HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 22 FEBRUARY, 1954 NUMBER 16

ANATOMY OF BARK OF BUD UNION, TRUNK, AND ROOTS OF QUICK-DECLINE-AFFECTED SWEET ORANGE TREES ON SOUR ORANGE ROOTSTOCK

HENRY SCHNEIDER

CONDITION OF PHLOEM OF SOUR ORANGE TREE TRUNK IN WINTER

HENRY SCHNEIDER

EFFECT OF TRUNK GIRDLING ON PHLOEM OF TRUNK OF SWEET ORANGE TREES ON SOUR ORANGE ROOTSTOCK

HENRY SCHNEIDER

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

ANATOMY OF BARK OF BUD UNION, TRUNK, AND ROOTS . . .

This paper concerns the sequence of anatomical changes occurring in sweet orange trees on sour orange rootstock after infection by quick decline. The primary symptom is necrosis of sieve tubes below the bud union. This symptom is followed by degeneration of the older sieve tubes above the union, accelerated cambial activity, and other reactions of a secondary nature.

CONDITION OF PHLOEM OF SOUR ORANGE TREE TRUNK IN WINTER

Since the sieve tubes of the functioning phloem of sour orange stock of sweet orange trees become necrotic when the tree is affected by quick decline, the condition of the functioning phloem of the trunk of the healthy sour orange, both as a rootstock and as a seedling tree, especially in winter, was investigated.

Throughout the winter months trunks of healthy sour orange trees, and of sour orange rootstock under sweet orange tops, maintained a band of functioning phloem averaging about 500 microns in width. A ring of degenerating phloem external to this was either absent or as much as 100 microns wide. Occasionally, there were abnormally wide bands of degenerating phloem or bands of necrotic sieve tubes within the functioning phloem.

EFFECT OF TRUNK GIRDLING . . .

. . . on phloem of trunk of sweet orange trees on sour orange rootstock was studied to discover whether the phloem above the removed bark reacts in the same way as that above the necrotic sieve tubes of the sour orange rootstock of quick-decline-affected trees. Sieve-tube degeneration above artificial girdling seems to be identical with that induced by girdling brought about naturally by necrosis of sieve tubes immediately below the union of a quick-decline tree.

EXPLANATION OF TERMS

Normal deterioration of sieve tubes after they have functioned for a year or two is termed degeneration. Abnormal deterioration of sieve tubes in diseased plants is termed necrosis. Which term should be used for some anomalous types of deterioration reported in these papers is open to question. The term induced degeneration has been applied to deterioration resulting from artificial or disease-produced girdling. For further clarification of terms, you are referred to the diagram presented on the inside of the back cover of this issue of Hilgardia.

EFFECT OF TRUNK GIRDLING ON PHLOEM OF TRUNK OF SWEET ORANGE TREES ON SOUR ORANGE ROOTSTOCK[1]

HENRY SCHNEIDER[2]

INTRODUCTION

IN AN ANATOMICAL STUDY of quick-decline-affected sweet orange trees on sour orange rootstock, it was noted that degeneration of the older sieve tubes of the functioning phloem immediately above the bud union followed an initial necrosis below the union (Schneider, 1954*a*). This degeneration was less extensive 1 inch above the union than it was immediately above, and little or no degeneration occurred 18 inches above the union until the tree deteriorated.

Degeneration immediately above the union is probably a result of the necrosis of the sieve tubes below the union, and not a result of the action of the virus. This is thought to be true for the following reasons: (1) The phloem of quick-decline-infected sweet orange trees on sweet orange stock is not affected by the disease. (2) The phloem 18 inches up the trunk from the bud union of diseased sweet orange trees on sour stock is not affected in early stages of the disease. (3) Degeneration of sieve tubes and companion cells above the bud union is secondary to the necrosis below the union. (4) Sieve-tube degeneration in peach follows girdling (Schneider, 1945).

Certain varieties of lemon trees on sweet orange, sour orange, grapefruit, mandarin, or Sampson tangelo rootstocks may be affected by lemon tree decline. This decline is brought about by a necrosis of sieve tubes just above the bud union (Schneider, 1948; Calavan *et al.*, 1951). The sieve tubes below the union do not degenerate. In other words, in lemon trees, girdling brought about by sieve-tube necrosis immediately above the bud union does not cause degeneration of sieve tubes below the girdle. This is in contrast to the condition in quick-decline-affected orange trees, in which sieve-tube degeneration above the girdle results from a virus-induced sieve-tube necrosis immediately below the union.

The purpose of the present study was to determine whether or not experimental girdling at the bud union of healthy-appearing sweet orange trees on sour orange rootstock would result in sieve-tube degeneration above the union and not below.

MATERIALS AND METHODS

Two groups of five trees each, growing in the orchard at the Citrus Experiment Station, were used for this study. The trees of one group were the Azusa strain of Valencia orange on Paraguay sour orange rootstock. These

[1] Paper No. 774, University of California Citrus Experiment Station, Riverside, California. Received for publication March 2, 1953.

[2] Associate Plant Pathologist in the Experiment Station, Riverside.

were vigorous, healthy-appearing 15-year-old trees having dense foliage, but prior to experimental girdling some of them did exhibit a necrosis of the older sieve tubes below the bud union. Degeneration of sieve tubes above the union was sometimes found in trees having necrosis below the union. This was probably a secondary response. Trees of the other group were Washington Navel orange on California standard sour orange rootstocks. These trees were 22 years old and in good condition, although not so vigorous or densely foliated as the trees on Paraguay sour stock.

Every 3 months a ⅜-inch-wide ring of bark was removed at the bud union of one of the trees of each group, until four trees of each group had been girdled. One tree of each group was left as a check. Bark samples for sectioning were taken 1½ inches and 18 inches above and below the bud union on the girdling date and 2 weeks, 6 weeks, 3 months, 9 months, and 1 year after girdling. Starch tests were made on finger-sized roots by cutting across them with pruning shears and applying a solution of iodine in potassium iodide, a method described by Fawcett (1945) for testing starch in roots. Color intensities were then recorded. The condition of the tops of the trees was recorded at the time of sampling.

OBSERVATIONS

Anatomic Alterations Induced by Ringing. In healthy trees the bands of developing and degenerating phloem are usually narrow in radial width. In ringed trees a portion of the outer functioning phloem degenerates. This is referred to here as *induced degenerating phloem.*

Results presented in tables 1 and 2 were obtained by dividing the radial width of functioning phloem, expressed in microns, by the combined widths of functioning phloem and induced degenerating phloem, and multiplying the quotient by 100. This gives the percentage of phloem that remains functioning, based on the amount that would normally be present. Since the induced degenerating phloem becomes part of the nonfunctioning phloem, the values are an inaccurate measure of phloem degeneration after trees have been ringed for considerable time. The percentage of functioning phloem based on what would be present if degeneration had not been induced is preferable, however, to measurements of phloem actually functioning, because of the normal variation in amount of functioning phloem.

Unfortunately, even before the ringing, sieve-tube degeneration from an unknown cause was evident in the phloem of some of the samples from below the bud union of three of the five Valencia orange trees on Paraguay sour stock, as indicated in table 2. It should also be pointed out that occasionally there may be excessively wide bands of degenerating phloem in apparently healthy orange trees (Schneider, 1954*b*).

From the data presented in tables 1 and 2, it is obvious that girdling a tree by removing a ring of bark at the bud union induced degeneration of the older sieve tubes in other parts of the trunk. The degeneration first occurred in about equal amounts 1½ inches above and below the girdle. The more distant points (18 inches above and below the bud union) were usually not affected until later.

The season of the year in which the girdling was done had a marked effect on the time required for the degeneration to begin to appear. When trees were girdled in October, degeneration was first observed on the collection date 9 months later; when they were girdled in January, degeneration was observed 3 months later. Six weeks were required for response when the trees were girdled in April, and only 2 weeks when girdled in July. Apparently, response to girdling does not occur between October and April.

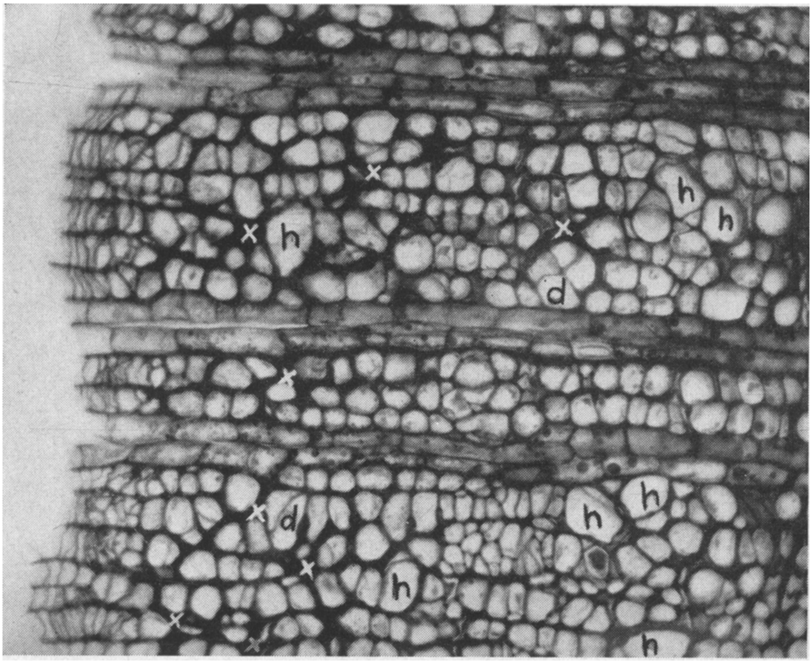


Fig. 1. Cross section of a root from a girdled tree, showing crushed sieve tubes (x) and hypertrophied (h) and divided (d) parenchyma cells, which sometimes occur. The cambium is at the left. (× 260.)

Induced degeneration of sieve tubes proceeded in a normal manner: Callus formed on sieve plates, the sieve-tube elements collapsed, and then the sieve-tube contents and callus were removed. In some cases hypertrophy of parenchyma cells accompanied sieve-tube necrosis. Hypertrophy was observed to be extensive in 12 roots (fig. 1) and occasional in 6 others. About half of the roots having sieve-tube degeneration showed some hypertrophy. In 11 of the trunk samples taken 1½ inches below the bud union, there was a moderate amount of hypertrophy, and in 35 samples there was a slight amount. At this point of sampling there was hypertrophy of parenchyma cells in about two thirds of the samples which had degenerating sieve tubes. At 1½ inches above the bud union, 11 of 68 trunk samples having degenerating sieve tubes exhibited occasional hypertrophy of the parenchyma; and at 18 inches above, 5 of 50 samples having degenerating sieve tubes also showed occasional hypertrophy.

In summary, hypertrophy of parenchyma cells accompanying sieve-tube

TABLE 1

PERCENTAGE OF PHLOEM WHICH REMAINED FUNCTIONAL IN TRUNKS OF WASHINGTON NAVEL ORANGE TREES ON CALIFORNIA STANDARD SOUR ORANGE ROOTSTOCKS AT INTERVALS AFTER GIRDLING (BY RINGING) AT BUD UNION

Bark sampling		Percentage of phloem functioning, as indicated by bark samples (A and B) from opposite sides of tree													
Direction from bud union	Distance from bud union (inches)	On date of girdling		After 2 weeks		After 6 weeks		After 3 months		After 6 months		After 9 months		After 1 year	
		A	B	A	B	A	B	A	B	A	B	A	B	A	B
Tree 13-12, girdled January 24, 1946															
		1–24–46		2–8–46		3–8–46		4–23–46		7–22–46		10–21–46		1–20–47	
Above	18	100	100	100	100	100	100	100	100	100	100	100	100	70	90
	1½	100	100	100	100	100	100	80	60	30	30	40	20	30	50
Below	1½	100	100	100	100	100	100	70	70	30	50	10	20	10	0
	18	100	100	100	100	100	100	100	100	100	70	20	0	70	0
Tree 14-13, girdled April 23, 1946															
		4–23–46		5–7–46		6–6–46		7–22–46		10–21–46		1–20–47		4–22–47	
Above	18	100	100	...	...	70	100	90	70	100	75	60	100	70	100
	1½	100	100	100	100	30	80	20	20	20	50	30	30	30	40
Below	1½	100	100	100	100	60	60	60	70	0	50	0	20	30	30
	18	100	100	...	...	100	100	100	100	100	0	0	100	70	70

Tree 13-13, girdled July 22, 1946

		7–22–46		8–5–46		8–30–46		10–21–46		1–20–47		4–22–47		7–22–47	
Above	18	100	100	80	80	70	70	50	80	40	40	50	60	60	30
	1½	100	100	30	50	40	40	30	50	20	40	30	40	10	10
Below	1½	100	100	30	60	40	40	40	40	50	40	50	50	40	40
	18	100	100	100	100	0	100	30	100	100	100	100	30	30	30

Tree 14-11, girdled October 21, 1946

		10–21–46		11–5–46		12–4–46		1–20–47		4–22–47		7–22–47		10–24–47	
Above	18	100	100	...	...	100	100	66	100	50	80	40	70	60	70
	1½	100	100	100	100	100	100	100	100	100	100	20	40	30	20
Below	1½	100	100	100	100	100	100	100	100	100	100	70	30	10	30
	18	100	100	...	...	100	100	100	100	100	100	100	70	90	70

Check trees (not girdled)

		2–8–46		3–8–46		6–6–46		8–30–46		12–4–46		1–20–47		4–22–47	
Above	18	100	100	100	...	100	100	100	100	100	100	100	100	100	100
	1½	100	100	100	...	100	100	100	100	100	100	100	100	100	100
Below	1½	100	100	100	...	100	100	100	100	70	100	100	100	100	100
	18	100	100	100	...	100	100	100	100	100	100	100	100	100	100

TABLE 2

PERCENTAGE OF PHLOEM WHICH REMAINED FUNCTIONAL IN TRUNKS OF VALENCIA ORANGE TREES ON PARAGUAY SOUR ORANGE ROOTSTOCK AT INTERVALS AFTER GIRDLING (BY RINGING) AT BUD UNION

Bark sampling		Percentage of phloem functioning, as indicated by bark samples (A and B) from opposite sides of tree													
Direction from bud union	Distance from bud union (inches)	On date of girdling		After 2 weeks		After 6 weeks		After 3 months		After 6 months		After 9 months		After 1 year	
		A	B	A	B	A	B	A	B	A	B	A	B	A	B
Tree 17-2, girdled January 24, 1946															
		1–24–46		2–8–46		3–8–46		4–23–46		7–22–46		10–21–46		1–20–47	
Above	18	100	100	100	100	100	100	100	100	80	70	100	100	80	40
	1½	100	50*	100	100	100	50*	50	100	50	20	20	50	30	50
Below	1½	50*	30*	50*	50*	100	20*	10	70	70	60	80	60	50	100
	18	100	100	100	100	100	100	100	100	70	90	70	50	90	70
Tree 17-5, girdled April 23, 1946															
		4–23–46		5–7–46		6–6–46		7–22–46		10–21–46		1–20–47		4–22–47	
Above	18	80	90	...	...	70	50	100	100	60	100	60	100	60	100
	1½	60*	100	80*	80*	60	50	20	30	30	20	30	30	20	40
Below	1½	20*	60*	30*	90*	40	70	60	80	40	60	50	100	50	50
	18	100	40	...	...	100	0	100	100	100	70	70	100	100	100

Tree 17-4, girdled July 22, 1946

		7-22-46		8-5-46		8-30-46		10-21-46		1-20-47		4-22-47		7-22-47	
Above	18	100	100	90	40	80	60	60	60	50	80	100	100	30	50
	1½	100	100	40	50	30	70	40	60	40	70	30	60	40	30
Below	1½	100	100	60	80	60	10	80	10	50	10	50	70	20	30
	18	100	100	100	100	70	60	100	100	80	100	100	100	100	30

Tree 17-3, girdled October 22, 1946

		10-21-46		11-5-46		12-4-46		1-20-47		4-22-47		7-22-47		10-24-47	
Above	18	100	100	...	...	100	100	100	100	100	100	50	60	30	40
	1½	100	100	100	100	100	100	100	100	100	100	20	30	10	20
Below	1½	60*	100	40*	100	100	100	100	100	100	100	70	30	40	40
	18	100	100	...	...	100	100	100	100	100	100	100	100	30	30

Check trees (not girdled)

		2-8-46		3-8-46		6-6-46		8-30-46		12-4-46		1-20-47		4-22-47	
Above	18	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	1½	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Below	1½	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	18	100	100	100	100	100	100	100	100	100	100	100	100	100	100

* Sections probably showing degeneration from some cause other than girdling by ringing.

degeneration in the phloem was most severe 18 inches below the bud union (in roots), less severe 1½ inches below the union, and only slight and infrequent at points above the union.

Time Required for Starch Depletion in Roots and for Appearance of Top Symptoms. Starch tests were made on roots from opposite sides of the tree. Finger-sized roots were cut with pruning shears in such a way as to crush the cells slightly in the process; iodine in potassium iodide was then applied, and color was noted.

The period required for starch depletion of the roots ranged from 6 weeks to 6 months and depended on the date of tree ringing. The least time (about 6 weeks) was required when ringing was done on July 22; the longest time (6 months), when ringing was done on October 21. Fawcett (1946) reported that roots of trees ringed on February 6, 1945, were almost depleted of starch 5 months later.

The time required for deterioration of the tree and the appearance of top symptoms—namely, yellowing and loss of leaves—ranged from 3 months to more than 6 months. Trees ringed in the spring and summer required the least time (3 to 6 months); those ringed in October required more than 6 months.

DISCUSSION

Presumably, in an evergreen tree there is a continuous downward movement of carbohydrates through the trunk phloem to the roots. When a tree is girdled, the sieve tubes above the girdle cease to have any place to transport materials, and carbohydrates therefore accumulate above the girdle. Sieve tubes below the girdle still have some function to perform, however. Although the amount of available carbohydrates is drastically lowered, these sieve tubes can still translocate the carbohydrates stored as starch in the woody part of the trunk to the roots.

Sieve-tube degeneration induced above girdling brought about by the removal of a ring of bark at the bud union of a healthy orange tree seems to be identical with that induced above girdling brought about naturally by the necrosis of sieve tubes immediately below the bud union of a quick-decline tree.

What happens to sieve tubes below a girdle in orange trees girdled by removal of a ring of bark, and in lemon trees girdled by necrosis of sieve tubes, is strikingly different. Degeneration occurred below the artificial girdle in orange trees, but not below the naturally occurring girdle in lemon trees. Effects of girdling by ringing differ in at least two respects from those of naturally occurring girdling caused by sieve-tube necrosis: (1) There is a wound involved in ringed trees, and there may be wound responses even 1½ inches below the union. (2) A few of the sieve tubes and all of the parenchyma cells remain intact in lemon trees naturally girdled by sieve-tube necrosis. These cells and sieve tubes may serve to let sufficient hormones and vitamins pass the girdle, even though the sieve-tube necrosis critically limits carbohydrate translocation. In trees artificially girdled by ringing, translocation of materials in the bark is completely stopped.

SUMMARY

The effect of girdling, by removing a ring of bark at the bud union, upon the condition of the phloem of the remainder of the trunk and roots of sweet orange trees on sour orange rootstock has been studied.

Artificial girdling of orange tree trunks caused degeneration of sieve tubes, the older sieve tubes being affected first and the younger ones later.

Degeneration usually occurred sooner and more extensively 1½ inches above and below the union than it did 18 inches above and below the union. Severe degeneration of sieve tubes and hypertrophy of parenchyma occurred in some roots in advanced cases, however.

The time required for sieve-tube degeneration to begin depended on the season of year in which the girdling was done. Two weeks were required for a response when trees were girdled in July, and more than 6 months when girdled in October.

The reserve starch in finger-sized roots of one tree ringed on July 22 was depleted after 6 weeks, but 6 months were required for trees ringed on October 21 to utilize their reserve starch.

Sieve-tube degeneration 1½ and 18 inches above the artificial girdle in healthy orange trees was similar in time of occurrence and mode of degeneration to that found in orange trees affected by quick decline.

Degeneration 1½ inches below the artificial girdle in orange trees was contrary to a condition recently found in lemon trees on various rootstocks, in which the sieve tubes of the scion become necrotic but those of the stock immediately below the union remain functional.

ACKNOWLEDGMENT

The author is indebted to Mr. Oscar F. Clarke for sectioning and staining of bark samples for this study.

LITERATURE CITED

CALAVAN, E. C., F. ARNOLD WHITE, HENRY SCHNEIDER, and J. M. WALLACE

1951. Lemon tree collapse and decline. Citrus Leaves **31**(11): 6–8, 16, 18, 38.

FAWCETT, H. S.

1945. A starch test for quick decline. California Citrog. **30**: 122.

1946. A progress report on quick decline studies. Starch relationships (Part II). California Citrog. **31**: 198.

SCHNEIDER, HENRY

1945. Anatomy of buckskin-diseased peach and cherry. Phytopathology **35**: 610–35.

1948. Sieve-tube necrosis, an early symptom of collapsing and declining lemon trees. Phytopathology **38**: 918.

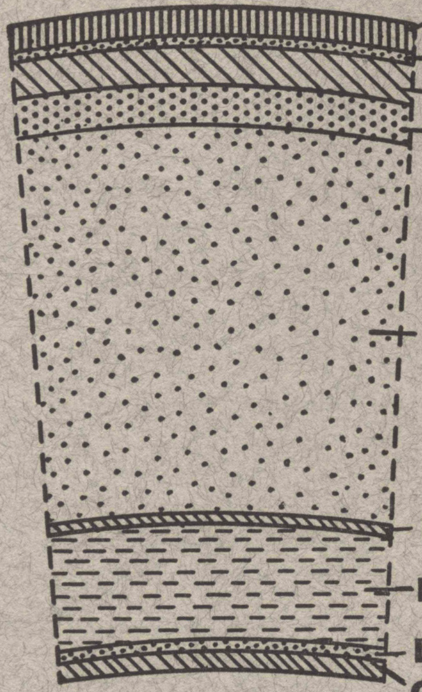
1952. The phloem of the sweet orange tree trunk and the seasonal production of xylem and phloem. Hilgardia **21**: 331–66.

1954*a*. Anatomy of bark of bud union, trunk, and roots of quick-decline-affected sweet orange trees on sour orange rootstock. Hilgardia **22**(16): 567–81.

1954*b*. Condition of phloem of sour orange tree trunk in winter. Hilgardia **22**(16): 583–91.

141

4*m*-2,'54(243)FH



The normal phloem of the orange tree trunk is a complex tissue. Its vertical system consists of sieve tubes, companion cells, parenchyma cells, fibers, and crystal idioblasts. The four zones of the phloem may be described as follows: (1) the developing phloem is the ring of phloem adjacent to the cambium, in which cells derived from the cambium divide further and then differentiate into mature phloem tissue. (2) The functioning phloem is the ring of phloem located just outside the developing phloem and containing mature sieve tubes. (3) The degenerating phloem is the ring of phloem located at the outer margin of the functioning phloem. In this tissue the sieve plates of the sieve tubes become callused, the sieve tubes lose their turgor and then collapse, and the contents are lysed. Some parenchyma cells also degenerate, lose their contents, and are crushed. (4) The vertical system of the nonfunctioning phloem contains blocks of degenerated sieve tubes and living and dead parenchyma cells.

The journal *Hilgardia* is published at irregular intervals, in volumes of about 600 pages. The number of issues per volume varies.

Subscriptions are not sold. The periodical is sent as published only to libraries, or to institutions in foreign countries having publications to offer in exchange.

You may obtain a single copy of any issue free, as long as the supply lasts; please request by volume and issue number from:

Publications Office
College of Agriculture
Berkeley 4, California

The limit to nonresidents of California is 10 separate issues on a single order. A list of the issues still available will be sent on request.