

REVIEW

Gravitropism of roots: an evaluation of progress during the last three decades

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INTRODUCTION

The response of plant roots to gravity has fascinated many botanists since the early days of plant physiology and much research has been devoted to the elucidation of the sequence of events between the physical reception of gravity and the visible growth response. In the last few decades the ideas on the graviresponse of roots have changed

profoundly and much progress has been made in understanding parts of the process. One of the reasons for writing this review was my curiosity to know what has happened since the time I myself was involved in the study of root geotropism, as it was called, about 30 years ago. Some excellent reviews have appeared since then, e.g. Audus (1975), Jackson & Barlow (1981) and Moore & Evans (1986), which were more restricted in scope and, moreover, there have been several fascinating developments. The aim of this review is to discuss briefly all aspects of the graviresponse of roots and the progress made in understanding during the last three decades. Some data on other plant organs are included where appropriate.

DEVELOPMENT OF GRAVICURVATURES IN ROOTS

The positive gravitropic curvature of a horizontally placed root is the result of a faster growth rate of the upper side of the extension zone relative to that of the lower side, which can be achieved by: (i) growth acceleration of the upper side; (ii) growth inhibition of the lower side, relative to the vertically growing control roots; (iii) both (i) and (ii); and (iv) by other variations in growth rate of the opposite sides. In order to understand and formulate a proper theory on gravitropism it is necessary to ascertain how bending develops. Many early reports do not allow firm conclusions about growth accelerations or inhibitions, because vertical controls were often not included for comparison and measurements were made only after several hours. In addition, gravitropic bending has been assumed for years to be the result of growth inhibition of the lower side effected by accumulation of auxin, as predicted by the Cholodny–Went hypothesis (Went & Thimann 1937).

Audus & Brownbridge (1957) were the first to make detailed measurements of the elongation of the upper and the lower side during the gravicurvature of pea roots in water culture; after a 40 min stimulation period, these were rotated on a clinostat. Growth measurements of continuously horizontally exposed pea roots in water culture were made by Konings (1964). In both experiments the roots first showed a rapid positive curvature, during which period the growth of the upper side accelerated in comparison with the vertical controls and the growth of the lower side diminished, but there were considerable differences between individual roots. After 1.5–2 h, inhibition of the lower side was reversed to a growth rate well over that of the vertical controls and the growth rate of the upper side decelerated to a value below it. Thus, the roots straightened partially (totally during rotation on a clinostat in the experiments of Audus & Brownbridge). In the following hours the roots showed alternating stimulations and inhibitions of the growth rate of the two sides, but in opposite directions; the growth differences between the upper and lower side were also smaller than in the first 2 h and the increase of curvature slower or absent. So, after a rapid positive curvature, the root tips showed an alternation of positive and negative responses, i.e. an oscillating behaviour more or less around an equilibrium value, or they slowly approached their final (liminal) angle (Konings 1964). More recently, this response pattern has essentially been confirmed by means of more sophisticated and detailed measuring methods for roots of *Lepidium sativum* by Selker & Sievers (1987), for roots of *Phleum pratense* by Zieschang & Sievers (1991) and for *Zea mays* roots by Ishikawa *et al.* (1991) and thus it seems to be a general occurrence. Stimulation of the upper side and inhibition of the lower side during the positive curvature was also found by Pilet & Ney (1981) and Barlow & Rathfelder (1985).

The overall elongation of graviresponding roots was often reduced (Audus & Brownbridge 1957; Konings 1964; Juniper 1976; Beffa & Pilet 1982; Zieschang & Sievers 1991), but in other cases was unaltered (Barlow & Rathfelder 1985; Selker & Sievers 1987; Ishikawa *et al.* 1991).

It follows from the above that, for proper understanding of the gravitropic behaviour of roots, both growth acceleration and retardation of the two opposite sides have to be explained.

Oscillations, also called circumnutations or (autonomous) nutations, occur in vertically growing roots and are considered to be feedback corrections of their liminal angle of deviation from the vertical (Spurný 1974; Barlow *et al.* 1993). In maize roots, for instance, the angle of deviation from the vertical necessary to induce a gravitropic response must be higher than the size of the natural oscillations in vertical roots of about 10° (Barlow *et al.* 1993). Spurný (1973, 1974) found that the oscillations in vertically growing maize roots had a higher frequency and a smaller amplitude than in pea roots corresponding with their higher growth rate. Ney & Pilet (1981) found that the frequency and the amplitude of oscillations in graviresponding maize roots were similar to those of the vertical controls.

Oscillations occurring in vertical roots will probably interfere with the gravitropic response when the roots are placed horizontally, depending on the direction in which the tip is moving at the time of horizontal exposure.

Oscillations of graviresponding roots started when the maximum angle of curvature of the roots was reached (Konings 1964; Ney & Pilet 1981; Selker & Sievers 1987; Ishikawa *et al.* 1991). Interestingly, the maximum of the first positive bending was often reached after approximately 2 h in several species, irrespective of the size of the bending and under various conditions (Konings 1964; Rufelt 1957a; Zinke 1968; Selker & Sievers 1987; Ishikawa *et al.* 1991). After that time the oscillations seem to take over, as if they had been transiently interrupted by the graviresponse of the horizontally placed roots. Roots that do not show a reversal of the curvature often shift their rate of bending after about 2 h, because the growth difference between the two sides decreases. This shift differs probably only gradually from partial straightening of the root tip or negative curvature. Tropic bending, therefore, could be considered as being superimposed on autonomous oscillations. However, the oscillations of horizontal roots that reached their liminal angle were often damped in time and are not necessarily similar to the oscillations found in vertically growing roots (Barlow 1992). Autonomous nutations of roots have been found to continue during space flights in microgravity (Volkman *et al.* 1986) and thus are not directed by gravity.

Removal of 1.3 mm of the root tip (Spurný 1974) or of the root cap (Hillman & Wilkins 1982) stopped the oscillations. Removal of the root cap from graviresponding pea roots blocked the positive curvature and/or the oscillations, depending on the time of decapping (Konings 1968). So, the oscillations are apparently controlled by the root cap.

The strong first positive gravicurvature and the oscillations that follow were found to respond similarly to various treatments (Konings 1964) and thus may be controlled by the same mechanism, a suggestion also expressed by Barlow *et al.* (1993). Further comparisons are needed to determine whether or not the various treatments that affect graviresponses, as discussed in the following sections of this review, do affect nutations and damped oscillations in a similar way.

The direction of root growth in the soil is probably not only determined by gravitropism, but also by mechanical resistance (thigmotropism), moisture gradients

(hydrotropism) and by temperature gradients (thermotropism). Roots in the soil may avoid obstacles, probably by touch, and follow the way of least resistance, as found for hypocotyls (Schwarzbach *et al.* 1991). Rufelt (1957c) observed that wheat roots in water culture showed a clearly stronger positive gravitropic behaviour at a temperature of 15°C than around 20°C. Root systems in the soil are often found to consist of different zones with increasing positive gravitropic response in deeper, cooler layers (Kutschera-Mitter 1971).

IMPORTANCE OF UNDERSTANDING WATER RELATIONS AND CELL WALL PROPERTIES OF THE GRAVIRESPONDING ROOT TIP

It should be noted that root pretreatment and experimental conditions affect the gravitropic response. The graviresponses of roots in water culture, for instance, were found to be influenced by pH, temperature, oxygenation and various ions (Rufelt 1957a,b,c; Nantiwisarakul & Newman 1992).

The influence of experimental conditions is especially clear when the behaviour of roots in water culture and in humid air are compared (Konings 1964; Zinke 1968; Jackson & Barlow 1981). Roots in humid air will probably have a lower hydraulic conductivity than in water culture and may also experience water stress. When pea roots, which were previously grown in humid air, were made fully turgid by dipping in water, the onset of gravitropic bending was postponed but, once started, the positive bending went on for a longer period than in untreated controls because no oscillations occurred after 2 h. When these pretreated roots were held in air with 70% relative humidity (RH) for 1 min and then placed horizontally, they again showed the straightening period after about 2 h. When kept in this drier air for 5 min their curvature was much delayed and smaller, but oscillations appeared. It was apparently more difficult to reverse the growth rate of the two sides when the water content was high (H. Konings, unpublished results).

In agreement with these results, Ishikawa & Evans (1992) reported reduced thigmotropic responses of roots in misty air compared to roots in slightly drier conditions, supposedly because the roots had their maximum growth rate under the wet conditions. At relative humidities between 96 and 90% RH the roots were found to develop hydrotropic curvatures that increased linearly with decreasing RH (Takahashi & Scott 1993), and under certain conditions hydrotropism may interact with gravitropism.

Excised roots, often used as an experimental system, behave differently, because their elongation, metabolism, plasticity and elasticity are reduced (Pritchard & Tomos 1994). Pea roots rapidly reduced their elasticity and plasticity (measured as reversible and irreversible extension of segments cut from the extension zone) and reduced their water uptake within 20–30 min of horizontal exposure; these properties continued to decrease as long as the gravitropic curvature increased. When the roots reversed their curvature, the values increased again (Konings 1964). Apparently, pea root cells altered their cell wall properties and water uptake soon after horizontal exposure, which corresponds with their reduced elongation.

It seems very likely that cell wall rheological properties and turgor are tightly balanced in such dynamic tissues as the gravireacting root tip (Pritchard & Tomos 1994). New insight into the factors which determine cell elongation must be applied to root gravitropism and exact changes in cell wall properties, of which the above presents

a simple example, should be measured on opposite sides of a bending root tip, to fill the gap in our present knowledge.

NECESSITY OF THE ROOT CAP FOR GRAVITROPISM

In the work of Darwin (1880), Jost (1912) and several subsequent authors, it has already been demonstrated that removal of 0.5–2 mm of the tip of the root abolished gravicurvature. However, the exact part of the root tip necessary for graviresponse remained controversial until the necessity of the root cap for gravitropism was demonstrated by accurate removal of the whole root cap from maize roots (which have a well-marked boundary between cap and root proper) by Juniper *et al.* (1966) and by progressive removal of the root cap from pea roots (Konings 1967, 1968). It was also found that the cells in the central part of the root cap, the columella, were essential for graviresponse. Removal of a part or the whole of the root cap did not affect the root elongation (Juniper *et al.* 1966; Konings 1968; Barlow 1974; Pilet 1971), or caused transient growth stimulation (Pilet 1972; Wilkins & Wain 1974). Wounding was not likely to affect the graviresponse because the difference between 0.4 and 0.5 mm removal of the cap, for instance, is very small in terms of wounding, but the curvature was greatly diminished and not the elongation growth (Konings 1968, and see Jackson & Barlow 1981 for discussion).

When the root cap (the most apical 0.5 mm in pea roots) was removed at any time during gravicurvature, the bending process was stopped shortly after and was even reduced to some extent (Konings 1968; Pilet & Nougarede 1974). The graviresponsiveness has been found to correlate with the size of the root cap in primary maize seedling roots (Pilet 1982) and also when primary and secondary roots of *Phaseolus vulgaris* were compared (Ransom & Moore 1985).

Replacement of a removed cap (with an aqueous phase between cap and root) restored the graviresponse, but the bending was about 50% reduced (Pilet 1971; Moore & Maimon 1993) and the location of the curvature was different compared to undamaged roots (Pilet & Nougarede 1974), which suggests that the contact between the root proper and the replaced caps was not as good as with the attached caps. Roots from which the cap had been removed regenerated a new cap, but the graviresponsiveness was already partly restored when only a small part of the prospective cap was regenerated (Barlow 1974; Hillman & Wilkins 1982). The possible reason for this will be discussed in a later section. Root caps were not regenerated and roots did not bend during space flights in microgravity, but this cannot be used as an argument for the cap being the gravisensing organ as suggested (Moore *et al.* 1987b), because all cell divisions are disturbed in weightlessness (Halstead & Dutcher 1987).

The above results do show clearly that the root cap is somehow of crucial importance for gravitropism of roots. It is generally believed, therefore, that the cap is the site of graviperception (Volkman & Sievers 1979; Moore & Evans 1986; Sievers & Hensel 1991). However, the above results do not *demonstrate* that the root cap is the only gravisensing part of the root; in addition, removal of the cap removes not only the presumptive site of graviperception, but also the source of the signal(s) that cause unequal growth in the extension zone (Feldman 1985; Poff & Martin 1989), as will be discussed in following sections.

Interestingly, the root cap has also been found to be essential in hydrotropism (Takahashi & Scott 1993), thermotropism (Fortin & Poff 1991), electrotropism (Ishikawa & Evans 1990b) and, though less distinctly, in thigmotropism of roots

(Ishikawa & Evans 1992). It is also the site where the light-stimulus is perceived in species and cultivars that require light for their graviresponse (Pilet & Ney 1978). So, the root cap is apparently essential for the root to respond adequately to various changes in the environment.

DIFFERENT BEHAVIOUR OF THE DISTAL ELONGATION ZONE AND THE PROXIMAL PARTS IN THE GRAVIRESPONSE

Barlow & Rathfelder (1985), Selker & Sievers (1987), Zieschang & Sievers (1991), Ishikawa *et al.* (1991) and Ishikawa & Evans (1992) observed that the bending response began close to the tip, in the region between the meristem and the rapidly elongating cells of the central extension zone, whereafter the more proximal cells of the extension zone caught up. Cells involved in the positive bending were closer to the tip at the upper side than at the lower side (Selker & Sievers 1987; Ishikawa *et al.* 1991). Thus, the contributions of the different regions changed during gravicurvature. In the thin translucent roots of *Phleum pratense* (Zieschang & Sievers 1991) the region of first visible curvature comprised only six cells on both the upper and the lower side, but these were not located in the region of highest relative growth rates, where hormone effects are most apparent (Sievers & Zieschang 1992). During the transient partial straightening of the roots, the corresponding group of six cells at the lower side of these roots elongated rapidly.

This region has been designated as the distal elongation zone and also, because the cells show isodiametric growth, as the postmitotic-isodiametric growth zone (Baluska *et al.* 1990; Zieschang & Sievers 1991; Ishikawa & Evans 1992, 1993). In the latter paper, adaptation to a growth-inhibiting concentration of auxin, measured as release from inhibition, was observed in cells at the upper side of the distal elongation zone, but not in similar cells in the more proximal part of the elongation zone, and gravicurvature developed in the distal zone only.

Another example of different behaviours in the distal compared with the more proximal part of the elongation zone is in roots of *Phleum pratense*, where the greatest proton efflux occurred in the region with the fastest growth at the upper side. The lower side behaved as in vertical roots. The highest intensity of proton transport (uptake), however, was found in the distal extension zone (Zieschang *et al.* 1993). Pritchard & Tomos (1994) reported that the cells of the distal part of the elongation zone were less affected by water stress than the cells in the proximal part.

Finally, the distal region may have, apart from the root cap, a specific capability to sense gravity and touch (Ishikawa & Evans 1992) and it displayed a characteristic electric pattern upon gravistimulation (Ishikawa & Evans 1990a). Thus, it seems very likely that not only the root cap, but also the distal cells in the elongation zone are involved in the early events of the root graviresponse.

Now that we recognize how and where the gravitropic growth responses occur in roots and acknowledge the necessity of a root cap and, by implication, the transmission of signals from cap to root, the signals from the cap to the responding cells some distance away in the elongation zone will be discussed in the following sections.

ROLE OF AUXIN IN THE GRAVITROPIC BENDING RESPONSE OF ROOTS

For many years the role of auxin (indoleacetic acid, IAA) in the graviresponse has been dominated by the Cholodny–Went hypothesis (Went & Thimann 1937); essentially, this

says that in horizontally placed plant organs auxin, assumed to be produced in the tip of the organ, is deflected to the lower side. There the higher concentration would promote the rate of elongation in organs like grass coleoptiles and hypocotyls, but inhibit the elongation of roots, which was known to be reduced by minor concentrations of the hormone.

The evidence for the hypothesis regarding roots was poor at the time of its formulation, because neither the production of auxin in the root tip, nor its deflection to the lower side of a horizontal root tip and its basipetal transport had been demonstrated (Audus 1975; Firn & Digby 1980). Even now the evidence is weak (Evans 1992; Scott 1992). In fact, the evidence obtained with grass coleoptiles and hypocotyls, which seems beyond doubt (Briggs 1992; Harrison & Pickard 1989) has been extrapolated to roots.

It is unlikely that such a simple concept could explain the growth accelerations and retardations of the opposite sides of the graviresponding root tips and the oscillations as described earlier (Audus & Brownbridge 1957; Konings 1964; Selker & Sievers 1987; Ishikawa *et al.* 1991).

Although the role of auxin in root gravitropism will probably not be as proposed by the Cholodny–Went hypothesis, several experimental results suggest that the hormone is of major importance in root gravicurvature.

1. IAA is preferentially transported to the lower side of the root tip when applied to the extreme tip (Konings 1967) and also when applied to the upper or lower side of the root cap (Young *et al.* 1990; Young & Evans 1994).

2. The distribution of externally tip-applied IAA in favour of the lower side, in the order of 2:1 (Konings 1967) or 1.6:1 (Young *et al.* 1990; Young & Evans 1994) may explain the growth differences observed, because the dose–response relation for root (Pilet & Saugy 1987) and shoot elongation (Migliaccio & Rayle 1989) is probably not logarithmic as has long been assumed, but arithmetic.

3. IAA applied exogenously at several cm from the root tip, promoted the gravitropic curvature within 30 min, suggesting a rapid acropetal transport of several cm per h (Konings 1969; Pilet 1977).

4. TIBA (2,3,5-triiodobenzoic acid) and NPA (naphthylphtalamic acid), both inhibitors of polar cell to cell IAA transport (which assumes that IAA enters the cell from the acidic apoplast and is trapped inside as anion, due to the higher pH inside; the anion is effluxed asymmetrically by the action of IAA-anion carriers located at the bottom of the cell; TIBA and NPA block these carriers), abolished the influence of acropetally transported IAA; when applied to the root cap they prevented the graviresponse (Konings 1968, 1969; Hasenstein *et al.* 1988).

5. Calcium-promoted lateral IAA transport in root caps is inhibited by IAA transport inhibitors (Hasenstein & Evans 1988; Young & Evans 1994); calmodulin-inhibitors applied to the root cap reduced the transport of exogenously applied IAA from the upper to the lower side in the elongation zone (Stinemetz *et al.* 1992).

6. Exogenously applied IAA inhibits root growth in very low concentrations, lower than any of the other growth regulators found in roots do (Jackson & Barlow 1981; Moore & Evans 1986).

7. Roots of the auxin-unresponsive mutant *aux 1* of *Arabidopsis thaliana* do not bend when horizontally exposed (Pickett *et al.* 1990; Okada & Shimura 1992).

8. IAA has been found in root caps in higher amounts than in the elongation zone (Rivier & Pilet 1974; Pilet 1977; and see Jackson & Barlow 1981). There is, however, no evidence for its *production* in root caps (Feldman 1981).

9. Transport of exogenously IAA, applied at various distances from the root tip, of intact seedlings is strongly polarly towards the tip (Morris *et al.* 1968; Konings & Gayadin 1971; Davies & Mitchell 1972; Juniper 1976; Feldman 1981). Endogenous IAA probably arrives in the tip from more basal parts of the root or from the shoot via the phloem (Eschrich 1968).

10. IAA-movement in the tip was found to be predominantly basipetal when the root cap was present and acropetal when the cap had been removed (Davies *et al.* 1976; Hasenstein & Evans 1988).

11. Gravicurvatures are connected with proton efflux patterns consistent with the rate of growth at the opposite sides of the curving root tip (Mulkey & Evans 1981). This different efflux pattern was abolished by orthovanadate, an inhibitor of auxin-stimulated proton excretion. Also inhibitors of auxin transport like TIBA and NPA inhibit asymmetric proton efflux and gravicurvature (Mulkey & Evans 1982).

Taken together, these findings present a strong body of argument that IAA is involved in root graviresponse.

As mentioned above, IAA is found in the root cap but it is not produced there and, therefore, must arrive from other parts of the root. The cap distributes applied IAA in favour of the lower side (Konings 1967; Young *et al.* 1990; Young & Evans 1994). It was proposed by Konings (1969) that IAA would be acropetally transported towards the root cap probably via phloem and plasmodesmata, would then become laterally distributed in the cap and then transported backwards (probably via another pathway) in unequal amounts to the extension zone where it would affect elongation differently and promote gravicurvature. This concept was endorsed by Young *et al.* (1990) and extended by Young & Evans (1994) who included calcium-promoted lateral IAA distribution in the root cap.

This concept assumes symplastic transport from the sieve tubes through plasmodesmata into the root cap. This could well take place, because plasmodesmata have their greatest density in transverse walls in the cap-root junction in maize roots (Juniper & Barlow 1969; Juniper & French 1970; Moore & McClelen 1989). Their density is lower in longitudinal walls of root cap cells, but the total number is judged to be similar in the two walls. A transversal pathway for IAA transport might thus be present in the root cap.

Moore & McClelen (1989) found that in maize roots the frequency of plasmodesmata was lowest at the site where the cap-root boundary is thickest and basipetal transport in a horizontal root is assumed to be greatest. They concluded from decapitation and recapping experiments that the signal from the cap could be transported apoplastically and that plasmodesmata are not necessary for *basipetal* cap to root transport.

To integrate auxin action and growth of graviresponding roots, Evans (1991) supposed that during the first period of rapid curvature the lower side was inhibited by a higher IAA concentration as the result of lateral displacement and that the upper side was promoted by a reduced level of IAA. When after about 2 h the pattern reversed, the lower side showed a dramatic increase in the rate of elongation, probably because the cells at the lower side became less sensitive to IAA, they were adapted, a phenomenon observed at several occasions (Gougler & Evans 1981). The IAA concentration then became stimulatory for growth. At the same time the reduced growth at the upper side would result from an enhanced sensitivity to IAA. Subsequently, the inhibited upper side would in turn be stimulated when these cells became adapted. This mechanism would be repeated and would cause the roots to oscillate. Supporting evidence is that the timing of the recovery of the growth inhibition of the lower side coincided with the

timing of recovery from IAA-induced growth inhibitions as found in vertical roots (Gougler & Evans 1981).

Although exogenously applied IAA can be unequally distributed in the root cap, the time it takes to establish the gradient is roughly equal to the time the curvature appears, suggesting a very rapid transport to the elongation zone (Young *et al.* 1990). However, the transport velocities found were generally only a few mm per h (Konings 1967; Pilet 1977; Young *et al.* 1990; Young & Evans 1994). To explain quick responses of the cells in the elongation zone, it has been supposed that gravity is detected directly by the responding cells (Ishikawa & Evans 1992) or that a rapid electric signal passes from cap to extension zone, which 'prepares' the cells for the auxin which will arrive soon (Sievers & Zieschang 1992).

Suggested alternative mechanisms for the cap-controlled unequal IAA distribution in the elongation zone are that the hormone could be unequally released from its transport path in the stele to the cells of the extension zone or that IAA could be differently released from a bound form in the opposite sides of the elongation zone (Evans 1991).

A problem has always been to determine auxin at its site of action. Auxin determined in extracts is of little value as long as the most responsive cells are not definitely known. When bulk extractable auxin is determined and no difference is found between the opposite sides, even with sophisticated methods, as by Mertens & Weiler (1983), there is still no convincing proof for the absence of a difference, because it seems probable that the auxin which was actually involved locally was masked by the extract of halved tips.

It has been found recently that an auxin-regulated RNA promoter, measured as GUS-expression, was enhanced by physiological doses of auxin and was in gravistimulated hypocotyls greatest in the lower side. The asymmetry of GUS-expression was blocked by inhibitors of polar auxin transport (Li *et al.* 1991). This seems to be an accurate, though indirect, determination of auxin in the tissue at the site of action.

Although IAA is obviously an important factor in root gravitropism, there are other possible putative regulating substances of the graviresponse, which will be discussed in the following sections.

ETHYLENE AND ROOT GRAVITROPISM

The young expanding cells close to the meristem produce the greatest amount of ethylene (Abeles 1973) and this region may well comprise the graviresponding cells which are now recognized as the postmitotic-isodiametric growth zone. The gas has been found to stimulate root elongation at low concentrations and to inhibit it at higher concentrations (Konings & Jackson 1979), so it is not hard to imagine that ethylene could interfere with graviresponse. Light-induced inhibition of root elongation was found in maize roots to result from enhanced ethylene levels (Jackson & Barlow 1981).

Enhanced ethylene release has been reported for slowly rotating cress roots corresponding with a reduced elongation, and application of $0.2 \mu\text{l l}^{-1}$ ethylene strongly inhibited the elongation and the curvature of gravitropically exposed roots (Hensel & Iversen 1980).

Mulkey & Vaughan (1986) and Lee *et al.* (1990) found that inhibitors of ethylene synthesis or action prevented gravicurvature of maize roots, which suggested that the gas is necessary for the graviresponse. The latter authors also found that applied ethylene (10 ppm) delayed the gravicurvature and that NPA, an auxin transport

inhibitor, not only inhibited the curvature, but also the ethylene effect. Ethylene probably inhibited the lateral transport of auxin.

Exogenously applied auxin above a certain level is known to promote ethylene production (Abeles 1973). It is not known, however, whether the endogenous auxin concentration in roots ever reaches that level under normal growth conditions or during gravistimulation. Interestingly, the agravitropic auxin mutant *aux 1-7* not only showed a strongly reduced sensitivity to auxin but also to ethylene, suggesting that the two are connected and that both are involved in the gravitropic response.

If a gradient in tension and stress is created between the two sides when a root is placed horizontally, as supposed by Pickard & Ding (1993), then the upper side might produce a transiently stimulating concentration of ethylene and the lower side a growth-inhibiting quantity. The growth inhibition of the lower side could disappear and be replaced by a growth stimulation because of outward diffusion of the gas. Oscillations could tentatively be explained by changes in ethylene production at the two sides as a result of alternating tension and compression.

Although ethylene is intimately involved in growth at the cellular level, its influence on graviresponses may not be a specific one. Further research is needed to confirm its role in gravitropism unequivocally.

A POSSIBLE ROLE FOR PHENOLIC COMPOUNDS IN ROOT GRAVITROPISM

After 20–30 min of horizontal exposure, the IAA-oxidase activity measured in homogenates prepared from lower halves of pea root tips was lower than that of the upper halves (Konings 1964, 1967). This suggested accumulation of some di- or polyphenolic compound in the lower side, which would inhibit the *in vitro* IAA-oxidase activity, but promote the graviresponse by enhancing the growth rate of the upper side of the root tip (Konings 1964). Neither the relevance of this finding was clear nor the presence and potential significance of IAA-oxidase found in the amyloplast membrane (Juniper 1976). Audus (1975) considered IAA-oxidase in the roots as being an evolutionary relict.

Interestingly, Jacobs & Rubery (1988) found that the polyphenols (flavonoids) quercetin and apigenin and related substances (Katekar *et al.* 1993), which are widely distributed in plants could remove bound naphthylphthalamic acid (NPA) from its receptor in zucchini hypocotyl tissue. This substance very probably inhibits the efflux of IAA at the cell base during the assumed chemiosmotic auxin transport from cell to cell. So, certain phenolic compounds could feasibly play a role in regulating cell to cell IAA transport in this tissue and possibly also in roots (Muday & Haworth 1994).

The pattern of activity of these phenols on IAA-oxidase activity was different from that on IAA transport and caffeic acid, which is a strong inhibitor of IAA-oxidase *in vitro*, had no effect on the transport process (Jacobs & Rubery 1988). So, if the reduced IAA-oxidase activity in the lower halves of horizontal pea root tips reflects an increased concentration of some polyphenol, the presence of it might facilitate auxin transport in the lower halves by abolishing the effects of IAA-transport inhibitors. In general, polyphenols in plants play an important role in the relation of the plant with its environment, notably light, and the example presented above suggests that they could also be of importance in the gravitropic response.

IS GIBBERELIC ACID INVOLVED IN ROOT GRAVITROPISM?

Stimulation of gravitropism by gibberellic acid (GA), has been reported many years ago (Konings 1961). El-Antably & Larsen (1974) found twice as much GA in the upper halves of *Vicia faba* root tips than in the lower halves after 30 min of horizontal exposure, and Webster & Wilkins (1974) found higher amounts in the upper halves of maize roots when GA was applied to the tips. GA-deficient mutants, however, were found to be graviresponsive as normal roots (Juniper 1976).

GA is crucial in shoot cell elongation (Métraux 1987) and mutants deficient in GA show a reduced elongation of root cells (Barlow *et al.* 1991). The reorientation of microtubuli from the normal transverse to an oblique position, which is connected with reduced cell elongation (Shibaoka 1993) has also been described for GA-deficient mutants. Notwithstanding the crucial role of GA in cell elongation, and some indications that the hormone is involved in early events of the graviresponse, its role has not been further established.

CONCEPT OF A CAP-PRODUCED GROWTH INHIBITOR CONTROLLING GRAVICURVATURE: THE CANDIDACY OF ABSCISIC ACID

The necessity of the root cap for gravitropism implies that some signal must travel from the cap to the responsive cells in the extension zone. Although this signal could well be IAA, as discussed before, a number of observations lead to the concept that a growth inhibitor other than IAA is involved in root graviresponse (see Audus 1975 and Jackson & Barlow 1981 for extensive discussion). Briefly, the major arguments in favour of a cap-produced inhibitor transported to the elongation zone are as follows.

1. Growth inhibition of the lower side of the gravicurving root tip was much stronger than stimulation of the upper side (Audus & Brownbridge 1957; Audus 1975; Pilet & Ney 1981), suggesting that it was not auxin redistribution that caused the reduced growth, but rather the synthesis of an inhibitor in the lower half of the root tip.
2. Exogenously applied auxin was found to inhibit the upper and lower side of a curving root tip to a similar extent, which would not be expected if IAA was the growth inhibitor present in higher concentration in the lower side (Audus & Brownbridge 1957; Audus 1975).
3. Decapped maize roots elongated temporarily faster than the intact controls (Pilet 1972; Wilkins & Wain 1974).
4. Placing a cap of a maize root eccentrically on the cut end of a root which had its own cap removed reduced the elongation of that side (Pilet 1972; Wilkins & Wain 1974); detached caps of maize roots inhibited the elongation of intact cress roots (Pilet 1972).
5. Removal of half the cap of a maize root resulted in a curvature towards the remaining half-cap, irrespective of the position of the root (Gibbons & Wilkins 1970; Shaw & Wilkins 1973).
6. Insertion of a small impermeable barrier perpendicular to the root axis, between cap and elongation zone on one side of a maize root, resulted in curvature away from the barrier; but a barrier placed proximal to the extension zone, at 4–5 mm from the apex of detached roots, did not interfere with gravicurvature (Shaw & Wilkins 1973).
7. In a number of maize cultivars, light reduced the elongation and promoted gravicurvature (Wilkins & Wain 1974, 1975a; Pilet & Ney 1978); illuminated caps had more growth-inhibiting activity than dark-grown caps (Wilkins & Wain 1974, 1975a).

All these results have readily been interpreted as support for the involvement of a growth inhibitor moving from the root cap to the root proper, at least in maize roots. However, pea roots (Konings 1968), maize roots (Pilet 1971) and roots of several other species (Juniper 1976) did not grow faster after decapping. The transient faster elongation after decapping found by Pilet (1972) and Wilkins & Wain (1974), may have been effected by thigmotropic stimulation (Ishikawa & Evans 1992). Further, the results of microsurgical experiments could tentatively also be explained by the presence of auxin in the (half-) caps, and IAA transported towards the root tip in the stele could probably pass a barrier placed at 4–5 mm from the apex undisturbed and promote gravicurvature.

For several years the growth inhibitions of the lower side received too much attention relative to the growth accelerations of the upper side. Jackson & Barlow (1981) discussed the inhibitor research extensively and concluded that the case for a cap-produced inhibitor was not strong and that growth acceleration of the upper side and inhibition of the lower side may result from release of an inhibitor from the upper side and its transport to the lower side and that the inhibitor does not need to arrive from the root cap.

However, once the general feeling was that an inhibitor other than IAA must be present in the root cap, and the research tools like GC-MS were available, it was attempted to identify the inhibiting substance. The inhibitor was first thought to be abscisic acid (ABA) for a number of reasons (see also review by Jackson & Barlow 1981).

1. Both ABA-like substances and ABA active in bio-assays were extracted from root caps in which IAA was not detected (Kundu & Audus 1974; Wilkins & Wain 1974); ABA was also detected in caps by GC/MS analysis (Rivier *et al.* 1977).

2. Exogenously applied ABA can inhibit root elongation (Pilet & Chanson 1981).

3. In horizontally placed maize root segments more of the ABA absorbed by the segments was found in the lower half of the extension zone than in the upper half; the upper half lost as much as the lower half gained (Pilet & Rivier 1981). El-Antably & Larsen (1974) found three times more ABA in the lower halves of *Vicia faba* roots stimulated for 30 min.

4. Cultivars of maize which did not curve in the dark, did so in the light and then contained more ABA in their caps (Wilkins & Wain 1974, 1975a,b; Pilet & Rivier 1980).

5. Wilkins & Wain (1975b) and Pilet & Rivier (1980) observed that the slow curvature of the light-requiring maize cv.LG11 could be enhanced in the dark by ABA pretreatment before gravistimulation. Abscisic acid thus substituted for the light treatment. Similarly, Leopold & La Favre (1989) found that red light promotion of curvature could be satisfied by ABA. Feldman *et al.* (1985) observed that light treatment produced a shift of ABA from the cap to the proximal region of root tips within the gravitropic reaction time. Leopold & La Favre (1989) detected more ABA in the growing region coinciding with red light-promoted graviresponse. These findings suggest the involvement of ABA in the light-promoted (maize) root graviresponse.

The role of ABA as a major growth inhibitor can, however, be questioned for the following reasons.

1. In contrast to other reports (Kundu & Audus 1974; Wilkins & Wain 1974), about 10 times more IAA than ABA was found in root caps (Pilet 1977).

2. No transverse gradient of endogenous ABA is detected in the root cap (Young & Evans 1992) and no polar basipetal transport from the cap to the extension zone has

been observed in non light-requiring roots (Jackson & Barlow 1981; Hasenstein & Evans 1988).

3. Replacement of a removed half-cap by ABA had no effect on the curvature which occurred towards the remaining half-cap, whereas IAA reversed it (Lee *et al.* 1990). Exogenously applied ABA in the concentration of 10^2 mmol m^{-3} does not inhibit root elongation significantly; for comparison IAA at 10^{-2} mmol m^{-3} causes strong inhibition (Jackson & Barlow 1981). Thus, ABA is a poor inhibitor of root elongation compared to IAA at similar concentrations.

4. ABA promotes rather than inhibits root growth when applied exogenously (Jackson & Barlow 1981; Mulkey *et al.* 1983); and also when its internal concentration increases at a low water potential (Saab *et al.* 1990).

5. The graviresponse was not affected when the level of endogenous ABA was reduced by treatment with its biosynthesis inhibitor fluridone (Moore & Smith 1984), or in mutants with very low ABA levels (Moore & Smith 1985).

6. Polar transport of IAA in root tips is promoted by Ca^{2+} , but ABA transport is not (Hasenstein & Evans 1988).

Taking all results together, these apparent contradictions suggest that ABA is unlikely to have a role as an important growth inhibitor transported from the root cap to the extension zone, with the possible exception of roots that require light for their graviresponse. In my opinion the arguments denying an essential role for ABA in root gravitropism seem stronger than the ones supporting it, but clearly its role in root growth and gravireaction must be further elucidated.

ROLE OF CALCIUM IN ROOT GRAVITROPISM

Although the stimulating influence in low concentrations of calcium ions (Ca^{2+}) on graviresponses of roots in water culture has already been shown by Rufelt (1957b) and Zinke (1968), its crucial role in root gravitropism has been recognized only during the last decade by the following results.

1. The tips of vertical roots bend towards the Ca^{2+} -source when it is asymmetrically applied (Lee *et al.* 1983a); the distal elongation zone is especially sensitive to Ca^{2+} (Ishikawa & Evans 1992).

2. Graviresponse was prevented by treating root tips with the Ca^{2+} -chelator EDTA, but was restored when EDTA was replaced by Ca^{2+} (Lee *et al.* 1983b).

3. $^{45}Ca^{2+}$ applied either at the upper or the lower side of a horizontally placed root tip, moved preferentially to the lower side; no polar movement across the tips occurred when the root cap had been removed (Lee *et al.* 1983a).

4. The agravitropic mutant (*agt*) of maize showed very little polar transport of Ca^{2+} in root tips (Moore *et al.* 1987a).

5. TIBA and NPA, both inhibitors of IAA transport, also block Ca^{2+} translocation in the root cap and prevent or stop gravicurvature (Lee *et al.* 1984).

6. Inhibitors of calmodulin (the Ca^{2+} -binding protein through which all further action is assumed to occur) inhibited the graviresponse of roots (Björkman & Leopold 1987b; Hasenstein & Evans 1988) and also the lateral transport of Ca^{2+} across root caps (Stinemetz *et al.* 1992).

7. Björkman & Leopold (1987b) measured a change in electric current in the root cap cells upon gravistimulation, which could be abolished by inhibitors of calmodulin action and thus was probably connected with Ca^{2+} transport.

8. Decapped maize roots developed a downward apoplastic gradient of Ca^{2+} in their regenerating root tips, coinciding with the return of graviresponsiveness; binding of the free Ca^{2+} prevented the curvature (Björkman & Cleland 1991b).

9. Suzuki *et al.* (1994) reported that maize roots, which were agravitropic in the dark, released more Ca^{2+} in their caps and became positive graviresponsive when illuminated. Diagravitropic maize roots in the dark contained much less Ca^{2+} than the positive graviresponsive roots in the light (Leopold & Wettlaufer 1988). Leopold & La Favre (1989) observed that red light or ABA treatment increased the Ca^{2+} -level in the root tip.

10. In horizontal maize roots the ratio of Ca^{2+} present in the mucilage at the lower side and at the upper side of the root cap and tip was 2.5–3 and about 6 in the mucilage surrounding the elongation zone (Moore *et al.* 1987c).

11. Ca^{2+} appeared to be indispensable for the graviresponse of maize roots in solution culture (Nantawisarakul & Newman 1992).

These data present good evidence that a transverse gradient of Ca^{2+} develops in caps of gravistimulated roots, which is probably transmitted to the elongation zone and is essential for the graviresponse.

Poovaiah & Reddy (1991) proposed the following sequence of events during root gravitropism. Calcium is assumed to increase in the cytosol of root cap cells following gravitropic stimulation (or by light, in the light-requiring maize cultivars). This increase activates calmodulin, leading to stimulation of Ca^{2+} - and Ca^{2+} -calmodulin-dependent enzymes such as Ca^{2+} -ATPase and protein kinase, ultimately leading to both intra- and extracellular Ca^{2+} -gradients. This asymmetric Ca^{2+} distribution could modify cytoskeletal proteins, microtubule orientation, and cell wall synthesis and deposition in different ways. The growth gradient would result in bending.

The role of Ca^{2+} was further endorsed by studies on its localization in root caps (Moore & Evans 1986, refs therein). By antimonate precipitation (assumed to represent free calcium) they found only small amounts of Ca^{2+} along the plasmalemma in vertical roots in the columella cells; it moved into the distal cell walls of the columella cells in large quantities within 5 min of horizontal exposure, but was absent from lateral walls. These findings suggested that Ca^{2+} did not move transversally through the horizontally oriented columella cells, but longitudinally towards the apex of the root cap.

It follows from this and an earlier section that both auxin and calcium are apparently intimately involved in the gravitropic response and their actions must somehow be integrated in root gravicurvature. Various data indicate that Ca^{2+} affects IAA transport.

1. It was found that the stimulation of root growth by IAA was dependent on the presence of Ca^{2+} (Hasenstein & Evans 1986).

2. IAA transport in root tips was predominantly basipetally, but when the cap (which is rich in Ca^{2+} and calmodulin) was removed, predominantly acropetally (Hasenstein & Evans 1988).

3. Ca^{2+} promoted the basipetal transport of IAA in the root cap and the Ca^{2+} -chelator EGTA reduced this Ca^{2+} effect (Young & Evans 1994).

4. Al^{3+} -ions applied to the root tip inhibited calmodulin and promoted the acropetal IAA transport (Hasenstein & Evans 1988).

Moore & Evans (1986) showed that the Ca^{2+} transported into the root cap was secreted distally into the cap-produced mucilage, both in vertically and horizontally oriented roots (Moore & Evans 1986 and refs therein). The preferential movement of

Ca^{2+} towards the lower side of a horizontal root cap was also assumed to occur in the mucilage surrounding it (Lee *et al.* 1983a,b). Ca^{2+} from endogenous sources was also found in higher amounts in the mucilage at the lower side of horizontal root tips (Moore *et al.* 1989). Thus, a transverse gradient of Ca^{2+} in the root cap mucilage was apparent. Moore & Evans (1986) and Moore *et al.* (1987c) suggested that an electrochemical gradient developing soon after horizontal exposure of roots (Behrens *et al.* 1985), could be the motive force for downward and basipetal movement of Ca^{2+} .

Calcium could be supposed either to sensitize the responsive cells in the extension zone to auxin, which would result in growth inhibition of the lower side without the necessity of IAA asymmetry, or Ca^{2+} could act as a sink for IAA, which would then be transported together with it and become transversely distributed. The first possibility would agree with the equal distribution of IAA in root tips (Mertens & Weiler 1983). However, other arguments support the second possibility.

1. Ca^{2+} promoted lateral distribution of IAA in the root cap (Young & Evans 1994) and treatment with the Ca^{2+} -chelator EGTA interfered with the longitudinal transport of IAA (Hasenstein & Evans 1988).

2. Labelled IAA, when applied to the root cap, was unequally distributed between the lower and the upper side in a ratio between 1.7:1 and 2:1 (Konings 1967; Davies *et al.* 1976) or 1.6:1 (Young *et al.* 1990; Young & Evans 1994). These values are close to the ratio of 2:1 found for unequally distributed Ca^{2+} after application to the cap (Lee *et al.* 1983a) and in the mucilage from endogenous sources (Moore *et al.* 1987c). These data suggest that Ca^{2+} and IAA displacement are connected and that Ca^{2+} may induce migration of IAA to the lower side of the elongation zone.

So, acropetally transported IAA may travel from the phloem via plasmodesmata into the root cap (Konings 1969; Young *et al.* 1990; Young & Evans 1994) and may be co-secreted with Ca^{2+} into the mucilage; both are transported in the mucilage (Moore & Evans 1986) or may even be displaced with bulk mucilage transport. In the extension zone a concerted action of Ca^{2+} and IAA would then lead to a gravitropic growth response. However, IAA and Ca^{2+} in the root cap might behave according to the model of Cleland (1992), which proposed that the higher concentration of Ca^{2+} in starch-containing cells (in the shoot, but is also applies to the columella cells in the root cap) following gravitropic stimulation would close the plasmodesmata in the lateral direction and activate the IAA-efflux carriers located at the lower walls, resulting in a polar transversal IAA transport (according to the chemiosmotic theory of IAA transport). In conclusion, one of the major roles of Ca^{2+} in root gravitropism is probably its control of IAA transport.

CAP-SECRETED MUCILAGE AS AN APOPLASTIC PATHWAY FOR TRANSMISSION OF SIGNALS FROM CAP TO ROOT

Moore & Evans (1986) described the lateral transport of Ca^{2+} in the cap-secreted mucilage and a number of observations suggests that it may function as an apoplastic pathway between cap and root.

1. Wiping mucilage from the root cap retarded the graviresponse and wiping it from one side of a vertical root resulted in a curvature to that side (Moore & Evans 1986).
2. Washing roots in distilled water removed their mucilage and delayed their graviresponse (Moore & Evans 1986).

3. Adventitious roots of *Allium* growing in water were not graviresponsive, but after transfer to moist air produced more mucilage and developed gravicurvatures. In case of a symplastic Ca^{2+} transport, no difference would be expected between response in water and air (Moore & Fondren 1986).
4. An inhibitor of Ca^{2+} -ATPase in the ER in caps of cress roots inactivated the secretion of mucilage by the Golgi-apparatus and also inhibited gravitropism (Busch & Sievers 1993).
5. Decapped roots of maize formed mucilage between plasmalemma and cell wall (Barlow 1974; Barlow & Sargent 1978) which coincided with the return of graviresponsiveness.
6. A downward transverse gradient of Ca^{2+} has been found in the apoplast (probably mucilage) of tips of decapped horizontal roots, coincident with the return of graviresponsiveness (Björkman & Cleland 1991b).
7. The non-graviresponsive maize cv. ageotropic, secretes very little mucilage and the edge of the root cap is not connected with the root. When the space between cap and root was filled with agar or jelly, the roots became graviresponsive (Moore *et al.* 1990; Moore & Maimon 1993).
8. The mucilage around the tips of horizontal maize roots contained more Ca^{2+} at the lower side than at the upper side (Moore *et al.* 1987c).
9. The graviresponsiveness correlated positively with the size of the columella tissue (Moore 1985); bigger caps are more graviresponsive (Pilet 1982) and create probably greater differences in concentrations of gravitropic effectors in the mucilage.

It has also been argued that removal of the root cap or part of it, abolished or reduced the gravicurvature (Juniper *et al.* 1966; Konings 1968) because the mucilage was removed. This argument is not valid, since decapping also removed the site where Ca^{2+} and probably also auxin, are laterally distributed.

The above arguments look convincing for the few species studied, but should now be extended to more species.

To underline the fact that the evidence is incomplete so far, Millet & Pickard (1988) reported no influence on curvature when mucilage was washed away from maize roots in distilled water and concluded that apparently the bulk mucilage was not required for normal curvature. Takahashi & Scott (1993) also found no support for a role of bulk mucilage in hydrotropism. So, it is probably not the bulk of the mucilage that is important, but the thin layer enveloping the root (Chaboud & Rougier 1985).

Root-secreted mucilage is assumed to protect the root meristem in the soil and to facilitate the sliding of the root through the soil. However, the shell of mucilage is only present under highly hydrated conditions so that lubrication does not seem likely in dryer soils (Guinel & McCully 1986). On the other hand, mucilage production is increased by mechanical resistance, which is higher in drier soils (Iijima & Kono 1992). However, too little is known about the behaviour of roots in the soil and it is difficult to imagine how the apoplastic transport of gravitropic effectors, which seems clear in roots in humid air, would function in a wet soil.

DO ROOTS HAVE AN INTERNAL TRANSPORT PATHWAY FOR GRAVITY EFFECTORS FROM ROOT CAP TO THE EXTENSION ZONE?

There is widespread agreement that a signal must be basipetally transported from cap to root potentially along an apoplastic mucilage pathway. An internal probably

symplastic pathway might also exist, being localized in the epidermis and/or the outer cortical layers, as the stelar cells presumably carry auxin towards the root tip (Shaw & Wilkins 1974; Young *et al.* 1990) and the epidermal layer probably limits growth of roots (Tomos *et al.* 1989) and shoots, and may even sense gravity (Firn & Digby 1980).

Microsurgical removal of a 0.5 mm wide girdle of tissue consisting of epidermis and one or two outer cortical layers at 1.5–2 mm behind the apex of maize roots almost abolished the gravicurvature (Yang *et al.* 1990). Their conclusion was that the signal moved in the outer cortex and/or epidermis. As filling the girdle with agar restored the bending, the signal could apparently be transported apoplastically. By contrast, Björkman & Cleland (1988) found that removal of the epidermis and the whole cortex of primary maize roots reduced the curvature, but did not prevent it, irrespective of the orientation of the cut surface (suggesting that wounding did not affect the response). Only when the endodermis was damaged was the root curvature blocked. In these roots the endodermal or stelar cells seemed the apparent transport path rather than the outer cortical layers. In a subsequent paper Björkman & Cleland (1991a) showed that removal of the epidermis between the root cap and the end of the elongation zone did not reduce the gravitropic response of the roots, thus confirming the earlier results.

Maimon & Moore (1991) found that microsurgical removal of a 1 mm wide circular layer of epidermis and 2–10 layers of the 20 layers thick cortex of the distal elongation zone did not alter the gravicurvature in the part distal of the incision, but there was no curvature in the zone proximal to it. When the removed tissue was replaced by jelly, the proximal part of the elongation zone also took part in the bending response. The effect of a shallow girdle (2–10 layers) was similar to that of a deep one (the whole cortex removed), which indicates that the outer cortical layers and/or the epidermis, play an important role in the internal transport of a growth inhibitor from the root cap to the extension zone.

A firm conclusion on the cell layers which function as the internal transport pathway of a signal from the cap to the elongation zone cannot be drawn on the basis of these conflicting results, although the epidermis does not seem to be as important for root growth as has been assumed. The signal can apparently pass a layer of jelly, which indicates apoplastic rather than symplastic transport. However, responses of surgically treated roots must be interpreted with great care as long as it is not unequivocally shown that the wounding does not affect the responsiveness of the roots.

It is accepted that microtubules align the cellulose microfibrils in the cell wall, which in turn determine the direction in which the cell expands. So, reorientation of the microtubules could give information on the growth of the cells and the pathway of effector transport.

Blancaflor & Hasenstein (1993) found that the microtubule orientation in the epidermis and the cortical cells of the upper side of the extension zone of gravistimulated maize roots remained perpendicular to the longitudinal axis, as in vertical roots. In the outer cortex layers of the lower side the microfibrils rearranged parallel to the axis of the root, but in the lower epidermis they remained transversely oriented. This situation agrees with the growth pattern as described for these roots, i.e. reduced elongation of the lower side and unchanged or accelerated growth at the upper side. A prominent role for the epidermis does not follow from these results. The orientation in the columella cells also changed from transverse to parallel, which might result from an enhanced IAA concentration in the root caps (Hasenstein & Evans 1988). However, using maize

coleoptiles, Nick *et al.* (1991) found that microtubule reorientation and tropistic bending were not closely related and that the relation between microtubule orientation and auxin was complex.

Conclusions about the relationship between microfibril orientation and growth can only be drawn if the timing of changes in microfibril angle and extension are accurately determined.

POSSIBLE SIGNIFICANCE OF RAPID CHANGES IN ELECTRICAL CURRENTS AND MEMBRANE POTENTIAL IN GRAVISTIMULATED ROOTS

Electric current flows around roots vary with time, root development and plant species. Iwabuchi *et al.* (1989) measured different electric profiles along roots coincident with differences in growth rate. The profiles were closely correlated with proton-efflux patterns and notably the pattern around the cap changed immediately upon gravistimulation. When Ca^{2+} was omitted from the test solution, the electric pattern changed and no graviresponse was observed. Weisenseel *et al.* (1992) observed that in cap and meristem of horizontal roots the current flow became asymmetric, an outwardly directed electric current at the upper side and inwardly directed one at the lower side of those roots that subsequently curved. These roots became gravitropic unresponsive when the Ca^{2+} -concentration was too low.

Behrens *et al.* (1982) observed that the symmetrical flow of current, with current flowing outwards at the elongation zone and inwards at the root cap, meristem and distal elongation zone, was replaced in gravistimulated roots by an acropetally directed current flow at the upper side of the root cap and a basipetally directed current at the lower side, followed a few minutes later by current flows in the same direction in the meristem region and distal elongation zone. No changes were observed in the proximal elongation zone in comparison with vertically oriented roots.

Behrens *et al.* (1985) measured transient changes in membrane potential in statocyte cells of the root cap upon gravistimulation, where the upper flank hyperpolarized and the lower depolarized. They supposed that in gravistimulated roots Ca^{2+} was released from storage compartments (ER), which affected the existing electrical pattern by stimulating proton pumping to the apoplast. A similar release of Ca^{2+} from ER-cisternae following gravistimulation and leading to an ion flux towards the upper side of the root cap has been postulated by Sievers & Hensel (1991). Since this change in electric pattern precedes root bending it may be closely linked to the transmission of a signal from the root cap to the elongation zone.

Within 30 s of horizontal exposure of roots, Ishikawa & Evans (1990a) observed hyperpolarization in cortical cells at the upper side of the distal elongation zone 2 mm behind the root tip and depolarization at the lower side (from -115 mV to -154 mV and -62 mV, respectively). This difference disappeared when the roots were placed vertically again. Such rapid changes suggest that perception of gravity may also be possible in the distal elongation zone.

It is essential, however, that in gravistimulated roots the events in the columella cells can be discriminated from the current related to physiological processes in the elongation zone; this has been done by Björkman & Leopold (1987a), who measured current density (ampère m^{-2}) with the aid of a vibrating probe and found that a

transient outwardly directed current appeared in the upper flank of the columella cells at a predictable time of 3.6 min, coinciding with the gravitropic presentation time, whereas no electrical changes were measured at the extension zone or at the extreme root tip (the cells in the mucilage). The membrane potential of the upper flank statocytes transiently hyperpolarized, while that of the lower side depolarized (the change being less distinct and less predictable than at the upper side), leading to an ion flux to the upper side of the root cap. Although these electrical changes were slow relative to others discussed above, the place and time of appearance suggest correlation with the graviresponse.

Björkman & Leopold (1987a,b) further found that the auxin transport inhibitors TIBA and NPA blocked the gravicurvature, but not the outward current. On the other hand, inhibitors of calmodulin activity blocked both current and curvature when applied to the root cap. In conclusion, auxin transport does not coincide with the displacement of electrical charges, but calmodulin activity does; thus, the process is probably linked to Ca^{2+} -release and transport, in agreement with the conclusions of Behrens *et al.* (1982, 1985).

The major components of the rapidly changing currents are H^+ -ions, but this proton extrusion is different from the well-known auxin-stimulated proton pumping connected with cell growth (Mulkey & Evans 1981; Cleland 1987; Zieschang *et al.* 1993).

In conclusion, electrical patterns change when roots are placed horizontally, and they are related to calcium in the root cap. They might be important for the transmission of a signal from cap to root, but causal correlations with the gravitropic response have not been determined yet.

ROOT CAP AS THE GRAVISENSING ORGAN: DO AMYLOPLASTS IN THE ROOT CAP BEHAVE AS STATOLITHS?

It has been demonstrated in various ways (by C. and F. Darwin, Piccard, Pfeffer and others, discussed in Jackson & Barlow 1981) that the gravisensitivity of roots is located in the distal 1.5–2 mm of the tip. Pilet (1977) showed with oblique re-heading experiments in maize roots that only the position of a small part consisting of the cap and 0.5–1.0 mm tissue behind it determined the direction of root growth. Demonstrating the necessity of the root cap for gravitropism, however, leads to the general belief that the cap is the gravisensing organ (Audus 1979; Volkmann & Sievers 1979; Sievers & Hensel 1991).

In their attempts to find something in plants similar to the statoliths of the invertebrate gravity sensing organ, Haberlandt (1900) and Nĕmec (1900) both discovered that roots of many, though not all, plant species contain relatively large starch grains. These starch grains were later found to be enclosed in amyloplasts, which sedimented in the core of the root caps, the columella cells, to the lower walls during gravistimulation. It was assumed that the sedimented amyloplasts would contact the plasmalemma and exert pressure on it. This physical stimulus (the *reception* of gravity) would then somehow be converted into a physiological response (the *perception*) leading to differential growth of the upper and lower side of the root tip. There is correlative evidence to support the functioning of the amyloplasts as statoliths.

1. The full sedimentation of the amyloplasts has often been found to be in time correlated with the onset of gravicurvature, the *reaction time* (Audus 1979; Sievers & Hensel 1991).

2. Other cell organelles in the root cap columella cells can be ruled out as gravity sensors (Audus 1979), with the possible exception of nuclei (Moore & Evans 1986).
3. Several experimental results suggest that full sedimentation of the amyloplasts is not necessary; only a small displacement, corresponding with the short stimulation period, is required (often less than 1 min) for a gravitropic response, the *presentation time* (Sack *et al.* 1985).
4. Measurable displacement of amyloplasts may not even be necessary. Evidence is increasing that the amyloplasts are suspended in a net of cytoskeletal elements like microfibril and actin filaments (Sievers *et al.* 1989; Volkmann *et al.* 1991; Buchen *et al.* 1991). Changing pull or pressure forces imposed by amyloplasts could be the actual gravity stimulus.
5. Displacement of amyloplasts has been assumed to lead to pressure on the plasma-lemma or on the membrane of another cell organelle, probably the endoplasmatic reticulum (ER), somehow triggering Ca^{2+} -release from the ER-cisternae (Volkmann & Sievers 1979; Sievers & Hensel 1991).
6. Complete removal of starch by kinetin+GA treatments made cress roots unresponsive to gravity (Iversen 1969). Graviresponsiveness was regained when starch was regenerated in their tips.
7. Amyloplasts do not sediment and the roots show no graviresponse under microgravity in satellite experiments (Moore *et al.* 1987b) or when the roots are rotated on a clinostat (Iversen & Larsen 1973). Starch is degraded during experiments under microgravity (Moore 1987b).
8. Decapped roots regained graviresponsiveness when starch was formed in the meristem during cap regeneration (Barlow 1974; Hillman & Wilkins 1982).

Prevention of graviresponse by decapping has been used as an argument in favour of statoliths, but it is clear now that this argument is not valid, because it can also be used in favour of the mucilage concept and in favour of the cap as the site of unequal distribution of auxin and/or calcium.

The above evidence presents a correlation between the presence and/or displacement of starch-statoliths and graviresponse, but does not really prove that amyloplasts function as statoliths. Moreover, other reports make their putative role less likely.

1. Roots of a maize cultivar (Moore 1987) and of some species (Moore & Evans 1986) are graviresponsive, whereas their amyloplasts are greatly reduced in size and sediment only poorly.
2. The displacement of nuclei in some plants is as obvious as that of the amyloplasts (Moore & Evans 1986).
3. Roots of a starchless mutant TC7 of *Arabidopsis thaliana* were almost normally responsive to gravity; the onset of curvature was delayed, but the rate of curvature equalled that of controls (Caspar & Pickard 1989; Kiss *et al.* 1989). This suggests that the transduction was reduced, rather than the perception, but Kiss *et al.* (1989) proposed that the slower response resulted from a reduced pressure of the starchless plastids on the sensitive surface with correspondingly reduced Ca^{2+} -release.
4. Busch & Sievers (1990) demonstrated that complete removal of starch by kinetin+GA treatments (Iversen 1969) not only abolished gravicurvature, but disturbed the entire structure of the columella cells. Similarly, perturbation of the cell organelles by centrifugation produced agravitropic roots until the normal orientation was restored (Wendt & Sievers 1986).

5. The regeneration of graviresponsiveness after decapping may not be due to reappearance of sedimenting amyloplasts (which cannot be observed in the reports of Barlow 1974 and Hillman & Wilkins 1982), but to regeneration of their mucilage secretion (Barlow & Sargent 1978), which coincided more closely with the return of graviresponsiveness. The role of mucilage seems to be supported by the result of Björkman & Cleland (1991b) who found a gradient of Ca^{2+} in the apoplast (probably the mucilage) between the upper and the lower side of decapped roots, while they regenerated their tips.

6. Sedimented amyloplasts neither contact the plasmalemma (Iversen & Larsen 1973) nor the ER (Barlow *et al.* 1984); a certain compression of material between amyloplasts and membranes, however, cannot be excluded.

In conclusion, despite an enormous effort in the last decades to establish the proper role of (sedimenting) amyloplasts in the root cap cells, their role in the mechanism of gravisensing remains obscure and more conclusive tests have to be developed to ascertain their involvement.

It seems beyond doubt, however, that the root cap columella cells are essential for graviresponse, but not necessarily as the gravisensing organ, as was the prevalent belief. The amyloplast starch degrades when the columella cells become peripheral and is probably an important source for the cap-secreted mucilage. The cap columella cells are probably the sites where Ca^{2+} and IAA first act upon gravistimulation and where an electrical signal is produced, which may be transmitted to the extension zone as has been discussed in an earlier section.

A special case is the graviresponse mechanism of *Chara* rhizoids, which also contain large sedimenting bodies composed of BaSO_4 -crystals. Recently, the notion has been confirmed that these bodies, when sedimenting, push away the Golgi vesicles from the lower wall, so that the growth of that cell wall is restricted by reduced excretion of building materials (Kiss *et al.* 1993). This, indeed, is a simple mechanism of graviresponse. Such a localized growth inhibition does not seem pertinent to roots as it cannot simply be extrapolated to multicellular root tips of higher plants.

If amyloplasts do not function as statoliths, then how could gravity otherwise be sensed by cells in the cap and possibly also in the distal elongation zone? An alternative will be discussed in the following section

MODEL FOR A NON-STATOLITH GRAVISENSING MECHANISM

Calcium is recognized as essential for graviresponse, but it is probably also of general importance in sensing the environment by means of mechanosensitive Ca-selective ion channels (Ding & Pickard 1993).

Pickard & Ding (1993) developed a model based on extensive literature studies and on results obtained with the patch clamp technique on plasmalemma of epidermal cells of onion bulb scales, gravistimulated shoots and some evidence from experiments with maize roots.

Essentially, mechanical stimulation of epidermal cells is transmitted through the cell wall by pressure or tension, probably by certain mechanosensitive proteins in the wall-plasmalemma border that activate transmembrane proteins. These in turn are linked, either directly by certain other proteins or indirectly via cytoskeletal elements (microfibrils, actin filaments) to the mechanosensitive calcium-channels in the plasmalemma. These channels are opened by pressure or tension and Ca^{2+} from the free space

of the walls enters the cytosol. There it is bound to calmodulin and activates, probably by phosphorylation, IAA-porters in the membrane which then transport IAA from inside the cell to the cell wall. This IAA in turn activates the proton pumps in the plasmalemma that acidify the cell wall, which is then loosened and will under proper conditions extend.

In a horizontally placed plant shoot or root the upper side will probably undergo a certain tension and the lower side a certain compression, and a small gradient may develop between the upper and lower sides. As a result, a small gradient of Ca^{2+} -release will develop, followed by a small difference in auxin export from the cells, creating asymmetric growth in each of the participating cells. According to the chemiosmotic transport of IAA it will lead to lateral transport of IAA in the organ and differential growth between the upper and lower side.

A feedback mechanism to stop the process will probably include saturation of Ca^{2+} -binding sites in the cytosol, no further stimulation of auxin transport, decreased proton pumping, dissipation of the acid in the wall free space followed by increase in the pH, decreased wall loosening and closing of the Ca^{2+} -channels by the high acidity of the wall. The model unifies a number of activities known or supposed to be located in or connected with the plasmalemma.

These mechanoreceptors may also participate in gravity reception, as suggested by the observation that gadolinium and lanthanum and certain xenobiotics interfere both with normal Ca^{2+} -channel behaviour and with graviperception of roots and shoots (Ding & Pickard 1993). In roots, these mechanosensitive Ca^{2+} -channels will probably be present in the root cap, but possibly also in the distal elongation zone. The concept should be adapted for Ca^{2+} release from cell organelles instead of release from cell wall free space.

Among mechanically regulated processes that have been studied are cell expansion, thigmotropism, gravitropism, turgor, and ethylene release (Pickard & Ding 1993).

Wayne *et al.* (1992) concluded that internodal cells of *Chara* contain mechanosensitive proteins that connect the cell wall and plasmalemma at either cell end. The proteins were held responsible for an altered cytoplasmic streaming, probably by changed Ca^{2+} -pumping, when the position of the cells was changed with regard to gravity. In this model of Wayne *et al.* (1992) small changes in pressure on these sensitive proteins are sufficient to trigger the gravity-induced change of protoplasmic streaming. This is an attractive proposition although, unfortunately, the data on cytoplasmic streaming could not be reproduced by Ackers *et al.* (1994).

The question has been discussed as to how a cell can detect the gravitational stimulus against the background of the very much greater hydrostatic pressure (Audus 1979). Staves *et al.* (1992) found that in *Chara* internode cells several treatments that affected the hydrostatic pressure also affected the gravity-induced change of cytoplasmic streaming, suggesting that the two are similarly controlled. Despite the presence of a large, but homogeneous hydrostatic pressure, the gravitational stimulus can probably be recorded, as small differences induced by gravity can be felt by appropriate sensors. Interestingly, plant roots are also capable of sensing small temperature differences (Fortin & Poff 1990) and small differences in moisture (Takahashi & Scott 1993).

The models of Pickard & Ding (1993) and of Wayne *et al.* (1992), although developed for different tissues, have the common principle that gravity is perceived by sensitive proteins, which quickly respond to small pressure differences without the need for displacement of bodies. The models also accommodate the very short presentation times measured in gravistimulated shoots and roots (Pickard 1985). The concept seems very

promising and a uniform idea could emerge on graviperception in roots, shoots and lower plants, in which the described system has a central position.

CONCLUDING REMARKS

In the past few decades the most obvious progress in understanding root gravitropism has been establishing the crucial role of calcium. Research into the action of calcium at the molecular level will greatly contribute to resolving its function in the graviresponse. The necessity of the root cap for graviresponse has been further supported, but the distal part of the elongation zone also appears to be important for gravisensing. Little is known of the early events in the sensitive cells of the root tip within the often very short presentation times, but the involvement of calcium is very likely. In this connection, the electrical phenomena in relation with the graviresponse of the root tip are intriguing and may contribute to our understanding of the initial processes triggered by the gravity stimulus. Notwithstanding much research, an important role for abscisic acid in root gravitropism, for years considered to be the growth inhibitor transferred from cap to root, has not been established. Similarly, a clear role for ethylene and gibberellin has not yet been established, although they are very important growth regulators. Only the involvement of auxin in root gravitropism has been further ascertained in various ways, although the predictions of the Cholodny–Went hypothesis have not been fulfilled.

Progress has also been made on the way in which growth regulators may be transported from cap to the extension zone. The cap-secreted mucilage is a good candidate for an apoplastic pathway, but basipetal transport inside the root tip may occur as well. Recent accurate measurements of the growth rates of the upper and the lower side of the root tip during the gravicurvature confirmed and extended earlier reports, and showed that both growth accelerations of the upper side and growth inhibitions of the lower side occur in the first phase of the positive bending and are reversed after some time. When the roots reach their maximum angle of curvature they often show an oscillating behaviour. These oscillations and the naturally oscillating behaviour of vertical roots (nutations) are probably controlled in a similar way.

The function of amyloplasts as statoliths in the root cap has not been proven, despite much correlative evidence, even after a century of research. On the other hand, gravisensing by sensitive proteins in the cell wall and plasmalemma, which probably control mechanosensitive Ca^{2+} -channels regulating Ca^{2+} -release into cells, opens a promising perspective for understanding several phenomena in which small differences in tension or compression between opposite sides of a cell, which probably also occur during horizontal exposure of roots, trigger adequate responses.

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