

TRANSPORT OF ROOT-FORMING HORMONE IN WOODY CUTTINGS

Thesis by

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## TRANSPORT OF ROOT-FORMING HORMONE IN WOODY CUTTINGS

It has been repeatedly observed since early times that if stems from some of our common woody plants are girdled adventitious roots may be formed above the girdle. Although this regeneration phenomenon may result in part from an interruption of food transport, recent evidence indicates that the regeneration is controlled by hormones which are transported in the phloem. The greater part of the experimental work on the nature and transport of these hormones in the plant has been done with Avena coleoptiles and pea (Pisum sativum) cuttings. Went<sup>(12)</sup> demonstrated that a growth-promoting factor from Avena coleoptile tips will diffuse out of them into a layer of agar, and that decapitated coleoptiles will grow considerably faster if blocks of this agar are placed on the cut surfaces than if they are supplied with pure agar. The chemistry of this growth substance has been worked out especially by Kögl, Haagen Smit and Erxleben<sup>(6&7)</sup>. Three different crystalline substances were isolated, which physiologically can not be distinguished. They have been named auxin a ( $C_{18}H_{32}O_5$ ); auxin b ( $C_{18}H_{30}O_4$ ); and hetero-auxin (indole-3-acetic acid-- $C_{10}H_9O_2N$ ). Later Thimann<sup>(10&11)</sup> found that synthetic hetero-auxin causes root formation on pea cuttings as well as promoting growth by cell elongation. Also, Cooper<sup>(2)</sup> has shown that hetero-auxin induces root formation on lemon, fig, Acalypha and Lantana stem cuttings, and Zimmerman and Wilcoxon<sup>(17)</sup> have found that hetero-auxin causes local initiation of adventitious roots on stems and leaves of tomato and tobacco plants.

Experimental work, especially by Van der Way<sup>(15,16)</sup>, on the transport of auxin in Avena has shown that auxin is transported basipetally

only, and that it is intimately connected with life processes. To cover these facts Went<sup>(13)</sup> proposed the theory that naturally occurring potential differences in coleoptiles and other organs (apical parts being negative against basal parts) would produce an electrophoresis of the negatively charged ions of auxin toward the positive base.

In addition, it was found by Went<sup>(14)</sup> that the transport of substances causing root formation in *Acalypha* is rectilinear, rigorously polar, and independent of the transport of carbohydrates. In contrast to these results showing polar transport of hormones as a basis of the well-known morphological polarity in *Avena*, *Acalypha*, and other plants, Hitchcock and Zimmerman<sup>(5)</sup> observed no strictly polar movement of several synthetic compounds, including hetero-auxin, in either stems or leaves of the tomato and tobacco plants. They found that these substances when applied to the soil in highly concentrated water solutions were absorbed by the roots and were transported upward in the xylem in the transpiration stream. Also, that when water solutions were admitted through the cut surface of a stem or leaf there was a longitudinal movement in either direction through dead stem tissue, this movement being influenced by transpiration. Thus they concluded that living cells were not essential for the transport of these substances, and that the main channel of transport is in the transpiration stream.

These results obtained by Hitchcock and Zimmerman, however, do not prove that the normal channel of transport of hormones in the plant is in the transpiration stream. The transpiration stream may possibly provide a means for the upward transport of substances absorbed from the soil by

the roots, but it does not provide for the downward transport of hormones found in leaves (Went<sup>(14)</sup> and Avery<sup>(1)</sup>). It is hardly possible that they would normally move downward in the xylem in the opposite direction from the transpiration stream. That root-forming substances, extracted from leaves, do move downward in the stem has been shown by Went<sup>(14)</sup> with Acalypha cuttings. Also, Cooper<sup>(2)</sup> has found that hetero-auxin, or some substance in the stem activated by hetero-auxin, will move downward in lemon cuttings. Therefore, with the above considerations in mind, it seems highly probable that root-forming substances normally move downward in the phloem. Results of girdling and local chilling experiments presented in this paper give evidence that root-forming hormones do move downward in the phloem in lemon and rose cuttings.

Synthetic hetero-auxin was used in all experiments and was applied to the cuttings either by the lanolin method of Laibach<sup>(8)</sup> or in water solution. By the former method one part of hetero-auxin was mixed with 2000 parts of pure lanolin; i.e., 0.5 mg hetero-auxin per gr lanolin.\* A small portion of this paste--roughly about 10 mg--was smeared both on the cut surface of the apical end of the cutting and on a small area of one side of the cutting near the top which had previously been scraped to remove the epidermis and outer cortical layers. This paste was left on throughout the experiment. Water solutions of various concentrations were applied to either the apical or basal end of the cuttings by soaking 8 to 24 hours in the solution; after treatment the cuttings were placed in sand

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\*This concentration was used in all experiments with the lanolin paste.



in the propagating frame. Control cuttings for the lanolin method were treated with pure lanolin, while control cuttings for the water-solution method were soaked in tap water for the same length of time and under the same atmospheric conditions as were the treated cuttings.

All lemon cuttings, usually about 12 cm long and 5 mm in diameter, were made from twigs of mature wood of the current season's growth and were obtained in all instances from the same grove in Claremont, Calif.

The cuttings were set in sand either in a sash-covered propagating frame without bottom heat in the greenhouse or in a thermostatically controlled propagating frame at Torrey Pines, Calif.\* At the latter place the temperature of the sand was kept at 85 to 88°F. At Pasadena the sand usually held a temperature near 75°F.

#### Girdling Experiments

Three types of rings, as illustrated in Figure 1, were used in these experiments. In type A (Fig. 1) a complete ring of phloem about 12 mm wide was removed from the stem of the cuttings about 4 cm from the base. Type B was only partly ringed, a straight vertical bridge (a) about 2 mm wide being left across the ring. Type C was also only partly ringed, but in this case a two-right-angled bridge of phloem (b,c,d) about 2 mm wide was left across the ring. These methods of ringing are similar to those used by Czapek<sup>(3)</sup> in 1897 in studying the effectiveness of lateral transfer

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\* The writer is indebted to Dr. L.C. Marshall of the U.S. Department of Agriculture, Field Station at Torrey Pines, Calif. for the use of the propagating facilities at Torrey Pines and for care of the cuttings while in the propagating frames.



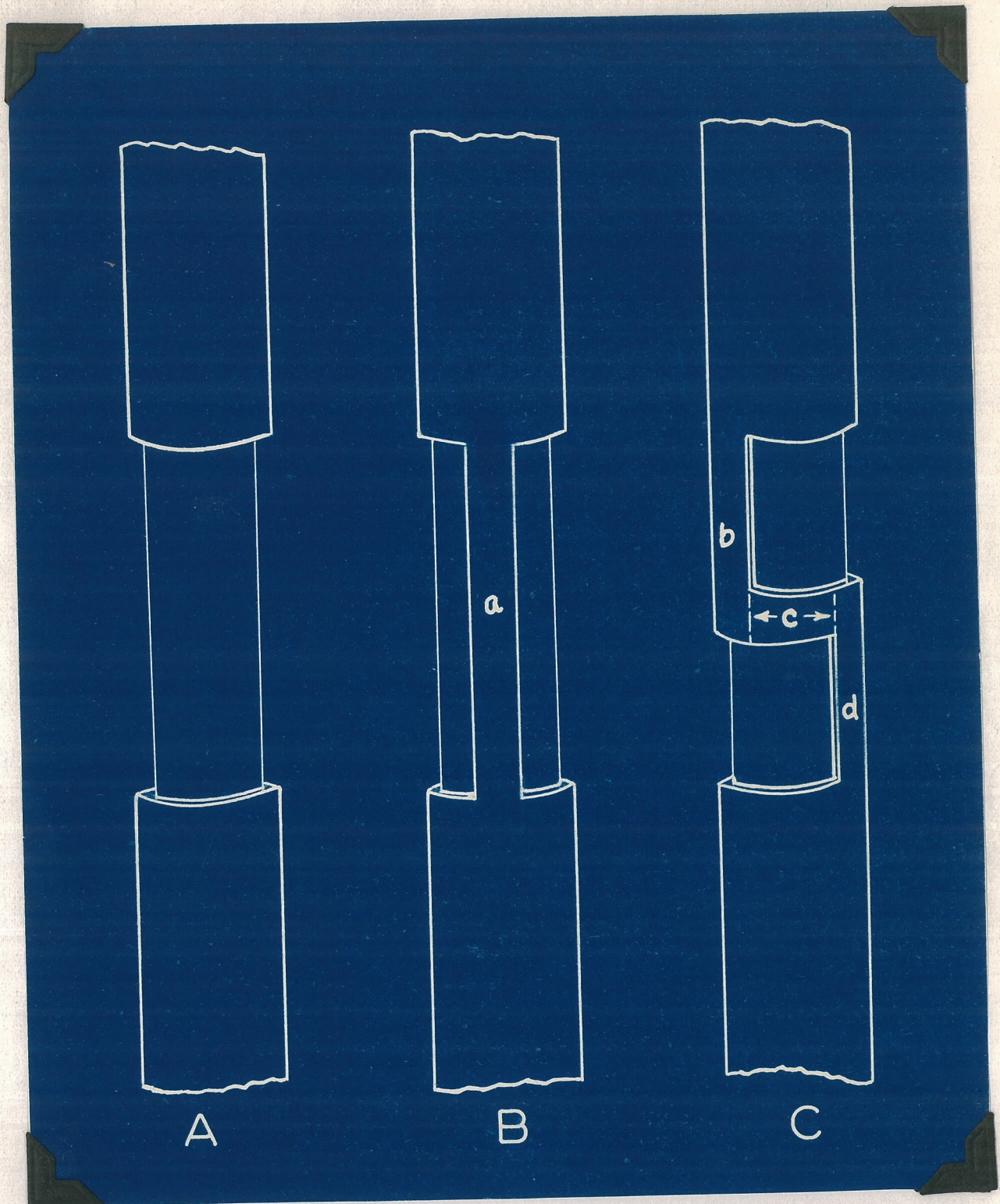


Figure 1. Diagrams of different types of girdles used. A, complete ring of phloem removed. B, partly ringed with straight vertical bridge of phloem (a) left across the girdle. C, partly ringed with two-right-angled bridge of phloem (b,c,d) left across the girdle. (b) upper vertical arm, (c) horizontal arm, (d) lower vertical arm.



of food through stem cuttings of several woody plants.

Since these cuttings were kept in sash-covered propagating frames where the relative humidity was always high, it was not necessary to take the precaution of coating the exposed area with warm paraffin to prevent drying out of the xylem tissue, as was found necessary by Curtis(2) with ringed tissue on trees out of doors. The fact that the cambium often became active and regenerated new tissue when the bark was removed is evidence that the xylem had not dried out.

The effect of ringing on root formation on lemon cuttings which had been treated with hetero-auxin is shown in Table I and figure 2. When both xylem and phloem above a complete ring were treated, either with hetero-auxin lanolin mixture or with hetero-auxin water solution, roots formed at the base of the cuttings. When a narrow vertical bridge of phloem was left across the ring roots would form at the base, though in smaller number than on the non-ringed cuttings. This is very good evidence that the hetero-auxin, or some root-forming substance present in the cutting and activated by the hetero-auxin, is transported downward mainly in the phloem.

Root formation at the base of the cuttings with a two-right-angled bridge of phloem across the ring (Fig. 1-C) was found to be influenced by the horizontal distance (c) between the side of the upper vertical arm (b) and that of the lower arm (d). Where this distance was greater than 2 mm there was usually a strong callus development at the sides and base of the upper vertical arm but very little on the horizontal arm and none on the lower vertical arm. In some instances roots would appear at the base of the upper vertical arm but none on the horizontal arm or at the base of the cutting. However, in cuttings where the horizontal arm (c) was less than 2 mm

Table I

Effect of Ringing on Root Formation of Hetero-auxin  
Treated Lemon Cuttings\*

Leaves	Hetero- auxin Treatment	Weeks after set in sand	Average number of Roots per Cutting**		
			Not Ringed	Complete Ring	Narrow Bridge of phloem straight across ring.
A	+ Lanolin mixture	6	4.8	0	3.4
	Pure lanolin	6	2.5	0	—
B	- .5 mg/cc water for 18 hours	3	4.2	0	1.1
	do	6	5.3	0.2***	2.0
	Tap water 18 hrs.	3	0.2	0	0.3
	do	6	1.6	0	0.6
C	- .17 mg/cc water for 15 hours	3	4.0	0	1.1
	Tap water 15 hrs.	3	1.7	0	0

\* All cuttings treated at apical end.

\*\* Average from 10 cuttings.

\*\*\* Two roots on one cutting.

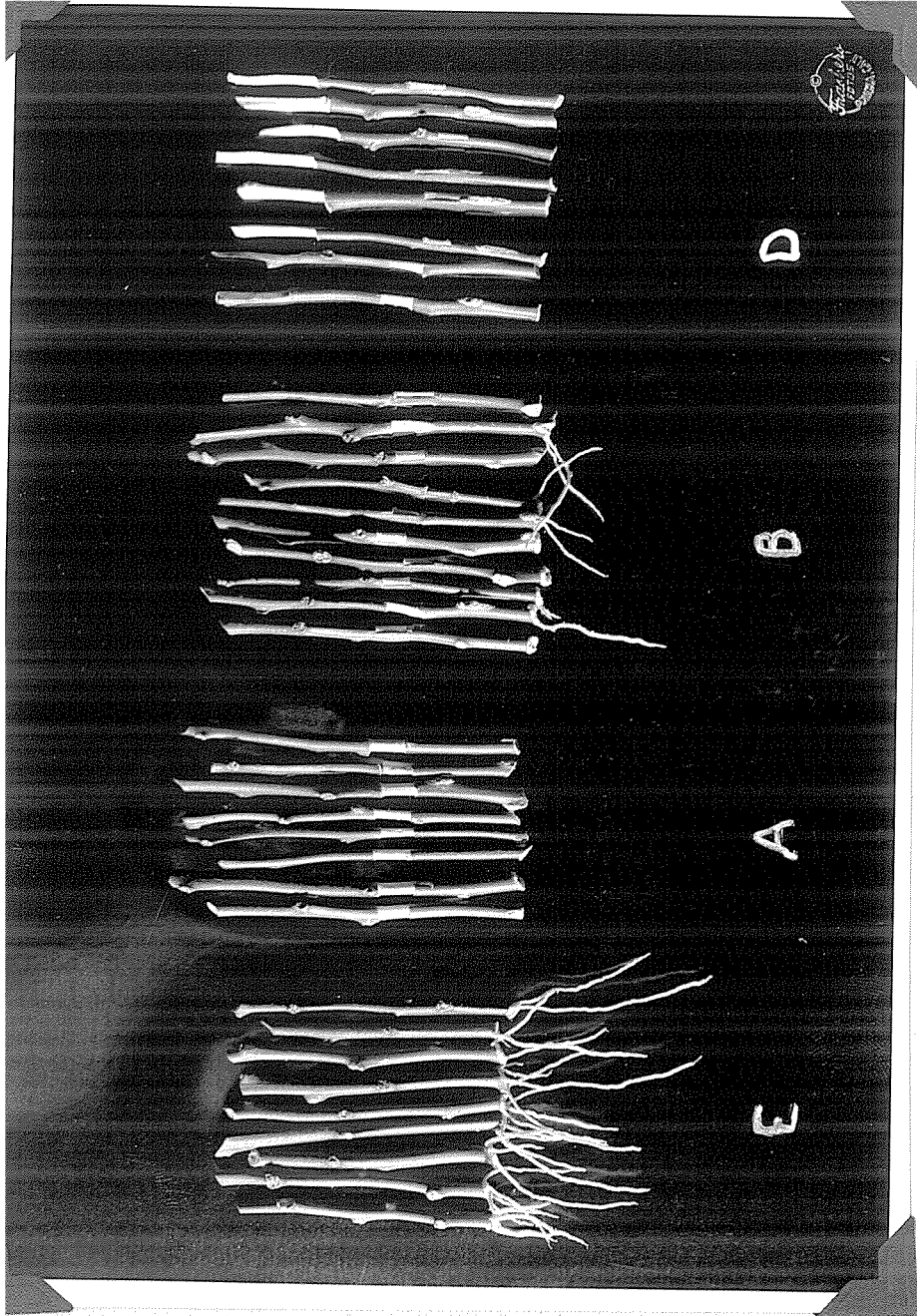


Fig. 2. Effect of ringing on root formation on leafless lemon cuttings treated at the apical end with a hetero-auxin solution (17 mg per cc of water) for 15 hours. E, not ringed; A, completely ringed; B, partly ringed with straight vertical bridge of phloem across the rings; C, same as B except one side of apex of cutting was removed in order that only the side of the apex opposite the phloem bridge was treated. Picture taken three weeks after treatment.

an occasional root would form at the base of the cutting, but at no time was root formation as great as on cuttings with a straight vertical bridge across the girdle.

In another experiment with two lots of partly girdled cuttings (type B) hormone solution was applied in one lot to the entire cut end of the apex (Fig. 2-B) and in the other lot only to the side of the apex opposite the phloem bridge across the ring (Fig. 2-D). No roots were formed on the cuttings to which hormone was applied only on the side opposite the bridge, but in the other lot roots formed at the base of the cuttings. These results, along with those obtained with the two-right-angled type girdle, indicate clearly that the hormone moves downward in the phloem mainly in straight lines parallel to the phloem elements.

MacDaniels and Curtis<sup>(9)</sup> report that when lateral transfer of food in apple tree trunks was forced by spiral ringing more rapid lateral conduction was provided for by structural changes in the phloem, beginning soon after ringing and resulting in the re-orientation of the cambium so as to be parallel with the spiral ring. They state that partial accommodation to the changed condition of conduction probably occurred immediately after ringing by the first formed elements being connected through their radial walls. Perhaps this would account for the slight lateral movement of the root-forming hormone observed with the two-right-angled type of girdle on lemon cuttings.

Local Chilling Experiment

Chilling at 33-40°F. and at 38-46°F. of about 50 mm of the stems near the mid-portion of leafless lemon cuttings was accomplished by inserting the cuttings through special insulated chilling units. These were set up in the propagating frame so that bases of the cuttings were in the sand which had a temperature near 30°F., 50 mm of the mid-portion in the chilling device, and the tips, treated with hetero-auxin-lanolin paste, in the air at a temperature near 70°F. The chilling unit consisted of small water-tight tin cans into which were soldered 10 copper tubes in a vertical position and parallel to each other. This arrangement of copper tubes permitted insertion of cuttings through the device so that when cold water was circulated through the can the portions of the cuttings in the tubes were chilled without actually coming in contact with the water. Two such chilling units insulated with one-half inch of celotex were connected with rubber tubing. Water at about 32°F. was circulated at a slow rate through the two-unit system for two weeks. Cuttings in the first unit were chilled locally to 33-40°F., and in the second unit to 38-46°F.

After two weeks of chilling the hetero-auxin-lanolin paste was removed from the tips, the cuttings were taken out of the device and re-set in the sand. There was no sign of callus formation at the base of either of the chilled lots, while a strong callus had formed on the cuttings which had been treated with hormone but not locally chilled. One week later, or three weeks from time of setting in sand, roots appeared on the non-chilled cuttings, while roots did not appear on the chilled cuttings until three weeks after chilling, or five weeks after setting in sand, and then largely on the 38-46-degree lot. (Table 2). Thus we see that root formation on the

Table II

Influence of Local Chilling of Lemon Cuttings on Downward  
Movement of Root-forming Hormone\*

Hetero- auxin	Chilling treatment	Average number of roots per cutting			
		End of 2 Weeks Chilling	One week after Chilling	Three weeks after Chilling	Five weeks after Chilling
-	not chilled	0	0.4	—	1.8
+	do	0	0.7	2.4	2.8
+	chilled 33-40°F.	0	0	0.1	0.4
+	chilled 38-46°F.	0	0	0.7	0.9

\*Hetero-auxin lanolin paste applied at top of cutting above chilled area.



locally chilled cuttings was delayed by two weeks--the length of the chilling period--and that root formation on chilled cuttings never did approach that of the non-chilled lot. Local chilling, then, must have acted in preventing the transport of hetero-auxin downward because the few roots which formed during the five weeks after chilling can be accounted for by naturally occurring root-forming hormones in the stems. This seems obvious since the untreated cuttings showed more roots than were formed on the chilled cuttings.

This evidence that local chilling actually does prevent the downward transport of hetero-auxin indicates that living cells take an active part in the transport of hetero-auxin or some substance in the stem activated by hetero-auxin. It therefore seems well established from the combined results of the girdling and local chilling experiments that the hormone is transported downward in the phloem.

#### Effect of Basal Application of Hetero-auxin

##### Solution on Root Formation

By soaking the base of lemon or rose cuttings in hetero-auxin solution of relatively high concentration (0.5 mg per cc of water) for eight hours before setting in sand a much greater number of roots were induced on the treated than on control cuttings (Figs. 3 and 4). Also it was found that the number of roots were from two to five times as great when treated at the base as when treated at the tip, provided a highly concentrated solution was used. The definite relation between the time of treatment, concentration of solution, and number of roots formed has not been determined.



Fig. 3. Lemon cuttings treated at the base with hetero-auxin solution (.5 mg per cc of water) for 8 hours. Picture taken 2-1/2 weeks after treatment.

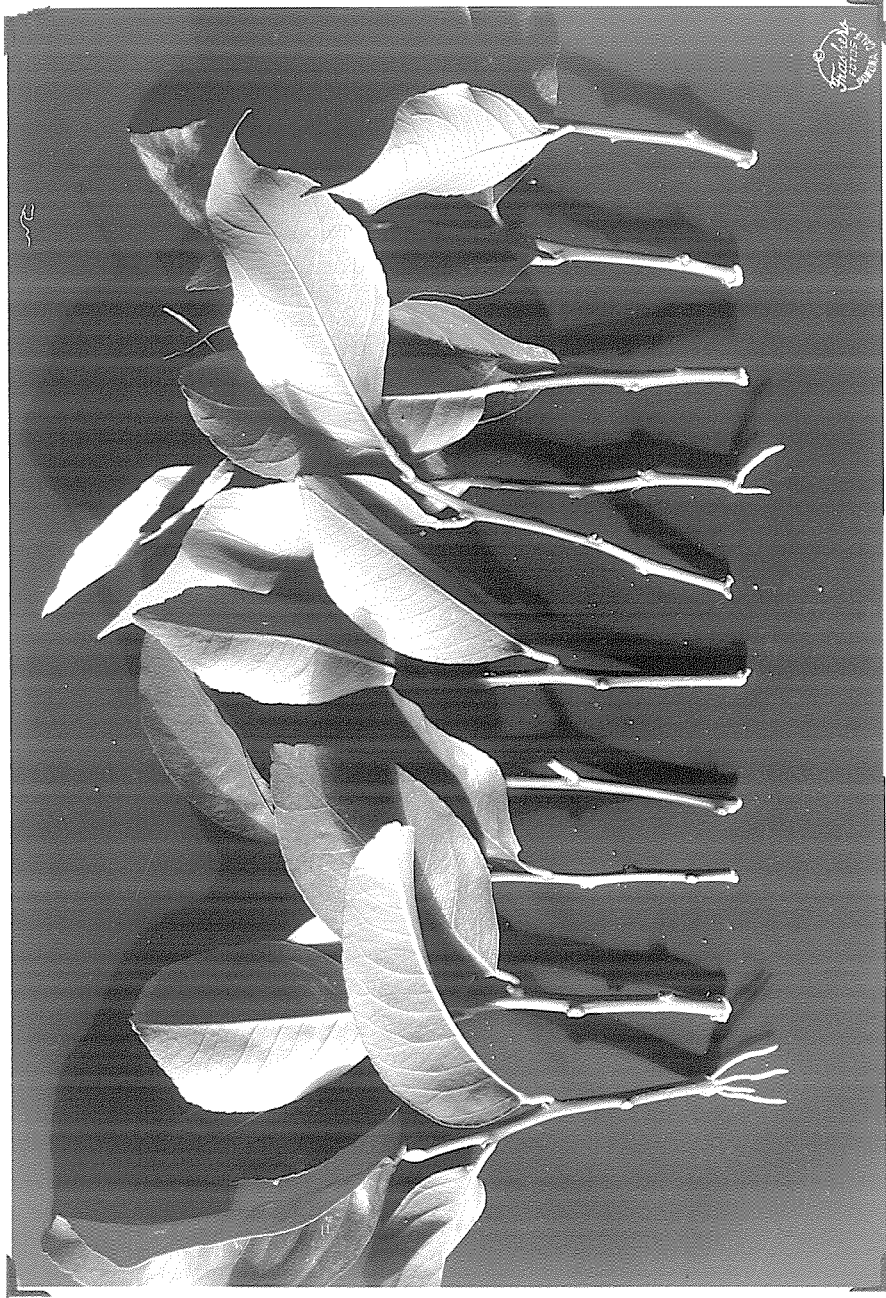


FIG. 4. Lemon cuttings treated at the base with tap water for 8 hours. Picture taken after 2-1/2 weeks.

However, results shown in Figure 5 for basal treatment of .04, .1, .2, .5 mg hetero-auxin per cc of water indicate that basal treatments are effective only in concentrations of .1 and above for a 15-hour treatment of leafy cuttings, and .2 and above for a 12-hour treatment of leafless cuttings. More dilute solutions applied at the base caused no more root formation than tap water. It was noted that .5 mg per cc solution applied at the base caused some injury, so very likely the effective range of concentration for basal treatment of lemon cuttings for 12 to 15 hours is from .1 or .2 to .5 mg per cc.

Some idea as to the reason for this rooting response to basal treatments of hetero-auxin solution is obtained from a study of Table 3. Cuttings in experiments A and B were placed in a nearly saturated atmosphere in the propagating frame at Torrey Pines during the period when the bases of the cuttings were soaked in hetero-auxin solution, thus very little opportunity was afforded for transpiration. Yet in both instances there was considerable increase in number of roots induced on the treated cuttings over that of the controls. However, when the portion of the base of the cutting which was actually in the hetero-auxin solution (about three-fourths of an inch) was cut off, the effect of the treatment was eliminated. This suggested that there was very little or no movement of the hetero-auxin solution up the stem. The solution was, however, effective only when applied at the cut end because, when the cut end was sealed over with paraffin before soaking in the hetero-auxin solution and the paraffin later removed after the treatment there was no increase in number of roots over the controls.



Figure 5.

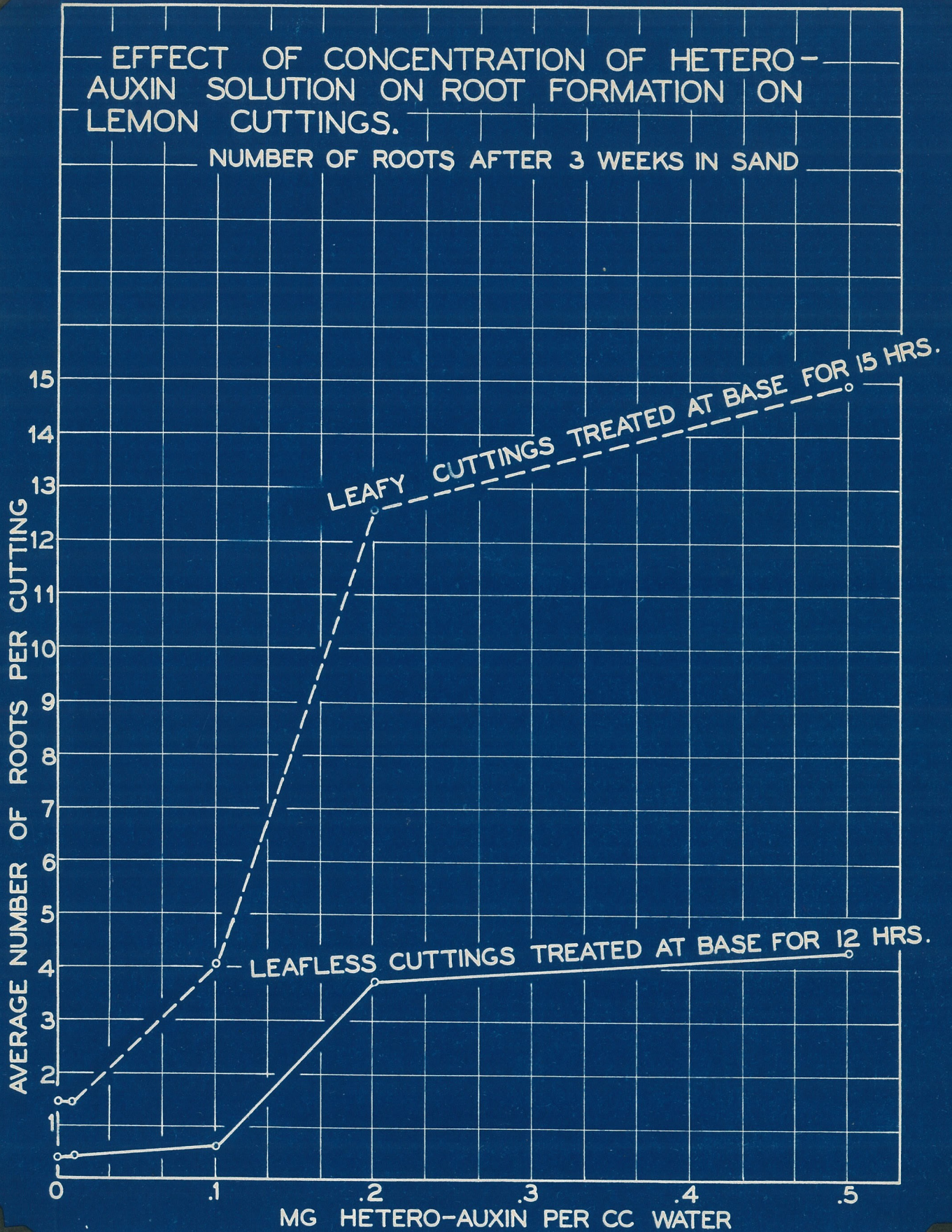




Table III

Experiments Showing the Effect on Root Formation of Treating the Basal Ends of Lemon Cuttings

Expt. leaves	Conc. of Hetero-auxin solution	Hours treatment	Weeks after treatment	Average number of roots per cutting			
				Tap water control	Base treated	Base and part treated	Base treated, cut off, and new base treated
A	+.5	20	2½	1.5	20.4	2.4	...
			6	4.3	33.5	3.6	...
B	+.1	8	2½	1.1	4.0	2.5	...
			6	4.0	8.3	4.3	...
C	+.17	15	3	1.7	12.6	4.9	4.8
			3	1.7	4.0	1.2	2.3
D	+.5	12	5½	1.1	4.3	0.9	0.8
			5½	1.3	5.9	1.7	1.6
			5½	1.1	0.6	0.8	0.5
			5½	1.3	1.6	1.6	1.4

\* Average of 10 cuttings in each instance.

In experiment C, leafy lemon cuttings were exposed to laboratory air (temp. 70°F., relative humidity about 75%) during the fifteen hours the cut end of the bases were in hetero-auxin solution, thus affording opportunity for transpiration. As a consequence, an average of 2 cc of solution was taken up by each cuttings, probably in the xylem in the transpiration stream. As a result of these conditions the number of roots on the cuttings with the treated portion of bases cut off was greater than the controls, yet the number was only about one-third that of the cuttings from which the treated portion of the base had not been cut off. This probable upward movement of the hetero-auxin in the xylem however should not be mistaken for the normal movement of naturally occurring hormones in the plant because, as stated by Curtis<sup>(3)</sup> "When solutions of most any sort of substance are introduced into cut stems these solutions are carried extensively and almost exclusively in the xylem tissues and it is obvious that transpiration determines both the direction and rate of movement of the solution introduced".

In experiment C, evidence of possible upward movement of hetero-auxin in the transpiration stream is of little significance, but the fact of greatest interest is that if the treated portion at the base of a cutting was excised and the base again treated the number of roots formed was no greater than that of a similar cutting which had not been re-treated. This was observed again with leafless lemon cuttings in experiment D, in which a solution of .5 mg of hetero-auxin per cc of water was used. In this instance the number of roots on cuttings with treated base cut off and on similar cuttings with base treated again was the same as on controls, while treated cuttings, but with the base not removed, showed nearly three times as many roots as controls. Results similar to these were also ob-

tained with leafy cuttings of the rose (var. Lady Perkins).

It is clear from these latter results that there is some factor other than hetero-auxin concerned in root formation. If only hetero-auxin were involved, re-treating the cutting after removing the treated base should give nearly the same response as the original treatment. In order to insure equal amounts of stored food and other substances the final length of the cuttings in all experiments was made the same. Cuttings whose treated bases were to be cut off were made longer in the beginning to allow for the removal of a portion of the stem at the base.

Summarizing, we find that (1) when applied at the base of cuttings for 15 hours only a strong solution of hetero-auxin is effective in inducing root formation, (2) cutting off the treated portion of the base nearly eliminates the effect of the treatment, (3) re-treating after cutting off the treated base causes no more roots than when not re-treated. To cover these facts it is suggested that a strong solution of hetero-auxin, when applied to the base, causes the rapid movement downward of a substance, rhizocaline, present in the leaves and stem and which is necessary for root formation. Cutting off three-fourths of an inch of the base after treatment cuts off most of the supply of rhizocaline and further treatment with hetero-auxin has little effect since hetero-auxin is only one of the substances necessary for root formation.

The effectiveness of treating the basal ends of lemon or rose cuttings with a strong solution of hetero-auxin in inducing root formation suggests a new line of attack in efforts to root cuttings of apple and other woody plants which do not root readily from cuttings. With lemon, rose, holly, and Chrysanthemum cuttings this method of treatment was much



more effective than the lanolin method of Laibach. The maximum number of roots per cutting obtained on lemon cuttings by the lanolin method was eight, while as many as seventy-five were obtained by soaking the base in hetero-auxin solution (5 mg per cc of water) for eight hours. The same concentration of solution induced formation of twentyfive roots per cutting on the Cecil Bruner rose and fourteen roots per cutting on a species of Chinese holly (Ilex cornuta) while the lanolin method produced only five roots per cutting on the rose and none on the holly. Even more striking results were obtained with Chrysanthemum cuttings as is shown in Figures 6 to 8, but in this instance a hetero-auxin solution of .1 mg per cc of water was found most effective as stronger solutions were toxic to the tissue of the base.\*

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\* Since preparing this paper it has come to the attention of the writer that A.E.Hitchcock and P.W.Zimmerman (Contrib. Boyce Thompson Inst. 8:63-79, 1936) obtained excellent results with the rooting of certain species of Ilex and Taxus by soaking the bases of cuttings in water solutions of hetero-auxin in a manner similar to the method described in the present paper. These authors in discussing a former paper by the present writer, published in Plant Physiology<sup>(2)</sup> state, "The qualitative and quantitative differences resulting from treatment of lemon cuttings having leaves are not clear, since there is no illustration of control lots with which to compare the three treated lots shown". Reference to the article will show that in Table I, page 79, are given the number of roots per cutting formed after two, three and four weeks on both treated and untreated leafy lemon cuttings. Although these figures in themselves provide complete proof of "qualitative and quantitative differences", there are also included illustrations of both treated and control cuttings. Reliable data on rooting can not, of course, be derived from illustrations alone, therefore in this paper both photographs and tables are included.

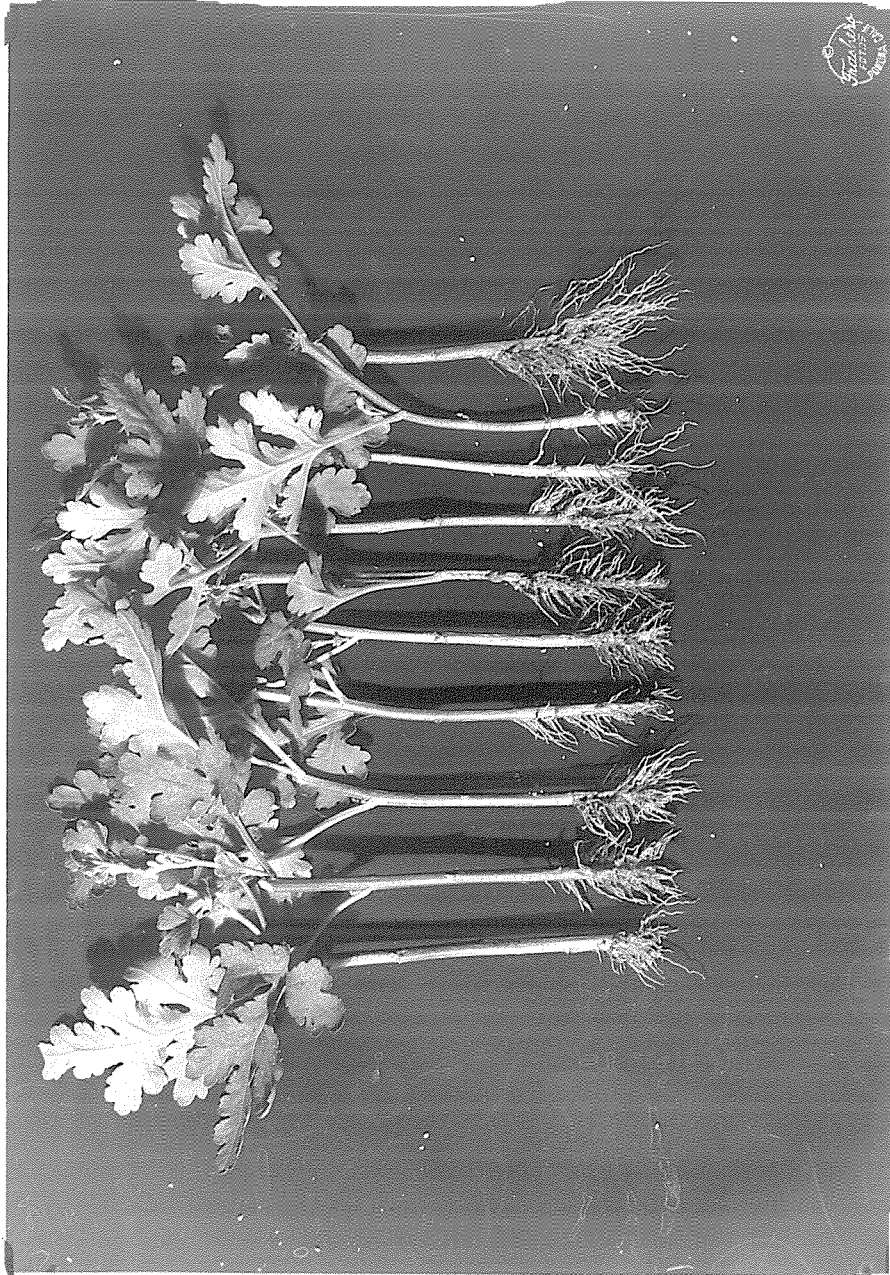


FIG. 6. Chrysanthemum cuttings treated at the base with hetero-auxin solution (.1 mg per cc of water) for 15 hours. Picture taken 2 weeks after treatment.

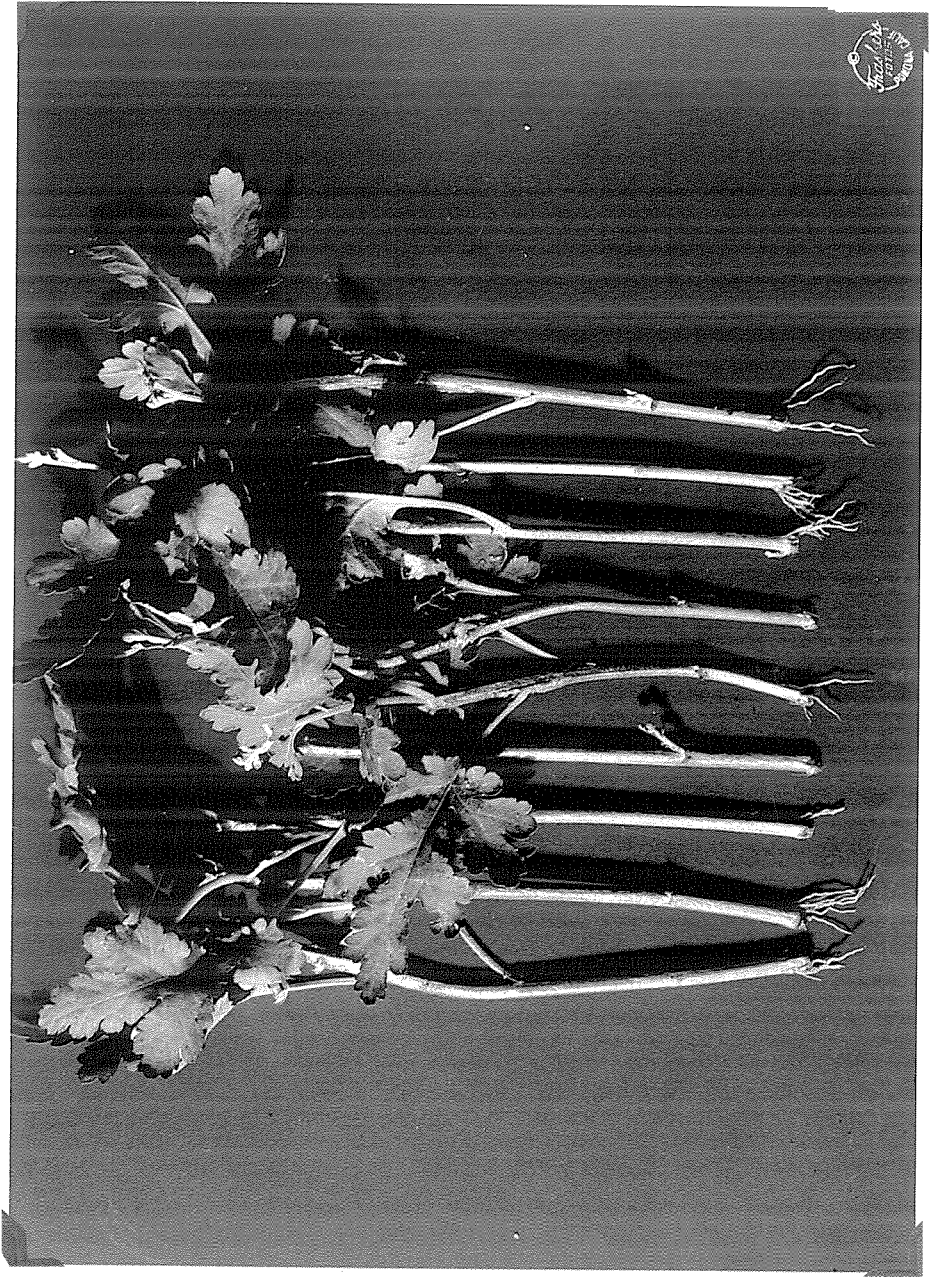


Fig. 7. Chrysanthemum cuttings treated near the top by the lanolin method. Picture taken 2 weeks after application of hetero-auxin lanolin mixture.

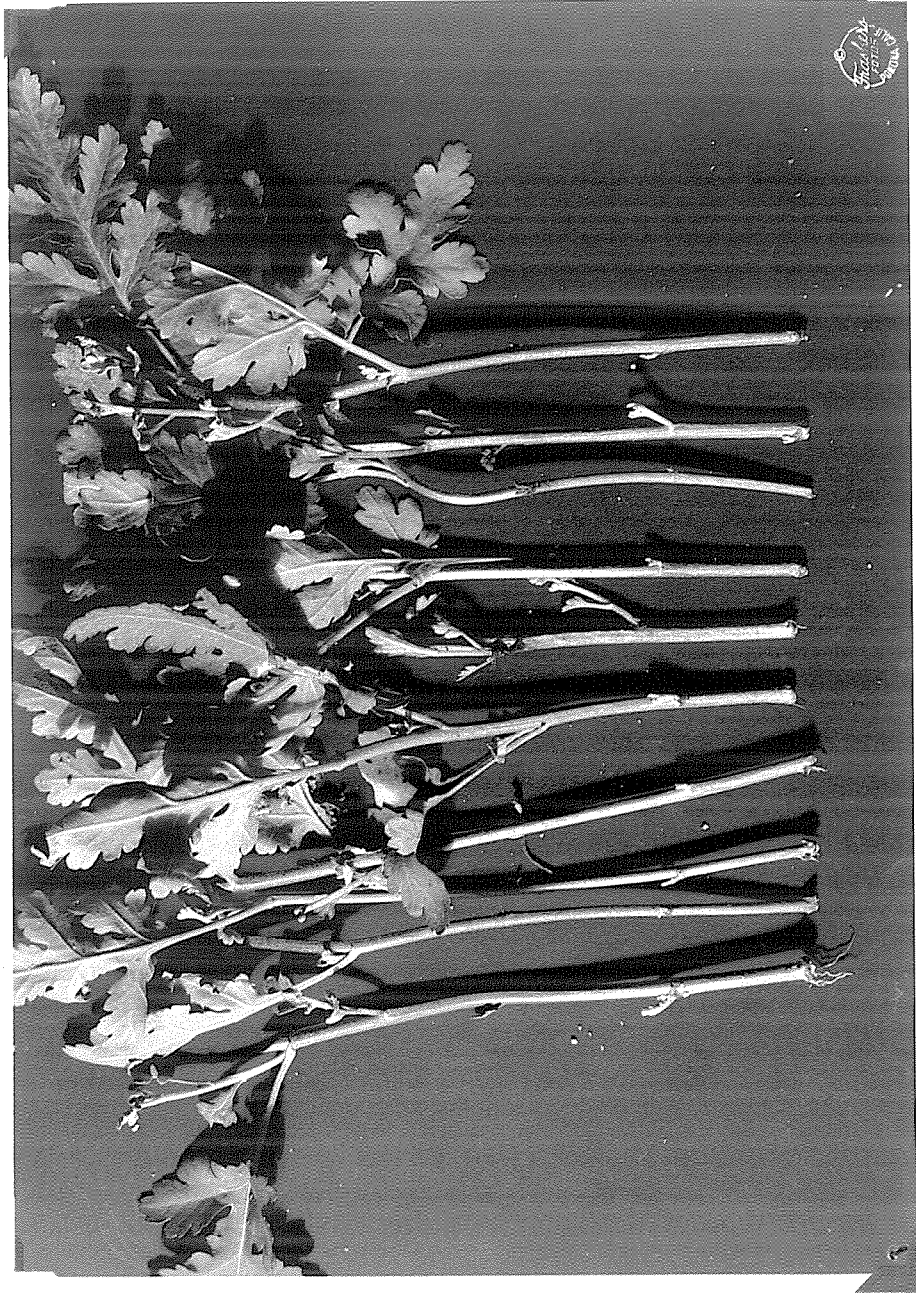


Fig. 6. Chrysanthemum cuttings treated at the base with tap water for 15 hours. Picture taken 2 weeks after treatment.



Summary

- (1) Ringing experiments with lemon cuttings indicate that hetero-auxin, or some substance in the stem activated by hetero-auxin, is transported downward in the phloem and in a straight line parallel to the phloem elements.
- (2) Local chilling experiments indicate that living cells take an active part in the downward transport of the hormone and supports the evidence, obtained in the ringing experiments, that downward transport of the hormone takes place in the phloem.
- (3) When the cut end of the base of a leafy lemon or rose cutting is placed in hetero-auxin solution there is some upward movement of the solution depending on the rate of transpiration.
- (4) When solutions of hetero-auxin are applied at the base of cuttings for 15 hours only strong ones are effective in inducing root formation.
- (5) Cutting off the treated portion of the base of cuttings nearly eliminates the effect of the treatment.
- (6) Re-treating with hetero-auxin solution after cutting off the treated base of cuttings causes no more roots than when not re-treated.
- (7) The hypothesis that a strong solution of hetero-auxin, when applied to the base of a cutting, causes the rapid downward movement of a substance, rhizocaline, which occurs in the leaves and stem and which is necessary for root formation, is offered as an explanation of the facts stated in 4, 5, and 6.
- (8) The effectiveness of treating at the base cuttings of lemon or rose with strong solutions of hetero-auxin in causing root formation suggests a new line of attack in efforts to root cuttings of apple and other woody plants which do not root readily from cuttings.

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