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The influence of gravity on bud development in apple trees and in poplars

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Abstract

The lower shoots in horizontally placed apple trees exhibited much weaker development as well in light as darkness. Removing a narrow strip of bark along both sides of a horizontally placed apple tree improved markedly the growth of the lower buds. In poplars the same effect was received by surrounding the lower buds with semicircular incisions. The inhibition of the lower buds was also released by removing the apical bud and the upper ones. The presented results and those published earlier show that the mechanism responsible for inhibition of the lower buds acts in two steps: 1) gravity influences directly the system composed of a bud and the adjacent tissue of the stem, 2) the lower buds partly inhibited in the step „1" are further inhibited by a correlative mechanism which supresses all weaker buds. The second „step" reaction takes place also after a tree have been reverted back to the normal vertical position.

INTRODUCTION

It is well known that the shoots of several woody plants inclined to the horizontal position show asymmetrical lateral growth on the upper and lower sides. The buds on the upper side grow much more vigorously, than those on the under side. Several authors claime that such differential growth is mainly the result of gravity action on plant morphogenesis (Wareing and Nasr 1958, 1961; Jankiewicz 1964, 1971; Borkowska 1966; Longman 1968). The phenomenon was called gravimorphism (Wareing and Nasr 1958).

This claim was confirmed by Smith and Wareing (1964 a) who reported that asymmetric lateral growth of horizontally placed willow shoots takes place also in complete darkness. It seemed necessary, however, to repeat horizontal treatment in the dark with apple trees, to have one more piece of evidence of this kind for a species which is much less sensitive to gravity than willow.

It was found by Mullins (1965) that in a horizontally placed apple tree the buds situated on the underside are inhibited due to the influence of upper shoots and buds. The results of Smith and Wareing (1964 a, b) on the other hand, have shown that the inhibition of the lower willow buds occurs also when the influence of the upper buds is eliminated.

The aim of our work was to elucidate this discrepancy of views with experiments on apple trees and poplars (*Salicaeae*), which differ markedly with their sensitivity to gravity stimulus.

MATERIAL AND METHODS

Part of the experiments were performed in the nurseries in Skierniewice and in Prusy near Skierniewice (Central Poland). The trees in the nurseries were growing on pseudopodsolic loamy sand, well fertilized. Some experiments were done in a greenhouse and in growth chambers on trees planted in 12 liter pails using a mixture of compost soil + washed medium sand + limed peat (4 : 1 : 2). The chilling requirements of trees were satisfied. The experiments were set up in randomized blocks using 6—7 replicates (blocks). There was one tree per plot. In most cases the results were worked out statistically with analysis of variance using the "t" or Duncan's test for significance.

RESULTS

1. Gravimorphic reaction of apple trees in darkness

Seven one-year old trees of the 'Starking' variety growing in pails were placed in a dark room in a horizontal position at the time of bud breaking. They were watered daily without changing their position, and kept for 17 days in a complete darkness in the temperature 15° ±1.5°C. After that time the apical group of 10—16 shoots was measured on each tree. The shoots situated further toward the base were not measured since their development was irregular, and they often did not develop.

The shoots which developed were yellow—white and showed typical symptoms of etiolations (Fig. 1). The results of measurements (Fig. 2) show that differential growth of buds takes place in darkness. In the trees grown in darkness the shoots on the underside had average only $^1/_5$ of the length of the upper shoots. In addition the lower shoots and buds show-

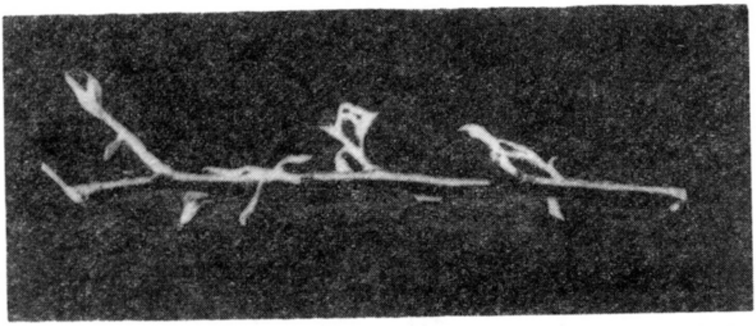

Fig. 1. Asymmetrical shoot development in darkness on a horizontally placed apple tree

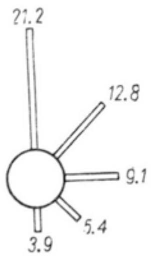

Fig. 2. Average length (in mm) of shoots depending on their position on an apple tree placed horizontally in darkness

ed a tendency to be shed off. On average 71% of the lower shoots and 43% of the semilower ones were shed off at the end of dark treatment or just after transfering the trees into light. Among upper and semiupper shoots none were shed off. Laterally situated shoots were shed off in 18% only.

2. Inhibition of lower shoots by the upper ones in horizontally placed apple trees

Trees of cv. Piękna z Rept grown in the nursery in Skierniewice were used. The experiment was set up in 7 randomized blocks on April 29, that is at bud bursting time. The treatments are presented in Fig. 3. The trees were measured periodically during their growth. The results of the last measurements on June 4 are shown in Fig. 4.

The trees of cv. Piękna z Rept were growing very vigorously. The horizontally bent trees, not otherwise treated (Fig. 4 *d*) showed weak shoot growth on their lower side. This inhibition was, however, significantly diminished when a strip of bark was removed along both lateral flanks of the tree (Fig. 4 *e*, *f*), showing that uninjured bark was important for the transport of inhibiting factor from the upper to the lower shoots.

The upper shoots in all horizontally treated trees (treatment *d*, *e*, *f*)

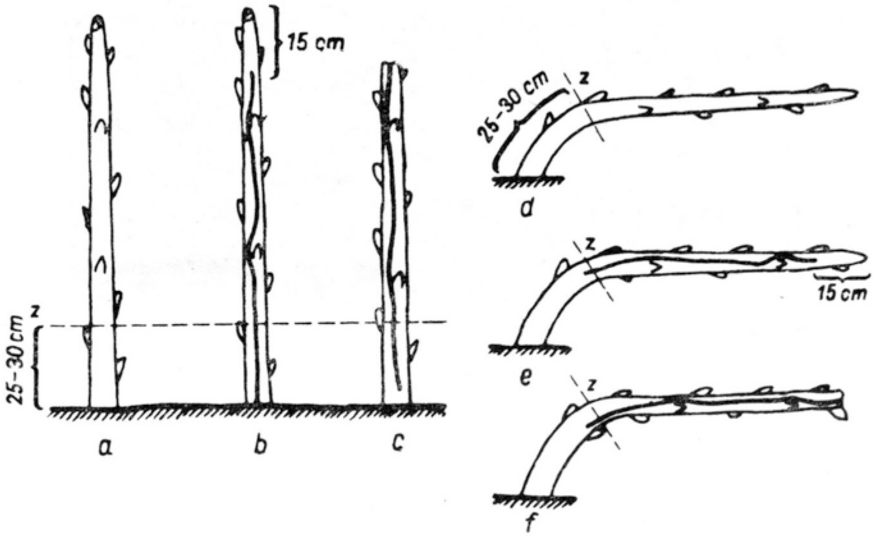

Fig. 3. Treatments applied to apple trees:
a — untreated, vertical — control; *b* — strips of bark were removed along two sides of a vertical tree, leaving the tip intact; *c* — decapitated, vertical tree — strips of bark removed; *d* — horizontal — control; *e*—*f* — treated as *b* and *c* but horizontally bent. Strips removed on both lateral flanks.
In all trees the basal part below the line "z" was not taken into account

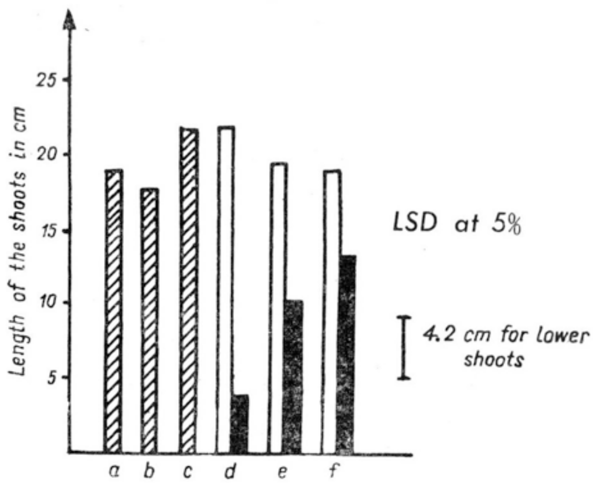

Fig. 4. Effect of treatment, shown in Fig. 3 on apple shoot length; cv. Piękna z Rept (measured on June 4)
White columns — upper shoots of horizontal trees. Black columns — lower shoots of horizontal trees. Hatched columns — shoots of vertical trees; LSD at 5%

did not differ significantly. In vertically growing trees the shoots of controls (treatment *a*) did not differ significantly from the shoots of both groups of vertical trees with the strips of bark removed (*b* and *c*).

This experiment was repeated a year later with Wealthy trees. Besides the treatments shown in Fig. 3 a treatment "*g*" similar to that applied earlier by Mullins (1965) was added: horizontal trees were split in a horizontal plane into two halves and impermeable plastic sheet

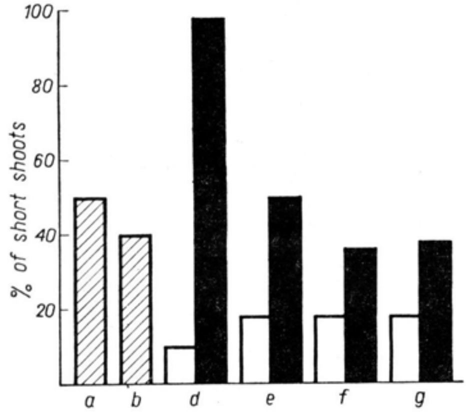

Fig. 5. Effect of treatments shown in Fig. 3 on the percent of inhibited shoots — less than 3.5 cm long, cv. Wealthy

In an additional treatment "g" an impermeable plastic sheet was inserted between the upper and lower sides of the longitudinally split tree. Columns as in Fig. 4.

was inserted between them. The results (Fig. 5) show that splitting the trees with insertion of impermeable sheet as well as removing the strips of bark along both sides of the tree, drastically reduced the inhibition of lower buds. The effect of both these treatments was similar (compare treatments "*f*" and "*g*" in Fig. 5).

Table 1

The influence of removing the leader and/or the upper buds on the development of lower buds, in horizontally placed 'Wealthy' trees. Vertically growing trees added for comparison

Position of the tree	Leader *	Upper buds *	Average number of spurs per 10 shoots
Vertical	+		5.6 a**
Vertical	—		4.8 a
Horizontal	+	+	10.0 b
Horizontal	+	—	9.8 b
Horizontal	—	+	10.0 b
Horizontal	—	—	5.4 a

* present: +; removed: —.

** The numbers marked with different letters differ significantly at P = 0.05. Duncan's test was used for significance.

In another experiment Wealthy trees growing in the nursery were partly debudded, at bud bursting time. Part of them was also decapitated. The results presented in Table 1 show, that when either the leader and/or upper shoots were left intact in horizontally placed trees almost all buds on the lower side were inhibited and formed only the spurs shorter than 3.5 cm. When both the leader and the upper shoots were removed, about half of the lower buds grew vigorously. In vertical decapitated and non decapitated trees about half of the shoots were inhibited.

3. Gravimorphism in poplar trees

Poplar hybrid No. 277 (Schneider and Stout 1934) growing in pails were taken into a heated greenhouse, in early March. After a few days when their buds started to swell, they were put into a horizontal position for 1 or 4 days. In half of the trees horizontally treated for 4 days a semicircular strip of bark was removed around each bud on the lower side (Fig. 6). After horizontal treatment finished, the trees were

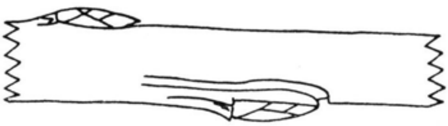

Fig. 6. Semicircular bark incision around a lower bud in a poplar tree

returned to a normal vertical position. The control trees were standing all the time in a normal, vertical position, half of them were left intact and the other half had semicircular incisions around the buds on the one side. There were 5 replicates (single tree) arranged in randomized blocks.

The results (Fig. 7) show, that 24 hours of horizontal treatment was not sufficient to evoke any gravimorphic effect, but 4 days treatment caused marked subsequent inhibition of the shoots growing on the previously lower side. The differences in the length between previously upper and previously lower shoots increased with time up to May 5, when the experiment ended. Apical dominance was seen in all non incised trees: the shoots in the basal half of these trees were growing less than those in the apical half. In horizontally placed trees the semicircular incisions around the lower buds abolished completely their gravity induced inhibition: they were growing as well or even better than the upper buds. The incisions also abolished the effect of apical dominance: the basal buds surrounded by incisions were growing better than the apical ones (treatment E). In vertical trees the buds surrounded with incisions became dominant over the intact ones and did not exhibit any influence of apical dominance.

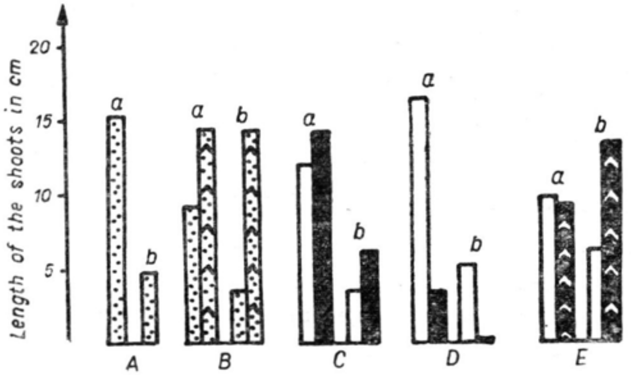

Fig. 7. Shoot length in one-year old poplar trees as affected by the following treatments:
A — vertical, control trees; B — vertical with semicircular incisions around all buds on one side; C, D — kept for 1 day (C) or 4 days (D) in horizontal position at bud bursting time; E — like D but with semicircular incisions around all lower buds
a — apical, b — basal shoots
columns: dotted — shoots of the trees kept all the time vertically
white or black — shoots which were respectively upper or lower during horizontal treatment
angles semicircular incisions around the buds as in Fig. 6.

This experiment was repeated with the same poplar cultivar and in similar conditions during the second spring. The results were similar: the semicircular incisions around the lower buds completely removed their inhibition causing the previously upper and lower buds to grow equally well. Incisions around the upper buds had no effect on their growth.

DISCUSSION

The claim that gravity causes the differential growth of the upper and lower shoots in horizontally placed trees is based among others on the observation of Smith and Wareing (1964 a) that lower buds on horizontal trees are inhibited as well in light as in darkness. That experiment was done by Smith and Wareing only with willow trees. Our experiment with apple trees fully confirmed the results of those authors. Shedding of portion of lower and semilower buds and shoots in horizontally placed dark grown apple trees might be caused by the exhaustion of sugar reserves or by the accumulation of ethylene on the lower side of the shoots (Galston, see Jankiewicz 1971).

In Mullins (1965) experiment separating the lower buds from the influence of the upper ones by splitting the trees longitudinally and inserting the impermeable barrier between the two halves caused marked allevation of the inhibition of the lower buds. Our results confirmed fully those of Mullins, and in addition showed that the hypothetical factor which inhibits the lower buds moves in the bark, because removing the strip of bark along both flanks of horizontal tree caused an effect similar to splitting the tree and inserting an impermeable barrier.

Further confirmation of Mullins' claim came from the experiments with poplars: semicircular incisions around the lower buds completely prevented their inhibition by 4 days of horizontal treatment. This results does not support the finding of Smith and Wareing (1964 a, b) obtained with willow in which the separation of the lower buds from the influence of upper ones did not prevent their inhibition. These authors used, however, different plant material: cuttings without roots, and they applied long lasting horizontal treatment.

Removing upper and lateral buds in horizontally placed willow cuttings did not release the lower buds from inhibition in Smith and Wareing (1964) experiment. Such treatment, however, gave a completely different results in our experiment with apple trees. If only lower buds were left on a tree their growth was much better than in the case when the other buds remained intact.

Taking into consideration the result presented in this paper as well as the results of the other authors we proposed the following "two steps" model of gravimorphic reaction in trees:

1. Gravity acts directly on a system composed of a bud and the immediately adjacent tissues. When the bud is on the underside of the stem it is partly inhibited. The existance of this step is shown in the experiments of Smith and Wareing (1964 a, b), and of Borkowska (1969) who applied in vitro culture of apple and poplar stem sections having a single bud.

2. The buds which are partly inhibited by the mechanism involved in the step "1" are further inhibited by a normal correlative mechanism of a tree. This mechanism (Jankiewicz, 1972) inhibits in apple trees all the smaller buds or the buds weakened for whatever reason. As it was shown by Borkowska (1966) and by Jankiewicz et al. (1967) the correlative mechanism of a tree is inhibiting the previously lower shoots further also after reverting a tree back to a normal, vertical position.

This "two step" model of gravimorphic reaction makes easier understanding the seemingly contradictory facts reported by different authors. In willow cuttings which are very sensitive to gravity (Smith and Wareing 1964) the "first step" reaction was probably so strong, that the "second step" was completely masked. Our experiments, however, with short time horizontal treatment of poplar — the other species very sensitive to gravity, belonging to *Salicaceae* — have shown evidently the existance also of the "second correlative step" in this plant material.

The treatment applied by Mullins (1965) permitted only to make evident the "second correlative step", however, Borkowska (1969) revealed in the same plant material — the apple shoots, the "first step" reaction: direct gravity induced inhibition of a single bud cultured with a stem section.

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Wpływ grawitacji na rozwój pąków jabłoni i topoli

Streszczenie

Badano przyczyny silniejszego wzrostu pędów na górnej stronie poziomo ułożonych drzewek jabłoni i topoli.

Drzewka umieszczone poziomo wykazywały silniejszy wzrost pędów znajdujących się po górnej stronie, nie tylko na świetle, ale i w ciemności, co wskazuje, że światło nie ma wpływu na zjawisko asymetrycznego wzrostu (Fig. 2).

Wykazano poza tym, że pędy górne wpływają hamująco na wzrost pędów dolnych. Oddzielenie pąków dolnych od górnych przez wycięcie wąskiego paska łyka po obu stronach drzewka poziomego, powodowało, że pąki dolne rosły znacznie silniej niż u drzewek poziomych, kontrolnych. Podobny wpływ miało przecięcie drzewek wzdłuż i umieszczenie nieprzepuszczalnej przegrody między górną i dolną częścią drzewka. Również usunięcie pąków górnych i pąka szczytowego znacznie zmniejszało zahamowanie pąków dolnych (Fig. 4 i 5).

Wysunięto hipotezę, że mechanizm powodujący zahamowanie pąków dolnych u drzewek umieszczonych poziomo jest dwustopniowy:

1. grawitacja działa bezpośrednio na system złożony z pąka i przyległych do niego tkanek łodygi — jeśli pąk znajduje się po dolnej stronie łodygi, zostaje częściowo zahamowany.

2. pąki dolne osłabione w pierwszym etapie, są dalej osłabiane przez mechanizm korelatywnego hamowania, nastawiony na zahamowanie wszystkich słabszych pąków.

Etap drugi przebiega nawet po ustawieniu drzewek w normalnej pozycji pionowej.