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Interaction of gravi- and phototropic stimulation in the response of maize (*Zea mays* L.) coleoptiles

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Abstract. The influence of gravitropic stimulation upon blue-light-induced first positive phototropism for stimulations in the same (light source and center of gravity opposite to each other) and in opposing directions was investigated in maize coleoptiles by measuring fluence-response patterns. As a result of gravitropic counterstimulation, phototropic bending was transient with maximum curvature occurring 100 min after stimulation. On a horizontal clinostat, however, the seedlings curved for 20 h. Gravistimulation in the opposite direction acted additively upon blue-light curvature. Gravistimulation in the same direction as phototropic stimulation produced a complex behaviour deviating from simple additivity. This pattern can be explained by a gravitropically mediated sensitization of the phototropic reaction, an optimal dependence of differential growth on the sum of photo- and gravistimulation, and blue-light-induced inhibition of gravitropic curvature at high fluences. These findings indicate that several steps of photo- and gravitransduction are separate. Preirradiation with red light desensitized the system independently of applied gravity-treatment, indicating that the site of red-light interaction is common to both transduction chains.

Key words: Coleoptile – Gravitropism – Phototropism – *Zea* (gravitropism, phototropism).

Introduction

Phototropism has been studied in some detail in both graminean coleoptiles and in fungal sporangiophores (Dennison 1979; Pohl and Russo 1984). It has long been known (Rothert 1894) that, in coleoptiles, a photogravitropic balance is obtained under conditions of continuous irradiation. This can also be observed in *Phycomyces blakesleeanus* sporangiophores (Galland 1983; Löser and Schäfer 1986) and in the hypocotyls of dicotyledons (Hart and MacDonald 1981). In the case of stimulation with light pulses involving the sensitive first rather than the time-integrating second positive reaction, however, no stable balance is observed. On stimulation, bending ceases after 100 min and straightening due to gravitropism begins. This leads to difficulties in quantifying the actual phototropic response (Curry 1969; Iino and Briggs 1984).

Gravitropic straightening can be expected to depend on the maximal curvature reached after phototropic stimulation, since gravitropic curvature has been shown to increase proportionally to the component of the gravitropic stimulus normal to the longitudinal axis of the coleoptile tip (Pickard 1972). One method of excluding distortions due to gravitropic counterinduction is the use of a clinostat. However, in such experiments, gravitropic stimulation is not absent but merely acting symmetrically, i.e. even on a clinostat "pure" phototropism does not exist.

Investigations into the interaction between photo- and gravitropism were begun as early as 1851 (Rawitscher 1932), but the use of continuous illumination meant that only the second positive curvature was involved. For first positive curvature, however, two principal approaches were considered:

(i) Summation of sub-threshold stimuli in oat (*Avena sativa* L.) coleoptiles (Pekelharing 1909). Sub-threshold stimuli of the same type (i.e. light followed by light, or gravity followed by gravity) showed an additive response up to the threshold,

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Abbreviations: BL = blue light; G^+ = stimulation by light and gravity in the same direction (i.e. light source and center of gravity opposite to each other); G^- = stimulation by light and gravity in opposing directions whereas this was not the case for stimuli of differing types (i.e. light followed by gravity or vice versa). This indicated that the two transduction chains are separated at the level of stimulus summation.

(ii) Adaptation after prestimulation (Hild 1977; Hild and Hertel 1972; Ullrich 1976; Blaauw and Blaauw-Jansen 1970). Coleoptiles prestimulated either by alternating gravitropic stimulation from opposite sides or blue-irradiation from above were then subjected to asymmetric gravitropic or phototropic induction. In all four possible combinations of symmetric prestimulation an adaptation to asymmetric stimulation could be observed. In the case of blue-light-induced adaptation, the time courses for both asymmetric photo- and gravitropic stimulation were the same. This indicates common adaptation of both signal chains (Hild 1977; Blaauw and Blaauw-Jansen 1970). In the case of gravitropically adapted coleoptiles, however, differences in the response to asymmetric stimulation could be observed. When asymmetric gravistimulation was tested, adaptation was confined to the azimutal axis of prestimulation (Hild and Hertel 1972). The adaptation to subsequent blue-light stimulation, however, did not depend on the angle between the azimutal axes of prestimulation and of stimulation (Ullrich 1976). It is not clear whether this deviation is caused by differences in transductional adaptation or merely by localized adaptation of gravity perception. In the latter case, one could conclude that the adaptation step is common to both transduction chains.

Symmetrical preirradiation with blue light reduces gravitropic curvature in both maize and oat coleoptiles. The fluence-response curve of this inhibition corresponds roughly to that for first positive curvature but is slightly (about half an order of magnitude) shifted towards higher fluences (Hild 1977; Blaauw 1961). Red-light prestimulation desensitized both gravitropic and phototropic bending (for the first positive reaction). Moreover the time courses for this effect were the same, indicating that red light acts upon transduction steps common to both signal chains (Hild 1977).

The present paper investigates the interaction between gravitropic stimulation and phototropic pulse stimulation as a contribution to understanding gravity-induced distortions of first positive phototropism. As a factor presumably affecting both tropisms in the same manner (Hild 1977), prestimulation with red light is used to indicate the part of the transduction chain common to both stimulations.

Material and methods

Plant material. Maize seeds (*Zea mays* L. cv. BRIO 42.HT, Asgrow, Buxtehude, FRG, stored at 3° C in the dark) were soaked for 24 h in running tap water and sown, embryo up, on one layer of absorbant paper (No. 914446/4; Hartmann, Heidenheim/Brenz, FRG) in clear plexiglas trays ($33 \cdot 22 \cdot 13$ cm^3, 80 seeds per tray), irrigated with 400 ml deionized water. They were kept for 60 h under continuous red light in a phytochamber (0.01 W·m^{-2}, 65% relative humidity, 25° C). Irradiation with red light enhances coleoptile elongation and inhibits mesocotyl growth (Kunzelmann and Schäfer 1985). After 60 h, seedlings were selected for straightness and length (about 7 mm), transferred in rows of seven to plastic trays (base area $14 \cdot 6$ cm^2, height 5 cm) filled with vermiculite (Deutsche Vermiculit; Dämmstoff, Sprockhövel, FRG) and irrigated with 300 ml deionized water. The seedlings were oriented in such a way that the flat sides of the seeds were perpendicular to the plane of the seed row. The trays were placed in cardboard boxes ($35 \cdot 27 \cdot 13.5$ cm^3) and kept in complete darkness at 25° C for one day.

Light sources. The red-light source used in the phytochamber was as described by Mohr et al. (1964). For phototropic induction (taking place in the dark), fluence rates lower than $25 \cdot 10^{-3}$ W·m^{-2} were obtained using a Prado Universal Projector (Leitz, Wetzlar, FRG). Higher fluence rates necessitated the use of a Zeiss-Ikon Xenosol III projector having an Osram XBO 2500 W Xenon arc (Osram, München, FRG). Blue light was isolated by means of a DIL interference filter (451 nm, half-bandwidth 10 nm, maximal transmission 18%) and fluence rates were regulated using neutral density filters (both filter types from Schott, Mainz, FRG). Irradiation time (30 s throughout) was controlled by means of an automatic shutter system. Between phototropic induction and excision, the seedlings were kept either in the dark or under saturating red light (1.0·W·m^{-2}, light source as described for phytochamber illumination). Light measurements were carried out with a digital photometer (J16/Option 2; Tectronix, Beaverton, Ore, USA).

Phototropic induction and gravistimulation. Complete shoots were irradiated unilaterally for 30 s with the longest transverse axis of the seedling parallel to the direction of the incident light. After irradiation, trays were tilted so that the gravity center was opposite to the light source enhancing phototropic bending ("G^+"). Alternatively, the gravity center was in the same direction as the light source had been, i.e. phototropic bending was inhibited ("G^-"). A control group of trays was kept in upright position. If not otherwise specified, gravistimulation was applied for 100 min. All treatments took place either in the dark or under continuous symmetrical red light beginning 1 h before the phototropic induction.

Curvature measurements. One hundred minutes after phototropic induction, the shoot was excised, attached to a strip of masking tape and fixed to a Plexiglas plate in such a way that the longest transverse seedling axis was parallel to the plate surface. The plate was photocopied with an IBM copier III Model 20 and coleoptile curvature marked by drawing lines. The angles were measured with an Hewlett-Packard 986417 digitizer connected to an HP 982017 calculator (Hewlett-Packard, Bad Homburg, FRG). Mean and standard error were calculated for 15 to 20 seedlings per treatment.

Kinetic measurements. Time courses for curvature development were measured after phototropic and gravitropic induction, respectively. For phototropic stimulation, one test group was kept

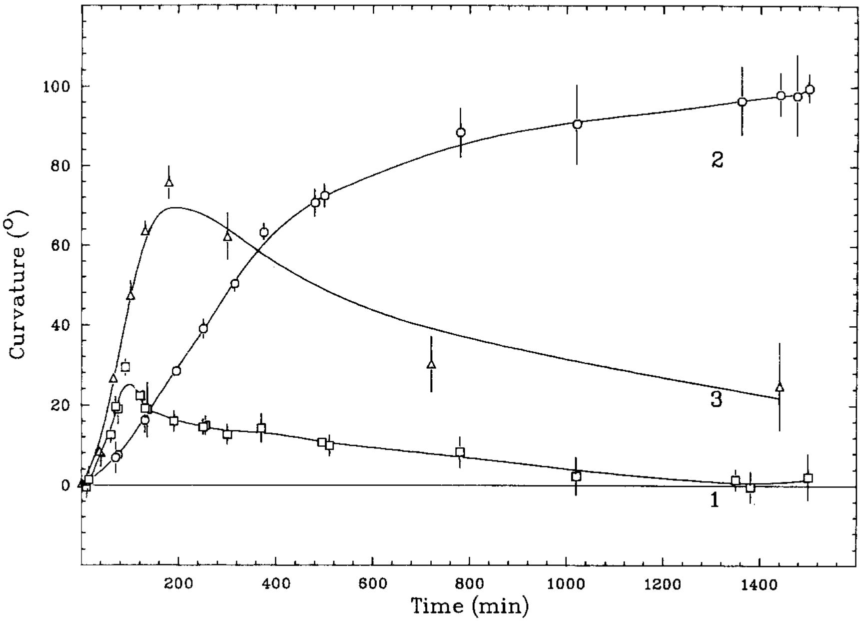

Fig. 1. Time course of curvature development after phototropic and gravitropic stimulation under symmetrical continuous red light ($2.3 \cdot W \cdot m^{-2}$) beginning 1 h before stimulation. *Curve 1*: Induction by 0.88 $\mu mol \cdot m^{-2}$ blue light, seedling trays upright during curvature development. *Curve 2*: As *1*, curvature development on a clinostat (0.5 rpm). *Curve 3*: Induction by 60 min gravistimulation (seedling trays tilted by 90°)

in an upright position, a second group was held horizontally on a clinostat at 0.5 rpm. For measuring the time course of gravitropic curvature, a further group was subjected to 60 min gravistimulation by tilting the seedlings into the horizontal position. After this treatment, these seedling were held on a clinostat as in the case of the second group. All seedlings were kept under symmetrical continuous red light starting 1 h before stimulation. Shadowgraphs were made using unilateral red light ($0.025 \, W \cdot m^{-2}$, DEPIL interference filter, maximal transmission at 665 nm, maximal transmission 10%). For shadowgraphing, seedlings had to be removed from the clinostat and stood upright for roughly 30 s. This treatment has been shown not to affect curvature development on the clinostat (Pickard 1972).

Results

Influence of gravitropic counterinduction on development of phototropic curvature. Time-course measurements. Kinetic measurements of first positive phototropism following unilateral irradiation with $0.88 \cdot \mu mol \cdot m^{-2}$ blue light show that a transient response reaches a maximum 100 min after phototropic induction and then returns slowly to zero (Fig. 1). This is consistent with earlier investigations (Curry 1969).

When curvature is allowed to develop on a clinostat, the initial phase is slightly slower but curvature increases continuously, saturating at about 20 h after induction at an angle of 95°–100°. Curvature is maintained even after the primary leaf has broken through the coleoptile 12 h after induction (Fig. 1).

In contrast to the first positive phototropism, 60 min of gravistimulation followed afterwards by growth on a clinostat produces an increase in bending for 3 h after induction reaching a maximum curvature of 75°. The angle then decreases slowly to a final value of 25° (Fig. 1). This decrease, however, is slower than that described for oat coleoptiles by Pickard (1972).

Interaction between gravitropism and first positive phototropism. Fluence-response patterns for curvature development in the dark. Fluence-response curves for upright unilaterally irradiated control seedlings show the familiar optimum curve for first positive phototropism. The threshold is at about $10^{-4} \, \mu mol \cdot m^{-2}$, maximum response at about $0.8 \, \mu mol \cdot m^{-2}$. Above this fluence, the response decreases and at fluences above $120 \, \mu mol \cdot m^{-2}$ no curvature can be observed (Fig. 2). Gravistimulation for 100 min without phototropic induction ("gravicontrol") results in 55° curvature (Fig. 2, dashed lines).

Upon gravistimulation in the same direction as photostimulation, the seedlings exhibit a complex fluence-response relationship. In the case of low fluences, which do not produce any curvature in the controls, the response is the same as that to gravicontrol curvature alone. Above the threshold fluence for the control curve, the curve for gravistimulation in the same direction shows a maximum followed by a deep trough and a second somewhat smaller peak at those fluences producing maximal curvature in control seedlings. On further increasing the fluence, the curve falls again to a constant value of 35°–40°. Thus, those fluences where the control curve shows no significant curvature, produce curvatures of approx. 55° for suboptimal and 35°–40° for supraoptimal fluences upon

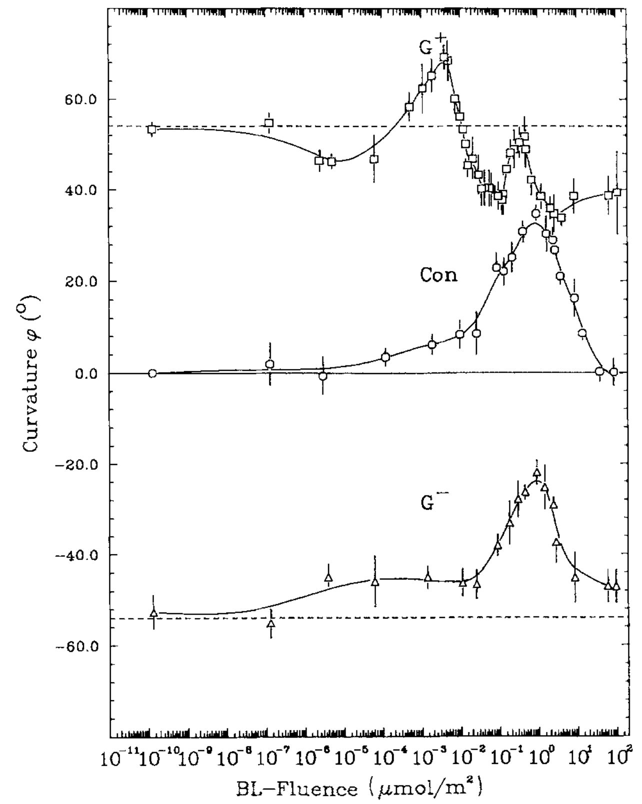

Fig. 2. Fluence-response curves for first positive phototropism with different gravity treatments. Responses measured 100 min after phototropic induction. Curvature development in the dark. *Con*: Seedling trays upright during curvature development. G^+: Trays tilted during curvature development. Gravity center opposite to light source. G^-: As G^+, but gravity center at the same side as light source. *Dashed lines*: gravicontrol (graviresponse without phototropic induction)

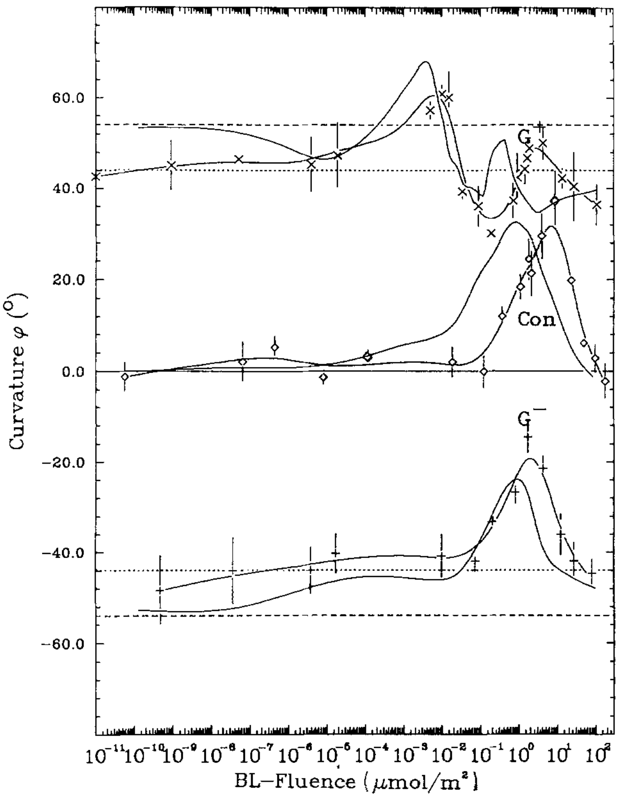

Fig. 3. Fluence-response curves for first positive phototropism with different gravity treatments. Curvature development measured after 100 min under continuous, symmetrical red light (2.3 W·m^{-2}) beginning 1 h before phototropic induction. *Dashed lines*: gravicontrol for curvature development in the dark. *Dotted lines*: gravicontrol for curvature development under red light. *Con*: Trays upright. G^+: Gravity center opposite to light source. G^-: Gravity center at the same side as light source. For comparison, curves from **Fig. 2** are given without points

gravistimulation in the same direction as photostimulation (Fig. 2).

If photostimulated coleoptiles are stimulated gravitropically in the opposite direction, the corresponding curve shows a shape very similar to the control. Curvature is, however, diminished by a constant value of roughly 55° (i.e. the value of gravicontrol curvature alone) for suboptimal fluences, 45° for supraoptimal fluences (Fig. 2). Additionally, the threshold of curvature is lowered by about two orders of magnitude. The position of the peak, however, is not significantly different from the control curve.

Interaction between gravitropism, first positive phototropism and red-light pretreatment. Fluence-response patterns. The experiments described above were repeated under continuous, laterally symmetrical irradiation with saturating red light (2.3 W·m^{-2}) starting 1 h before phototropic induction. Regardless of the gravistimulation applied, a shift of somewhat less than one order of magnitude towards higher fluences occurs as compared to experiments where curvature developed in the dark (Fig. 3). The response patterns appear to be unaltered if one takes into account the fact that the curvature induced by 100 min gravistimulation without phototropic induction (gravicontrol) is diminished by about 10° by red light (Fig. 3, dotted line).

Interaction between first positive phototropism and weak gravistimulation. Fluence-response patterns for curvature development under continuous red light. In order to test whether the complex pattern for gravistimulation in the same direction as photostimulation is caused by saturation of curvature due to supraoptimal gravistimulation, the previous experiment with red-light irradiation was repeated but the gravistimulation was reduced by using a

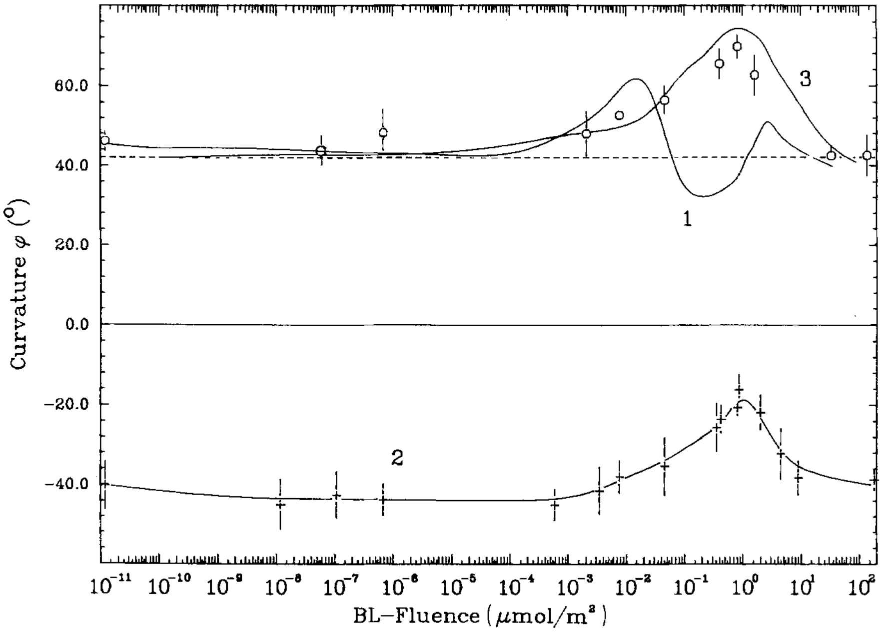

Fig. 4. Fluence-response curves for first positive phototropism with different gravity treatments. Curvature development measured after 100 min under red light. Weak gravistimulation (tilting angle 45°). *Dashed line*: gravicontrol for a stimulation angle of 45°. *Circles*: G^+-curve for 45°-gravistimulation. *Curve 1*: G^+-curve for 90°-gravistimulation (**Fig. 3**). *Curve 2*, *crosses*: G^--curve for 45°-gravistimulation. *Curve 3*: Addition of 45°-gravicontrol and control curve of first positive phototropism (**Fig. 2**)

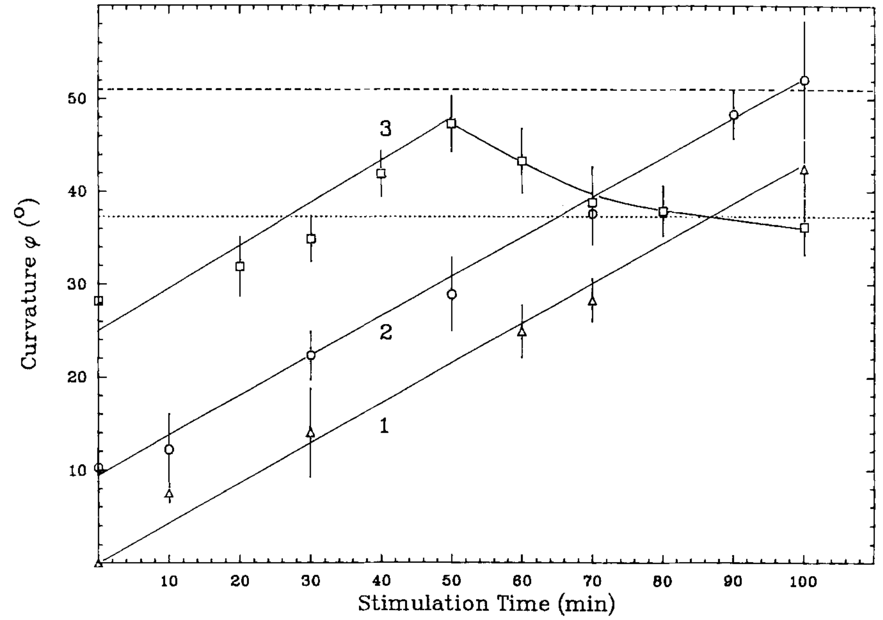

Fig. 5. Dependence of G^+-effect on gravistimulation time (stimulation angle 90°). Curvature development was measured after 100 min under symmetrical, continuous red light ($2.3\ \mathrm{W \cdot m^{-2}}$) beginning 1 h before phototropic induction. *Curve 1*: gravicontrol (without blue-light irradiation). *Curve 2*: $1\ \mathrm{nmol \cdot m^{-2}}$ blue light. *Curve 3*: $1\ \mathrm{\mu mol \cdot m^{-2}}$ blue light. *Dashed line*: value from **Fig. 3** ($1\ \mathrm{nmol \cdot m^{-2}}$ blue light, curvature development under $2.3\ \mathrm{W \cdot m^{-2}}$ red light). *Dotted line*: value from **Fig. 3** ($1\ \mathrm{\mu mol \cdot m^{-2}}$ blue light, curvature development under $2.3\ \mathrm{W \cdot m^{-2}}$ red light)

smaller stimulation angle (45°). This reduction of the stimulus angle simplifies the response for stimulation in the same direction dramatically. Curvature is again increased as compared to the control by the value of the gravicontrol (Fig. 4, dashed line). However, instead of two peaks there is only one (Fig. 4) with a maximum corresponding exactly to the maximum of the control. Thus, the curve can be described by addition of the control curvature and the gravicontrol. As in the experiments described above, additivity is also found for weak stimulation opposite to photostimulation (Fig. 4).

Interaction between first positive phototropism and various times of gravistimulation in the same direction: Time course of gravity influence. To investigate the possible role of saturation phenomena in the pattern for photo- and gravistimulation in the same direction, gravistimulation time was varied for two blue-light fluences using a stimulation angle of 90°. The blue-light fluences were chosen as $1\ \mathrm{nmol \cdot m^{-2}}$, where the fluence-response curve for gravistimulation in the same direction is rising, and $1\ \mathrm{\mu mol \cdot m^{-2}}$, where it shows a trough. The experiments were carried out under continuous irradiation with red light. After different times of gravistimulation the trays were returned to the upright position. As previously, seedlings were excised 100 min after phototropic induction. In the case of phototropic stimulation with 1 $\text{nmol} \cdot \text{m}^{-2}$ blue light and in the dark controls, there is a linear increase in curvature with increasing gravistimulation time (Fig. 5). The curves are also parallel to one another. With 1 $\mu\text{mol} \cdot \text{m}^{-2}$ blue light, however, the curve is only linear (and parallel to the other two curves) for up to 50 min gravistimulation. On attaining 50° curvature, further gravistimulation results in a decrease in the response.

Discussion

Response kinetics. First positive phototropic induction only results in transient curvature which decreases again 100 min after stimulation (Fig. 1). This decrease could be caused by gravitropic counterinduction, by endogenous feedback mechanisms or simply by basipetal curvature migration (Firn 1986). The fact that phototropic curvature is stable in clinostat experiments, where it reaches values of more than 90° indicates that gravitropic counterinduction ("gravitropic straightening") is responsible for the transient response.

Stabilization of the original growth gradient must occur, since this moves towards the base of the coleoptile at a speed of about 10–20 $\text{mm} \cdot \text{h}^{-1}$ (Iino and Briggs 1984), i.e. 2 h after induction, the initial growth gradient might be expected to reach the mesocotyl. Further increases in curvature must presumably be produced by secondary growth gradients. In contrast, gravitropic bending is transient even on the clinostat (Fig. 1); this might indicate that gravitransduction is incapable of initiating such secondary growth gradients.

Fluence-response patterns for photo- and gravistimulation in opposing directions. The fluence-response pattern for photo- and gravistimulation in opposite directions can be described by subtraction of gravicontrol curvature from the control curve regardless of the light conditions during curvature development (dark or red light) and of the angle of gravistimulation. Thus, if applied in opposing directions, gravistimulation and photostimulation appear to act independently upon curvature. During first positive phototropism exactly this situation is given. Thus, gravity-caused distortions of first positive phototropism are restricted to mere addition of gravitropically induced (negative) curvature.

Dependence of the effect of gravistimulation in the same direction as photostimulation on gravistimulation time. In the case of the dark control there is a linear increase in curvature with increase in gravistimulation time (Fig. 5). The same situation occurs for weak blue light which causes only slight phototropic curvature, differing only in a shift, by a constant angle, in the positive direction. This indicates additivity of phototropic and gravitropic curvature as found for stimulations in the opposite direction. For blue-light fluences eliciting maximum curvature in control seedlings, additivity is only found for weak (stimulation times shorter than 50 min) gravistimulation. Longer stimulation times appear to be supraoptimal. These findings indicate that additivity of stimulations in the same direction is obscured by a non-linear dependence of growth on the preceding transduction step. Neither gravistimulation nor photostimulation alone are sufficient to attain this region, where the dependency is non-linear. Combined action can, however, reach this point and result in "overstimulation".

Fluence-response patterns of phototropism for gravitropic stimulation in the same direction: sensitivity-shift and overstimulation. Except in the case of weak gravistimulation in the same direction as photostimulation (45°, Fig. 4), it is obviously impossible to explain the complex fluence-response curve for stimulations in the same direction by simple addition at the growth level without assuming a sensitization of the first positive reaction by gravistimulation. The shape of the fluence-response curve for the first positive reaction has been shown to depend mainly on the light gradient (Kunzelmann 1986). One would not expect it to be changed by gravistimulation since sensitization of the first positive reaction would simply shift the whole curve towards lower fluences without affecting its shape. On this assumption and taking into account addition of phototropic and gravitropic curvature, one would expect for stimulations in the same direction a single-peaked curve, whose maximum is shifted to lower fluences and increased by the gravicontrol curvature (Fig. 6, curve 1). In the centre of this curve overstimulation occurs causing curvature to cease. This would explain the trough between the two peaks. These peaks should, however, then be symmetrical. The observed asymmetry of the two peaks and the biphasic behaviour of the baseline (Fig. 6, curve 3) can, however, be explained by the inhibition of gravitropic curvature by high fluences of blue light found in both oat (Blaauw 1961) and maize coleoptiles (Hild 1977; Fig. 6, curve 2). Thus, the rather complex response for gravistimulation in the same direction as pho-

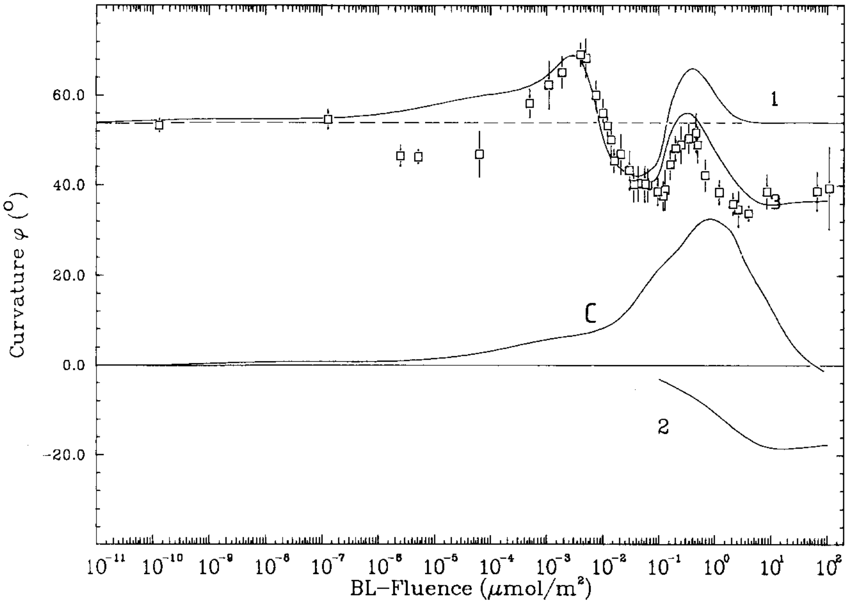

Fig. 6. Description of G^+-response pattern. *Dashed line*: gravicontrol (100 min gravistimulation); *C* Control curve for first positive phototropism (see **Fig. 2**). *Squares*: G^+-curvature in the dark (see **Fig. 2**). *Curve 1*: Expected G^+-curve under the assumption of additivity on the growth level and overstimulation. *Curve 2*: Fluence-response curve for blue-light-induced inhibition of gravitropic curvature (data according to Hild 1977). *Curve 3*: Expected G^+-curve taking into account the data of *Curves 1* and *2*

tostimulation can be described by assuming three factors: (i) Addition of photo- and graviresponses at the growth level with an optimum dependence of the response on the corresponding sum of stimulations (Fig. 5). For 1 nmol·m^{-2} this optimum is not reached. For 1 µmol·m^{-2}, however, this optimum is reached at 50 min gravistimulation, if both stimulations occur in the same direction. (ii) Sensitization of phototropic bending by gravistimulation in the same direction. (iii) Inhibition of gravitropically induced curvature by high fluences of blue light.

Phototropic and gravitropic transduction are different. (i) On the clinostat, phototropic curvature is stable, whereas gravitropic curvature is only transient. (ii) Simple additivity of curvature is found, if gravi- and photostimulation are applied in opposing directions. Together with (i) this can be interpreted by assuming the existence of separate transduction chains. (iii) Additivity is also valid for parallel suboptimal stimulation.

Perception, summation (Pekelharing 1909) and site of signal-chain interaction are thus followed by an transductional adaptation step (Hild 1977; Hild and Hertel 1972; Ullrich 1976; Blaauw and Blaauw-Jansen 1970) common to both signal chains, and the site of red-light interaction (red-light pretreatment shifted all fluence-response curves to the same degree regardless of how gravistimulation was applied). Gravistimulation in the opposite direction and weak gravistimulation in the same direction as phototropic stimulation do not affect the confluent part of the transduction chains. This can, however, be influenced by strong, near-optimal gravistimulation in the same direction.

Both, gravi- and photoperception must occur at the cellular level, leading to the formation of a putative transverse polarity. On account of the nature of the inducing agents, gravity-induced transverse polarity is considered to occur at the cellular level. Phototropic transverse polarity, on the other hand, has been shown to originate from integration over the whole coleoptile (Buder 1920). In both cases, however, the final growth gradient requires a trans-organ polarity, i.e. the cellular gravitropic polarity must be transformed into a systemic polarity. The difference between gravistimulation in the same and in the opposite direction, respectively, with respect to the observed sensitization, involves such a transformation mechanism, whereby the gravity-induced cell polarity is expressed as a systemic polarity equal in quality to, and able to interact with, phototropic polarity.

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References

Blaauw, O.H. (1961) The influence of blue, red and far red light on geotropism and growth of the *Avena* coleoptile. Acta Bot. Neerl. **10**, 397–450

Blaauw, O.H., Blaauw-Jansen, G. (1970) Third positive (c-type) phototropism in the *Avena* coleoptile. Acta Bot. Neerl. **19**, 764–776

Buder, J. (1920) Neue phototropische Fundamentalversuche. Ber. Dtsch. Bot. Ges. **38**, 10–19

Curry, G.M. (1969) Phototropism. In: Physiology of plant growth and development, pp. 253–254, Wilkins, M.B., ed., McGraw-Hill, London

Dennison, D.S. (1979) Phototropism. In: Encyclopedia of plant physiology, N.S., vol. 7: Physiology of movements, pp. 506–566, Haupt, W., Feinleib, M.E., eds. Springer, Berlin Heidelberg New York

Firn, R.D. (1986) Phototropism. In: Photomorphogenesis in plants, pp. 367–389, Kendrick, R.E., Kronenberg, H.M., eds. Martinus Nijhoff, Dordrecht Boston-Lancaster

Galland, P. (1983) Action spectra of photogeotropic equilibrium in *Phycomyces* wild type and three behavioural mutants. Photochem. Photobiol. **37**, 221–228

Hart, J., MacDonald, I.R. (1981) Phototropism and geotropism in hypocotyls of cress (*Lepidium sativum* L.). Plant Cell Environ. **4**, 197–201

Hild, V. (1977) Wirkung von Vorbestrahlung mit Rot- oder Blaulicht auf die geotropische Empfindlichkeit von Maiskoleoptilen. Planta **133**, 309–314

Hild, V., Hertel, R. (1972) Initial phases of gravity-induced lateral auxin transport and geotropic curvature in corn coleoptiles. Planta **108**, 245–258

Iino, M., Briggs, W.R. (1984) Growth distribution during first positive phototropic curvature of maize coleoptiles. Plant Cell Environ. **7**, 97–104

Kunzelmann, P. (1986) Analyse von Photonenflußgradienten in biologischen Geweben – Die Beziehung des Lichtgradienten zum Phototropismus. Doctoral Thesis, University of Freiburg, FRG

Kunzelmann, P., Schäfer, E. (1985) Phytochrome-mediated phototropism in maize mesocotyls. Relation between light and Pfr gradients, light growth response and phototropism. Planta **165**, 424–429

Löser, G., Schäfer, E. (1986) Are there several photoreceptors involved in phototropism of *Phycomyces blakesleeanus*? Kinetic studies of dichromatic irradiation. Photochem. Photobiol. **43**, 195–204

Mohr, H., Meyer, U., Hartmann, K. (1964) Die Beeinflussung der Farnsporenkeimung (*Osmunda cinnamomea* (L.) und *O. claytoniana* (L.)) über das Phytochromsystem und die Photosynthese. Planta **60**, 483–496

Pekelharing, C.J. (1909) Onderzoekingen over de perceptie van den zwaartekrachtprikkel door planten. J. van Boekhoven, Utrecht

Pickard, B.G. (1972) Geotropic response patterns of the *Avena* coleoptile. I. Dependence on angle and duration of stimulation. Can. J. Bot. **51**, 1003–1021

Pohl, U., Russo, V.E.A. (1984) Phototropism. In: Membranes and sensory transduction, pp. 231–329, Colombetti G., Lenci, F., eds. Plenum, New York London

Rawitscher, F. (1932) Der Geotropismus der Pflanzen, p. 251. Gustav Fischer, Jena

Rothert, W. (1894) Über Heliotropismus, pp. 43–45, Kern, J.U., ed. Breslau

Ullrich, C.H. (1976) Kontinuierlich registrierende Messung der Krümmungsbewegung von Maiskoleoptilen: schnelle Effekte von Auxinapplikation, Schwerkraft und Blaulicht, pp. 78–81. Doctoral Thesis, University of Freiburg, FRG

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