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Apical Dominance in Shoots and Proximal Dominance in Roots As Related to Structural Framework of the Apple

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INTRODUCTION

The potential longevity of the apple tree makes it imperative to preserve intact the larger structural members. Smaller twigs are more readily replaced, but once the framework begins to deteriorate from winter injury, or other cause, the decline of the tree is hastened. Casual attention to the framework produced by the so-called conventional method of training demonstrates clearly that existing deficiencies of this system must be overcome if more satisfactory trees are to be produced.

The complexity of the problem is little realized until one attempts to secure proper spacing of limbs, crotch angles of sufficient size or the maintenance of balance between branches.[16*] For example, when the terminal bud is not removed, the one-year-old tree grows vigorously as a rule with a high head and few or no lower scaffold lambs.[3] If the tree is headed back, as is usually done in the nursery, a cluster of branches forms with the upper ones the most vigorous and the desired lower limbs, when present, often become unimportant because of being outgrown. Should the tree be disbudded to groups of buds, a more desirable framework will develop but, according to work at the Arkansas Station,[1] some varieties which form few branches fail to respond very well. Without summer tipping even in Jonathan, a free branching variety, the upper limbs on laterally and terminally disbudded trees may be too vigorous, resulting in lack of balance within the tree. The desirable situation is to have the main branches started so that they all grow with equal rapidity.[15]

A suitable distance between scaffold limbs is required if the limbs are not to interfere with one another. Limbs which seem well placed in the two-year-old tree may encroach on one another with time to produce a jammed framework which is the most difficult of all problems for the pruner.[14] A more ideal framework

*Numerals refer to "References", page 22

often described in part but not easy to attain is one on which there are four or five wide-angled scaffold branches with crotch angles of 45° or more depending upon the variety. Such limbs spaced not less than eight inches apart along a central leader should be arranged so as to balance the tree in all directions.[12]

APICAL DOMINANCE

A troublesome obstacle partially underlying the framework difficulties in the early training of the apple tree is the inhibition of lateral bud growth by the more distal buds. It is a fundamental fact that despite the profusion of mature viable buds on the trees only a few normally develop into branches. This phenomenon termed apical dominance, thought to be brought about by hormone action, and exhibited by diverse plant forms, has until the last decade, been but little understood.

It would seem that the dormant bud in the axil of each leaf would grow forth into a lateral shoot, if only it were freed from the retarding influences which are normally operative. Soon after the initiation of this study, which originally dealt with crotch injury, it was observed that faulty framework composition and narrow angles were contributory causes to low temperature crotch injury.[9] This resulted in a search for some means to stimulate lateral bud development at desired locations on young tree trunks. Talbert[17] reported the loss of apical dominance in cut-back trees: disbudding was investigated by Fagan,[8] Ruth,[16] and others. Denny's[6] work with tubers of *Solanum tuberosum* demonstrated that treatment with thiourea is a possible chemical means to overcome inhibition of lateral buds.

TREATMENT OF APPLE TREES WITH THIOUREA

In the spring of 1935, one hundred unbranched yearling Jonathan trees were immersed in solutions of thiourea from two to five per cent, the time being varied from two to four hours. Each tree was inserted singly in a glass tube three-fourths inch in diameter and four feet long. This tube, one end closed, was laid on a table with the open end raised four inches above the horizontal. Distilled water solutions of thiourea of the desired concentration were then added so that the whole tree, except the roots, was entirely immersed, care being taken that the roots did not become dry.

Fig. 1.—Jonathan. Greenhouse trees disbudded and soaked in thiourea solutions as shown. Note lower limbs are longest in the trees on the right.

After treatment the trees were rinsed with tap water and set in a warm greenhouse. With the advent of spring the later work was carried on in the field. Using the thiourea as a means to better framework development, it seemed inadvisable to retain too many buds because the draft on the tree would perhaps result in short undesirable laterals. In consequence of growth in too many buds, disbudding after treatment to groups of three buds 8 inches between centers, was done in all later work.

With the two and three per cent solutions of thiourea the results indicate a slight retardation in growth of the uppermost branches to give a better balance than is usually obtained. All branches were about equally long, none gaining the ascendancy. (Figures 1, 2 and 3.)

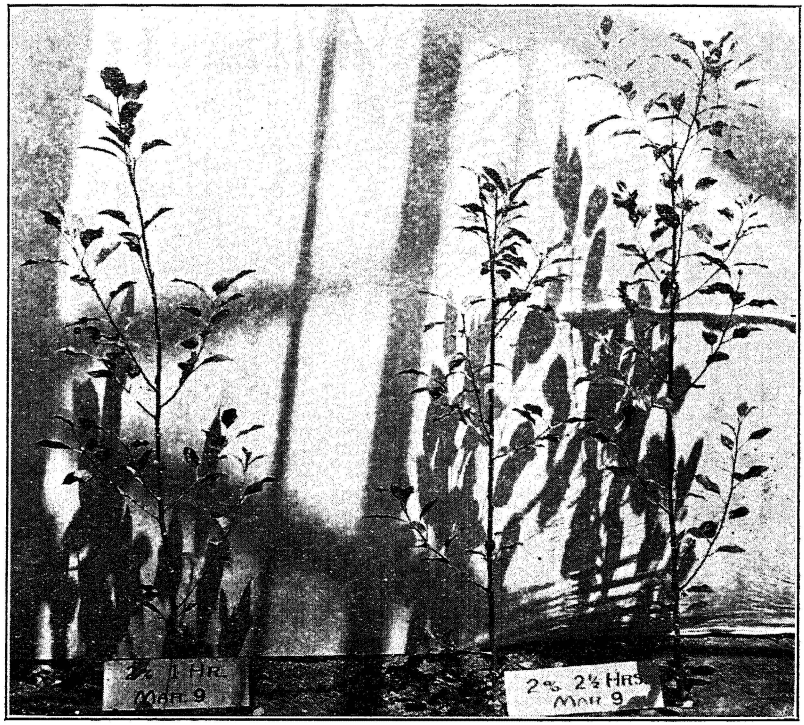

Fig. 2.—Jonathan. Greenhouse trees disbudded to groups of buds and soaked in thiourea solutions as shown. Branches from apex to base are approximately the same length.

All solutions of the thiourea which were used killed the terminal buds. In several instances these buds grew out a half-inch or more and died. Often with the higher concentrations the terminal end of the shoot died back slightly but the buds making a start immediately below the dead area seemed uninjured except for a slower growth rate. Buds far removed from the terminal were apparently not adversely affected for they made good growth. The increasingly lower limbs were longer and longer with the outline of the tree assuming somewhat the form of a cone, the lowest limbs being the longest. This loss of dominance of the upper limbs is an outcome

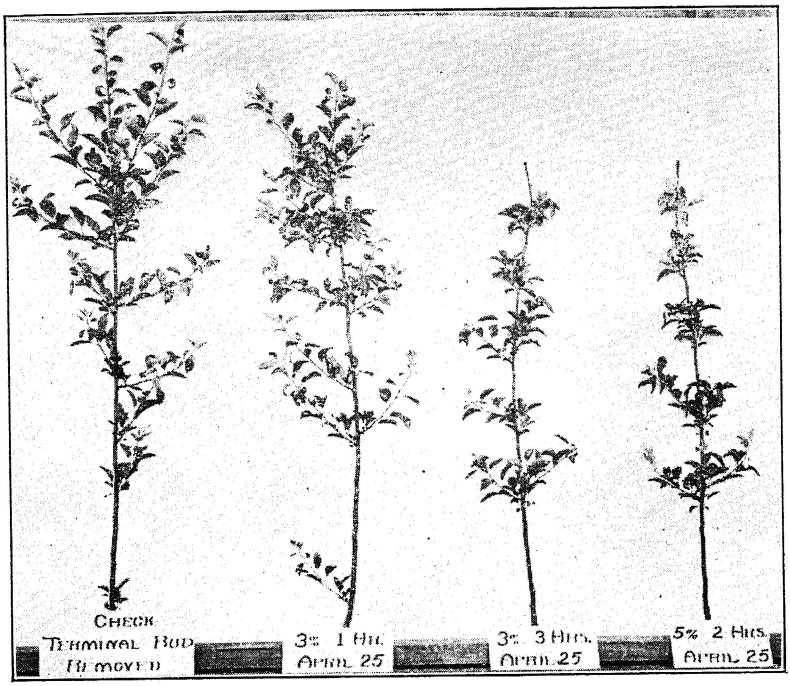

Fig. 8.—Jonathan. Trees set in field April 25. Picture made July 8. Prior to planting trees disbudded and soaked in thiourea solutions as indicated. Note lack of balance between branches of tree on the left as compared with the second tree from left.

somewhat to be expected if some sort of gradient in physiological activity exists with the more distal buds increasingly less able to resist the thiourea. Or as between the distal and sub-apical buds the action may possibly be one of differential toxicity with the terminal bud most susceptible and the correspondingly lower buds more and more resistant.

CUT-BACK APPLE TREES

Talbert[17] found that, in comparison with the conventionally headed tree, cut-back apple trees are abnormal in that they do not exhibit marked apical dominance and that they form scaffold branches well distributed low in the tree (Figures 4 and 5). The laterals developed by the cut-backs form wide angles with the trunk. Since cutting back offers a means to prevent the clustering of limbs, study has been given to this subject. The loss of apical dominance may involve the production and fate of auxins in the

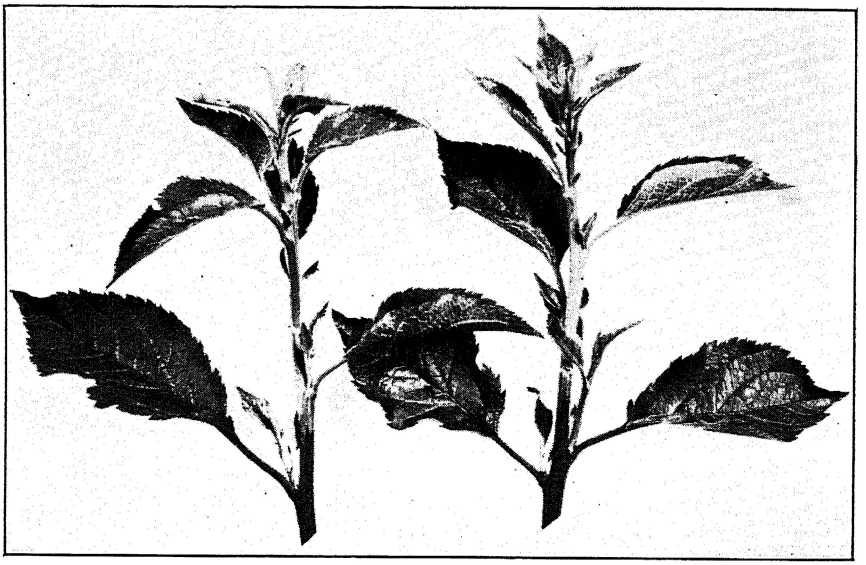

Fig. 4.—Jonathan. Wide angles of scaffold limbs in cut-back trees originate as narrow angles. Compare with Fig. 5.

plant. While the formation of wide-crotch angles is so characteristic of these trees, it is but little different from non-cut-backs which also form wide angles low in the tree if somehow the lateral buds grow out (Figures 8 and 9). The difference is that in the conventionally treated trees the lower buds either fail to grow as a rule or, if they do push out, the branch is small and soon becomes outgrown and insignificant as a framework member.

In a number of specimens of different varieties observed, cutting back two-year-old trees forced the growth only of axillaries, but four-year-old Delicious similarly treated also initiated a large number of adventitious buds, some of which grew out to form shoots.

When only one vertical shoot was retained on these four-year-old Delicious, a reversal of dominance was found in some cases. Every lateral on such trees made a very rapid growth with the main axis soon being far outgrown. This seems to indicate a progressive loss of apical dominance as the age at which the trees are cut back increases.

Several conditions were found which were associated with the reappearance of apical dominance in cut-back trees. When more than one main shoot is allowed to grow, lateral buds fail to grow. Likewise, lack of sufficient water and light reduction to 380 foot candles were found to favor inhibition of laterals.

The apple tree is a plant which does not normally form laterals on wood of the current season, a fact which delays somewhat the formation of the framework. Young apple trees which are cut back depart from the usual in that they do form laterals on current season wood and this must be taken into account when considering crotch angle size in such trees. (Figure 5.)

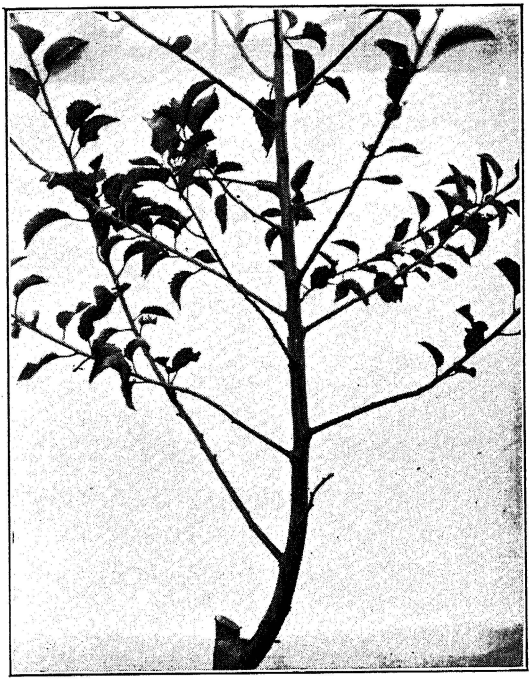

Fig. 5.—Jonathan. Wide crotches of this cut-back tree began growth at a narrow angle. Compare with Figures 4 and 6.

In observing the growth of cut-back trees, the question arose as to why it is that the axillaries which begin growth at a very narrow angle of 10° or less from the vertical (Figure 4), produce a scaffold limb forming a very wide angle, often close to the horizontal position. With the young limb, the cells are differentiated and the crotch tissues are no longer meristematic; consequently no basal growth of the limb can take place as occurs in some latent buds.* Since the trunk rapidly enlarges, the young shoot is forced

*Eames and MacDaniels[7] state that adventitious buds, by building up central cylinders as the tree trunk increases, maintain their position in the bark of the tree. Some similar mechanism must be present for axillary buds which at least for a time maintain their position at the surface.

from the vertical position while its tissues are yet too soft to resist the growth pressure. Later when the deposition of cellulose occurs, the limb is at a wide angle where it becomes fixed.

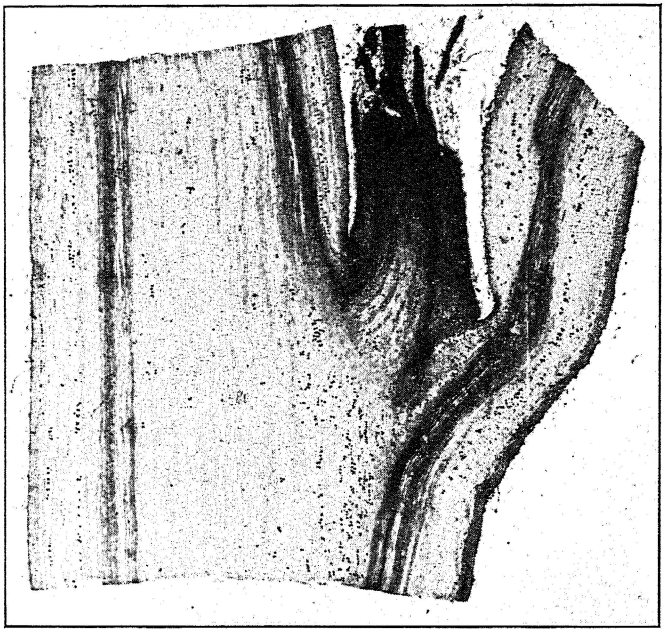

Fig. 6.—Axillary bud on a cut-back tree starting growth at a narrow angle.

The change of limb angle from narrow to wide in the cut-back trees suggested that perhaps the influences operative in the tender young limbs might also be active to some extent in the buds of the normal one-year-old tree during its first year's growth. Histological studies show that apparently the enlargement of the trunk during the first season causes the lower buds to lie with the median line far from the vertical. Since these lower buds have an axis often only slightly elevated from the horizontal, the scaffolds originating from such buds grow at a wide angle with the trunk.

Figure 6 shows that the axillary bud as first laid down has its axis in nearly the vertical position, while Figure 7 shows that with growth of the main stem the axis of a lateral bud is turned more toward the horizontal.

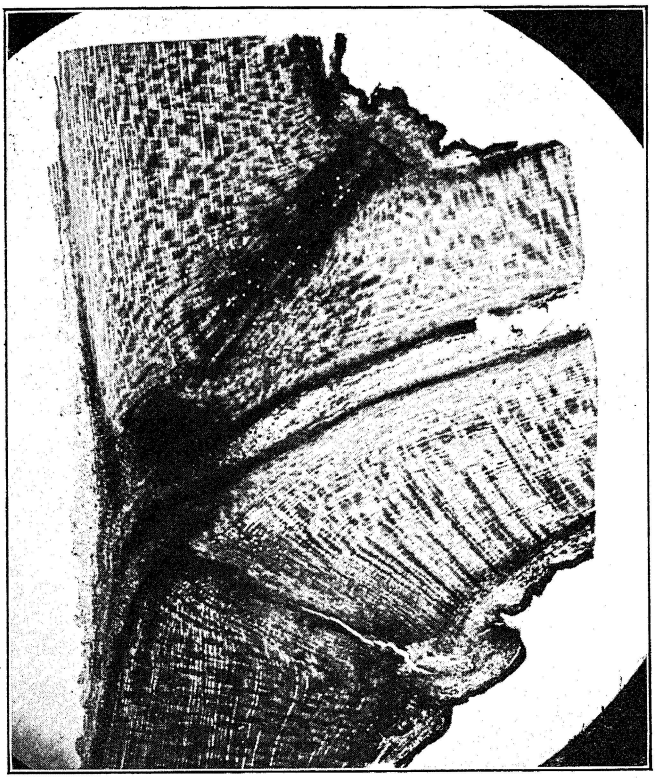

Fig. 7.—Scaffold branch of a cut-back tree one-year-old. Note the wide angle of the limb and the distortion of the leaf trace. The pith at the left is largely broken away.

SHADING INVESTIGATIONS

Auxins, the growth promoting and inhibiting substances, are produced only in the light by some plants, but light seems to inhibit their growth promoting property.[18] Since no reference was found in the literature as to the effect of reduced light intensity on axillary inhibition, a shading experiment was carried out with Jonathan to learn if reduced light intensity would cause the reappearance of apical dominance and prevent the outgrowth of lateral buds in cut-back trees.

The trees were set in an inclosure, covered with a double thickness of cheese-cloth, which was dyed almost black. The illumination in this structure was found to be 380 foot-candles* on a clear

*Measured with a Westinghouse foot-candle meter.

day, June 7, 1935, at 1:45 p. m. As so much of the time was cloudy, the average strength of light was somewhat below the measured intensity. Except in the cases of very few axillaries, apical dominance was complete.

Unfortunately as the illumination is decreased below 1000 foot-candle, photosynthesis is reduced and the complicating food deficiency factor enters which Thimann and Skoog[18] believe to be effective in retardation of axillaries. The near failure of grass and weed growth under the tent strongly indicates the part that reduced photosynthesis may have had in the effect of the shading.

HISTOLOGICAL WORK

In the study of the origin of angle size in scaffold limbs, median sections of woody stems of yearling apple trees were made by the paraffin method. Suitable pieces of tissue were cut and fixed in chromoacetic killing agent. They were then washed for 24 hours in running water. One part of technical 48 per cent hydrofluoric acid, diluted with one or two parts of water, depending on the hardness of the material, was used one to two weeks for softening. The acid was washed out and the tissue carried through the procedure to imbed in paraffin.

Before clamping in the microtome holder, a pair of lines in two directions marking the median plane of the tissue were cut in the paraffin to prevent the difficulty otherwise encountered in making the finer adjustments necessary to insure that a median section would be obtained.

The tissue was set in the microtome holder with the bud turned toward the knife. Excess paraffin above that nearly covered by the tip of the index finger was pared away from the two ends and from the bud side of the block. Paraffin was left on the fourth side and pared later up to the line left by the trailing end of the sliding razor passing over the surface. Drops of half and half glycerine and distilled water were placed just far enough apart along the cutting edge of the knife that they would not coalesce. These furnished a lubricant to prevent the sections from adhering to the razor.

The cutting edge of the razor was brought up to the edge of the block before the index finger was put in position on top of the tissue. The stroke was then made, the finger preventing the section from curling up. By the use of a small brush dripping with distilled water, any excess glycerine was cleared from the section before transferring to the slide.

Slides were prepared some time before needed by smearing with two drops of Szombathy's[4] fixative* and two drops of 2 per cent formalin and allowing to become well dried under a petri dish or some similar cover to exclude dust. The section fresh from the microtome and still adhering to the finger tip was applied directly to the slide, no water being used to float into place. Any inclosed air bubbles were forced out by means of a rolling motion of the finger tip moistened with the glycerine and distilled water mixture.

While it is a time-consuming necessity, the razor must be kept free of flakes of paraffin by use of xylene. Room temperatures below 70°F. materially expedite the work because harder paraffin is less likely to absorb sufficient heat from the finger to cause it to adhere to the razor.

Sections were made as a rule about 20 to 25 microns thick. While thinner sections could have been made, for the purpose this thickness was satisfactory.

The operator may be inclined to be nervous because of the proximity of the finger tip to the passage of the razor. Unscathed, however, a large number of sections were made by the procedure described. There is no attendant danger of injury if the knife is brought to the side of the paraffin block at the proper height before the finger is applied and the paraffin has been so pared that the trailing end of the razor, by the barest margin, fails to pass entirely through the block.

Difficulty was encountered in the staining process because the sections easily came off the slides in 50 and 95 per cent alcohols. This was not serious because the free sections could be manipulated in watch glasses.

REDUCTION IN SIZE OF CROTCH ANGLE IN LOWER SCAFFOLDS

Limbs that grow at very wide angles with the trunk are likely to droop and fail to persist because of being outgrown.[16] Well pruned trees appear too thick until the first crops of fruit weigh down and spread the main branches.[2] Even Transparent, an upright variety, may have to be pruned at times when 30 or more years old to keep the branches off the ground.[13] To have the limbs at excessively wide angles in young trees then would seem to be a poor practice.

As shown in Figure 7, the lower buds before growing out on a one-year whip have the longitudinal axis far from the vertical with

*One drop of LePage's glue was added to each 16 cc. of Szombathy's fixative.

the consequence that, if such buds are stimulated to grow, the resulting laterals form too wide an angle with the trunk.

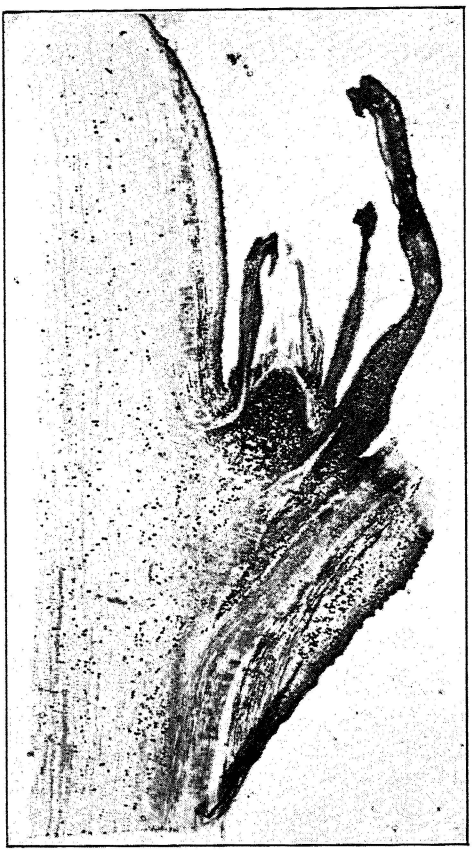

Fig. 8.—Bud from near the top of a one-year-old unbranched tree. This bud would have grown out to form a narrow angle. Compare with Figure 9.

In an attempt to reduce the angle of lower laterals from 80° to around 45° a short section of adhesive tape ½ inch wide was wound 2 or 3 turns about the trunk and young limb while it was yet only an inch or two long and quite tender. After the limb had grown out and become rigidly set, the tape was removed with the crotch angle seemingly permanently fixed at the predetermined angle. No "choking" or other ill effects were noted, except that the adhesive tape held so tenaciously to the trunk that the underlying epidermis was destroyed when the tape was unwrapped. To overcome this it

was found that before applying the tape, it could be doubled back upon itself in such a way that the viscid surface did not come against the tree.

Fig. 9.—A lower lateral bud from the trunk of an unbranched year-old tree. Median line of the bud is far from the vertical. Buds in the position of this one usually produce a wide angle limb.

SPIRAL GIRDLES ON SCAFFOLD LIMBS

Possibly as a result of adaptation to maximum exposure of leaves to the sunlight, the secondary branches from scaffold limbs seem to arise more frequently from the sides and outer or lower part of the scaffold limbs rather than from the upper part.[5] As conduction along the limb takes place in more or less straight lines, the place where most of the leaf elaborated substances must move is determined by the point where this material enters the scaffold limb. It would seem that scaffold limb crotches are effectively cut off from most of the food supply from the limb forming the crotch

because the movement is in the sides and lower part of the scaffold limb and not through the crotch. In the specimens of crotch and limb tissues studied, it was observed that the upper part of the scaffold limb enlarges more slowly than the remainder of the limb. This retarded development may be related to the movement of substances from the leaves.

Fig. 10.—Spiral girdles cause the phloem and xylem subsequently formed to change the axis from parallel with the limb to parallel with the spiral. A = more than one complete girdle. B = girdled only half way around the limb.

Spiral girdles on the trunks of apple trees have been shown to cause the regenerated conductive tissues to change the direction of longitudinal axes from normally vertical to parallel with the spiral.[10] It was found in these studies that likewise on a scaffold limb the orientation of conducting elements formed subsequent to spiral girdling was changed so that the long axes were parallel with the spiral (Figure 10). Crotch tissues particularly subject to winter injury because of framework structure in the tree might acquire increased hardiness by so placing a spiral girdle as to divert the elaborated food from the lower side of the limb into the crotch areas. The peculiar ensuing development associated with spiral girdles might, however, introduce structural weakness in the limb.

EFFECT OF THIOUREA UPON PROXIMAL DOMINANCE IN THE SWEET POTATO

Denny[6] in working with tubers of *Solanum tuberosum* discovered that thiourea in proper concentration overcame the inhibiting effect, which the main bud in each eye exerts, upon the subsidiary buds and also partially nullified the capacity of the terminal bud to prevent the development of the basal buds on the same seed piece. The analogy between apical dominance in stems and proximal dominance in roots suggested the use of thiourea on the sweet potato.

Porto Rico sweet potato roots, as near 2 x 4 inches in size as could be found, were selected from a grocer's stock. The roots had not sprouted but the rudiments of buds were visible on the proximal end. The potatoes were immersed in distilled water solutions of 2 to 4 per cent thiourea for one to two hours. Excellent results as shown by Table 1 were obtained from the treatments, especially those for one hour. (See Table 1, Figures 11, 12, 13, 14, 15 and 16.)

TABLE 1.—EFFECT OF THIOUREA UPON PROXIMAL DOMINANCE IN THE PORTO RICO SWEET POTATO.

Root Treatment	No. of Roots	Mean Number of Slips		
		Proximal 1/3	Middle 1/3	Distal 1/3
2% Thiourea 1 hour	13	21.1	8.2	9.7
2 hours	5	4.2	1.8	5.0
3% Thiourea 1 hour	4	14.2	6.8	13.8
2 hours	4	5.0	.0	1.2
4% Thiourea 1 hour	10	7.1	5.2	14.2
2 hours	3	.0	.3	11.3
No Thiourea	9	11.4	1.7	.1

When the time of immersion in the solutions was longer than one hour, a retarding effect was evident which was also true of the 4 per cent solution for both one and two hours. Despite the retardation, the roots treated with 4 per cent solution for one hour, later made a fine crop of sprouts well distributed over the surface. All treated roots showed a loss of proximal dominance in a second crop of slips. The lot in the 4 per cent solution for one hour produced the second drawing of plants well distributed over the surface as readily as any of the concentrations.

The temperature of the plant bed used was too low. McGinty and Miller[11] found that the largest number of plants from a given

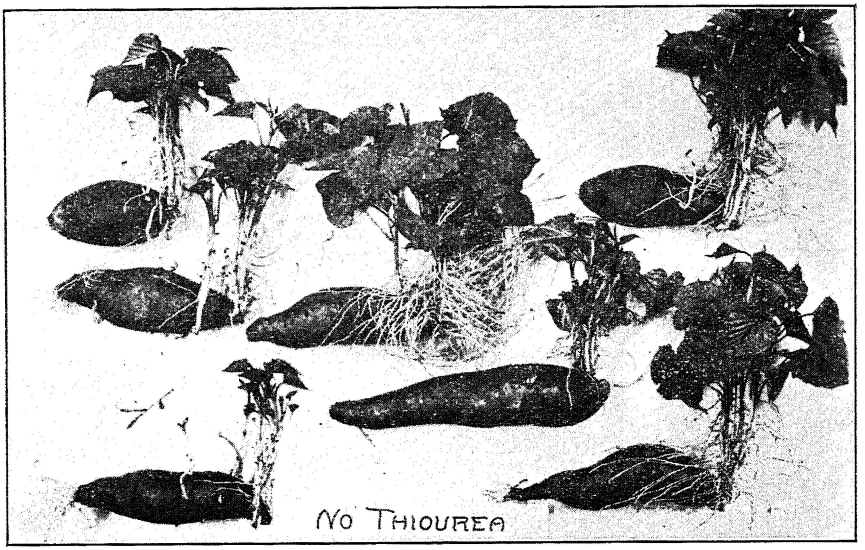

Fig. 11.—Porto Rico sweet potatoes. These roots demonstrate the normal proximal dominance. Distal end in all pictures is to the reader's left.

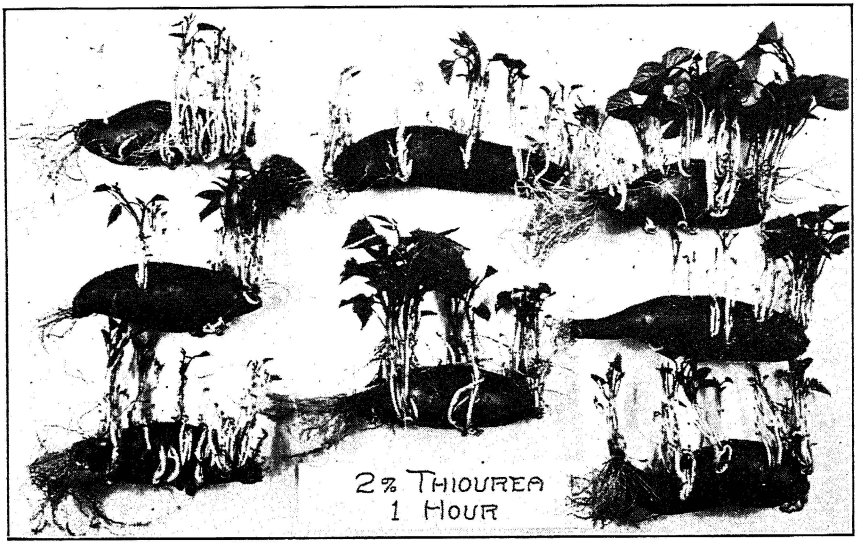

Fig. 12.—Porto Rico sweet potatoes. Roots soaked in 2 per cent distilled water solution of thiourea for one hour. Slips arise over the surface of the potato and not from the proximal end only.

quantity of seed stock is to be obtained at about 85° Fahrenheit. Much of the time the plant bed used in this experiment was below 70° Fahrenheit.

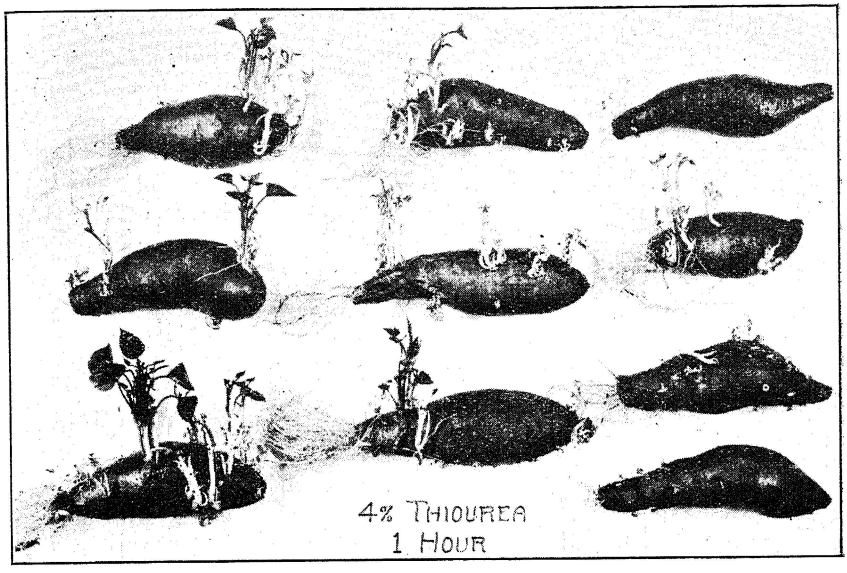

Fig. 13.—Porto Rico sweet potatoes. Soaked in thiourea 4 per cent for one hour. Roots are retarded and do not exhibit dominance of the proximal end.

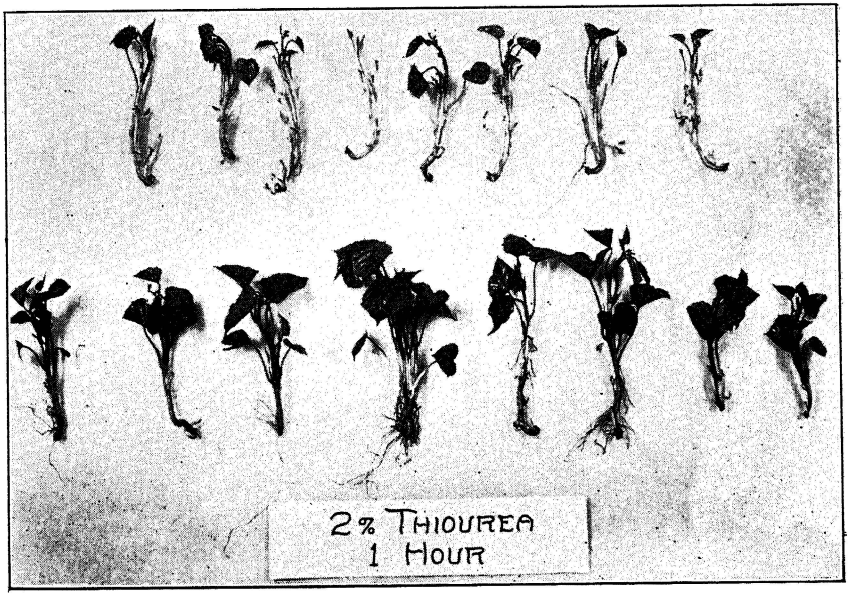

Fig. 14.—Porto Rico sweet potato slips. Soaking in thiourea solution previous to bedding the roots has caused axillary bud development in the slips. Such plants later, while still attached to the root, exhibited normal apical dominance.

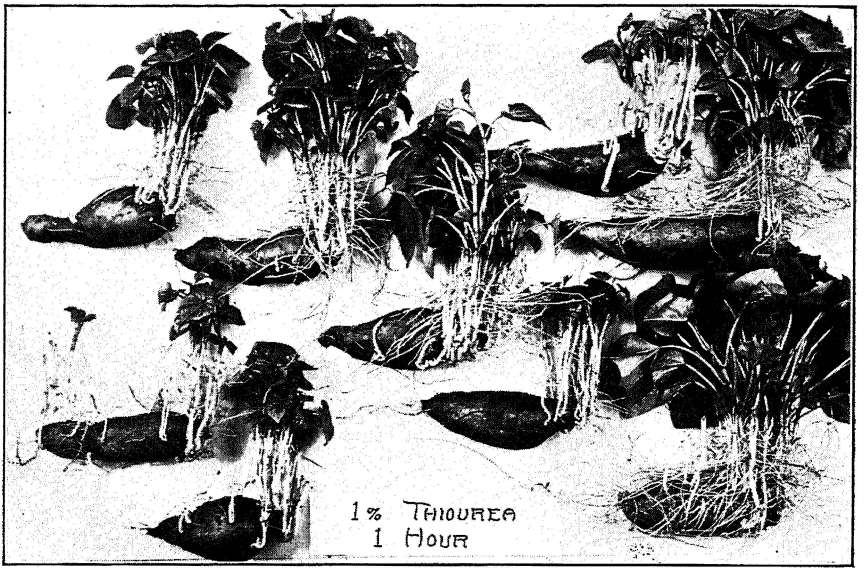

Fig. 15.—Nancy Hall sweet potatoes. Concentration of thiourea too weak to materially affect proximal dominance. These roots were similar to the controls. Distal end to the left in all pictures.

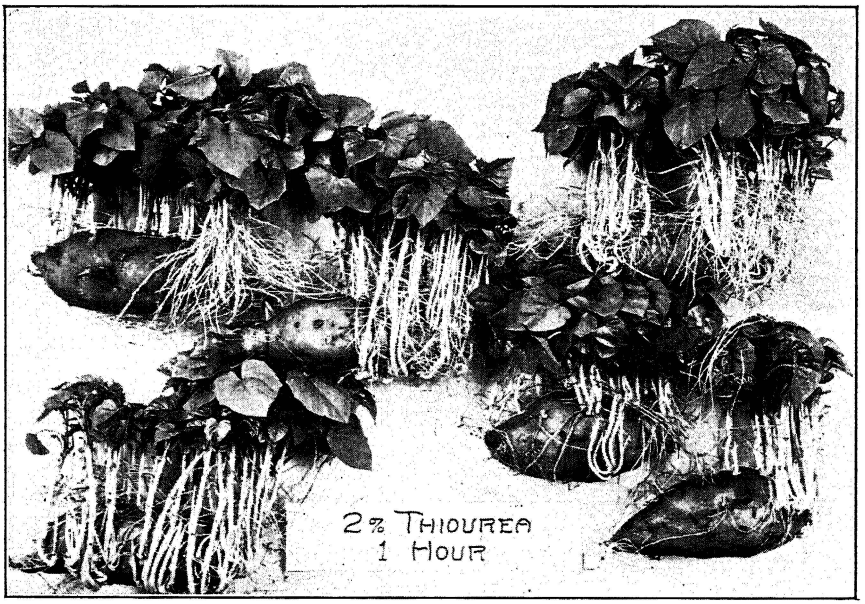

Fig. 16.—Nancy Hall sweet potatoes. Proximal dominance overcome in most cases.

SUMMARY

Certain combination treatments of disbudding and aqueous solutions of thiourea retarded the growth of the distal buds on one-year-old apple trees, so that the upper branches were not dominant the first year.

A reversal of apical dominance was found in some cases when four-year-old Delicious trees were cut back. The lower laterals outgrew the terminal shoot.

Several conditions were found which were associated with the reappearance of apical dominance in cut-back trees. When several shoots were allowed to grow, lateral buds fail to grow. Likewise, lack of sufficient water and light reduction to 380 foot-candles were found to favor inhibition of laterals.

After the cells are differentiated in the young scaffold branch of cut-back trees, the rapid enlargement of the trunk forces a change of angle from narrow to wide while the tissues of the lateral are yet too soft to resist the growth pressure. This accounts for the large size angle.

Lower lateral buds on a one-year-old tree lie with their axes far from the vertical; consequently, scaffolds originating from such buds usually grow at a wide angle with the trunk.

During the second year of growth of the tree, short sections of adhesive tape wound 2 or 3 turns about the trunk and young limb, when the latter is only an inch or two long and quite tender, markedly reduced the spread or angle of the crotch.

Spiral girdles on one-year-old scaffold branches are shown to cause the regenerated conductive tissue to change the direction of longitudinal axis from parallel with the limb to parallel with the spiral.

Soaking the thickened roots of the sweet potato in distilled water solutions of thiourea overcame proximal dominance, so that slips originated from points well distributed over the surface. In a second crop of slips, all roots exhibited a loss of proximal dominance.

Immersing sweet potato roots in thiourea solutions previous to bedding caused axillary bud development in the slips. Such plants later even while still attached to the bedded root exhibited normal apical dominance.

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