THE CIRCUMNUTATION OF THE AVENA COLEOPTILE, ITS AUTONOMOUS NATURE AND ITS INTERFERENCE WITH THE GEOTROPIC REACTION

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SUMMARY

The circumnutation of intact and decapitated *Avena* coleoptiles is not influenced by indole-acetic acid in whatever concentration it is added. This supports the hypothesis that circumnutation is a purely autonomous movement, unconnected with geotropism.

The nutative movements inconveniently interfere with induced movements. A way of dealing with them when determining a geotropic curvature is discussed on the basis of relevant data.

1. THE CIRCUMNUTATION

The growth of grass seedlings is not rectilinear. Shadowgraphs made at intervals of growing coleoptiles reveal that slight oscillating movements are carried out during the elongation. From investigations by ARNAL (1953) and JOERRENS (1959) we know that the tip describes an irregular spiral. This way of growing is called circumnutation.

The present paper is a contribution to the discussion on the nature of the circumnutation. The evidence obtained is in favour of the hypothesis that it is an autonomous movement. The alternative view, the so-called "geotropic hunting theory" (see further on), which describes nutations as corrective *geotropic* reactions, cannot apply to the *Avena* coleoptile since the circumnutation is insensitive to auxin addition, whereas the geotropic reaction is highly sensitive to the auxin concentration.

2. METHODS

The method of cultivating the *Avena* seedlings as well as their preparation for the experimentation has been described in ANKER (1971). The experiments were performed with 18 mm sections submersed in IAA solutions. The sections comprised the apical part of the coleoptile. In case of decapitation a tip of exactly 1 mm was cut off in advance. The nutational movements were measured on shadowgraphs made of the sections at intervals of one hour. The sections were arranged in such a way that the oscillations carried out in the plane through the vascular bundles were recorded.

The data presented here have been taken from experiments on straight growth (ANKER 1971). Coleoptiles used for that purpose are always selected on account of their straightness. Perfect straightness is an exception because of the nutations.

In *tables 1* and *2* coleoptiles were included that had a relatively large initial curvature. Some of them accomplished a complete swing in the course of the experiment. Others were straight or nearly so at the beginning.

On account of the irregularity of the movements it did not seem necessary to give more than two examples per concentration. For the same reason a determination of the average period of the circumnutation was impossible. In this respect the oat sections conform to similar sections of wheat coleoptiles (JOERRENS 1959).

3. RESULTS AND DISCUSSION

ARNAL (1953) defends the hypothesis that the circumnutation of the wheat coleoptile is due to periodical variations of the release of auxin from the tip. JOERRENS (1959), on the other hand, is of the opinion that the elongating cells' sensitivity to auxin changes periodically.

At first sight it seems possible to solve this controversy in the following way: remove the tip and check up whether the remaining stump, if externally supplied with auxin, still nutates or now grows rectilinearly. The latter experiment has been carried out by Joerrens. She administered a paste with 0.2% IAA to the cut surface and found that the nutations continued for at least 20 hours. This result, together with additional observations, strongly support her hypothesis that the cause of the nutations is localized in the zone of elongation and not in the tip.

Arnal (personal communication to Baillaud) and BAILLAUD (1962), however, remark that the IAA concentration in Joerrens' experiments was high and that the movements deviated from the normal "spontaneous" circumnutation.

To test the possibility that the irregular movements observed by Joerrens were actually caused by the abnormally high IAA concentration, similar experiments are needed with decapitated coleoptiles supplied with IAA in physiological concentrations.

The present author had at his disposal a large amount of shadowgraphs of decapitated coleoptiles growing in both diluted and concentrated solutions of IAA. The growth system of the decapitated coleoptiles was already saturated in a solution of 0.2 mm/l IAA, that of intact coleoptiles at 5 mg/l IAA.

As is shown by *tables 1* and *2*, the oscillations were independent of the IAA concentration. A clear effect of decapitation on the nutations was not observable. Many coleoptiles nutated during the full length of the experimental period whereas others stopped oscillating after one or two hours. This variation of behaviour agrees with Joerrens' observations of deseeded wheat coleoptiles.

The presence of nutations in the diluted solutions of IAA weakens the criticism by Arnal and Baillaud of Joerrens' experiments.

The fact that the nutations persisted at saturation concentrations, however, is neither consistent with Arnal's hypothesis nor with that of Joerrens. For Arnal attributes circumnutation just to variations of the hormone concentration, and the mechanism proposed by Joerrens (variability of the sensitivity to

Table 1. The nutations of *non-decapitated* coleoptiles in water and in solutions of indoleacetic acid.

Concentration of indoleacetic acid	Degrees curvature after:				
	0 hours	1 hour	2 hours	3 hours	4 hours
0	−5	−2	+6	+2	0
	+5	+2	−1	0	+2
0.05 mg/l	−6	−4	+2	−3	−3
	+4	+1	−3	−4	−4
0.10 mg/l	−11	−4	+3	0	+4
	−14	+2	0	−5	−3
1 mg/l	−5	+4	+1	0	+1
	0	+3	+4	+5	+2
5 mg/l	−2	+3	−2	−4	−6
	+1	+3	+3	0	0
10 mg/l	+4	+3	+2	+1	−5
	−3	+2	0	−2	−2

Table 2. The nutations of *decapitated* coleoptiles in water and in solutions of indoleacetic acid.

Concentration of indoleacetic acid	Degrees curvature after:				
	0 hours	1 hour	2 hours	3 hours	4 hours
0	−12	−11	−6	−1	+2
	+3	+5	+5	+2	−2
0.01 mg/l	−10	−2	0	+1	0
	−5	−5	0	+3	+3
0.05 mg/l	−3	+2	+1	+2	+1
	−2	+1	+4	+3	+3
0.075 mg/l	0	−5	−2	0	0
	+9	+2	+1	+2	+3
0.2 mg/l	+5	−1	−3	0	−4
	+2	+2	+3	0	−3
0.6 mg/l	−5	+1	+2	+3	+3
	−4	0	+2	+1	+2

auxin) can only work as long as the auxin concentration limits the growth.

The presence of circumnutation at saturation concentrations must therefore be explained by a mechanism differing from the hormonal regulation of the growth *rate*.

If auxin is abundant, a periodic change in the capacity of the tissue to respond to IAA will cause fluctuations in the growth. Since Joerrens observed that the presence of the seed is important for the continuation of the circumnutation over a long period of time, variations in the supply of a food factor could be a link in the chain of events.

From the above discussion it will be evident that we consider the circumnuta-

tion to be an autonomous movement. This view is opposed to a theory, coming from GRADMANN (1926), and still supported by others, called by HEATHCOTE & ASTON (1970) the "geotropic hunting theory". This theory describes the nutations as corrective *geotropic* reactions through which the plant is hunting for the vertical position, a mark which is overshot again and again.

To the present author it is impossible to imagine that the nutational movements of the *Avena* coleoptile have a geotropic component. In his own experience (ANKER 1954, 1956) the geotropic response of the coleoptile is very sensitive to the auxin concentration. Its occurrence is restricted to internal auxin concentrations which are infra-optimal for the growth rate of the cells.

Since circumnutation appeared to be independent of the IAA concentration, it is very improbable that geotropism contributes to the circumnutation. This improbability is rendered even greater by the observation that removal of the tip did not affect the nutational movements, for the tip of the coleoptile is much more sensitive to the direction of the gravitational force than the rest of it is. This fact counts heavily since the small deviations from the vertical will cause only a minimum of geoinduction.

During the preparation of this manuscript the author came across the article by Heathcote and Aston on the circumnutation of *Phaseolus* seedlings referred to above. In spite of a great difference in the way of approaching the problem, these authors came to the same conclusion "that the movements of nutation of *Phaseolus* have an endogenous origin unconnected with geotropic reactions".

The second purpose of this publication is to suggest a way of dealing with the nutations when studying a tropism. How to make allowance for the movements that interfere with the geotropic reaction?

Because of the nutations coleoptiles are seldom perfectly straight. They show small upward or downward curvatures when put horizontally for geotropic studies. It is common practice in research of photo- and geotropism to take this initial curvature into account. If, for instance, a horizontally placed coleoptile has an initial curvature of 5° downwards and if after one hour of horizontal exposition an upward curvature is measured of 15°, then a geotropic curvature of 20° is recorded. This practice may be wrong because it is not improbable that the coleoptile referred to above was on the point of nutating in upward direction, in which case an overestimate of the geotropic activity would be obtained. The same is true for initially upwards curved coleoptiles, *mutatis mutandis*.

The alternative practice is to neglect the initial curvature. The advice to do so seems justified by the results presented in *fig. 1* A.

The geotropic reactions of 2 groups of 8 coleoptiles were followed until the final curvature of roughly 70° was attained (see ANKER 1971). At the beginning of the experiment one of the groups had an average downward curvature of about 8°, while the other had an upward curvature of about 4°. After one hour of horizontal exposition the average curvature of both groups was 17°, and a significant difference of geotropic activity during the rest of the experiment was not observable. This points to equality in physiological respect. The different
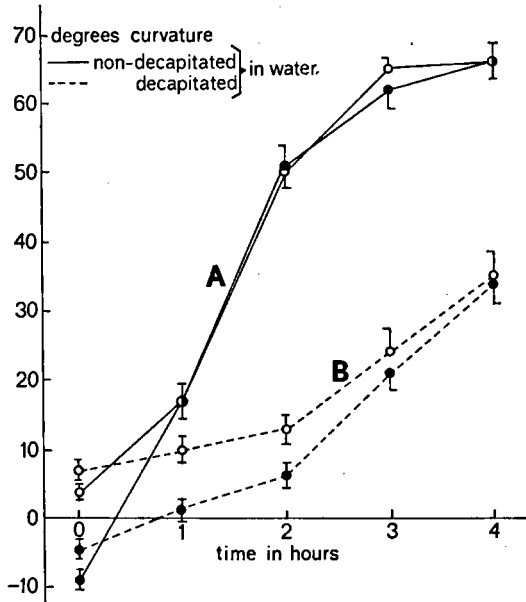
Fig. 1. The effect of the initial curvature on the subsequent development of the geotropic curvature. A. Non-decapitated coleoptiles, B. Decapitated coleoptiles, in water. The vertical lines represent standard deviations of the means.

rates of curvature displayed during the first hour may therefore be attributed to the interference of the circumnutation with the geotropic reaction. They cannot be attributed to a stronger geoinduction of the downward-curved coleoptiles since at continual exposition the "amount of geoinduction" is abundant. Moreover, DE WIT (1957) demonstrated with *Avena* that coleoptiles placed at angles of 45° and 135° from the vertical show the same rate of curvature during the first 1½ hour of the exposition.

These facts and considerations result in the advice not to pay attention to the initial curvature of the coleoptile in case one is interested in its geotropic activity alone, a proceeding which also decreases the spread.

With decapitated coleoptiles in *water* (not in auxin solutions) the situation is different (*fig. 1*B). The influence of the nutations is relatively large during the first and the second hour of the experiment because the concentration of the residual auxin is low. After the regeneration of the physiological tip the picture becomes comparable with that of *fig. 1* A. The way to proceed with the measurements will depend on the part of the reaction one is studying.

In *fig. 1* A and B the reactions of two extreme groups are compared. In practice the *average* initial curvature of the coleoptiles is near to zero, but the interference of the nutations with the geotropic reaction legalizes or even necessitates the assumption that every coleoptile is straight at the beginning.

REFERENCES

ANKER, L. (1954): A comparative study on the recovery of the geotropic response of decapitated Avena coleoptiles by indoleacetic acid, indoleacetonitrile, and naphthylacetic acid. *Proc. Kon. Ned. Akad. Wet.* C **57**: 304–316.
— (1956): The auxin concentration rule for the geotropism of Avena coleoptiles. *Acta Bot. Neerl.* **5**: 335–341.
— (1971): The permeation of indoleacetic acid through the cuticle of the Avena coleoptile and its effects on the growth and the geotropism. *Acta Bot. Neerl.* **20**: 275–281.
ARNAL, C. (1953): Recherches sur la nutation des coléoptiles. I. Nutation et croissance. *Ann. Univ. Saraviensis* II: 186–203.
BAILLAUD, L. (1962): Mouvements autonomes des tiges, vrilles et autres organes à l'exception des organes volubiles et des feuilles. In: W. RUHLAND, *Handbuch der Pflanzenphysiologie* XVII/2: 562–634.
GRADMANN, H. (1926): Die Bewegungen der Ranken und die Überkrümmungstheorie. *Jb. wiss. Bot.* **65**: 224–278.
HEATHCOTE, D. G. & J. T. ASTON (1970): The physiology of plant nutations. I. Nutation and geotropic response. *J. exp. Bot.* **21**: 997–1002.
JOERRENS, G. (1959): Nutationsbewegungen bei Triticum-Koleoptilen. *Z. f. Bot.* **47**: 403–420
WIT, J. L. DE (1957): Growth-substance relations in the Avena coleoptile, studied by means of the geotropic response. *Acta Bot. Neerl.* **6**: 1–45.