown released in 1979). Tree 4 was crown released in 1979 but not root released.

IV. DISCUSSION

A. Sprouts' use of root system

Pressure gradients in the xylem are usually such that a sprout in a clump uses resources only from roots which have direct vascular connections with the sprout (Figure 13a). Only roots which are associated with junctions between two or more sprouts will share their xylem sap with more than one sprout. Because many growth rings in the diffuse porous maple are functional, the association may be deep within the stump and not easily detected from the outside, except by the direction in which the root penetrates the root collar. The physiological connections between root and stem follow the direct anatomical connections. Not only are some vessels continuous between the stem and the roots, but connections between vessels allow xylem sap to travel axially from one vessel to the next. Little lateral movement through the tissue occurs because the vessels are directly connected along the pressure gradient (Figure 13b).

There can be little doubt that a sprout remaining after removing all other sprouts from the clump has access to a large part of the root system. In Tree 1, where the root through which dye was applied angled away from a group of 2 year old sprouts, evidence indicates that even small sprouts can use a much greater portion of the root system than they would under competition with other stems. Root releasing a sprout neutralizes competing pressure sinks by removing other transpiring crowns from the clump and changes the pressure gradients so that the sprout has access to the xylem sap in many more roots (Figure 14a). Although direct physiological connections between the root system and the sprout result, the anatomical connections are not direct, and the transpiration stream

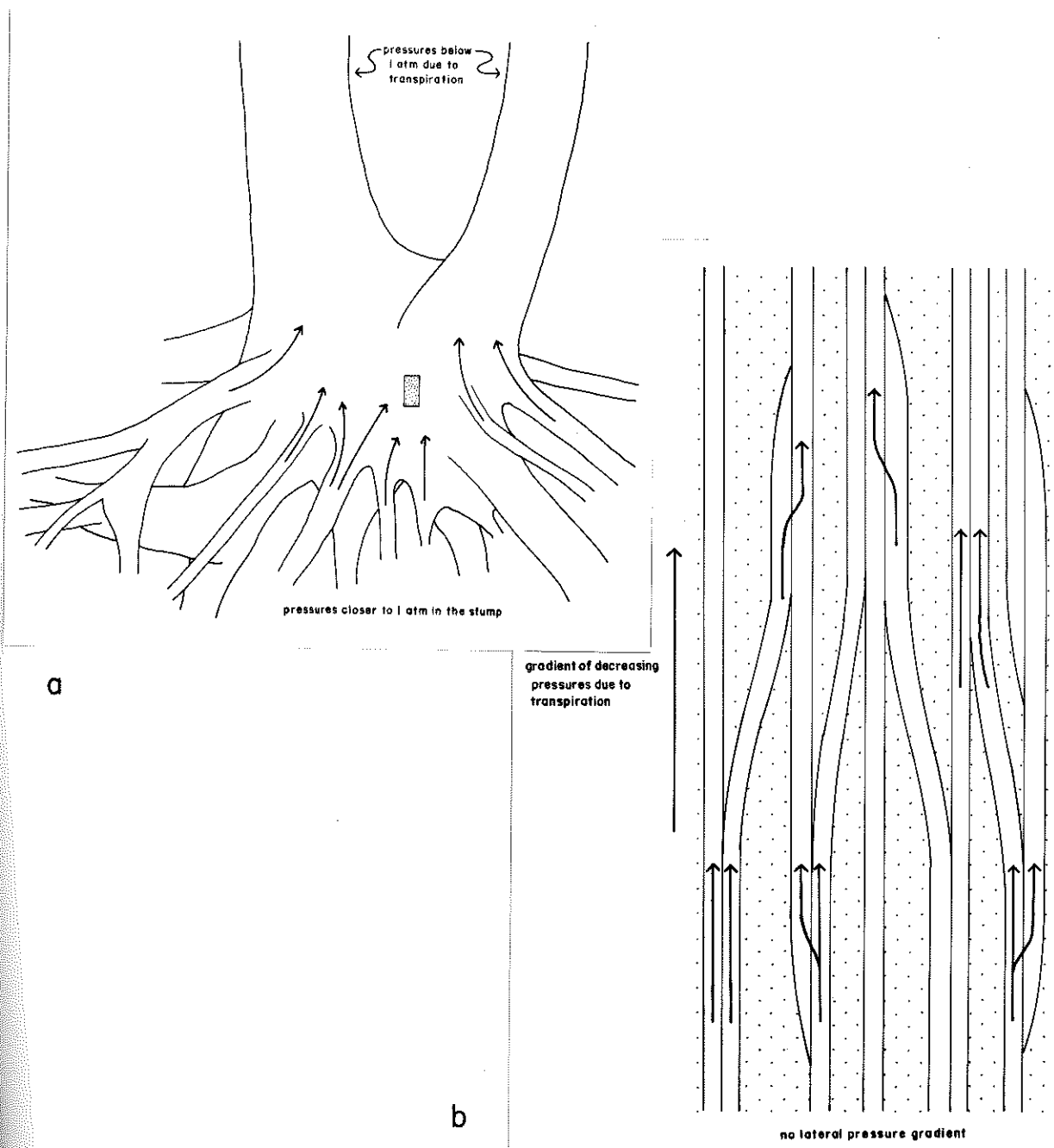


FIG. 13. Presumed pressure gradients in an intact sprout clump. (a) The arrows indicate the general directions of the gradients of decreasing pressures in a sprout clump which correspond to the directions of xylem sap flow from the roots. The shaded area is magnified in b. (b) This schematic diagram indicates the likely path of xylem sap flow through the vessels. Little lateral flow occurs because the pressure gradient favors axial movement. Thus xylem sap from the roots flows only into closely associated sprouts.

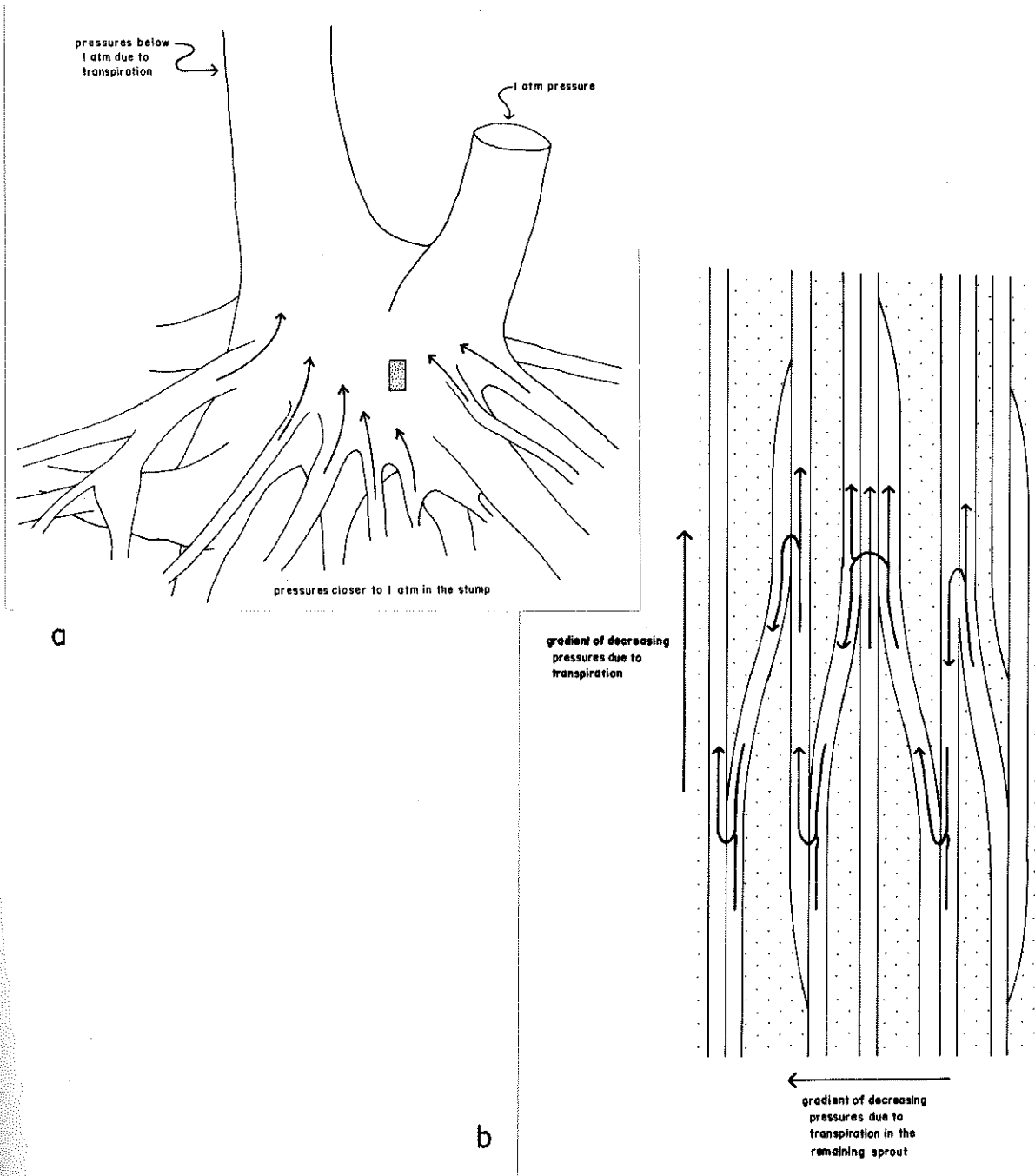


FIG. 14. Presumed pressure gradients in a root-released tree. (a) The arrows indicate the general directions of the gradients of decreasing pressures in a sprout clump after root release. These gradients correspond to the direction of xylem sap flow from the roots. The shaded area is magnified in b. (b) This schematic diagram indicates possible paths of xylem sap flow through the vessels after root release. A significant amount of lateral flow occurs because there is not only an axial component to the pressure gradient, but also a lateral component. Xylem sap from the roots flows into the transpiring sprout. Some of this sap comes from roots which previously supplied only the sprout which has been removed.

must take advantage of the intertwining vessels to flow laterally from one part of the clump to another (Figure 14b). Creating new vascular tissue in which vessels are angled restores a path with direct anatomical connections from sprout to utilized roots.

B. Vascular reorientation

Wilson (1964) described the reorientation of tissue developing under the influence of sprout stubs within the first year after removal of the parent stem. He said that as a result of this reorientation "even if there is only one sprout, it is in direct vascular connection with the whole of its root system, rather than just the portion directly below the sprout which was originally in direct vascular connection." He found red maple tissue in which the vessels grew at angles of up to 45° from the vertical, and described the process of reorientation as being the same as the process which reorients vessels in tissue around wounds. As the current study found, the reorientation process also occurs in tissue under the influence of remaining sprouts if one or more stump sprouts are removed from the clump. As the results of the dye applications through the roots indicate, the redirecting of vascular tissue in the wood does not create new physiological connections, but may lessen the resistance to xylem sap flow from a large area of the root system to a sprout.

Presumably, the tissue reorientation occurs as a result of the directional influence of auxin waves produced in the remaining stem. Zajaczkowski and Wodzicki (1978) postulate auxin waves in tree stems propagated primarily in the cambial region and moving basipetally. Transport also occurs in the differentiating xylem and phloem. In addition to producing the waves,

cambial cells are capable of detecting the direction of propagation and adjusting their orientation accordingly by localized growth and asymmetric divisions. The work with Pinus silvestris L. suggests that tissue orientation and thus plant morphology is regulated by the vectors of propagation of auxin.

In red maple sprout clumps where the sprouts have grown large enough to encircle the parent stump, the vectors of auxin propagation would be expected to be approximately parallel at the root collar. Removal of one or more of the sprouts should disrupt the wave front causing deflection of the wave fronts produced by adjacent sprouts (or the single remaining sprout). The change in direction of propagation should be detected by those cambial initials formerly under the influence of the removed sprout(s), causing a change in orientation of the cambial cells and the vascular tissue derived from them. Over the years, as the remaining sprout(s) increases in diameter and the new wood encompasses the entire stump, the vectors of propagation would be expected to regain parallelism. Using this model, the auxin produced in Sprout A of Tree 10 must have been carried through the root which traversed from Sprout B to Sprout A (Figure 15), in a direction opposite the original flow of auxin and against the flow of xylem sap in the root after thinning. In Sprout B, it influenced the orientation of new tissue. However, most of the dye in this root was not carried in the outer wood layers but deeper within the root, so that it is unlikely that the auxin was carried through the xylem against the transpiration stream. Additionally, since auxin transport is polar, it is not likely to have been transported along the cambium of the root whose polarity was directly opposite the hypothetical direction of auxin transport.



FIG. 15. A view of Tree 10 showing vascular reorientation and the root through which growth hormones may have been transferred. Refer to Figure 11 for details.

An alternate explanation for the vascular reorientation involves the detection of the presence of two poles by the cambial initials and growth responses based on the poles' positions (Zimmermann, 1982, personal communication). Here, the two poles would be the end of the root directly below the reoriented tissue and the apex of the remaining stem (Sprout A). Before thinning the upper pole was represented by Sprout B's own apex. The method of detection is unknown. As yet, the mechanism by which the vascular orientation on Sprout B occurred is unexplained. As described by Tupper-Carey (1930) working with tissue bridges across rings through the phloem of Acer pseudo-platanus and Laburnum vulgare, these cambial changes probably took place gradually during 2 or 3 months.

C. Management implications

Deciding on the best management strategies for red maple coppice stands is a complex problem. The final product (e.g. sawtimber, cordwood, or pulpwood) will determine whether the management goal is to maximize overall growth or to maximize increment growth on select trees. Let us assume that the goal is to optimize the growth on certain trees. Exactly which trees we choose as the future crop trees will depend largely on growth form and on the potential for butt rot to enter from thinning. In current thought, the problem of decay entering from thinning wounds in red maple is minimized. It is suggested that potential crop trees be selected primarily by growth form, so the important question is: Should one opt for 2 or 3 well formed stems in a sprout clump or choose to thin to one sprout per stump? On wet sites where water and nutrients are not limiting, there may be little growth advantage in the second thinning

method. There may be an advantage during dry years, but gains are more likely to come from removing crowns which compete with the selected stem for light. On drier sites where water and nutrients are limiting growth, there may be great advantage in selecting a thinning pattern which gives the future crop trees larger root systems to exploit. Stumps whose roots are not utilized by vigorously growing stems are a resource lost to the current timber harvest. It is unlikely that sprouts elongating after root release are serious competition for a clump's resources. Within a few years the canopy should close and reduce the third generation growth to a minimum by limiting the light that reaches the young shoots.

D. Remaining questions

In the tradition of scientific investigation this study has raised more questions. Assuming that red maple is typical of diffuse porous species, do ring porous species (e.g. oaks) behave in the same manner after thinning to one sprout per stump? There are at least 2 characteristics of ring porous trees that lead one to suspect that they may have different reactions to "root release" from those of red maple. Only the outer growth ring has efficient earlywood vessels which are functional. These vessels are extremely long compared to the vessels of diffuse porous trees (Zimmermann and Jeje, 1981). Cutting one or more sprouts on an oak, or other ring porous species, may embolize a sufficient number of vessels in the root collar to disrupt the pathway that water and nutrients would use to reach the remaining stem from the more remote parts of the root system. On the other hand, the roots of ring porous species have diffuse porous characters, at least with respect to vessel

distribution within a growth ring. This may enable ring porous trees to take advantage of root release in a manner similar to red maple. In part, this ability should depend on the wood anatomy in the transition from stem to root. It would be valuable to know if and how a remaining oak sprout can take advantage of most of the clump's root system.

Tangential sections of reoriented tissue showed blocky vessel elements with small lateral connections between elements and short contact areas between vessels. How does transport through this tissue compare in efficiency with transport through the normally oriented tissue? In healthy root-released clumps is the preferred pathway through the older tissue or through the reoriented tissue?

There are a variety of factors which contribute to the overall pressure value in any part of a tree. These include transpiration rate, vessel diameter, number of functional vessels, height above ground level, and root pressure. Exactly what role these play in local pressure differences at any given height is unknown. One would expect that differences in transpiration rates among branches would have little effect on the local pressures in a section just above the root collar. Vessel diameters, the number of functional vessels, and, possibly, root pressures should be more important. If, in this study, some of the unstained tissue in the stumps was functional, it would be interesting to know what prevented it from conducting the dye solutions.

Another puzzle, mentioned previously, is the mechanism by which the cambium detects changes in apical dominance and in direction of sap flow. In this case, cambial cells may recognize concentration gradients of growth hormones (e.g. gibberellins or cytokinins) transported through the xylem (Hess and Sachs, 1972), or they may be sensitive to the effects of

small pressure gradients transferred through the differentiating xylem. Knowing how the cambium is controlled is a fundamental problem in plant physiology.

LITERATURE CITED

- Campbell, W.A. 1938. Preliminary report on decay in sprout northern hardwoods in relation to timber stand improvement. U.S.D.A., Forest Serv., Northeast. Forest Exp. Sta. Occas. Paper 7.
- and P. Spaulding. 1942. Stand improvement of northern hardwoods in relation to diseases in the Northeast. U.S.D.A., Forest Serv., Allegheny Exp. Sta. Occas. Paper 5.
- Hepting, G.H. and M.E. Fowler. 1962. Tree diseases of eastern forests and farm woodlands. U.S.D.A., Forest Serv., Agric. Infor. Bull. 254.
- Hess, T. and T. Sachs. 1972. The influence of a mature leaf on xylem differentiation. *New Phytol.* 71: 903-914.
- Jemison, G.M. and G.H. Hepting. 1949. Timber stand improvement in the southern Appalachian region. U.S.D.A., Forest Serv., Misc. Pub. 693.
- Lamson, N.I. 1976. Appalachian hardwood stump sprouts are potential sawlog crop trees. U.S.D.A., Forest Serv. Res. Note, Northeast. Forest Exp. Sta., No. NE-229.
- Lees, J.C. 1981. Three generations of red maple stump sprouts. Maritimes Forest Res. Centre, Canad. Forest Serv., Environment Canada, Information Report M-X-119.
- Lyford, W.H. and B.F. Wilson. 1964. Development of the root system of Acer rubrum L. Harvard Forest Paper, No. 10.
- Riedl, H. 1937. Structure and function of root wood. [transl. by M.H. Zimmermann. Copies available from National Translations Center, 35 West 33rd St., Chicago, IL 60616] *Jahrb. wiss. Bot.* 85: 1-75.
- Roth, E.R. and G.H. Hepting. 1943. Wounds and decay caused by removing large companion sprouts of oaks. *J. Forestry* 41: 190-195.
- and G.H. Hepting. 1969. Prediction of butt rot in newly regenerated sprout oak stands. *J. Forestry* 67: 756-760.
- and B. Sleeth. 1939. Butt rot in unburned sprout oak stands. U.S.D.A., Forest Serv., Technical Bull. 684.

- Shigo, A.L. 1965. Decay and discoloration in sprout red maple.
Phytopathology 55: 957-962.
- Tattar, T.A. 1973. Management of sprout red maple to minimize defects.
Northern Logger and Timber Processor 21: 20, 26.
- Trimble, G.R., Jr. 1974. Response to crop tree release by 7 year-old stems of red maple stump sprouts and northern red oak advance reproduction.
U.S.D.A., Forest Serv., Res. Paper NE-303.
- Tupper-Carey, R.M. 1930. Observations on the anatomical changes in tissue bridges across rings through the phloem of trees. Proc. Leeds Phil. Lit. Soc. (Sci. sect.) 7: 86-94.
- Wendel, G.W. 1975. Stump sprout growth and quality of several Appalachian hardwood species after clearcutting. U.S.D.A., Forest Serv., Res. Paper NE-329.
- Wilson, B.F. 1964. Structure and growth of woody roots of Acer rubrum L.
Harvard Forest Paper, No. 11.
- 1968. Red maple stump sprouts: development the first year.
Harvard Forest Paper, No. 18.
- Zajaczkowski, S. and T.J. Wodzicki. 1978. On the question of stem polarity with respect to auxin transport. Physiol. Plant. 44: 122-126.
- Zimmermann, M.H. 1971. "Dicotyledonous wood structure (made apparent by sequential sections)." Encyclopaedia Cinematographica, ed. G. Wolf; Institut fur den Wissenschaftlichen Film: Gottingen.
- and C.L. Brown. 1971. "Trees: Structure and Function."
Springer-Verlag: New York.
- and A. Jeje. 1981. Vessel length distribution in stems of some American woody plants. Canad. J. Bot. 59: 1882-1892.