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Mechanism of crotch angle formation in apple trees

II. Studies on the role of auxin

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INTRODUCTION

The marked influence of the auxin on crotch angle formation in apple trees was reported by Verner (1938, 1955) and by Jankiewicz (1956). Indoleacetic or indolebutyric acid applied in lanolin paste on young, not yet fully lignified lateral shoots caused a considerable increase of the angle width. Several authors tried afterwards to take advantage of this phenomenon in nursery and orchard practice with apple trees (Łysenko 1958; Jankiewicz at al. 1961; Jankiewicz 1964a; Poll 1966) and with plum trees (Preston and Barlow 1951). Spraying the apple trees with auxin solutions in order to improve crotch angles was also applied by Poll (1968) and by Jankiewicz et al. (1969 — in press) but without success.

In non treated apple trees crotch angle formation depends probably on natural hormone of the auxin type (Verner 1938, 1955). There is evidence that such a hormone is produced by each actively growing shoot and is transported in basipetal direction causing an increase of crotch angles of branches situated lower on the stem (Jankiewicz 1956, 1961).

The role of natural and synthetic auxin in the mechanism of crotch angle formation is, however, little known. The aim of the present experiment was to throw some light on this problem.

It was shown previously (Jankiewicz 1964) that the mechanism of crotch angle formation is complex. The following factors were recognized to take part in it:

1. Negative geotropism — especially well visible in the first two branches below the decapitation point or below the ring (Münch 1938; Jankiewicz 1964).

2. Geoepinasty i.e. epinasty induced in the branches by prolonged

influence of gravity. Geoepinasty usually counteracts geotropism in plagiotropic growth (Münch 1938; Jankiewicz 1964).

3. A factor which probably is the mechanical pressure generated by the newly-formed tissues situated in the crotch: This pressure acts on the base of a not yet fully lignified lateral shoot and shifts it towards a more horizontal position. (Horsfall and Vinson, 1938; Jankiewicz, 1956, 1964). The true nature of this third factor is not yet definitely established, however, its existence has been proved (Jankiewicz 1964).

There exist an easy method of separating the first and second of these factors from the third one (Jankiewicz, 1964). In branches situated laterally on horizontally placed trees (Fig. 1), negative geo-

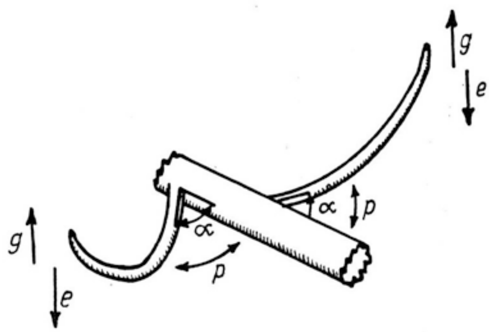

Fig. 1. In horizontally placed trees the angles were measured in horizontal plane The arrow "p" indicates the direction of action of mechanical pressure produced by the tissues situated in the crotch; the arrow "g" shows the direction of geotropic bending; "e" indicates the direction of action of epinasty

tropism and geoepinasty act in vertical plane whereas the mechanical pressure generated by tissues situated in the crotch acts on a branch base in horizontal plane. For this reason the experiment was performed mainly with horizontally placed trees in which the first two buds below the decapitation point were situated laterally. The branches which developed of them were used by the author to establish — what component of the mechanism of crotch angle formation in influenced by auxin.

MATERIAL AND METHODS

The studies were performed in the nursery in the vicinity of Skierniewice in central Poland. The soil was of medium fertility. The experiment was started around April 14-th, at the time of bud swelling. It was ended on May 30-th, at the time when the process of crotch angle formation was almost completed.

Eight combinations of treatments were applied in the spring before growth had started (in their description the term "horizontal trees" will be used instead of "horizontally bent trees" and "vertical trees" instead of "the trees growing in normal, vertical position"):

1. vertical, untreated trees
2. horizontal, otherwise non treated trees; only the laterally situated branches were taken into account, those situated on the upper and under side of the tree being omitted,
3. vertical, decapitated, trees with pure lanolin on the decapitation wound,
4. vertical, decapitated, trees with indoleacetic acid (IAA) paste, on the wound,
5. vertical, decapitated, trees with 2,4D paste on the wound,
6. horizontal, decapitated trees with two first buds below the decapitation point situated laterally; decapitation wound covered with pure lanolin,
7. trees treated as in 6 but with IAA paste, applied,
8. treated as in "6" but with 2,4D paste, applied.

In all decapitated trees only the 2—3 uppermost branches were taken into account. In horizontal or vertical non treated trees the branches analogous to those in decapitated trees were measured.

Auxin pastes consisted of dehydrated lanolin with an admixture of 1% IAA or of 0.15% 2,4D. The cut end of the which was covered with the paste and protected from the light with the aluminum foil.

The angles between the branch and the main axis were measured at the branch base and also at a 5 cm distance from the main axis (Fig. 2). The measurements of branch angles were made with a pro-

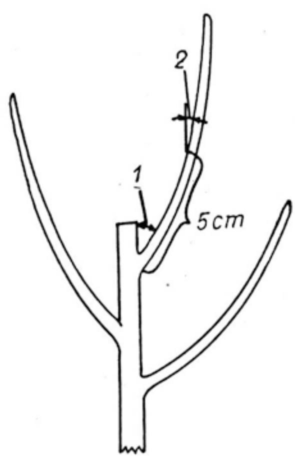

Fig. 2. In vertical trees the branch angle was measured in two places: at the base of a branch *(1)* and at 5 cm apart from the main axis *(2)*

tractor with an accuracy of ±2—4°. In horizontal trees the crotch angles were measured in horizontal plane (Fig. 1). The measurements of shoot length were made with an accuracy of about ±2 mm.

The experiment was set up according to the method of randomized blocks. One tree was a plot. There were 6 blocks (replications). The method of analysis of variance was applied with the "t" test for significance. Two levels of P were used: $P = 0.05$ and $P = 0.01$. The transformations were applied using the formula $x = \sqrt{z+0,5}$, where z denotes leaf number, shoot length or crotch angle.

RESULTS

The branches of vertical, non treated trees formed large angles, usually exceeding 60° on May 30-th (Fig. 3, VN). The branches situated laterally on horizontal non treated trees had also angles exceeding 60°. The branches of both groups of trees were short and had about 7—8 leaves on May 30-th (Fig. 3 *b, c, e, f*). These branches showed only very weak or no geotropism. In general they behaved similarly to the trees investigated previously (J a n k i e w i c z 1964).

In horizontal, decapitated trees with pure lanolin applied, the two uppermost shoots formed very narrow crotches (Figs. 3 a, d, and 5). They formed on the average 26° for the first shoot and 37° for the second, on May 30-th. These shoots showed distinct geotropic curvatures in vertical plane (which were, however, not measured).

Horizontal trees with IAA or 2,4D paste applied on the decapitation wound had wider crotch angles than the trees treated with lanolin only (very significant differences for the first shoot and both auxins on May 10-th, 18-th, and 30-th; very significant differences for the second shoot and both auxins on May 18-th and only for IAA on May 30-th). This shows clearly that the component "p" (see Fig. 1) is influenced by auxins (Figs. 5, 6, 7).

It was characteristic for 2,4D that it influenced powerfully the angle of the first shoot but had only small effect on the angle of the second shoot. Another characteristic feature of 2,4D was that its effect on crotch angles was very strong shortly after repplication i.e. between April 14-th and May 10-th, and much weaker later.

In decapitated horizontal trees there seemed to be some inhibitory influence of the auxin on first shoot growth, however, it was not proved statistically. There was no influence of auxin on the growth of the second shoot. The influence of auxin on leaf formation was not significant.

Vertically growing decapitated trees formed narrow crotch angles

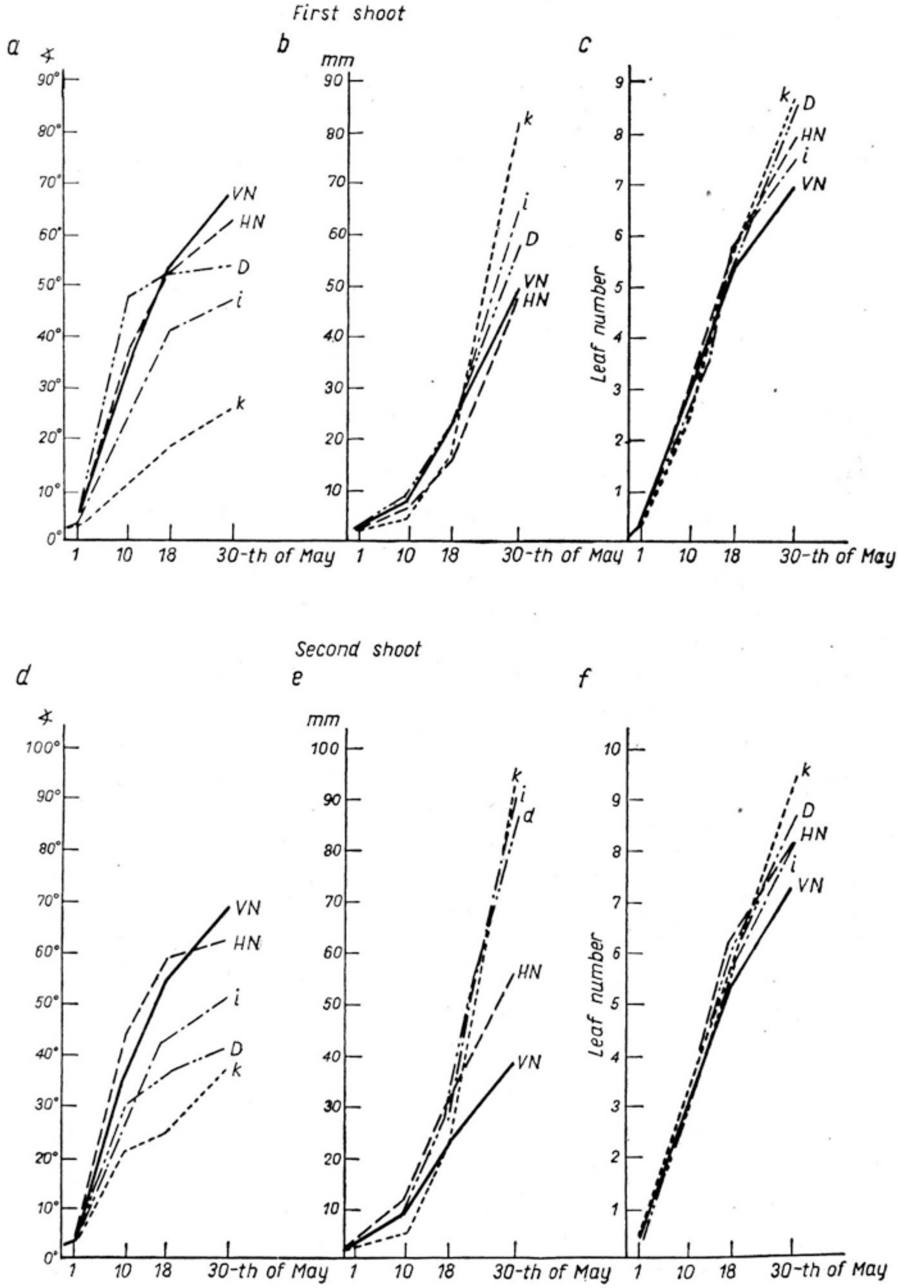

Fig. 3. Crotch angle width *(a, d)*, shoot length *(b, e)*, and leaf number *(c, f)* in the first and in the second shoot of horizontally placed trees. These two shoots were situated on the lateral sides of the tree (see Fig. 2)

k — decapitated trees, decapitation wound covered with pure lanolin; *i* — decapitated, covered with 1% IAA paste; D — decapitated, smeared with 0.15% paste of 2,4D; *HN* — horizontal non decapitated, only laterally situated branches were measured; *VN* — nondecapitated vertically growing control trees are shown for comparison

On the abscissa the dates of measurements.

Table 1

Curvature of a branch expressed as a difference of branch angles measured at the base of a branch and at 5 cm departure from the main axis (see Fig. 2) in vertical decapitated trees

Shoot below decapitation	Decapitated: wounds covered with		
	pure lanolin	IAA paste	2,4D paste
1-st	18.7° +	10.8° +	2.6° + +
2-nd	11.5° +	7.4°	14.0° +
3-rd	5.9°	5.4°	4.8°

* The values marked with one cross differed significantly from the value marked with two crosses.

when the decapitation wound was covered with pure lanolin (Fig. 4 a, d). Application of IAA paste caused an increase of the angle width in both uppermost shoots (very significant differences with lanolin treated trees on May 18-th and 30-th). The paste with 2,4D did not influence significantly the angle of the second shoot. The influence of 2,4D on the first shoot angle was very marked and significant up to May 10-th but on May 30-th the difference between lanolin and 2,4D treated plants was already non significant. Such peculiar behaviour may be partly connected with strong inhibition imposed by 2,4D on the growth of the first shoot (Fig. 4 b). The paste with 2,4D as well as with IAA did not influence significantly the leaf production (Fig. 4 c, f).

The geotropic bending of the branches in vertically growing, decapitated trees was diminished by auxin treatment (Table 1). The difference between the branch angle measured at the base of the branch and at a 5 cm distance from the main axis was used as a measure of geotropic bending. Indoleacetic acid paste seemed to diminish the geotropic bending of the first two uppermost branches (non significant differences), whereas 2,4D influenced significantly only the first branch. There was no influence of auxins on geotropic bending of the third and further branches.

DISCUSSION

The results presented show that the influence of auxins on crotch angle formation is two-directional, on the one hand the auxins act on the geotropism and geoepinasty of a branch in such a way that negative geotropism diminishes. On the other hand auxins influence the "third factor" which is probably the mechanical pressure exerted on a branch base by the tissues situated in the crotch.

The effect of exogenously applied auxins on geotropism was noted by several authors (K a l d e w e y 1962). Auxin, when given in high

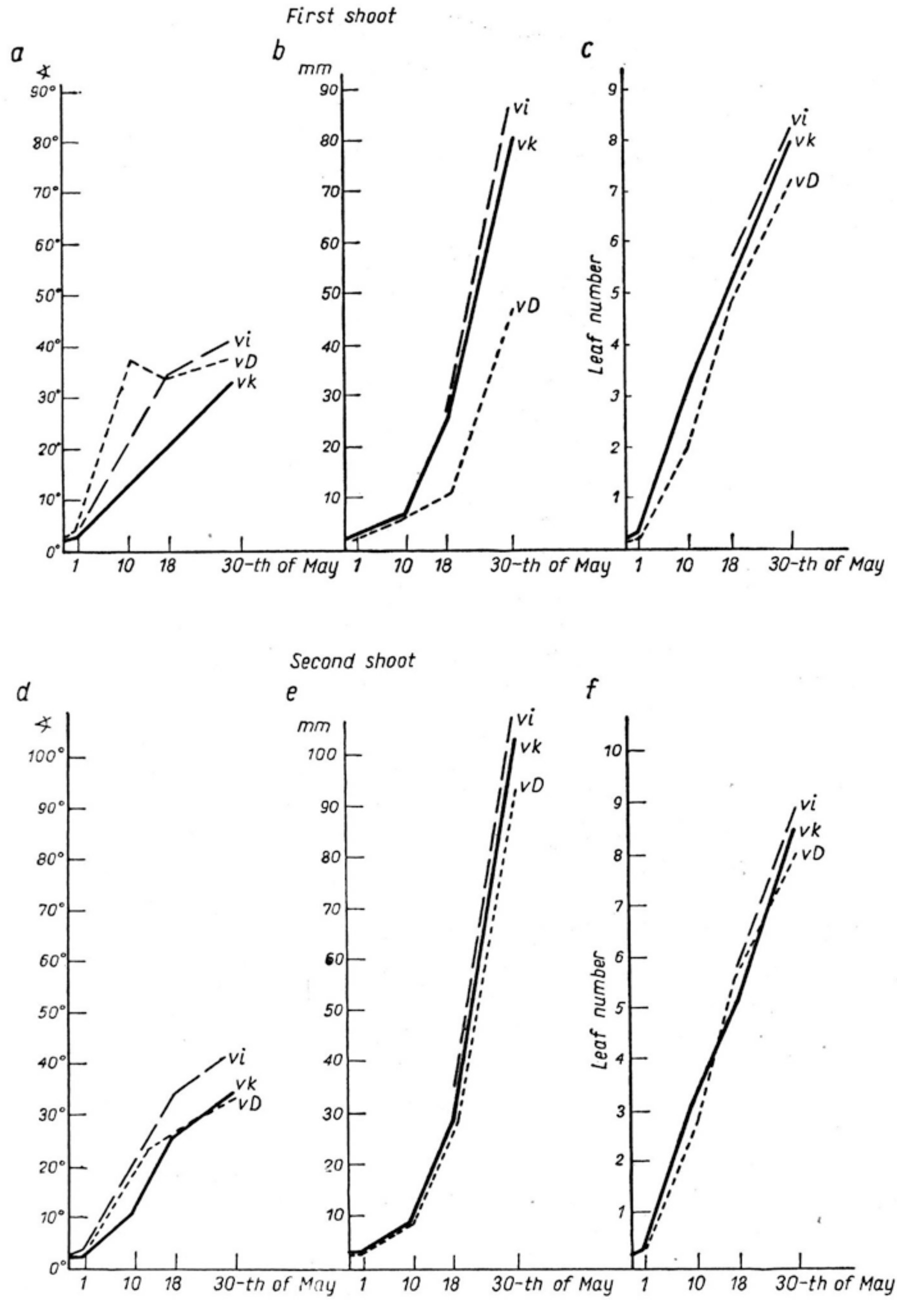

Fig. 4. Crotch angle width (*a, d*), shoot length (*b, e*) and leaf number (*c, f*) in the first and second shoot of decapitated, vertically growing trees. Decapitation wound covered with:

vk — pure lanolin; *vi* — lanolin paste with 1% IAA; *vD* — 0.15% 2,4D paste

On the abscissa the dates of measurements

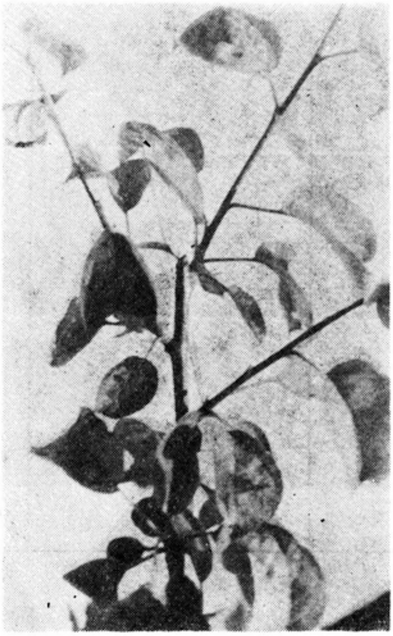

Fig. 5. Horizontally placed, decapitated tree photographed from above. Decapitation wound covered with pure lanolin. Note narrow angles of the first and the second branches

concentration or when transported in transpiration stream (Leike 1962) tends to diminish negageotropic reaction. Our results seem to be in agreement with those findings.

The effect of auxins on the mechanical pressure exerted on a lateral branch by the tissues situated in the crotch seems very probable in the light of recent publications. Auxin, especially in combination with other growth regulators like gibberellins or cytokinins stimulates very markedly the activity of cambium (Wareing et al. 1964; Digby and Wareing 1966; Pieniążek and Jankiewicz 1966, 1967; Pieniążek and Saniewski 1968). The new tissues produced by cambium of a young shoot may generate considerable pressure directed outward, which may deviate the branch base. In pines such pressure exceedes 0,5 kg/cm² (Jankiewicz and Stępień — in press).

The effect of 2,4D was very distinct in the first shoot but not in the second. This may be considered as a result of weak transport or of quick inactivation of this compound in the apple tissues. The data found in the literature do not support fully this supposition. Day (1952) demonstrated that 2,4D moved in the bean phloem rather fast 10—100 cm per hour but the movement from outside the epidermis into the phloem was only some microns per hour. Batjer and Thompson (1946)

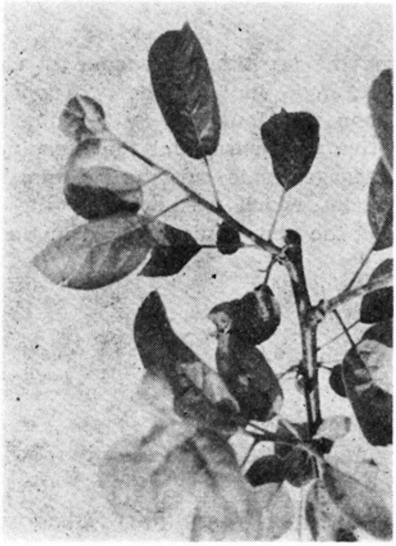

Fig. 6. IAA paste on decapitation wound caused increase of crotch angles (horizontally placed tree photographed from above)

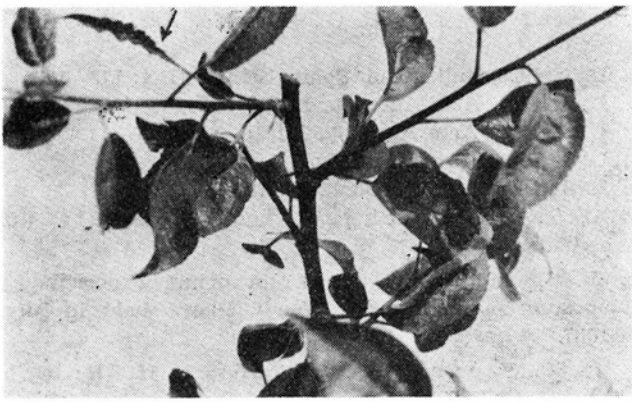

Fig. 7. Paste containing 2,4D caused also marked increase of crotch angles but sometimes evoked also characteristic leaf deformations (shown by arrow)

found that 2,4D was ineffective as a spray preventing preharvest drop of McIntosh apples. Although this compound injected into the McIntosh branches gave marked and long-persisting effect.

Further experiments are under way to elucidate the mechanism of crotch angle formation in apple trees and in other woody species.

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SUMMARY

Auxin paste applied on the decapitation wound of a young apple tree caused a marked increase of crotch angle width of the two uppermost branches. The role of auxin in this phenomenon was found to be two-directional. On the one hand the auxin influenced negative geotropism and the geoepinastic reaction of a shoot in such a way that the negageotropic curvature diminished. On the other hand auxin increased another factor which was probably the mechanical pressure exerted on the branch base by the new tissues formed in the crotch by cambium.

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Mechanizm formowania się kątów rozwidleń jabłoni

II. Badania nad rolą auksyn

Streszczenie

Jeśli zastosuje się pastę z auksynami na zdekapitowany wierzchołek jednorocznego drzewa jabłoni, kąty rozwidlenia dwóch najwyższych gałązek zwiększą się znacznie. Wykazano, że rola auksyn w tym zjawisku jest dwukierunkowa. Z jednej strony auksyna wpływa na ujemny geotropizm pędu i na jego reakcję geopinastyczną w taki sposób, że skrzywienie geotropijne się zmniejsza. Z drugiej strony wykazano, że auksyna wpływa na inny czynnik, którym jest prawdopodobnie mechaniczne ciśnienie wywierane na podstawę gałązki przez tkanki nowo utworzone przez kambium w rozwidleniu.