Phototropic Stimulation can Shift the Gradient of Crown Root Emergence in Maize

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Abstract: **The crown roots in the coleoptilar node of maize emerge asymmetrically: emergence at the dorsal flank of the node (opposite to the caryopsis) precedes emergence at the ventral flank (facing the caryopsis). This asymmetry can be altered by phototropic stimulation: emergence of crown roots is delayed in the lighted flank and promoted in the shaded flank causing an inversion of the endogenous asymmetry. The curvature induced by the phototropic stimulation is transient, the effect on crown root emergence, in contrast, persists. This stable effect is not a consequence of curvature *per se* and becomes irreversibly fixed between one and two hours after stimulation. The emergence of crown roots depends on directional signalling from the coleoptile to the node. The data are discussed in terms of a stable blue light induced transverse polarity of the coleoptile that can imprint a stable asymmetry upon the coleoptilar node guiding the emergence of crown roots.**

Key words: Blue light, coleoptile, crown roots, phototropism, polarity, *Zea mays* L.

Abbreviations:

IAA: 3-indoleacetic acid
NPA: 1-N-naphthylphthalamic acid

Introduction

Environmental signals such as light or gravity can control various aspects of plant morphogenesis throughout development. Induction or alignment of polarity is one of the most fundamental events in this context and has fascinated researchers over the last two centuries (du Monceau, 1764; Goebel, 1908; Quatrano, 1978; Sachs, 1991).

In higher plants, the shoot – root polarity is established during the first stages of development (Mayer et al., 1991), when the developing embryo is still embedded in the embryo sack. After germination, this polarity has already become fixed and often persists even in the presence of counteracting environmental gradients (Vöchting, 1878; Goebel, 1908, for review see Nick and Furuya, 1992). Nevertheless, it is sometimes possible to change polarity, when the original polarity is disturbed by wounding. This has been shown for vessel regeneration in *Coleus* stem sections (Sachs, 1991), or for formation of adventitious roots in various species (Van Tieghem, 1873; Sachs, 1880). Shoot – root polarity can change naturally in response to gravitropic stimulation, when adventitious roots form at the lower half of the node (Goebel, 1908).

It is not clear, however, whether this new polarity can exist independently of the inducing asymmetry, or whether it is just maintained by an asymmetric environment. In a classical experiment with roots of *Taraxacum*, Vöchting (1878) could demonstrate that the expression of polarity can be shifted, although the polarity itself remains unaltered (for review see Nick and Furuya, 1992). In order to separate both phenomena, it is necessary to find conditions, where transient stimuli can induce a polarity that persists after the stimulus has been removed.

This requirement is met by the response of maize coleoptiles to phototropic stimulation: in parallel to the transient bending response to pulses of unilateral blue light, a stable transverse polarity is established that is expressed as stable curvature under conditions of symmetric gravity (Nick and Schäfer, 1988a). This polarity becomes irreversibly fixed two hours after induction (Nick and Schäfer, 1991), and is correlated to a gradient in the orientation of cortical microtubules between the two flanks of the stimulated organ (Nick et al., 1990) – this gradient is irreversibly fixed at the same time as the blue light induced transverse polarity (Nick and Schäfer, 1994). The physiological role of this transverse polarity has remained enigmatic, however. Moreover, the coleoptile is an ephemeral organ that is soon afterwards torn open by the emerging primary leaves. This renders the role of a stable transverse polarity even more obscure.

In the search for potential long-term consequences of phototropic stimulation, it was observed that the nodal crown roots of maize emerge asymmetrically and that this asymmetry can be shifted by a phototropic stimulus that had been administered several days earlier. In the present work, this phenomenon is described and characterized physiologically.

Materials and Methods

Plant cultivation

Caryopses of maize (*Zea mays* L. cv. Percival, Asgrow GmbH; Bruchsal, Germany) were soaked in running tap water for 2 h and sown equidistantly on moist tissue paper (Verbandszellulose, Hartmann; Heidenheim, Germany) with the embryo facing upwards, in boxes made from clear plexiglass (300 mm × 200 mm × 100 mm). After cultivation for two days at 25 °C under red light (1.53 μmol · m^{-2}s^{-1}, λ_{max} 660 nm), seedlings were transplanted into moist vermiculite in small plastic trays (120 mm × 60 mm × 70 mm). The seedlings were transplanted in a row such that the long cross-axis of the coleoptile was parallel to the long axis of the tray and the caryopses were all pointing to the same side of the row. After a further day in complete darkness at 25 °C, seedlings were selected for straightness and length (30–35 mm for the coleoptile) under dim green safelight (λ_{max} 550 nm) and then subjected to phototropic stimulation. For details on the light sources and the isolation of broad-band red and green light refer to Mohr et al. (1964).

Phototropic stimulation

The seedlings were kept, from 2 h prior to phototropic stimulation, under the red light that had been used for cultivation (see above) so as to exclude potential effects of phytochrome gradients that might be induced by the blue light used for phototropic induction (Nick and Schäfer, 1988a). Blue light for phototropic stimulation was isolated from a slide projector through an interference filter (λ_{max} 450 nm, half band with 12 nm, Schott; Mainz, Germany), and was administered unilaterally in the dorsiventral (short) cross-axis of the coleoptile, either to the dorsal flank (opposite to the caryopsis), or, alternatively, to the ventral flank (at the side of the caryopsis). The coleoptiles were illuminated along their entire length. For fluences up to 200 μmol m^{-2} of blue light the duration of the stimulation was confined to 30 sec (first positive phototropism *in sensu* Iino (1991)), for higher fluences, the stimulation time was varied between 1 and 20 min (time-dependent phototropism *in sensu* Iino (1991)). The exposure time was controlled by an automatic shutter system. Phototropic curvature was measured 2 h after induction as described in Nick and Schäfer (1988a). Following phototropic induction, the seedlings were maintained under red light until curvature measurement. Alternatively, the plants were kept at high humidity in a moist chamber under red light (0.27 Wm^{-2}) until response evaluation. In the phototropic fluence-response curves shown in Figures **3 A**, **B**, each data point represents mean and standard deviation from ten individual seedlings. For the experiments shown in Figures **1**, **2** and Tables **1**, **2** 10 μmol · m^{-2} blue light was chosen as stimulus, because this fluence was found to cause maximal shifts of crown root emergence (Figure **3**).

Drug application and excision experiments

In order to facilitate drug penetration, the cuticle was abraded with a fine polishing cloth (Schopfer, 1993) along the entire axis of the seedling. 1-N-naphthylphthalamic acid (NPA) was applied symmetrically in the form of microdrops (10 μl) either to the node, to a zone 5 mm above the node, or to a zone 5 mm below the node, in a concentration of 5 μM (diluted from an ethanolic stock solution yielding a final concentration of 0.01 % v/v ethanol). Following drug application, the trays with the seedlings were kept in moist chambers at high humidity for 4 d at 25 °C under 0.27 Wm^{-2} of red light. For the excision experiments (Table **3**), either the coleoptile alone or both, coleoptile and primary leaves were excised 1 mm above the node. The cut surface was immediately covered with a drop of water, or indoleacetic acid (IAA) at various concentrations. The plants were then kept in a moist chamber at high humidity at 25 °C for 4 d under red light, whereby the liquid (water or IAA) was replaced twice daily during that incubation period.

Evaluation of crown root emergence

The emergence of crown roots at the dorsal and the ventral side of the coleoptilar node was followed over time after the various treatments. The emergence of nodal crown roots was scored for each side of the seedling and the relative frequency of emergence in a seedling population was taken as a measure for crown root development. The criterion for emergence was the visibility of the root apex. For photographic documentation, the plants were recorded under red light on a sensitive film (TriX, 400 ASA, Kodak Ltd; Rochester, U.K.) with an automatic camera (OM4, Olympus; Tokyo, Japan) and a 400 mm Macro-objective (Zeiss, Oberkochen; Germany). Each experiment was repeated at least twice on independent days.

Results

Crown root emergence is shifted by phototropic stimulation

The nodal crown roots emerge at four predictable sites: At the dorsal side, distal to the caryopsis, the root emerges first (Figure **1 B**, Figure **2 A**), whereas at the ventral side, proximal to the caryopsis, despite an early local swelling of the node, the root emerges only a few days later (Figure **1 B**, Figure **2 B**). Perpendicular to those nodal roots, a second pair of roots emerge from the two flanks in the long cross-axis, but even later than the root in the ventral side (data not shown). In the following, only the dorsal and the ventral crown roots were considered.

Phototropic pulse stimulation interfered with the temporal pattern of crown root emergence. If the stimulus was administered to the dorsal side, this promoted the emergence of the ventral crown root (Figure **1 C**, Figure **2 B**), whereas the emergence of the dorsal crown root was delayed (Figure **1 C**, Figure **2 A**). If the light was administered to the ventral flank, the emergence of the dorsal crown root was promoted (Figure **1 A**, Figure **2 A**), whereas the emergence of the ventral crown root was delayed (Figure **1 A**, Figure **2 B**).

Crown root emergence is not a mere consequence of curvature

To test whether crown root emergence is just the consequence of curvature, fluence-response curves were measured in parallel for phototropic curvature (Figures **3 A**, **B**), and crown root emergence (Figures **3 C**, **D**). In a second set of experiments, the curvature was induced not by blue light, but by gravity (Table **1**).

The fluence-response curves for phototropic curvature exhibit the familiar pattern known from red light pretreated maize (Iino and Briggs, 1984): a threshold at 0.2 μmol m^{-2}, a maximal response at around 10 μmol · m^{-2}, and a decrease for higher fluences with minimal curvature around 200 μmol · m^{-2} (Figures **3 A**, **B**). For higher fluences that could be obtained only by prolonged irradiation, a new rise of curvature is observed. The pattern is fairly similar for irradiation in the

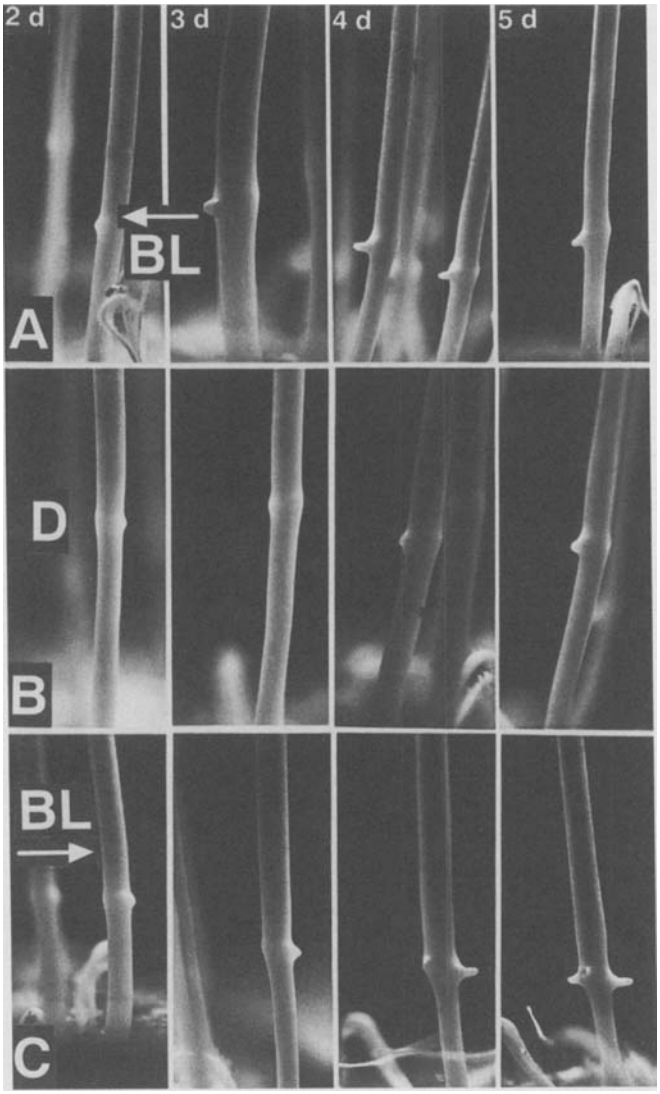

Fig. 1 Effect of phototropic stimulation with 10 μmol m^{-2} of blue light on the emergence of dorsiventral crown roots in the maize coleoptilar node.
The plants were irradiated and then maintained under red light throughout the experiment. (**A**) Stimulation of the ventral side 4 d after sowing, (**B**) Unstimulated control, (**C**) Stimulation in the dorsal side. The dorsal side is oriented to the left, the ventral (facing the caryopsis) to the right.

dorsal flank (Figure **3 B**) as compared to irradiation in the ventral flank (Figure **3 A**).

The comparison of the fluence-response curves for crown root emergence (Figures **3 C**, **D**) and for phototropic curvature (Figures **3 A**, **B**) reveal the following similarities and differences: for irradiation in the dorsal side, the emergence of crown roots in the shaded, ventral side is promoted in parallel to the induced phototropic curvature (Figure **3 D**). Only for prolonged irradiation does this promotion break down (Figure **3 D**), although the curvature still rises (Figure **3 B**). Nevertheless, there is some correlation between phototropic curvature and the promotion of crown root emergence at the shaded side.

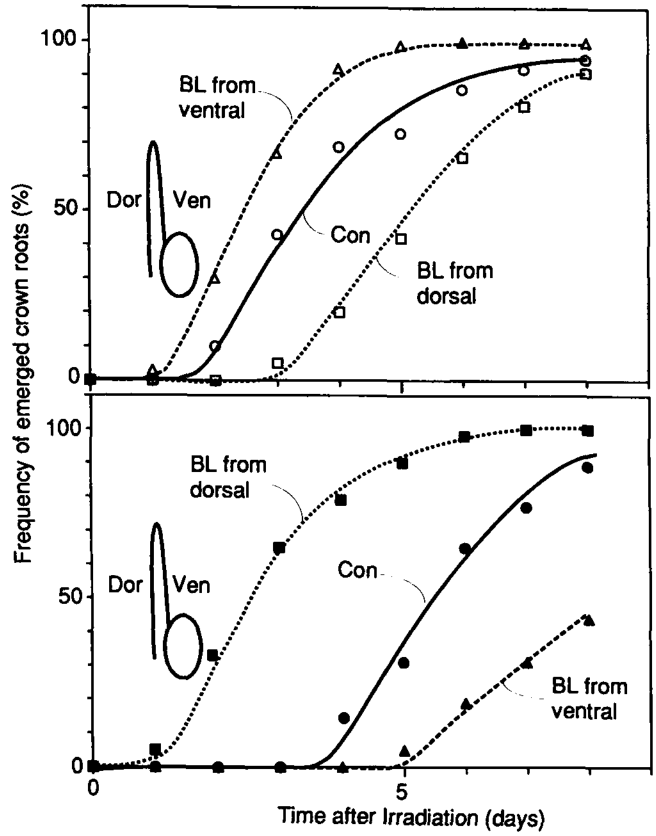

Fig. 2 Time course of crown root emergence after stimulation with 10 μmol · m^{-2} of blue light.
Upper panel: dorsal crown root, lower panel: ventral crown root. The frequency of emergence is given in %. Squares, dotted curves: stimulation of the dorsal flank. Triangles, dashed curves: stimulation of the ventral flank, circles, solid curves: controls in red light. n = 100.

In contrast, in the dorsal (lighted) side, the emergence of crown roots is increasingly inhibited with rising fluences. Only after prolonged stimualtion does this inhibition ease off. However, under these conditions, the curvature rises again (Figure **3 A**).

For irradiation in the ventral side, the emergence of dorsal crown roots is inhibited by low fluences that cause only weak curvature. For increasing fluences, the inhibition disappears, reappears for phototropically super-optimal pulses, and disappears again for prolonged irradiation (Figure **3 C**). Again, the curves for curvature and crown root emergence coincide roughly, if very low and very high fluences are ignored.

In the ventral (lighted) side, crown roots are promoted by weak light and very strong pulse light (Figure **3 D**, triangles, dashed curve). They are inhibited by light that induced maximal first positive phototropism (Figure **3 B**). This inhibition is to be expected, if curvature and crown root emergence are correlated. The stimulation of ventral crown root emergence by weak and very strong pulses, however, cannot be attributed to curvature.

To test the relation between curvature and the emergence of crown roots further, the response of nodal crown roots was

Treatment	curvature °]	Dorsal side	Ventral side	n
Control (7d)	– 0.2 ± 0.9	66%	5.9%	72
2 h gravitropic stimulation (4 d after stimulation, 7 d after sowing)				
ventral side down	28.3 ± 1.3	42%	0%	66
ventral side up	27.5 ± 2.3	76%	0%	69
phototropic stimulation with 10 µmol · m^{-2} BL (4 d after stimulation, 7 d after sowing)				
in dorsal side	25.6 ± 1.9	21%	79%	42
in ventral side	24.6 ± 2.6	89%	11%	39
Control (10d)	0.5 ± 0.4	90%	82%	73
2 h gravitropic stimulation (7 d after stimulation, 10 d after sowing)				
ventral side down	29.7 ± 2.5	67% [62%]	142% [72%]	79
ventral side up	27.9 ± 1.8	130% [89%]	55% [39%]	85

Table 1 Effect of photo- and gravitropic stimulation on curvature and crown root emergence at 4 and 7 days after stimulation. The plants were maintained under continuous red light for 2 h prior to stimulation until the end of the experiment. The values indicate frequencies of emerged crown roots with 100% indicating that one crown root per flank has emerged in all seedlings. At 7 d after stimulation, in addition to the nodal crown roots [values given in brackets], additional roots emerged from the mesocotyl, causing frequencies that were higher than one root per flank of a plant. Controls were subjected to the same precultivation protocol as the samples, but were kept under red light only.

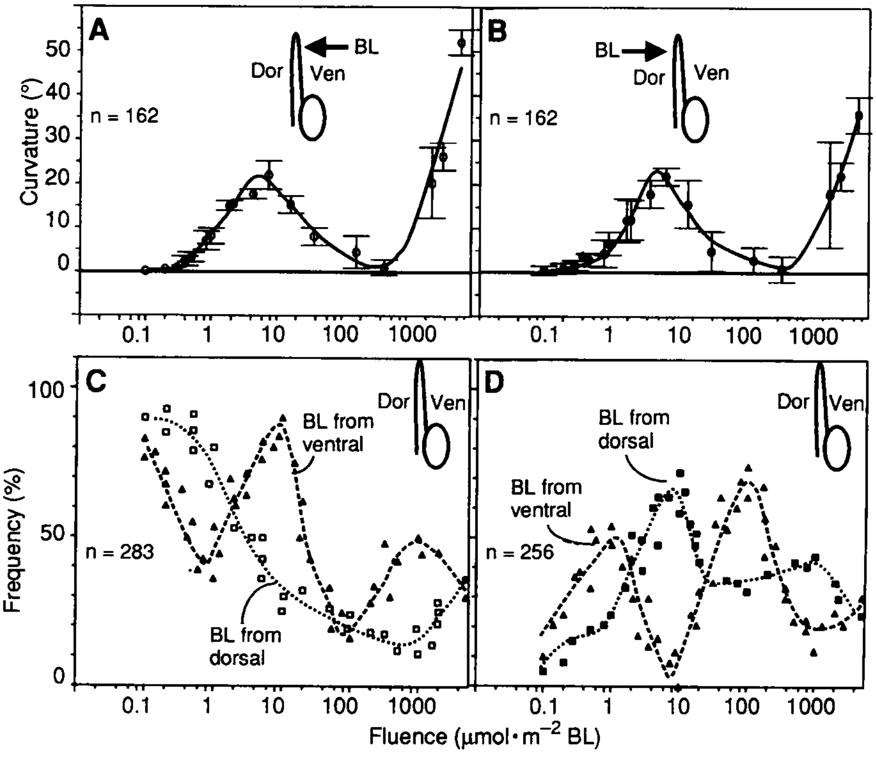

Fig. 3 Fluence-response curves for phototropic curvature and crown root emergence.

(A, B) Fluence-response curves for phototropic induction in the ventral (**A**) and the dorsal (**B**) flank of the coleoptile. Curvature was measured 2 h after induction. (**C, D**) Frequency of emerged crown roots in the dorsal (**C**) and ventral (**D**) flank of the node, scored 4 d after induction (8 d after sowing). For details refer to Figure **2**.

assayed for a gravitropic stimulation that caused similar curvatures as the most effective phototropic pulse stimulation (Table **1**):

When the caryopsis was facing downwards (equivalent to dorsal phototropic stimulation with respect to curvature), the coleoptile exhibited negative gravitropism, but crown root emergence was not promoted in the ventral side. Such a promotion is seen, however, if a comparable curvature is induced by phototropic stimulation (Table **1**). Crown roots emerged in the dorsal side, although to a lesser extent than in the equivalent phototropic stimulation.

When the caryopsis was facing upwards, no significant difference in root emergence was observed relative to the control, either in the dorsal, or in the ventral side. The equivalent phototropic induction (in the ventral side) causes a promotion of crown root emergence in the shaded dorsal side, as well as in the ventral side.

If the response is evaluated a week after stimulation (Table **1**, lower half), the discrepancy is even more pronounced: for gravitropic stimulation with the ventral side facing downwards, the emergence of nodal crown roots (values in brackets) is inhibited on both flanks as compared to the control and this is true for stimulation in the opposite direction as well. Interestingly, in addition to the "true" (nodal) crown roots, mesocotyl roots can be observed. These mesocotylar roots are always more abundant at the side that was facing downwards.

Table 2 Stabilisation of the effect of phototropic stimulation on crown root emergence with time. At time 0 the plants were stimulated phototropically in the dorsal side with 10 μmol · m^{-2} blue light and counter-stimulated with a stimulus of equal strength 0, 1, or 2 h later. The emergence of crown roots was scored 4 d after irradiation (for details refer to Table 1).

Treatment	Drosal side	Ventral side	n
Control (4 d RL)	72%	11%	41
stimulus in dorsal side	27%	78%	50
stimulus in ventral side	98%	13%	38
stimulus in dorsal side, then, after an interval, stimulus in ventral side			
interval 0 h	41%	89%	40
interval 1 h	76%	32%	45
interval 2 h	31%	132%	53

Table 3 Stimulation of crown root emergence by removal of coleoptile and primary leaf (pl) and the effect of indoleacetic acid (IAA). For the highest concentration of IAA, in addition to nodal crown roots [value given in brackets] additional roots emerged from the mesocotyl, sometimes causing frequencies that were higher than one root per flank of a plant.

Treatment	Drosal side	Ventral side	n
Control (4 d RL)	78%	3%	42
removal of the coleoptile	100%	0%	55
removal of coleoptile and primary leaves	132%	65%	60
Application of IAA after removal of coleoptile and primary leaf			
1 μM IAA	160%	60%	20
3 μM IAA	135%	75%	20
10 μM IAA	120%	80%	20
30 μM IAA	110% [95%]	55% [25%]	20
100 μM IAA	120% [80%]	10% [10%]	20
300 μM IAA	100% [60%]	25% [20%]	20

Table 4 Inhibition of crown root formation by application of 1-naphthylphthalamic acid (NPA), an inhibitor of polar auxin transport to intact seedlings after abrasion of the cuticle. If not stated otherwise, the drugs were administered directly to both sides of the node.

Treatment	Dorsal side	Ventral side	n
Control (4 d RL)	74%	9%	47
Abrasion + Water	81%	7%	50
Abrasion + 5 μM NPA (in the node)	8%	0%	45
Abrasion + 5 μM NPA (5 mm above the node)	67%	7%	39
Abrasion + 5 μM NPA (5 mm below the node)	5%	0%	49

This comparison of photo- and gravitropic stimulation demonstrates that the effects of phototropic stimulation on crown root emergence cannot be mimicked by gravitropic stimulation. It demonstrates further that the nodal crown roots respond in a different way to gravity than the roots emerging from the mesocotyl.

Tropistic curvature is transient, the light effect on crown root emergence is stable

To find the time point, when the light effect on crown root emergence becomes stable, the response to a phototropic pulse induction was challenged by a counter-stimulation of equal strength after various time intervals (Table **2**). A stimulus, administered to the dorsal side, inhibited crown root emergence in the dorsal side and promoted the emergence in the shaded, ventral side. A counter-stimulation, administered to the ventral side, conspicuously increased the frequency of emerged crown roots in the shaded, dorsal side. If the counter-stimulus in the ventral side was administered immediately after the first pulse in the dorsal side (time interval 0), the emergence of crown roots was strongly promoted in the ventral side and slightly reduced in the dorsal side (Table **2**). For a time interval of 1 h, however, this promotion in the ventral side was much weaker, suggesting that now the response to the second, opposing pulse had become more prominent. Moreover, the two flanks produced crown roots at a very similar frequency, suggesting that the interaction of the two pulses resulted in a nearly balanced, symmetrical situation. For a longer time interval of 2 h effects of the first stimulus became dominant again: a slight reduction of the frequency in the dorsal side was accompanied by dramatic increase in the ventral side. In this case, some of the lateral nodal crown roots appeared earlier than usual and they did not emerge in their usual axis perpendicular to the dorsiventral axis, but were diverted towards the ventral side, causing emergence frequencies that exceeded 100%.

The experiment suggests that the directional effects produced by phototropic induction that eventually will guide crown root emergence, are still labile 1 h after stimulation. They have become stable against counter-stimulation 2 h after induction.

Crown root emergence depends on directional signals

If the coleoptile is excised, leaving the primary leaf intact (Table **3**), this increases the frequency of crown roots in the dorsal side, but not in the ventral side. If, in addition, the primary leaves are removed, the frequency rises even further, this time on both sides. But the dorsal dominance is maintained. Again, some of the lateral crown roots emerge precociously and diverted, this time to the dorsal side, causing a frequency exceeding 100%. Addition of the auxin, indoleacetic acid (IAA), at 1 μM to the cut surface causes a further increase on both sides, whereby the dorsal side remains dominant. At higher concentrations, this stimulation disappears again, first in the dorsal side (at the transition between 1 and 10 μM of IAA), later, but more dramatically, in the ventral side (at the transition between 10 and 100 μM of IAA). At the highest concentration of auxin, additional formation of mesocotyl roots was observed (Table **3**).

These experiments indicate that the emergence of nodal crown roots is influenced by the coleoptile and that auxin can control the emergence as well. In an attempt to possibly interfere with these signals that potentially mediate the communication between different organs, 1-N-naphthylphthalamic acid (NPA), a potent inhibitor of auxin transport (Morgan, 1964) was either symmetrically applied to the node itself, or 5 mm above or below the node (Table **4**). Cuticle abrasion did not impede crown root emergence (Table **4**), whereas application of NPA to the node inhibited crown root emergence dramatically (Table **4**). The same inhibition could be achieved, if the drug was applied 5 mm below the node (Table **4**). In contrast, application of NPA 5 mm above the node had almost no effect (Table **4**). This indicates directional signalling that is involved in the control of crown root emergence.

Discussion

Phototropic induction induces a stable transverse polarity of the coleoptile that is imprinted upon the node

Phototropic stimulation causes several phenomena in maize seedlings: (1) A phototropic curvature (Figure **3 A**, **B**) that is transient with a maximum at 2 h after induction disappearing within a few hours (Nick and Schäfer, 1988a). (2) A gradient of microtubule orientation with longitudinal microtubules in the lighted flank and transverse microtubules in the shaded flank of the coleoptile (Nick et al., 1990). This response is complete within 1 h and remains stable (Nick et al., 1991). (3) A transverse polarity ("directional memory") that can be separated from fast curvature responses. This polarity becomes irreversibly fixed at 2 h after induction (Nick and Schäfer, 1988b, 1991). It can be rendered manifest as stable, long-lasting curvature under symmetric gravity (rotation on a horizontal clinostat). (4) A fixation of microtubule orientation at 2 h after induction that is tightly correlated to the transverse polarity (Nick and Schäfer, 1994). (5) A shift of crown root emergence with a promotive effect in the shaded, and an inhibitory effect in the lighted flank of the coleoptilar node (Figures **1**–**3**). This response becomes manifest several days after phototropic induction.

A detailed phenomenological analysis (Nick and Schäfer, 1988b, 1991, 1994) supports a model, where the fast phototropic bending and the gradient of microtubule orientation are parallel phenomena that are not causally linked. In contrast, the fixation of microtubule orientation 2 h after induction appears to be the cellular expression of the stable transverse polarity that is observed on the physiological level.

The relation of crown root emergence to these phenomena can be infered from the fluence-response relations (Figure **3**) and the experiments involving gravitropic stimulation (Table **1**). These data clearly demonstrate that there is no close relation between phototropic curvature and the shift in crown root emergence. It is not possible to explain the shift of crown root emergence in terms of a promotion at the convex and an inhibition at the concave side of the organ, irrespective of the signal that triggered the curvature. This contrasts with the situation for adventitious roots, where the curvature itself defined a gradient in root emergence that was independent of the manner how this curvature was achieved (by gravitropism or by manual bending) in the classical experiments by Goebel (1908).

The light effect that guides crown root emergence becomes manifest a few days after induction. Nevertheless it is already stabilized much earlier (Table **2**): already 2 h after induction, this directional light effect has become stable against counter-stimulation, i.e. a long time before it is expressed as a shift of crown root emergence. The stabilisation at 2 h after induction and the long lasting persistence place this stable light effect in the close neighbourhood of the blue light induced transverse polarity (Nick and Schäfer, 1988b, 1991) and the fixation of microtubules (Nick and Schäfer, 1994).

There is one important difference, however: the blue light induced transverse polarity and the fixation of microtubules are located in the basal part of the coleoptile (Nick and Schäfer, 1994), whereas the crown roots emerge from the node (Figure **1**). Moreover, at the time, when the crown roots emerge, the coleoptile has already been pierced by the primary leaves and ceased to elongate. This means that the transverse polarity of the coleoptile must have been imprinted upon the node. This requires signalling between the two organs.

In this context it should be emphasized that even in unstimulated control plants there is a distinct dorsiventrality of crown root emergence with a clear dorsal dominance (Figure **1 B**, Figures **2 A**, **B**, circles, solid curves). The coleoptile as well is characterized by a clear dorsiventrality (Rothert, 1894) that can be made manifest, on the physiological level, as nastic curvature observed during rotation on a horizontal clinostat (Nick and Schäfer, 1989).

These observations indicate that the coleoptile can imprint a polarity upon the node and that this polarity is then expressed as gradient of crown root emergence at a time, when the coleoptile itself has already ceased to elongate.

The spatial pattern of crown root emergence seems to be defined by events that take place in the coleoptile several days earlier (Figure **2**). At the time of phototropic induction, the primordia of the nodal crown roots have either not formed yet, or are too small to be detected in cross-sections (data not shown). The excision of the coleoptile promotes the emergence of nodal crown roots (Table **3**) and this is even more pronounced if the primary leaves are excised as well. This indicates that, in intact plants, the disruption of the coleoptile by the primary leaf might be the signal that triggers crown root emergence. Is it the basipetal flow of auxin in intact coleoptiles that suppresses crown root emergence? However, if NPA, a potent inhibitor of auxin transport (Morgan, 1964) applied above the node, such that the basipetal flow of auxin from the coleoptile to the node should be interrupted, this hardly affects the emergence of crown roots (Table **4**). If NPA is administered below the node or in the node itself, it causes a dramatic inhibition. Moreover, auxin, that is applied to the cut surface of the node, enhanced the emergence of crown roots conspicuously. These findings might be interpreted in terms of a factor (that could be auxin or another signal that is impaired by NPA) being transported in the acropetal direction through the mesocotyl and promoting crown root emergence in the node, if the coleoptile has been removed or has been disrupted by the expanding primary leaves. This point warrants further investigation.

The inhibitory influence of the coleoptile on crown root emergence might be caused merely by a sink function for this factor that is transported acropetally. Alternatively, together with the basipetal flow of coleoptilar auxin, a second factor might move towards the node that locally, in the node, alters the sensitivity for auxin that is transported in the mesocotyl towards the node. Future work will be directed to assay for changes in hormone sensitivity in response to light.

The coleoptile is generally believed to have the function of guiding the primary leaves through the soil towards the surface. The ephemeral nature of the coleoptile, at first glance, seems to exclude a formative role of this organ for plant development. The present work attempted to demonstrate that even transient events can have long lasting morphogenetic consequences, if they fall into a period of competence. The organ that senses and processes the polarity, the coleoptile, is ephemeral and vanishes – the morphogenetic traces transduced by this organ upon the node, remain stable for a long time.

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