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The possible rôle of xanthoxin in plant growth and development

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In higher plants, abscisic acid and xanthoxin are two potent growth regulators. Although similar properties in both substances have been demonstrated in several biological tests including biochemical interconversion of the substances, evidence is available that in the plant as a whole, xanthoxin has regulatory functions other than those of abscisic acid.

Several environmental factors, such as water supply, photoperiod and low temperature, which affect growth and development also greatly change the level of abscisic acid in the plant; however, only small variations in the xanthoxin level have been observed in response to changes in the environmental conditions. On the other hand, a strong enhancement of the xanthoxin level can be induced when dark-grown seedlings are briefly illuminated; this treatment, however, has no influence on the abscisic acid level. This observation supports the hypothesis that light-induced inhibition of growth may be mediated by an increased formation of the growth inhibitor xanthoxin. Light-induced enhancement of the xanthoxin level may also contribute to the phototropic bending in dictyledonous seedlings.

Evidence has been obtained from experiments in this laboratory that xanthoxin may be involved in the regulation of root branching. Decapitation of root tips causes a significant increase in the number of lateral root primordia. Chromatographic studies reveal the presence of two substances in the root, which, in a specific bioassay, are active inhibitors of the development of root primordia. The activity of these root inhibitors in the basal part decreases when the root tip is removed. They are probably produced in the root tip and are transported to the base. One of these inhibitors has been identified as xanthoxin, the other is cytokinin.

The hormonal regulation of abscission is another process where xanthoxin may have a regulatory function. Senescent, abscinding petioles contain a factor called 'senescence factor' which promotes the abscission of leaves. In an attempt to identify its chemical nature, it was found that at least three different abscission accelerating substances, including xanthoxin, participate in the composition of the senescence factor.

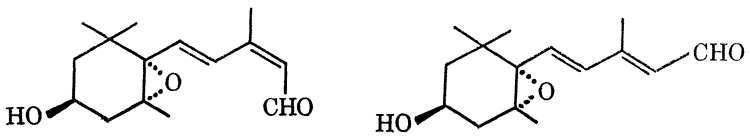
Introduction

Although the plant growth inhibitor xanthoxin (figure 1) was discovered by Taylor and his coworkers only a few years after the discovery of abscisic acid, the literature concerning xanthoxin has not reached a fraction of the volume of that currently available on the physiology and chemistry of abscisic acid. One reason for this may be the fact that, in contrast to abscisic acid, synthetic xanthoxin is not commercially available. Methods to isolate and purify natural xanthoxin and methods to produce synthetic xanthoxin have been described (Firn, Burden & Taylor 1972); but to date the A.R.C. laboratory at Wye College is the only source for authentic xanthoxin. Although Dr Taylor has generously provided xanthoxin to his colleagues, including myself, this source is too small to stimulate xanthoxin research in a similar manner to that when abscisic acid became commercially available.

A second reason may be the fact that abscisic acid was discovered in connection with two important physiological processes, namely dormancy and abscission. The question at once arose whether this newly discovered hormonal factor was causally involved in the regulation

of these processes – a question which until now could not be answered unequivocally, but which considerably stimulated experimental research.

Xanthoxin, on the other hand, was detected as a result of experiments on the biogenetic origin of abscisic acid. It was found that oxidation of certain xanthophylls, especially violaxanthin, gave rise to a substance which was inhibitory to the germination of cress seeds. Besides its possible biochemical rôle as a precursor of abscisic acid, there was at that time no evidence for a physiological rôle of xanthoxin in the plant. Since then, knowledge about the biochemistry of xanthoxin has increased to a considerable extent, especially through the efforts of the group at Wye, but information on the physiological function of xanthoxin in the plant as a whole, and not only in bioassays with isolated plant organs, is still lacking.



FIGURE, 1. *Cis,trans*- (left) and *trans,trans*-xanthoxin (right).

Even the basic question, whether xanthoxin exerts its different biological effects *per se* or via transformation into abscisic acid, is still open to question. Results recently obtained by Raschke and his coworkers (1975) strongly point to the second possibility. When xanthoxin was applied to isolated epidermal strips of *Commelina* or *Vicia*, it proved to be completely inactive in closing the stomata. However, when xanthoxin was applied to detached leaves of these species, the stomata closed nearly as fast as after application of abscisic acid. Xanthoxin was approximately half as active as abscisic acid. One explanation for these observations may be that xanthoxin does not act directly on the guard cells, but only after conversion to abscisic acid which occurs in the mesophyll of the leaf but not in the epidermis. This conversion must take place in less than 10 min, because the lag phase between application of abscisic acid and beginning of stomatal closure is about 10 min.

Conversely, a comparison of xanthoxin and abscisic acid in their effect on lateral root formation shows a significantly higher activity of xanthoxin, at least at lower concentrations. Böttger (1974), who made this observation, took this as evidence that xanthoxin acts *per se* as an inhibitor of root formation and not via conversion into ABA.

PROBLEMS OF DETECTION AND ESTIMATION

In comparison with abscisic acid, the detection and estimation of xanthoxin in plant extracts is much more difficult. This also may contribute to the relatively slow progress in our knowledge about the physiological rôle of xanthoxin. A gas chromatographic method has been described by which xanthoxin is chromatographed in acetylated form and detected by a flame ionization detector (Firn *et al.* 1972). The sensitivity and selectivity of this detector is, however, relatively low in comparison with electron capture detectors widely used for the gas chromatographic detection of abscisic acid.

Moreover, during the acetylation procedure the ratio of *cis,trans* : *trans,trans*-xanthoxin is affected. Authentic xanthoxin normally is a 1 : 1 mixture of the two isomers *cis,trans*- and *trans,trans*-xanthoxin. This ratio shifts during the acetylation procedure towards 1 : 1.5 or

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1 : 2, and, in some cases, even 1 : 3, as Fenner (1976) recently found. These disadvantages may be overcome by reduction of the aldehyde group, which prevents isomerization, and esterification of the hydroxyl group with perfluorobutyric acid anhydride. This derivatization allows subsequent detection with an electron capture detector. Less than 30 pg can be detected in plant extracts by this method (Böttger 1978).

It should be mentioned, however, that xanthoxin can be submitted to gas chromatography under standard conditions without any derivatization. A mixture of *cis,trans*- and *trans,trans*-xanthoxin in a 1 : 1 ratio can be easily separated and yields two peaks of the same height and area, indicating that the ratio is not changed during this procedure. However, a greater amount of the biologically inactive *trans,trans*-xanthoxin is detected in plant extracts.

Is xanthoxin involved in light-induced growth processes?

The fact that xanthoxin is produced by photo-oxidation of violaxanthin and other xanthophylls raises the question whether light-induced changes in growth and development are mediated via changes in the levels of xanthoxin. The possibility has been repeatedly discussed that photomorphogenetic processes, such as growth inhibition by light, are caused by light-induced changes in the hormonal balance. A reduction of the gibberellin level has been postulated as well as an increase in growth inhibitors. However, here we shall give primary consideration to the growth inhibitors.

One of the first reports that light influences the growth inhibitor system in plants came from Bayer (1961). Hypocotyl segments from dark-grown sunflower seedlings were illuminated for about 2 h with low light intensity. During that time, a factor was produced in the tissue which moved into agar blocks and reduced the auxin-induced curvature in the common *Avena* curvature bioassay. Diffusates from control segments which were not illuminated increased the curvature induced by suboptimal indoleacetic acid concentrations. Thus, Bayer concluded that a transportable growth inhibitor, antagonistic to the effect of auxin, was formed during the light treatment. The growth inhibiting effect was more pronounced in diffusates from basal segments. This may be due to the fact that these contain less endogenous auxin than diffusates from apical segments.

No attempts were undertaken by Bayer to characterize this inhibitor in more detail. Studies carried out recently by Thompson & Bruinsma (1977) raise the possibility that the inhibitor was xanthoxin. Thompson & Bruinsma found that light-grown sunflower seedlings contained much higher amounts of xanthoxin than seedlings grown in the dark, whereas no significant differences could be found in the levels of abscisic acid. This result resembles observations of different researchers with pea seedlings, where red light was found to enhance strongly the level of xanthoxin (Burden *et al.* 1971; Firn 1974; Anstis, Friend & Gardner 1975). Results pointing in the same direction have also been obtained in our laboratory by R. Fenner (figure 2). The content of xanthoxin in seedlings, which were illuminated each hour for 5 min with red light of low intensity was several times higher than in dark-grown seedlings.

Moreover, seedlings of a dwarf variety, 'Kleine Rheinländerin', had significantly higher amounts of xanthoxin than plants of a normal variety, 'Senator', either on the basis of nanograms per gram fresh mass or nanograms per plant. In dark-grown Senator seedlings there was almost no detectable xanthoxin. This observation, of course, cannot be generalized, but it seems noteworthy to point to similar observations made by Higgins & Bonner (1974). They

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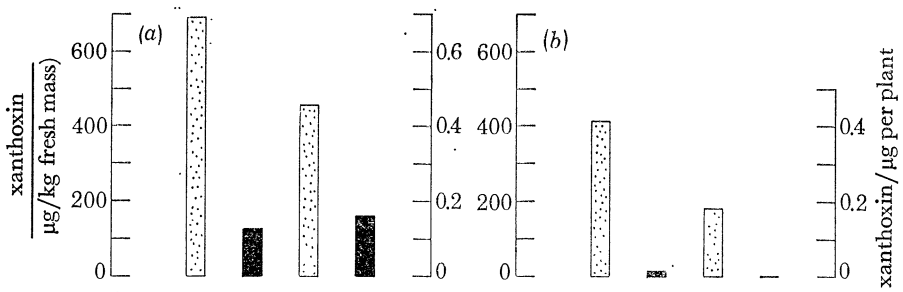
found significantly higher amounts of a xanthoxin-like inhibitor in the dwarf variety 'Radio' in comparison with 'Alaska'. The level of abscisic acid was the same in both varieties. From the work of Firn (1974), there is, moreover, evidence that the xanthoxin level is phytochrome dependent, as is the case with the internode growth of the seedlings. Thus, clear correlations exist between the level of the growth inhibitor xanthoxin and the intensity of growth.



FIGURE, 2. Xanthoxin contents in pea seedlings of (*a*) a dwarf variety (Kleine Rheinländerin) in comparison with (*b*) a normal variety (Senator). The seedlings were grown in the dark (black columns) or under intermittent red light (5 min per hour, for 8 days) (stippled columns). The xanthoxin contents are expressed as micrograms per kilogram fresh mass (columns on the left) and micrograms per plant (columns on the right). Means of two experiments. With permission of R. Fenner.

However, serious objections must be made against the hypothesis that a causal relation exists between light, xanthoxin and growth inhibition. The most important argument is the observation that growth inhibition in dark-grown pea seedlings by red light is observable within one hour, but elevated levels of xanthoxin could be measured only after 12 h had elapsed (Firn 1974). Evidence for an intermediate rôle of xanthoxin in the control of internode growth is, therefore, doubtful. The situation is the same here as with abscisic acid and with gibberellic acid, where earlier studies (Mohr & Appuhn 1966; Dörffling 1973) have shown that these hormones obviously are not involved in the chain of events which start with absorption of photons by phytochrome and end with reduction in internode growth rate. This conclusion must be restricted, however, to dark-grown seedlings. It cannot be excluded that more rapid changes in xanthoxin concentration occur in light-grown plants.

Bruinsma, in two recent papers (Bruinsma, Karssen, Benschop & van Dort 1975; Thompson & Bruinsma 1977), has discussed the possibility that xanthoxin controls phototropism in dicotyledonous seedlings such as sunflower. The idea is, of course, attractive. If the illuminated side of an organ could produce more inhibitor via photolysis of violaxanthin or other xanthophylls than the shaded side, then the organ would bend towards the light.

In favour of this idea, first expressed by Taylor (1968), is the fact that, for example in mung beans, 5,6-epoxyxanthophylls are present in higher amounts in illuminated plants than in dark-grown seedlings (Valadon & Mummery 1969). However, kinetic studies have shown that phototropic bending of the seedlings occurs without any detectable change in the xanthophyll content of the illuminated and shaded side (Valadon & Mummery 1971).

Bruinsma emphasizes the finding that the phototropic response of the sunflower hypocotyl occurs without any change in the distribution of indoleacetic acid (IAA). When a phototropically bending hypocotyl is halved longitudinally in a plane perpendicular to the cotyledonary axis and to the light direction, the shaded and the lightened sides do not differ in their IAA content. The Cholodny–Went theory of phototropism, which postulates translocation of

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auxin (IAA) from the illuminated to the shaded side of the organ as a prerequisite for differential growth, is therefore, not applicable to this plant.

In this connection, an observation made by Lam & Leopold (1966) is of great importance. They found that sunflower seedlings with one darkened cotyledon bent in diffused light towards the illuminated cotyledon. The explanation was that more auxin is delivered to the hypocotyl by the darkened cotyledon than by the illuminated one. In fact, darkened shoot tips yielded more auxin into agar than illuminated shoot tips.

An alternative hypothesis to the Cholodny–Went theory and, moreover, an alternative explanation of the results obtained by Lam & Leopold is proposed by Thompson & Bruinsma (1977). It involves the production of xanthoxin in the illuminated cotyledons and its translocation down the hypocotyl, where it causes differential growth inhibition. The cotyledons are necessary for phototropic bending. When they are removed or covered by black cloth, the curvature of the hypocotyl is greatly reduced. This can be partly explained by assuming that they are the main source of the light-induced inhibitor. However, although increase of the xanthoxin level in sunflower after illumination has been shown, up to now the crucial experiment demonstrating unequal distribution of xanthoxin in the phototropically bending hypocotyl or in the diffusate has not been made, so that the evidence for this hypothesis remains insufficient.

Lateral root formation, root growth, and xanthoxin

I should now like to discuss another subject possibly related to xanthoxin which has been recently investigated in our laboratory by Böttger (1974). Böttger studied the hormonal regulation of lateral root formation in pea seedlings. It is well known that in this plant, as well as in many others, the root apex inhibits the formation and outgrowth of the lateral roots. If the apical 3 mm of the apex are removed, the number of root primordia in the following basal 3 cm segment is increased within a few hours. The root primordia are easily detectable after staining with Feulgen's reagent. The effect of decapitation demonstrates that lateral root formation is a correlative phenomenon, as with lateral bud inhibition by the shoot apex.

However, the hormonal systems involved in both correlations seem to be quite different. Torrey (1962) has shown that auxin in the root medium stimulates lateral root formation while kinetin inhibits it. Chromatographic studies revealed the presence of two inhibitors of root formation in the alkaline-soluble ether fraction of root extracts. One of these inhibitors was, with high probability, a cytokinin. The other, more active inhibitor seemed to be a phenolic compound. The acidic ether-soluble fraction contained an inhibitor with chromatographic properties of inhibitor β (Torrey 1959).

By means of a special root formation bioassay using pea root segments it was shown by Böttger (1974) that paper chromatograms of the alkaline ether fraction of pea root extracts developed in isopropanol–ammonia–water (10 : 1 : 1) contained a strongly inhibitory region of root formation with R_f 0.7–1.0. This inhibitory activity was not present 12 h after decapitation (when lateral root formation was initiated). Surprisingly, neither the region where IAA occurs on the chromatogram of the acidic fraction nor the region of abscisic acid showed significant changes after decapitation. Further detailed analysis of the inhibitor region at R_f 0.7–1.0 in two different bioassays – the *Amaranthus* bioassay for cytokinins, and the *Avena* coleoptile segment test for auxins and growth inhibitors – showed that the respective fraction

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obviously contained cytokinin-active substances as well as cell growth inhibitors. Again, it was obvious that the activity of both substances decreased after decapitation. It is well known that cytokinins as well as xanthoxin have chromatographic positions in this region. Xanthoxin and cytokinins such as zeatin have been shown to be very active inhibitors of root formation in the respective bioassay. It was, therefore, concluded that the root tip forms cytokinin as well as xanthoxin. Both xanthoxin and cytokinin are supposed to be translocated basipetally and inhibit lateral root formation.

Subsequent gas chromatographic studies confirmed that xanthoxin is present in pea roots, and the root tips contained four to five times as much as the basal tissue. Intact basal root tissues contained about 20 ng *cis*,*trans*-xanthoxin per gram fresh mass. The same quantity, dissolved in water, is sufficient to inhibit the root formation in the respective bioassay. When the root tip was removed, the concentration decreased by about 50% (Böttger 1978). Thus there is evidence that xanthoxin may play a rôle in the regulation of lateral root formation.

However, it has still to be established that the relatively small decrease of the xanthoxin level is in itself sufficient to allow the development of lateral root primordia. The shape of the dose–response curve of xanthoxin in the root formation bioassay does not support this claim. Even when the level decreases to one-tenth of the initial concentration, there is only a relatively small difference in the number of roots initiated. Also to be taken into account is the fact that the cytokinin concentration decreases, too; both these factors together may regulate the formation of root primordia.

Whether xanthoxin has other functions in the root beside that which has just been discussed is an unresolved question. The roots of many plant species, for example maize, show enhanced geotropic response after illumination (Scott & Wilkins 1969). Furthermore, it is known that light inhibits not only shoot growth, but also root growth (Burström 1960). It seems to be of great interest, therefore, to study whether the xanthoxin level in roots is increased by light as in shoots. To date this has not been done.

There is, however, good evidence that abscisic acid plays an important rôle in the orientation of the root, but the rôle of xanthoxin needs further investigation. An earlier paper of Masuda (1962) showed that illuminated wheat roots contain higher amounts of inhibitor β, which is in all probability mainly abscisic acid, than dark-grown roots. The data of Masuda do not provide evidence for the increase of an xanthoxin-like inhibitor. Higher amounts of ABA in illuminated roots of pea have also been found in our laboratory by Tietz (1974). In addition, we know from a series of papers discussed during the most recent conference on plant growth substances at Lausanne in 1976 that, at least in maize, ABA is present in the root cap and, in all probability, regulates geotropic curvature. On the other hand, Kundu & Audus (1974) and Audus (1975) have shown by mass spectrometry that root tips, but not root caps, of maize contain xanthoxin. Thus, much work on this question remains to be done.

Xanthoxin and the control of abscission

The last part of this report deals with some recent data concerning the possible rôle of abscisic acid and xanthoxin as abscission accelerating factors in senescent leaves. We have started to analyse the endogenous substances which are present in abscinding leaves and which may participate in the regulation of abscission (Dörffling *et al.* 1978).

We wished to identify the nature of the so-called 'senescence factor' in senescent *Coleus* leaves,

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the existence of which was postulated first by Osborne in 1955 (see also Osborne, Jackson & Milborrow 1972). This factor, being present in higher activity in senescent, abscinding leaves and petioles than in young, growing ones can be obtained from petioles by extraction with organic solvents or by diffusion into agar. Agar blocks containing the factor showed enhanced abscission accelerating activity in comparison with diffusates from young or adult petioles.

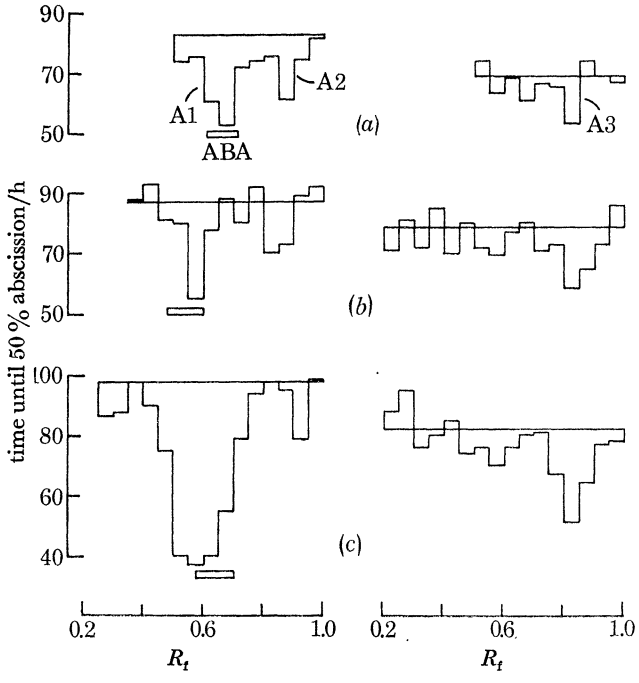

FIGURE 3. Abscission accelerating activity in chromatograms from ethanolic extracts of senescent petioles (*a*, *Coleus rehneltianus*; *b*, *Phaseolus multiflorus*; *c*, *Acer pseudoplatanus*). Acidic ether-soluble fractions on the left, neutral ether fractions on the right. Thin-layer chromatography in isopropanol–ammonia–water (10 : 1 : 1). Biassay: abscission test with *Coleus* explants. Each fraction was bioassayed with 21 explants. Three abscission accelerating substances called A1, A2, A3 are present in all species examined. The position of marker ABA is indicated. A3 has been identified as xanthoxin.

A chromatographic separation of the active substances in extracts and diffusates from different plant species and subsequent bioassay of the various fractions in a special abscission bioassay showed the presence of at least three different abscission accelerating substances (figure 3). Two of them were acidic in nature; one of these acidic substances was conclusively identified by gas chromatography in different systems as ABA. The alkaline ether-soluble fraction contained an abscission accelerator which had a position on the thin layer plate similar to that of xanthoxin. In fact, gas chromatography of this fraction showed that xanthoxin was present.

The activity of xanthoxin in the abscission bioassay was found to be lower than that of abscisic acid. The amount of xanthoxin (*cis*,*trans*- and *trans*,*trans*- taken together) in extracts of senescent *Coleus* leaves was about 220 ng/g fresh mass. According to the dose–response curve of xanthoxin, an aqueous solution of this concentration significantly stimulates abscission in the respective bioassays. Up to now it was not possible to analyse the variation of xanthoxin concentration in the petioles during development. We know, however, from earlier data of Taylor & Burden (1974), that in *Phaseolus* leaves the xanthoxin content decreases with increasing age. We found a similar pattern for the variation of abscisic acid levels in *Coleus* petioles. Senescent petioles always contained the lowest amount of ABA, absolutely, and in relation to

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fresh mass and to dry mass. The third abscission accelerating substance, which has not been identified yet, did not vary significantly during development.

The significance and relation of these findings is not fully clear at the moment. We can conclude, however, that the higher abscission accelerating activity of diffusates and extracts of senescent petioles is a composite effect of a mixture containing at least three substances: abscisic acid, xanthoxin and a third unknown factor.

The important question remains as to the actual cause of the higher abscission speeding activity of diffusates and extracts from senescent petioles, since the amount of all these substances does not seem to increase from young to senescent petioles. One of several possible answers is that the amount of auxin declines in the petioles with increasing age. This has been found in the past by several authors. Determinations of the IAA content of *Coleus* leaves by the method of Knegt & Bruinsma (1973) have shown that the concentration decreases to less than one-tenth of its initial concentration from the juvenile to the senescent stage. It may be assumed, therefore, that the abscission speeding factors become gradually more active as the amount of the abscission-retarding hormone, IAA, decreases in the petiole.

Concluding remarks

In attempting to summarize what is known about the physiological rôle of xanthoxin in plants, we should state first that xanthoxin is a very potent growth regulator, active in many biological assays. It resembles abscisic acid, both qualitatively and quantitatively. This high activity, however, does not imply that it has a regulatory function in the plant. A specific rôle for xanthoxin in plant growth and development has not been established. In any case, it must be assumed that xanthoxin is only one factor in a complex hormonal system that regulates growth and development.

Regarding this hormonal system, three important areas for future xanthoxin research present themselves. First, although not without contradiction, there is some evidence that xanthoxin may be involved in light-mediated growth inhibition. Its postulated rôle in phototropism of sunflower hypocotyls is an attractive idea as is a similar postulation with regard to root growth and root formation. Further investigation of both phenomena is necessary. Secondly, more work has also to be done to establish whether xanthoxin functions as a precursor or as a storage form of abscisic acid. As already mentioned, xanthoxin obviously affects stomatal movements only after conversion into abscisic acid. Since this conversion takes place when xanthoxin is applied exogenously, it must be assumed that endogenous xanthoxin occurs in well isolated compartments within the leaf. We have no further information about these compartments. Finally, nearly nothing is known about the transport properties of xanthoxin. Before we can define xanthoxin as a plant hormone, we have to show that it is transportable within the plant. These unanswered questions show us that xanthoxin research – extremely interesting, but still in its infancy – must be continued.

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