

## ON A GEO-GROWTH REACTION OF THE AVENA COLEOPTILE

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(received October 8th, 1960)

### INTRODUCTION

In several investigations, particularly in those from the period before the discovery of the auxins, the question has been raised whether the rate of growth of an organ is influenced by its position with regard to the direction of the gravitational force. Is there any measurable difference between the straight growth of an organ in the normal position and that shown on the horizontal clinostat or in the inverse position? HERING (1904) observed that plants which were kept continuously in the inverse position, prematurely end the grand period of growth. BREMEKAMP (1912) noticed that stems of *Pharbitis*, placed alternately for 24 hours in the normal and in the inverse position, show a reduction of their growth in the latter position.

As to the effect on the growth exercised by a rotation on the clinostat, the results are less uniform. Exact measurements made by KONINGSBERGER (1922) with his auxanometer revealed that the transfer of vertical *Avena* seedlings to the clinostat caused a decrease of the growth rate whereas the seedlings showed an increased growth when they were taken from the horizontal clinostat and were put vertical. BREMEKAMP (1925) and DOLK (1930, 1936) who in principle obtained the same results, are of opinion that all the seemingly growth accelerations and retardations in reality are due to dorsoventral curvatures of the seedlings. In view of the smallness of the gold plate of the auxanometer, however, the obscuring action of dorsoventral curvatures has been overestimated. They may have accounted for maximally 0.01 percent of the observed effects on the growth rate.

BARA (1957), on the other hand, found an acceleration of the growth of coleoptiles on the horizontal clinostat. Since the speed of revolution of his clinostat was much higher than that of Koningsberger's, this factor may have caused the opposite result. From LARSEN's (1953) investigation with *Artemisia* roots we have learned that the speed of revolution of the clinostat may indeed be regarded as a possible cause of contrasting results.

Another obvious comparison was that of the increase in length of a horizontal plant which carries out a geotropic curvature, with that of an upright one which remains straight. According to SACHS (1872), CHOŁODNY (1929) and NAVEZ and ROBINSON (1933) there would be no difference.

DE WIT (1957) compared the rate of curvature of horizontal coleoptiles with that of the back curvature after an opposite geo-induction. He found that the straightening out, followed by a curvature in the opposite direction, is faster than the forwards curvature. The question arises whether the higher rate of back curvature was due to an extra fast growth of the new convex side or to an extra slow growth of the new concave side, or to both. This question, though not studied as such, gave rise to the present investigation, which is concerned with the growth rate of curving and straight-growing coleoptiles in different positions, and in auxin solutions of different concentration.

The main result was that under the conditions of the experiment the geo-growth reaction of the *Avena* coleoptile consists in a reduction of the growth rate in the horizontal position, which is explained by a decreased rate of auxin transport.

#### MATERIAL AND METHODS

The investigation was carried out with isolated coleoptiles from which the primary leaf had been pulled out, and which had all been cut to the same length, viz. of 19 mm. Of these sections the growth rate was studied. The control coleoptiles remained in the normal vertical position, whereas the test plants were treated in one of the following ways:

*Treatment A.* After the determination of the initial length to tenths of a millimeter, the coleoptiles were placed in a horizontal position. When the geotropic curvature had attained a value between 25 and 35 degrees, the coleoptiles were turned over 180 degrees. On account of the opposite geo-induction received now in the second horizontal position, the coleoptiles straightened out and began to curve in the opposite direction. When the curvatures in the new direction had attained 10 to 20 degrees, the coleoptiles were turned again over 180 degrees and thus brought back in the first horizontal position. As soon as the greater part of the 12 coleoptiles used in one experiment, had straightened out their second curvature, the other coleoptiles which had not yet done so, were smoothly straightened (not stretched) by finger, and the length was compared with that of the controls. The duration of the experiment was  $5\frac{1}{2}$ -7 hours.

*Treatment B.* After the determination of the initial length the coleoptiles were placed in a horizontal position. However, in contrast to treatment A, the coleoptiles were prevented from curving geotropically by reversing them every ten minutes. After four hours their length was compared with that of controls which had remained in the normal vertical position during the experimental period.

The first part of the investigation was carried out with non-decapitated coleoptiles in tap water, whereas in the second part the effect was studied with decapitated coleoptiles (2 mm removed) in solutions of indoleacetic acid (IAA) of different strength.

Detailed descriptions of the method and of the apparatus used in

the experiments have been given in previous publications, more especially in ANKER (1954).

### RESULTS AND DISCUSSION

The results have been summarized in the Table, which shows in the first place that intact coleoptiles (tip not removed) attain the greatest length in the normal, vertical position; in the second place that it is *not* the bending which reduces the growth of horizontal coleoptiles, since the reduction caused by treatment B was even slightly more pronounced than that caused by treatment A; finally that in decapitated coleoptiles an inhibition of the same magnitude is present in the 0.05 mg/l IAA solution, but that it is absent in the 0.1 mg/l IAA solution.

TABLE  
Comparison of the growth of vertical and horizontal coleoptiles

Col. tip	IAA concentr. in mg/l	Treatment	Growth in mm/100		Mean inhibition
			control col.	treated col.	
Present	0	A	168 ± 8	150 ± 6	
„	0	A	190 ± 7	167 ± 9	
„	0	A	273 ± 7	221 ± 9	17 %
„	0	A	477 ± 20	385 ± 10	
„	0	A	274 ± 16	222 ± 15	
Present	0	B	133 ± 8	105 ± 6	
„	0	B	160 ± 3	113 ± 3	21 %
„	0	B	197 ± 9	169 ± 7	
Removed	0.1	A	260 ± 13	269 ± 12	
„	0.1	A	304 ± 15	292 ± 15	0 %
„	0.1	A	265 ± 15	266 ± 15	
Removed	0.2	B	284 ± 9	291 ± 9	
„	0.1	B	292 ± 13	297 ± 15	— 2 %
„	0.1	B	268 ± 9	273 ± 6	
Removed	0.05	B	243 ± 8	205 ± 8	
„	0.05	B	217 ± 14	205 ± 10	
„	0.05	B	206 ± 12	173 ± 10	14 %
„	0.05	B	227 ± 8	187 ± 8	

The explanation of the above effect of gravity is not easy, since growth may be influenced in many ways. However, it seems improbable that the inhibition was caused by a decreased auxin production, as the same reduction of growth was observed with decapitated coleoptiles in the 0.05 mg/l IAA solution, in which the vertical and horizontal coleoptiles were supplied with the same quantity of auxin. As a matter of fact, in those instances reported in literature where a change of the auxin production was really found, the lateral action of gravity always caused a stimulation in stead of an inhibition of the auxin production (SCHMITZ, 1933; VAN OVERBEEK *et al.* 1944).

It is further not likely that a change of the reactivity or the sensitivity of the tissue to auxin was involved, since in that case a reduction of the growth should have occurred at both IAA concentrations, since the 0.1 mg/l concentration is still sub-optimal for the growth. For the same reason the idea of a production of growth inhibiting substances may be disregarded.

Finally the inhibition of the growth by gravity could have been effected by a decrease of the rate or the intensity of the transport of auxin; if auxin is added in limiting concentrations, as was done here, a slowing down of the speed of transport must be followed by a decreased rate of growth. With this mechanism the inhibition of intact coleoptiles and that of decapitated ones at the 0.05 mg/l IAA solution can be explained, but the absence of any geo-growth reaction at the 0.1 mg/l IAA concentration, which is still suboptimal (ANKER, 1956), seems to come in conflict with this explanation.

From previous investigations (ANKER, 1956; DE WIT, 1957), we know that IAA permeates through the cuticle, but that in short-lasting experiments (75 minutes) the growth of intact coleoptiles submersed in a 0.1 mg/l IAA solution is not yet measurably influenced. At slightly higher concentrations it is. The possibility, therefore, was investigated, whether in the present, relatively long-lasting experiments, a penetration of IAA from the 0.1 mg/l solution through the cuticle could have obscured effects due to differences in the auxin transport from the cut surface to the base. In three separate experiments of 4½, 5½ and 6 hours duration an increase of the growth was indeed observed; the growth in the IAA solution proved to be 19, 25 and 21 percent respectively higher than that of the controls in water. By this result a serious objection against the idea of a gravity-controlled rate of auxin transport has been removed. As in the earlier experiments of ANKER (1956) and DE WIT (1957), this stimulation was not yet visible after an immersion of 75 minutes.

Measurements of small differences in auxin transport are extremely difficult. They were carried out by PFAELTZER (1934), who obtained variable results, and by VAN DER WEY (1932), whose results provide some support to the transport hypothesis, as a slight decrease of the auxin transport was observed with the *Avena* coleoptile in the inverse position. However, we are in need of a direct proof that gravity affects the auxin transport, as several gravity-induced phenomena are easily explainable by this mechanism. Among the latter are the geo-growth reactions of the *Avena* seedling studied by KONINGSBERGER (1922). The present investigation carried out with relatively small, isolated coleoptile sections, in which dorsoventral curvatures are absent, confirms the results of Koningsberger, and supports the correctness of his interpretation.

The possibility to explain other phenomena by a gravity-controlled rate of auxin transport has been discussed in the Chapter "Orthogeotropism in shoots and coleoptiles" in: Encyclopedia of Plant Physiology Vol. 17II, yet to appear.

## SUMMARY

The growth of *Avena* coleoptiles during a period of 5½–7 hours in which they carry out two geotropic curvatures (in opposite directions), and finally are allowed to straighten out, remains behind that of coleoptiles in the normal vertical position. This is true for non-decapitated coleoptiles in water, and for decapitated ones in a 0.05 mg/l IAA solution.

The decreased growth of curving coleoptiles is not due to the bending, since the same reduction is observed when horizontal coleoptiles are prevented from curving geotropically by reversing them every ten minutes.

The above retardation was not found in the 0.1 mg/l IAA solution.

A gravity-induced decrease of the auxin transport is proposed as a possible explanation of the retarded growth of horizontal coleoptiles.

## ACKNOWLEDGEMENT

The author wishes to express his indebtedness to Prof. Dr. V. J. Koningsberger and to Dr. H. P. Bottelier for many stimulating discussions.

## REFERENCES

- ANKER, L. 1954. Proc. Kon. Ned. Ak. Wet. C **57**: 304–316.  
———. 1956. Acta bot. neerl. **5**: 335–341.  
———. Encyclopedia of Plant Physiology 17ii (yet to appear).  
BARA, M. 1957. Rev. Fac. Sc. Univ. Istanbul B **22**: 209–238.  
BREMELAMP, C. E. B. 1912. Rec. trav. bot. neérl. **9**: 281–381.  
———. 1925. Ber. dtsh. bot. Ges. **43**: 159–165.  
CHOLODNY, N. 1929. Planta **7**: 702–719.  
DOLK, H. E. 1936. Rec. trav. bot. neérl. **33**: 509–585.  
HERING, G. 1904. Jb. wiss. Bot. **40**: 499–562.  
KONINGSBERGER, V. J. 1922. Rec. trav. bot. neérl. **19**: 1–136.  
LARSEN, P. 1953. Physiol. Plantarum **6**: 735–774.  
NAVEZ, A. E. and T. W. ROBINSON. 1933. J. gen. Physiol. **16**: 133–145.  
OVERBEEK, J. VAN, G. D. OLIVO and E. M. S. DE VASQUES. 1944. Bot. Gaz. **106**: 440–451.  
PFAELTZER, J. W. 1934. Diss. Utrecht (in dutch).  
SACHS, J. 1872. Arb. bot. Inst. Wurzburg **1**: 193–208.  
SCHMITZ, H. 1933. Planta **19**: 614–635.  
WEY, H. G. VAN DER. 1932. Rec. trav. bot. neérl. **29**: 379–496.  
WIT, J. L. DE. 1957. Acta Bot. Neerl. **6**: 1–45.