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On the relation between photo- and gravitropically induced spatial memory in maize coleoptiles

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Abstract. The interaction of photo- and gravitropic stimulation was studied by analysing the curvature of maize (*Zea mays* L.) coleoptiles subjected to rotation on horizontal clinostats. Gravitropic curvature in different directions with respect to the stimulation plane was found to be transient. This instability was caused by an increasing deviation of response direction from the stimulation plane towards the caryopsis. The bending angle as such, however, increased steadily. This reorientation of the gravitropic response towards the caryopsis is thought to be caused by the clinostat-elicited nastic curvature found in maize coleoptiles. In contrast, the response to phototropic stimulation was stable, in both, orientation and curving. Although stimulation by gravity was not capable of inducing a stable tropistic response, it could inhibit the response to opposing phototropic stimulation, if the counterstimulation was given more than 90 min after the onset of gravistimulation. For shorter time intervals the influence of the phototropic stimulus obscured the response to the first, gravitropic stimulation. For time intervals exceeding 90 min, however, the phototropic effects disappeared and the response was identical to that for gravity stimulation alone. This gravity-induced inhibition of the phototropic response was confined to the plane of gravity stimulation, because a phototropic stimulation in the perpendicular direction remained unaffected, irrespective of the time interval between the stimulations. This concerned not only the stable phototropic curving, but also the capacity of the phototropic induction to elicit a stable directional memory as described earlier (P. Nick and F. Schäfer, 1988b, Planta **175**, 380–388). This was tested by a second blue-light pulse opposing the first. It is suggested that gravity, too, can induce a directional memory differing from the blue-light elicited memory. The mechanisms mediating gravi- and phototropic directional memories are thought to branch off the respective tropistic signal chains at a stage where photo- and gravitropic transduction are still separate.

Key words: Coleoptile (gravi-, phototropism) Gravitropism – Phototropism – *Zea* (coleoptile, gravitropism, phototropism)

Introduction

The response of graminean coleoptiles towards tropistically effective stimulation supposedly involves the formation of a tropistic polarity as a mediating step between asymmetric stimulation and asymmetric growth. It appears that this step implies different mechanisms for photo- and gravitropism, as classical experiments by Johannes Buder (1920) showed phototropic polarity to be a systemic organ polarity resulting from integration of locally perceived stimulation over the organ cross-section, whereas gravitropic polarity, due to the nature of the inducing agents, is presumed to be cell-based (Rawitscher 1932). From this it may be concluded that the early parts of photo- and gravitropic transduction are separate. In agreement with that conclusion Pekelharing (1909) observed stimulus summation for subthreshold stimuli of the same quality (light-light or gravity-gravity), whereas stimuli of different quality (light-gravity or gravity-light) were not summed up. A separation of both transduction chains at the level of formation of tropistic polarity was also indicated by the additive behaviour of counteracting photo- and gravitropic stimulations (Nick and Schäfer 1988a).

In addition to the polarities causing tropistic curvature, both, gravi- and phototropic stimulations have been found to elicit the formation of a stable transverse polarity, which is not necessarily expressed as curvature (Nick and Schäfer 1988b). This stable transverse polarity became manifest as increasing stability of the stimulus-induced directional effects against counterstimulation of equal strength. It was stable even in those cases where tropistic curvature, caused by gravitropic straightening, remained transient, and could be rendered visible as strong curvature by transfer to a horizontal clinostat at a time when the initial tropistic response had already

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disappeared. Thus, this stable transverse polarity is clearly distinct from the tropistic polarity mentioned above. This was confirmed by the fact that stable transverse polarity attains its stability only 90 min after the first, inducing pulse, whereas the lag of appearance of tropistic curvature is between 20 and 30 min, which means that the formation of tropistic polarity has been completed at this time.

There seems to be no immediate interaction between photo- and gravitropic transduction on the level of tropistic polarity. The observed interactions appear to reside in the late stages of transduction rather than in the early steps of the signal chains (Nick and Schäfer 1988a). There seems to be, however, a direct interaction of photo- and gravitropic responses on the level of stable transverse polarities (Nick and Schäfer 1988b). The bending response to a blue-light pulse was stable against a gravitropic counterstimulation of equivalent strength administered 120 min later and vice versa. Thus, the capacity of the coleoptile to form a second stable transverse polarity was abolished by the stabilisation of the first polarity. This inhibition was independent of the respective stimulus qualities, and could not be explained by simple addition of the opposing responses, as individual seedlings either performed a strong bending according to the first or according to the second stimulus or remained straight. Intermediates between those three distinct types of behaviour, as would be expected after mere response addition, were not observed. Thus, the interactions on the level of the presumed stable transverse polarity are not at all graded, but follow an all-or-none pattern yielding only a few discrete outcomes. Such an all-or-none behaviour of individual seedlings is also encountered during the interaction of phototropism with the clinostat-elicited nastic response (Nick and Schäfer 1989) and the reversion of the gravitropic response on the clinostat following symmetric blue irradiation (Sailer et al. 1989). It appears to be a general feature of the putative stable transverse polarities, which can be made visible by rotation on horizontal clinostats.

Although it is obvious that the transduction mediating stable transverse polarity is not identical to that causing the immediate tropistic response, it remains unclear at which point it branches off the tropistic signal chain. One prominent feature of tropistic transduction is sensory and-or transductory adaptation, which was analysed in relation to interaction phenomena between photo- and gravitropism (Hild and Hertel 1972; Ullrich 1976, pp. 78–81). These experiments showed that gravitropic sensory adaptation, tested by a perpendicular gravity stimulus, was confined to the plane of prestimulation, i.e. remained localised. Gravitropic transductory adaptation as testable by a perpendicular pulse of blue light, however, appeared to be global. This transductory adaptation was presumed to be a common step of both, photo- and gravitropic signal chains.

Based upon these observations we assessed the question of how a stable gravitropic transverse polarity interacts with a phototropic stimulus administered in the perpendicular plane. The outcome of this experiment might provide valuable insight into the question of whether gravi- and phototropically induced stable transverse polarities involve the same mechanisms.

Material and methods

Plant material and light sources. Straight maize coleoptiles (*Zea mays* L. cv. BRIO 42. HT; Asgrow, Bruchsal, FRG; harvest 1988, stored at 3° C in the dark) were raised in a phytochamber as described elsewhere (Nick and Schäfer 1988a). For details of light conditions and blue light used for phototropic induction see Nick and Schäfer (1989).

Stimulation treatments. In order to evaluate the interaction of the applied stimulations with the clinostat-elicited nastic response (Nick and Schäfer 1989), a gravitropic stimulus of 30 min was administered within the longer and the shorter coleoptile cross-section and seedlings then rotated for 24 h on a horizontal clinostat. Alternatively, a blue-light pulse of 1.9 $\mu mol \cdot m^{-2}$ (inducing maximal first positive phototropism) was given in the longer coleoptile cross-section and the response was measured after 24 h of clinostat rotation.

Antiparallel-interaction experiments. A gravitropic stimulation of 30 min within the longer coleoptile cross-section was followed by rotation on the clinostat for variable time intervals. Then, seedlings were subjected to a phototropic stimulus (1.9 $\mu mol \cdot m^{-2}$ blue light), whose direction opposed that of the gravity stimulation. Thereafter, seedlings were mounted again on the clinostat and rotated until 24 h after the onset of gravity stimulation.

Perpendicular-interaction experiments. This experimental design was varied such that the gravitropic stimulus was applied within the shorter coleoptile cross-section (caryopsis upwards), whereas the light pulse was irradiated within the longer coleoptile cross-section. An additional experiment involved a second light pulse of equal fluence, but opposing the first. Hereby, the time interval elapsed between the end of the gravistimulation and the first pulse was 120 min, the time interval between the first and the second pulse amounted to 45 or 120 min, respectively. The details of gravi- and phototropic stimulation and clinostat rotation are given in Sailer et al. (1990) and Nick and Schäfer (1989).

Response evaluation. Time courses of curvature and final curvatures were estimated as described elsewhere (Nick and Schäfer 1988a, b). At the time of excision, 24 h after the onset of stimulation, the respective responses are expected to be completed, even in those experiments involving multiple stimulations. As the direction of responses very often deviated from the stimulation plane, the azimuth of response had to be recorded (Nick and Schäfer 1989). The system used therefore characterised bending away from the caryopsis by an azimuth of 0°, whereas 180° indicated curving towards the caryopsis. 90° and 270° meant those curvatures orientated parallel to the plane of the longer coleoptile cross-section. For the time courses of gravi- and phototropic curvature (Figs. 1, 2) the curvature components within the stimulation plane (average from 16 seedlings) were plotted versus time. For the antiparallel and perpendicular interaction experiments, final curvature (average from eight seedlings) was plotted versus the time interval after the onset of gravity stimulation, at which the phototropic stimulus was administered (Figs. 3, 5). In those curves, error bars indicate standard deviations. In order to understand the spatial response pattern, frequency distributions over the azimuth of final curvature were constructed for all experiments using data from 39 to 79 seedlings.

Results

The gravitropic response on the horizontal clinostat. The gravitropic response of maize coleoptiles on the clinostat

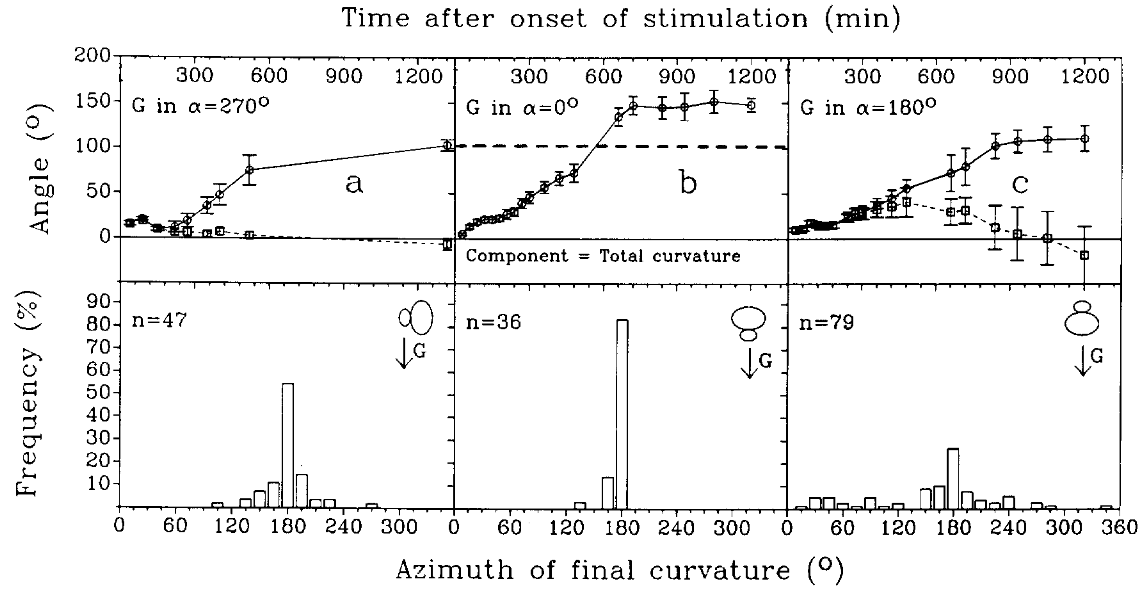

Fig. 1a–c. Total curvature and curvature component parallel to the stimulation plane (*upper row*) and azimuth distribution of the final curvature for gravitropic stimulation in different directions of the maize coleoptile cross-section (*lower row*). **a** Gravity vector (*G*) parallel to the longer coleoptile cross-section; **b** gravity in $\alpha = 0°$, i.e. gravity vector pointing away from the caryopsis; **c** gravity in $\alpha = 180°$. Seedlings were gravistimulated for 30 min (for the spatial relations, see *lower row*, *insets*: the smaller ellipse denoting the coleoptile, the larger ellipse the caryopsis cross-sections), and then rotated on the horizontal clinostat under red light until 24 h after the onset of stimulation. Time course of total curvature irrespective of the orientation of the coleoptiles (*circles*, *solid curves*) and time course of the curvature component parallel to the gravitropic stimulation (*squares*, *dashed curves* in **a** and **c**; $n = 16$, each). Final curvature for nastic bending alone without preceding stimulation by gravity is given in **b** (*dashed line*). *Lower row*: azimuthal distribution of final curvature 24 h after the onset of stimulation, with 180° indicating curvatures towards the caryopsis. It should be noted that, for total curvature, the azimuth is different in each individual coleoptile, whereas for the component the negative gravitropic response irrespective of the orientation of the caryopsis is plotted

appears to be not very stable and depends on several external and internal factors (Sailer et al. 1990). Thus, the analysis of the response to gravitropic stimulation in different directions is a prerequisite for understanding the interaction of gravi- and phototropic stimulation on the clinostat. For this, the seedlings were gravitropically stimulated for 30 min either in the plane of the long coleoptile cross-section (gravity vector pointing in azimuthal direction 270°, Fig. 1a) or in the short axis with the coleoptile downwards (gravity vector pointing in azimuthal direction 0°, supporting the nastic response (Fig. 1b) or gravity in azimuth 180°, counteracting the nastic response (Fig. 1c), respectively. Then, they were rotated on a horizontal clinostat with constant red light as background illumination. As was expected, a rather complex spatial pattern was found, requiring an appropriate representation of data. Therefore, time courses of total curvature (irrespective of its azimuth) are given together with the time course of the curvature component parallel to the stimulation plane, and frequency distributions over the azimuth of final curvature.

Gravitropic stimulation in the longer coleoptile cross-section (Fig. 1a) resulted in transient bending opposing the gravity vector. After reaching 25°, 100 min after the onset of stimulation, curvature returned to a minimum of 10° 50 min later. Then, the curvature component within the stimulation plane slowly decreased, which was the consequence of a change of azimuth rather than an actual decrease of the bending angle. This is indicted by the fact that total curvature increased steeply up to 100° at the same time. The frequency distribution peaks at an azimuth of 180°, indicating curvatures towards the caryopsis. Thus, the increase of curvature after 150 min is accompanied by a growing deviation of the response direction from the stimulation plane towards the caryopsis.

For gravitropic stimulation in an azimuth of 0° (Fig. 1b), the response pattern is more simple. Again, an initial bending opposing the gravity vector of 20 to 25° 100 min after the onset of stimulation is followed by a period of about 50 min duration when curvature does not develop further, and a final sharp increase of curvature reaching final values of 150° towards the caryopsis, which at the same time is the direction opposing the gravity vector. The frequency distribution over the azimuth of final curvature peaks more distinctly at 180° than for stimulation in the longer coleoptile cross-section. This explains why the curvature component within the stimulation plane is identical to total curvature. There are no deviations from the stimulation plane. It should be mentioned that the final total curvature is much higher than that for stimulation within the longer coleoptile cross-section (150° as compared to 100°).

The corresponding curves for an azimuth of 180° (Fig. 1c) are identical to the curves in Fig. 1b in the initial parts (until 150 min after the onset of gravity stimulation), i.e. seedlings bend in a direction opposing the gravity vector. Then, the curvature component parallel

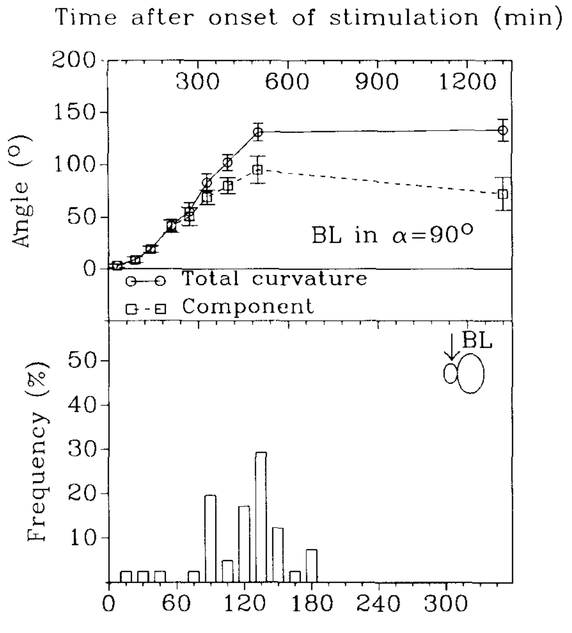

Fig. 2. As for Fig. 1, but for phototropic stimulation (1.9 µmol · m^{-2} blue light (*BL*)) parallel to the longer coleoptile cross-section and subsequent clinostat rotation. *Circles, solid curve*: total curvature irrespective of azimuth. *Squares, dashed curve*: curvature component parallel to the stimulation plane. For the spatial relations see the *inset* in the *lower row*. An azimuth of 90° corresponds to a phototropic response not affected by nastic bending, i.e. the direction of curvature is identical to the situation in Fig. 1a. An azimuth of 180° indicates bending towards the caryopsis, i.e. perpendicular to the stimulation plane. $n = 41$

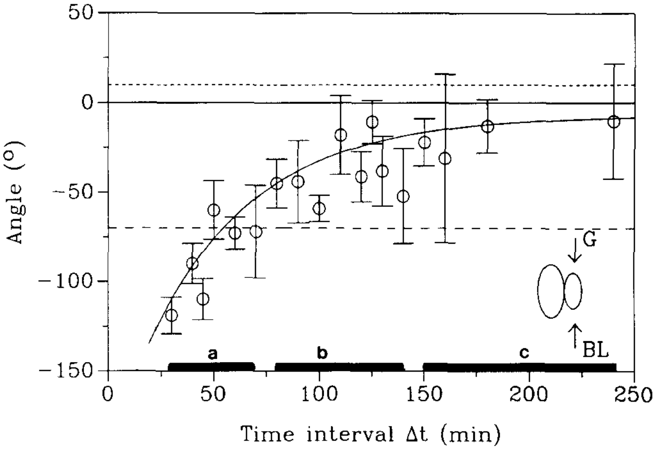

Fig. 3. Final curvature component parallel to the stimulation plane after 24 h of clinostat rotation observed for gravitropic stimulation (30 min) followed by a phototropic stimulation (30 s, 1.9 µmol · m^{-2}) in the opposite direction at the time interval after the onset of gravity stimulation given on the *abscissa*. Negative values indicate curving towards the light. *Dashed line*: final curvature component for phototropic induction alone. *Dotted line*: final curvature component for gravitropic induction alone, which is a mirror image of the situation in Fig. 1a. *Error bars* denote ±SD. The *horizontal bars a–c* on the abscissa define the time ranges used for the frequency distributions of Fig. 4a–c

to the stimulation plane grows only slowly and, from 8 h after the onset of stimulation, it gradually returns to zero. At the same time total curvature increases to a final value of 110°. The corresponding frequency distribution, though peaking at 180° as those in Figs. 1a, b, is much broader with a significant portion (15%) of seedlings pointing in directions almost opposing that of the distribution maximum. This means that some seedlings maintain the direction defined by the gravity stimulation, whereas most seedlings deviate more and more from this direction yielding a decrease of the curvature component parallel to the plane of stimulation.

The phototropic response on the horizontal clinostat. As a second precondition for the interaction analysis the behaviour after phototropic stimulation in the longer coleoptile cross-section was checked (Fig. 2). For about 300 min total curvature and the component of curvature parallel to the stimulation plane were almost indistinguishable. Then, the curvature component within the stimulation plane did not rise much further, but even decreased slightly to a final value of about 70° 24 h after stimulation. At the same time total curvature increased to a final value of 130°. The corresponding frequency distribution over the azimuth of final curvature reveals that, in addition to those seedlings curving within the stimulation plane (azimuth 90°), many seedlings were oriented in a direction deviating 45° from the stimulation plane towards the caryopsis.

Antiparallel-interaction experiments. It was demonstrated previously that the development of a stable directional memory in maize coleoptiles takes about 90 min after phototropic stimulation (Nick and Schäfer 1988b) and about 240 min during rotation on a clinostat without prestimulation (Nick and Schäfer 1989). Using a delay time of 120 min, Nick and Schäfer (1988b) showed that gravity, too, can induce a stable spatial memory. In order to determine the point at which this memory becomes stable against equivalent phototropic counterinduction, the seedlings were transferred to a clinostat after gravitropic stimulation for 30 min in the plane of the longer coleoptile cross-section. Then, after variable time intervals they were subjected to a phototropic counterstimulation with 1.9 µmol · m^{-2} blue light. The component of final curvature within the stimulation plane was plotted as a function of that time interval after the onset of gravity stimulation, after which the light pulse had been administered (Fig. 3). For time intervals up to 70 min a curvature component of −120° to −70° was obtained, indicating that the final response is dominated by the phototropic induction. This is confirmed by the analysis of the frequency distribution over the azimuth of final curvature (Fig. 4a), which is almost identical to that for blue light alone (Fig. 2). For time intervals exceeding 130 min, values approach zero and the corresponding frequency distribution shows a sharp peak at an azimuth of 180°, i.e. the seedlings curved towards the caryopsis (Fig. 4c). This corresponds to the spatial pattern of final curvature for a gravity stimulus in the plane of the longer coleoptile cross-section as

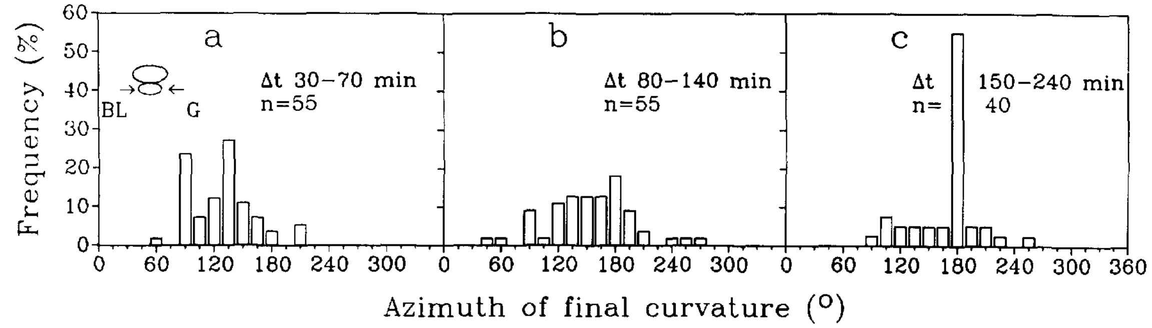

Fig. 4a–c. Frequency distribution over the azimuth of final curvature for the time ranges a–c of the curve in Fig. 3, constructed from the data presented therein. Azimuths of 90° indicate bending towards the light pulse, azimuths of 270° bending according to the gravitropic stimulation. Phototropic stimulus administered 30–70 min (**a**), 80–140 min (**b**), and 150–240 min (**c**) after the onset of gravitropic stimulation

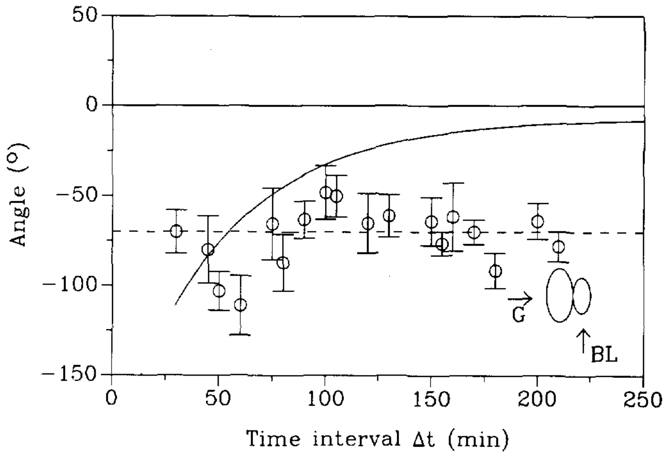

Fig. 5. As for Fig. 3, but for blue light administered perpendicular to the gravitropic stimulation. Again, error bars indicate standard deviations. *Dashed line*: response for phototropic induction alone. The smooth curve represents the corresponding values from Fig. 3. Here, the curvature component parallel to the plane of phototropic stimulation is considered. For this arrangement of stimulations, curving according to the gravitropic stimulus is characterised by zero values

shown in Fig. 1a. The transition between those two parts of the curve is characterised by large standard deviations and a broad azimuth distribution smeared between azimuths of 90° (indicating curvature towards the light pulse) and 180° (indicating curving towards the caryopsis, i.e. perpendicular to the stimulation plane).

Perpendicular-interaction experiments. As in the antiparallel-interaction experiments the component of curvature parallel to the plane of phototropic stimulation was plotted versus the time interval after the onset of the first, gravitropic, stimulus (Fig. 5). This curve is strikingly different from that shown in Fig. 3 in that values oscillate around −70°, indicating curvatures directed towards the light pulse. The azimuth distributions for short (30 to 75 min, Fig. 6a) and long (110 to 210 min, Fig. 6b) time intervals are not significantly different and are almost indistinguishable from that found after phototropic induction alone, administered parallel to the longer coleoptile cross-section (Fig. 2). It should be noted that, in these experiments, gravitropic stimulation was given such that the gravitropic response alone should yield a very sharp frequency peak at an azimuth of 180°

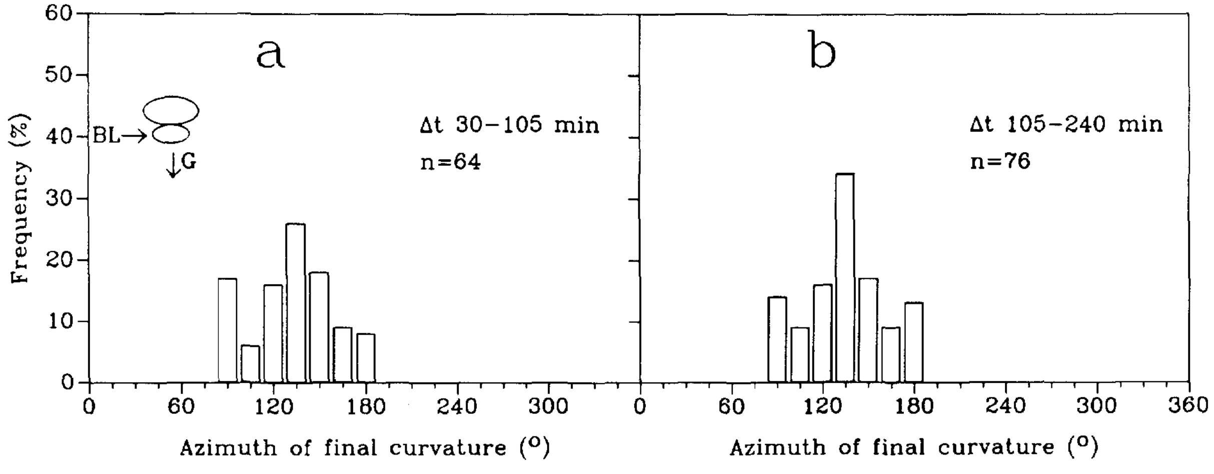

Fig. 6a, b. As for Fig. 4, but for the data of Fig. 5 with blue light irradiated 30–105 min (**a**), and 110–240 min (**b**) after the onset of stimulation by gravity. An azimuth of 90° indicates curvatures towards the light pulse

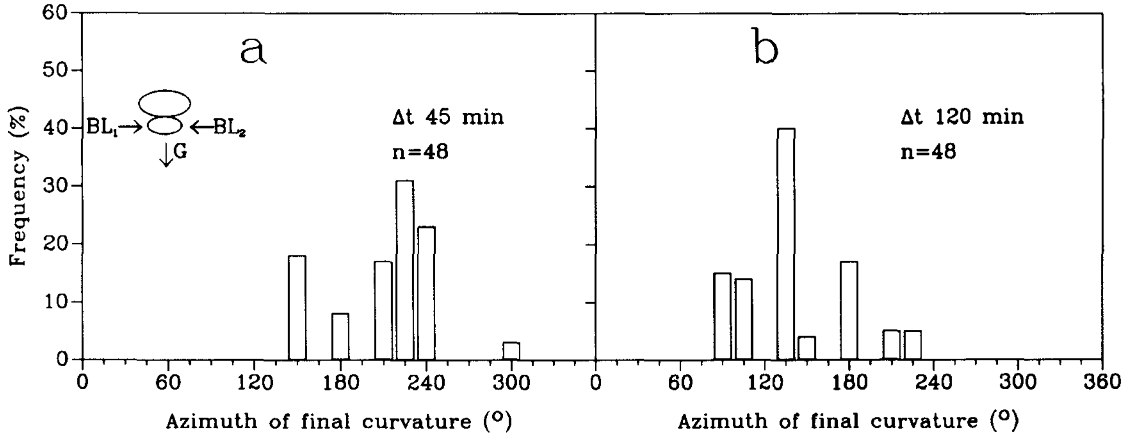

Fig. 7a, b. Frequency distribution over the azimuth of final curvature of maize coleoptiles for gravitropic stimulation (30 min) in $\alpha = 0°$ (nastic bending enhancing the gravitropic response), phototropic induction ($1.9\ \mu\mathrm{mol} \cdot \mathrm{m}^{-2}$) parallel to the longer coleoptile cross-section (i.e. perpendicular to the gravity vector) 150 min after the onset of gravistimulation, and phototropic stimulation of equal strength opposing the first light pulse 45 min (**a**), and 120 min (**b**) later. An azimuth of 90° indicates bending towards the first, an azimuth of 270° towards the second light pulse. The average curvature component parallel to the plane of phototropic stimulations amounts to 53° in **a**, indicating bending towards the second pulse, and + 56° in **b**, indicating curvature towards the first pulse

(Fig. 1b) corresponding to a curvature component of zero in Fig. 5.

In order to assess whether the blue-light pulse, which in this experimental set-up is the second stimulus, is really not influenced by the preceding perpendicular gravitropic stimulation, it was tested whether it still could induce a stable directional memory. For this, a second blue-light pulse of equal fluence but opposing direction was administered 45 min or 120 min after the first pulse. The azimuth of final curvature was analysed by construction of a frequency distribution (Figs. 7a, b). For the short time interval, the distribution is clearly shifted in the direction of the second pulse (applied in an azimuth of 270°), whereas for the long time interval the peak was clearly in the direction of the first pulse (azimuth 90°). In both cases, a certain portion of seedlings curved towards the caryopsis. It should be noted that the distribution peaks deviated about 45° from the exact direction of phototropic stimulations. This "aiming-error" in both cases, was oriented towards the caryopsis.

Discussion

Separation of gravitropic memory and stable gravitropic curving. The analysis of the response to gravitropic stimulation in different directions (Figs. 1a–c) revealed that the gravitropic response is easily reoriented towards the caryopsis, which is probably due to the influence of the nastic bending found to occur in this direction during clinostat rotation (Nick and Schäfer 1989). Only in a situation where gravitropic and nastic curving enhance each other (Fig. 1b), can a stable response according to the direction of stimulation be achieved on the clinostat. In those cases where both responses do not coincide in direction, one gets a large discrepancy between curvature as such and that component of curvature which is oriented according to the gravitropic stimulation (Figs. 1a, c). It might be argued that the steady increase of total curvature is not due to the gravitropic response itself, but to nastic bending, whose direction is shifted by the gravitropic stimulation. However, if this held true, it is difficult to explain the fact that for the situation of Fig. 1b, where both responses run parallel, the curvature is much higher than expected from an exclusively nastic bending (Fig. 1b, dashed line). This implies that, in fact, the observed instability of the gravitropic response on the clinostat in the seed batch used here (harvest 1988) is not the result of a transient bending response, but is a consequence of reorientation of the response direction. What one can conclude from these observations is that the gravitropic response as such on the clinostat remains very labile. This lability, here, becomes manifest as an increasing deviation of the response from the stimulus orientation to the direction of the nastic response.

In contrast to the instability of gravitropic curvature on the clinostat, the phototropic response seems to be very stable in both direction and bending (Fig. 2). This is consistent with earlier reports (Nick and Schäfer 1988a, b).

Surprisingly, the response pattern seen in the antiparallel-interaction experiments (Figs. 3, 4) suggests that gravitropic stimulation, although not capable of inducing a stable tropistic response, is able to produce a stable directional memory. Whereas the final response for short time intervals is obviously dominated by the second, phototropic, stimulation (Figs. 2, 3, 4a) for long time intervals the response is indistinguishable from that for gravitropic stimulation alone (Figs. 1a, 3, 4c). This indicates that the gravitropic stimulation induced a stable effect preventing the expression of a stable phototropic curvature. This effect becomes stable at about 90 min after the onset of gravistimulation. For short time intervals (up to 30 or 40 min after the onset of gravity stimulation) the second, phototropic response is even enhanced by the first, gravitropic, stimulation, although its direction was opposing that of the light pulse (Fig. 3, dashed line, Figs. 2, 4a). For intermediate time intervals, the azimuth distribution was smeared over a wide range of azimuths rather than resuming a clear position somewhere in between the two stimulation vectors. Those three observations, the increase of the response to the second stimulation at short time intervals, suppression of the response to the second stimulus for long time intervals, and large inhomogeneity of the response for intermediate time intervals, were typical for the expression of directional memory induced by a phototropic stimulation, which was equivalent in its tropistic effect to the gravity stimulation used here (Nick and Schäfer 1988b). This phototropically induced directional memory was interpreted in terms of a stable transverse polarity. The results of the antiparallel-interaction experiments presented here allow the conclusion that not only phototropic, but also gravitropic stimulation can induce a stable transverse polarity. However, whereas phototropic stimulation produces a stable bending response on the clinostat, this effect cannot be achieved by gravitropic stimulation. Thus, the stable transverse polarity detectable as increasing stability against counterstimulation has to be separated from the stable tropistic response on the clinostat.

Gravitropic memory remains localised. Sensory adaptation to gravity remains localised to the stimulation plane (Hild and Hertel 1972), whereas transductory adaptation, a step common to both, photo- and gravitropic signal chains, was spread over the whole organ cross-section (Ullrich 1976). This was concluded from experiments involving tropistic stimuli administered perpendicular to each other. Those investigations delivered the motivation for the perpendicular-interaction experiments described here (Figs. 5, 6). Compared to the corresponding curve for antiparallel stimulation (Fig. 3), no clear dependency of final curvature upon the time interval after the onset of gravity stimulation can be detected for perpendicular stimulation (Fig. 5). Mainly, there is no tendency to approach the zero level for long time intervals as it was observed for antiparallel stimulation, which is consistent with the striking similarity of the corresponding azimuth distributions for short and long time intervals (Figs. 6a, b) with that for phototropic stimulation alone (Fig. 2). The response pattern, independently of the time interval, does not reveal any traces of the gravitropic stimulation. This is the more surprising as the used stimulus constellation (gravitropic and nastic response are supposed to enhance each other) is the one where the expression of gravitropic curvature is favoured as much as possible. The clear dominance of the second, phototropic response in these experiments not only involves stable phototropic curving, but also the formation of a blue-light-elicited stable transverse polarity, which can be inferred from the behaviour after a second blue-light pulse after a short and a long time interval opposing the first light pulse (Fig. 7a, b). When the time interval was short, the response was directed towards the second pulse, whereas for long time intervals seedlings curved towards the first pulse. This is exactly the behaviour to be expected, if the first light pulse really induces a stable transverse polarity (Nick and Schäfer 1988b).

These observations lead to the following conclusions: (i) Whereas gravitropic stimulation can induce a stable transverse polarity suppressing the response to phototropic counterstimulation in the same plane (Figs. 3, 4c), it cannot prevent a perpendicular phototropic stimulation from being expressed as stable curvature (Figs. 2, 5, 6). Moreover, the second stimulus does not only elicit a stable bending response, but also a stable transverse polarity (Figs. 7a, b). (ii) The proportion of seedlings pointing towards the caryopsis in all the experiments involving perpendicular stimulation (Figs. 6, 7) compared with that for the gravitropic stimulation alone (Fig. 1b) is much smaller than one would expect, if in addition to the phototropic bending a certain gravitropic response took place. The data of Fig. 6 compared to those of Fig. 2 do not show any influence of the gravitropic stimulation at all. This indicates that there is not only no suppression of the responses to blue light by a preceding gravitropic stimulation in perpendicular direction but that additionally, the phototropic stimulation inhibits the expression of the gravitropic response. This favours the assumption that, in contrast to gravitropic stimulation, the effect of phototropic stimulation, manifest as suppression of the gravitropic response in perpendicular direction, is global, rather than being localised.

On the relation between photo- and gravitropic signal chains. The following properties of photo- and gravitropic signal chains await an explanation: (i) Adaptation of that part of the gravitropic signal chain, which is not accessible to phototropic stimulation is confined to the plane of stimulation (Hild and Hertel 1972). (ii) Adaptation of that part of transduction which gravitropism shares with phototropism is global, not localised (Ullrich 1976). (iii) The suppressing effect of gravitropic transverse polarity upon the responses to phototropic stimulation is restricted to the plane of gravitropic stimulation (Figs. 5–7). (iv) The suppressing effect of blue-light-elicited transverse polarity upon gravitropic responses is not localised (Figs. 1b, 2, 6, 7).

Thus, the mechanism mediating gravitropic transverse polarity must branch off gravitropic transduction in that part, where the effects of gravitropic transduction are still localised, i.e. before the point of confluence of gravi- and phototropism (labeled by the global transductory adaptation step mentioned in (ii). On the other hand, the bifurcation between phototropism and blue-light-elicited transverse polarity cannot occur in that part of the signal chain which is used by both stimulus qualities. Otherwise it could be triggered also by a gravitropic prestimulation. As the effects of tropistic transduction are supposed to be global in that part of the signal chain (Ullrich 1976), a gravitropic stimulation in one plane should prevent the formation of transverse polarities in other directions. This was not observed.

Thus, the simplest model that can describe the observations assumes that the signal chains mediating gravity and blue-light-elicited stable transverse polarities split from the respective tropistic transduction before the point of confluence of both tropisms. This, however, means that not only the early tropistic polarities (Buder 1920; Rawitscher 1932), but also the respective stable transverse polarities imply different mechanisms for the different stimulus qualities.

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