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Interactions Between Gravitropism and Phototropism in Plants

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Abstract

To receive adequate light and nutrients for survival, plants orient stems and stem-like organs toward light and away from the gravity vector and, conversely, orient roots into the soil, away from light toward the direction of gravity. Therefore, both gravity and light can influence the differential growth of plant organs. To add to the complexity of the interactions between gravity and light, each stimulus can enhance or reduce the effectiveness of the other. On earth, the constant presence of gravity makes it difficult to determine whether plant growth and development is influenced by gravity or light alone or the combination of the two stimuli. In the past decade, our understanding of the gravity and light transduction pathways has advanced through the use of mutants in either gravitropic or phototropic responses and the use of innovative techniques that reduce the effects of one stimulus on the other. Thus, both unique and common elements in the transduction pathways of the gravitropic and phototropic responses have been isolated. This article is focused on the interactions between the light- and gravity-transduction pathways and describes methods used to separate the influences of these two environmental stimuli.

Key words: Gravity; Light; Signal-transduction; Auxin transport; Photoreceptors; *Arabidopsis thaliana*

Introduction

Plants rely on sophisticated mechanisms to interpret the constant bombardment of incoming signals so they can adjust their growth accordingly. The environmental cues of gravity and light are of particular influence on plant development (Hangarter 1997). Although the initial sensing mechanisms of plants to gravity and light appear to be quite different, the resulting differential growth patterns are similar (Hangarter 1997). The signal transduction pathways of both gravity and light appear to result in the redistribution of auxin (Went and Thimann 1937), thus it is not surprising that they have common elements in their pathways (Watahiki and others 1999). Consequentially, the gravity and light signals can act synergistically or antagonistically on influencing the final form of a particular organ (Hangarter 1997; Okada and Shimura 1992). The ubiquitous nature of gravity on earth makes it a constant influence on the developmental changes induced by light. To further complicate light and gravity interactions, certain wavelengths of light are known to alter the gravity-induced responses (reviewed in Hangarter 1997). Therefore, not only does gravity influence phototropic responses (phototropism), but light can also influence gravitropic responses (gravitropism). These interactions can make it difficult to separate the influences from one stimulus from that of the other.

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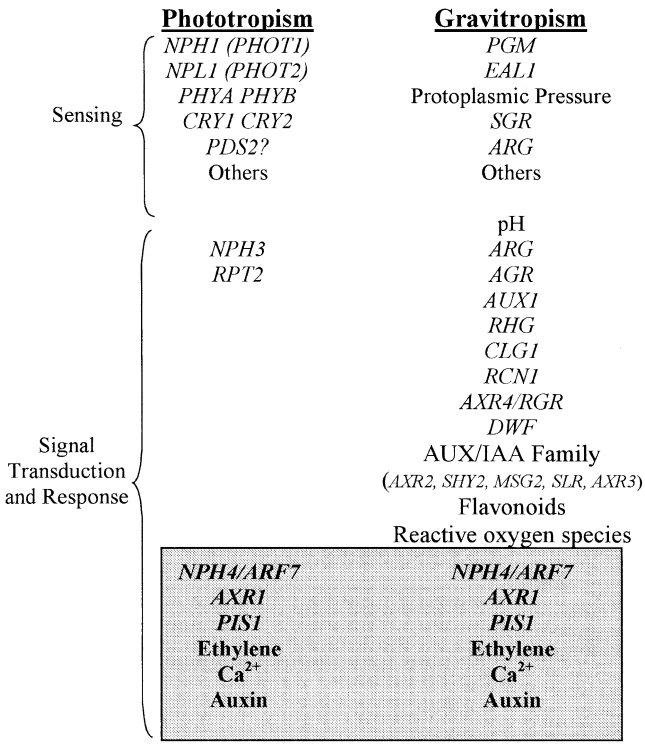

Figure 1. Some of the components involved in phototropism and gravitropism of *Arabidopsis*. Abbreviations are for genes described in the text. The box highlights components that are similar between the gravitropism and phototropism pathways.

Much research has focused on separating gravity and light influences by using mutants with deficiencies in gravitropism and/or phototropism (Figure 1), clinostats to reduce gravity effects, bilateral illumination to nullify the directional influence of light, or microgravity (Grolig and others 2000; Kern and Sack 1999; Ruppel and others 2001; Vitha and others 2000). This article provides a review of the interaction between gravitropism and phototropism and addresses the techniques used to study the two tropisms and separate their influences. Recent review articles on photoreceptors and phototropism include: Batschauer (1999), Briggs and Olney (2001), Casal (2000), Christie and Briggs (2001), Fankhauser (2001), Lin (2000), Liscum and Stowe-Evans (2000), and Neff and others (2000). Recent review articles on the many aspects of gravitropism include: Chen and others (1999), Firn and others (2000), Hemmersbach and others (1999), Kiss (2000), and Renjeva and others (1999).

PHOTOTROPISM

Phototropism is the bending of an organ in response to light (Liscum and Stowe-Evans 2000). In general, stems and stem-like organs of flowering plants are positively phototropic, that is, they bend toward the light source. Typically, roots are negatively phototropic in blue and white light, that is, they bend away from the light source. Other organisms (for example, fungi) and lower plants such as ferns and mosses also have differential growth in response to light, although this occurs by somewhat different mechanisms than flowering plants (Grolig and others 2000; Hartmann and others 1983; Nozue and others 1998). Phototropism in all organisms can be separated into three distinct events (Figure 1): sensing of the light signal (perception), transduction of the signal (transduction), and the differential growth of organs (response).

Light Sensing

In recent years, there has been progress in the elucidation of the pathways involved in flowering plant phototropism due in part to the use of *Arabidopsis* mutants with reduced phototropic responses. Studies with mutants with reduced phototropic responses are revealing the proteins involved in various aspects of light sensing (Figure 1). The primary photoreceptors in angiosperms associated with phototropism are the blue light photoreceptors (also involved in the perception of UV-A and green wavelengths) in the phototropin family, nph1 (*n*on *p*hototropic *h*ypocotyl; also known as phot1) and npl1 (*n*on *p*hototropic *h*ypocotyls-*l*ike; also known as phot2; Christie and Briggs 2001). The nph1 photoreceptor seems to function in phototropic responses in conditions of light pulses or low fluence

rates, whereas npl1 seems to be activated in high fluence rates of light (Sakai and others 2000, 2001). *NPH1* encodes a light-activated protein kinase that is associated with the plasma membrane and can undergo blue-light-induced phosphorylation (Liscum and Briggs 1995; Liscum and Stowe-Evans 2000). *NPL1* has considerable homology to *NPH1* (Jarillo and others 1998). Other proteins have been isolated with similar structural and sequence homology to phototropin, but their role in phototropism is unknown (Liscum and Stowe-Evans 2000). In ferns, a gene has been cloned (*PHY3*) that encodes a protein similar to NPH1 and phytochrome, the red/far red photoreceptors (Nozue and others 1998). The role of this chimeric protein in fern photosensing may provide an insight into how the photoreceptors in flowering plants evolved.

Phytochromes, the red/far-red photoreceptors, are known to absorb blue light and can also be involved in the phototropic responses (Ahmad and Cashmore 1997; Lin 2000; Parks and others 1996). In *Arabidopsis,* five phytochrome genes (*PHYA-E*) have been isolated (Clack and others 1994). The *Arabidopsis* double mutants *phyA phyB,* when exposed to low to moderate fluences of blue light, have reduced phototropic curvature compared with the wild-type plants (Janoudi and others 1997). However, in high fluences of blue light, *phyA phyB* mutants have an equivalent magnitude of phototropic response compared with wild-type plants, although they are reduced in sensitivity (Janoudi and others 1997; Liscum and Stowe-Evans 2000). Therefore, under low fluences, the magnitude of the phototropic responses appears to be regulated by both phyA and phyB whereas at high fluences, another photoreceptor appears to govern the response (Liscum and Stowe-Evans 2000). However, the other photoreceptor involved in regulating phototropism does not appear to be one of the other phytochromes (phyC-E) since the double mutant *nph1, hy1* (*hy1;* heme oxygen) fails to make the phytochrome-chromophore phytochromobilin has phototropic response similar to that of the single *nph1* mutant when grown at a high fluence rate of blue light (Sakai and others 2000). Cryptochromes, other blue light receptors, can modulate phototropic responses, although the extent to which they influence phototropism is debatable (Ahmad and others 1998; Christie and Briggs 2001). The recently identified proteins with similar homology to NPH1 may be involved in modulating the phototropic responses at high fluence of blue light (Liscum and Stowe-Evans 2000).

The phototropic curvature of plant organs can also be induced by red light. For instance, in the protonemata of the moss *Ceratadon,* red light induces a strong positive phototropic response, which is mediated primarily by phytochrome (Hartmann and others 1983; Lamparter and others 1998). Recently, a red-light-induced positive phototropism in *Arabidopsis* roots was discovered, suggesting a possible role of phytochromes in red-light phototropism (Kiss and others 2001; Ruppel and others 2001). However, this positive phototropism is weak and only evident in plants that are reduced in gravitropism. Thus, the identification of the phytochrome(s) involved in the red-light-induced phototropism in roots may require the use of mutants impaired in gravitropism.

Seedlings of several flowering plants, when pretreated with red light, have increased blue-light-induced phototropic bending (Chon and Briggs 1966; Janoudi and Poff 1992; Liu and Iino 1996). The red-light dependence of this response implicates phytochrome in the enhanced response and, in *Arabidopsis,* it is attributed to phyA and phyB (Hangarter 1997; Parks and others 1996). The phototropic enhancement under low fluence, long-term irradiation in *Arabidopsis* is mediated primarily by phyA through a red/far-red-reversible response (Stowe-Evans and others 2001). The enhancement of the phototropic curvature by phytochrome in red light may be the result of reduced gravitropism: plants irradiated by red light can also exhibit reduced gravitropism (Parks and others 1996). Jin and others (2001) have implicated another factor in the red-light-induced enhancement of phototropism. Mutants that lack mature chloroplasts, *pds2* (*p*hytoene *de*saturation), are devoid of the wild-type phototropic responses in hypocotyls, suggesting that the mature chloroplasts are required in the phototropic bending. The degree of the phototropic response in wild-type plants depends on the extent of greening caused by varying the duration of the red-light pretreatments (Jin and others 2001). These authors propose that the chloroplasts may be involved in regulating the intercellular auxin concentrations associated with the asymmetric growth of phototropism.

Other proteins downstream of photoreceptors in the phototropism signal transduction cascade include NPH3 (Motchoulski and Liscum 1999) and RPT2 (*r*oot *p*hot*o*tropism; Sakai and others 2000). NPH3 is essential for normal phototropism and is known to be associated with the plasma membrane and can bind NPH1 in vitro in yeast (Motchoulski and Liscum 1999). NPH3 is an 82-kD protein with two protein-protein interaction domains (Albagli and others 1995; Aravind and Koonin 1999; Lupas 1996). RPT2 is a 66-kD protein that belongs to a

family that includes NPH3 and plays a role in the second-positive phototropism (Sakai and others 2000). It has been suggested that NPH3 and RPT2 function as scaffold or adaptor proteins to bring together the early components of the phototropic signal cascade (Liscum and Stowe-Evans 2000; Sakai and others 2000). All three proteins (NPH1, NPH3, and RPT2) are required for normal phototropic responses (Liscum and Stowe-Evans 2000).

Light Activated Signal Transduction and Response

Once the light signal is absorbed, conformational changes in the photoreceptors' apoproteins lead to the activation of the kinase domain and initiation of phototropic signal transduction elements perhaps regulated by Ca^{2+} (Sakai and others 2001). Although the photoreceptors involved in phototropism are becoming increasingly well-characterized, the downstream signal transduction pathway is just beginning to be elucidated. Calcium appears to play a role as a secondary messenger in the phototropic responses. For example, transient increases in cytosolic Ca^{2+} were evident in wild-type plants upon illumination but not in the *nph1* mutant (Baum and others 1999). Calcium has also been suggested as an important second messenger in gravitropism (Sinclair and Trewavas 1997) and thus, calcium may be a point in the signal transduction pathway where light and gravity influences converge.

The light-induced transduction cascade leads to the differential growth apparently caused by lateral redistribution of auxin (Went and Thimann 1937). It appears that the auxin mechanism involved in phototropism is divided into two pathways: one associated with *NPH4/MSG1* (*m*as*s*u*g*u 1)/*T1R5* (*t*ransport *i*nhibitor *r*esponse 5) loci (hereafter referred to as *NPH4*), and the other associated with *AUXIN RESISTANCE* (that is, *AXR1;* Harper and others 2000; Leyser and others 1993; Sakai and others 2001; Watahiki and others 1999). The *NPH4* gene encodes an *a*uxin *r*esponse *f*actor (ARF7), which is part of a family of auxin transcriptional regulators (Guilfoyle and others 1998; Harper and others 2000). NPH4/ARF7 functions late in the phototropic signal response pathway and is a converging point for gravitropism and phototropism (Harper and others 2000; Liscum and Briggs 1996; Stowe-Evans and others 2001). In addition to having reduced phototropic responses, *nph4* mutants also have reduced red light enhancement of blue-light-induced phototropism when grown in light-limiting conditions (Stowe-Evans and others 2001). Treatment of *nph4* mutants with exogenously applied ethylene, a plant growth regulator involved in many developmental pathways, can recover phototropic and gravitropic responses (Harper and others 2000). However, when the NPH4 mutation is combined with a second mutation in an enzyme involved in the degradation of repressers of auxin responses, AXR1 (reviewed in del Pozo and Estelle 1999), ethylene is ineffective in recovering the tropic responses (Harper and others 2000). Thus, ethylene seems to act in a redundant pathway to NPH4 that includes AXR1. The *axr1* mutant has reduced phototropic curvature in hypocotyls (Watahiki and others 1999) and reduced root gravitropism (Leyser and others 1993), although hypocotyl gravitropism in the *axr1* mutant appears to be affected only in a limited manner (Watahiki and others 1999). Further characterization of AXR1 and NPH4 may lead to a better understanding of the interaction between gravitropism and phototropism in specific plant organs.

Another phototropic and gravitropic mutant associated with auxin is *pis1* (*p*olar *a*uxin transport *i*nhibitor-*s*ensitive 1). The roots of *pis1* mutants are hypersensitive to N-1-naphthyphthalamic acid (NPA) and 2,3,5-triiodobenzoic acid (TIBA), auxin transport inhibitors, and have reduced gravitropic and phototropic responses (Fujita and Syōno 1997). It has been suggested that the *PIS1* gene product may act as a negative regulator of the action of certain auxin transport inhibitors (Fujita and Syōno 1997). Shoots and hypocotyls of *pis1* retain normal gravitropic and phototropic responses. Thus, PIS1 appears to be a factor in the interaction between gravitropism and phototropism only in roots.

Gravitropism

Gravitropism is the bending of an organ in response to gravity (Chen and others 1999, Kiss 2000; Sack 1991). In general, stems and stem-like organs are negatively gravitropic, that is, they bend away from the gravity vector, and roots are positively gravitropic, that is, they bend toward the gravity vector. However, many plant organs do not grow either toward or away from gravity but exhibit intermediate orientation. Thus, the angle that maintains this stable position has been termed the gravitropic-set-point angle (GSA; Digby and Firn 1995). Most research has focused on plant organs, such as roots or stems, in the context of either being negatively or positively gravitropic, and this review focuses on gravitropism in this context. Gravitropism can be separated into the similar three temporal events as those defined in phototropism (Figure 1): sensing of

the gravity signal (perception), transduction of the signal (transduction), and the differential growth of organs (response; Kiss 2000).

Gravity Sensing

There are several different cellular mechanisms by which organisms sense gravity (Chen and others 1999; Kiss 2000). In the protonemata of the moss *Ceratodon,* gravity perception appears to be located in the apical cells containing starch-filled plastids (amyloplasts) that function as statoliths (dense organelles; Kuznetsov and others 1999). In contrast, in the alga *Chara,* the apex of the rhizoid has membrane-bound vesicles that appear to be involved in sensing gravity (Kiss 1997; Sievers and others 1996). In the sporangiospores of the fungi *Phycomyces,* gravity sensing appears to be through three sensory mechanisms: wall strain (bending stress), the sedimentation of protein crystals, and the floating of lipid globules (summarized in Grolig and others 2000).

There are two predominant hypotheses on how gravity is sensed in flowering plants: the starch-statolith hypothesis and the protoplast pressure hypothesis (Fujihira and others 2000; Kiss 2000, Sack 1997; Salisbury 1993). The starch-statolith hypothesis proposes that sensing of gravity is through the settling of statoliths that interact with other cytoplasmic structures (reviewed in Kiss 2000). A starchless mutant *(pgm*; *p*hospho*g*luco*m*utase) of *Arabidopsis* shows reduced sensitivity to gravity compared with wild-type plants and these results suggest a strong correlation between gravity sensing and total mass of plastids (Kiss and others 1996, 1997; MacCleery and Kiss 1999). Another starch mutant, *eal1* (*e*ndodermal-*a*myloplast *l*ess), has no amyloplasts in hypocotyl endodermal cells and also exhibits a reduced gravitropic response (Fujihira and others 2000). Therefore, it seems that starch-statoliths play a key role in sensing gravity. Alternatively, the protoplast pressure hypothesis proposes that the weight of the entire mass of the cytoplasm is involved in gravity perception (Staves 1997; Wayne and others 1992). The receptor molecules involved in sensing protoplast pressure changes have yet to be isolated. Another possibility is that the initial perception of gravity occurs by a combination of mechanisms suggested by both hypotheses (Barlow 1995; Kiss 2000; Sack 1997).

The location of gravisensing has been isolated in roots of flowering plants to the columella cells, and the response phase occurs in the zone of elongation (Kiss 2000; Sack 1991). The location of gravity perception in hypocotyls and inflorescence stems appears to be the site of amyloplast sedimentation, that is, the endodermis (Fujihira and others 2000; Fukaki and others 1998; Moctezuma and Feldman 1999; Weise and others 2000). Mutants that lack an endodermis *(sgr1* (*s*hoot *gr*avitropism)/*scr* (*s*care*cr*ow) and *sgr7/shr* (*sh*ort-*r*oot)), have no gravitropic response in stems or hypocotyls, although roots respond normally (Fukaki and others 1996a, 1996b). Other differential growth responses in *sgr* mutants such as phototropism appear normal (Tasaka and others 1999). In mutants with no amyloplasts in their endodermal cells of the hypocotyls, *eal1,* gravitropism is impaired (Fujihira and others 2000). Taken together, these observations substantiate the role of the endodermis and statoliths in gravisensing.

Another cellular component that may be involved in the early sensing stage and/or transduction in gravitropism is the cytoskeleton (Baluška and Hasenstein 1997; Nick and others 1997; Sievers and others 1996). Mutations in the *ARG* gene (*a*ltered *r*esponse to *g*ravity) result in the disruption of the gravitropic response, although other differential growth responses, that is, phototropism, are not affected (Sedbrook and others 1999). *ARG1* encodes a DNA-J-like protein that may interact with the cytoskeleton (Sedbrook and others 1999). The amyloplasts are enmeshed in microfilaments and upon sedimentation, these cytoskeletal elements may transmit the signal to receptors (Baluška and Hasenstein 1997). In addition, there appears to be a strong correlation between proteins that bind auxin transport inhibitors and the cytoskeleton (Muday and DeLong 2001). However, treatment of plants with chemicals that disrupt actin microfilaments (cytochalasin D or latrunculin B) results in normal or enhanced gravitropic responses (Staves and others 1997; Yamamoto and Kiss 2002). Therefore, an intact actin cytoskeleton may not be a necessary component of the gravitropic-signaling pathway but the cytoskeleton still may play a role in modulating the response.

Gravity Activated Signal Transduction and Response

Once gravity is sensed, there are a series of events that cause the activation of auxin-dependent transduction pathways. Calcium may also play a role in the signal transduction, although the cytosolic calcium concentration does not appear to change in response to gravity (Legué and others 1997). However, components that interfere with

calcium-binding proteins (that is, calmodulin or calcium ATPase) also reduce gravitropic responses (Sinclair and Trewavas 1997). Therefore, the role of calcium in the signal transduction cascade of gravitropism needs further evaluation. Sensitive new detection techniques may help resolve these issues.

Other elements involved in the gravitropic transduction pathway may include reactive oxygen species (Joo and others 2001). Root bending is induced by reactive oxygen species in plants pretreated with auxin transport inhibitors. In addition, the application of scavengers of reactive oxygen species (antioxidants) inhibit the gravitropic curvature in roots (Joo and others 2001). These authors propose that the reactive oxygen species may act downstream of auxin movement to mediate gravitropic responses. Other modulators of auxin transport in gravitropism may include flavonoids. Root gravitropism is impaired in wild-type plants grown on agar plates containing a flavonoid precursor. In addition, mutants in flavonoid biosynthesis, *tt4* (*t*ransparent *t*esta), have higher levels of auxin transport in inflorescence stems and hypocotyls (Brown and others 2001). Future experiments with *tt4* mutants, may help resolve the potential role of flavonoids in auxin regulation in both gravitropism and phototropism.

The gravitropic signal transduction pathways in the aerial organs and the roots appear to be quite different. These differences are most evident in mutants that have agravitropic responses in one organ and normal gravitropic responses in the other. For instance, *agr1* (*a*bnonnal *g*ravitropic *r*esponse)/*eir1*(*e*thylene-*i*nsensitive *r*oot)/*pin2* (*pin* formed)/wav6 mutants (hereafter referred to as *agr*) have disruptions in the gravitropism of roots while retaining normal gravitropism in the hypocotyls and inflorescence stems (Utsuno and others 1998). The *AGR* gene is only expressed in the roots so this discrepancy is not surprising (Utsuno and others 1998). The *AGR* gene encodes a protein that has homology to a bacterial transporter. It appears to encode one of the multiple auxin efflux carriers and is posttranscriptionally regulated (Chen and others 1998; Lushnig and others 1998; Sieberer and others 2000; Utsuno and others 1998). In addition, *agr* mutants have decreased sensitivity to ethylene, therefore in roots, ethylene seems to target AGR (Rosen and others 1999). AGR activity also appears to be dependent on a component of an enzyme involved in activating proteins that degrade repressers of auxin responses (that is, AXR1; Sieberer and others 2000). It is hypothesized that activation of AXR1 causes the degradation of AGR that is essential for establishing an auxin gradient involved in gravitropism. The *agr* mutants respond normally to light, indicating another step where the gravitropism and phototropism transduction pathways differ (Okada and Shimura 1992).

As with *agr* mutants, *axr1* mutants also show organ-specific tropic responses. Roots of *axr1* mutants have no gravitropic response and hypocotyl gravitropism is affected only in a limited manner, although hypocotyl phototropism is impaired (Watahiki and others 1999). AXR1 provides an interesting link between root gravitropism and hypocotyl phototropism. As described previously, *nph4* mutants also have reduced phototropic and gravitropic responses in hypocotyls (Watahiki and others 1999), and these defects can be recovered in the presence of ethylene (Harper and others 2000). The hypocotyls of the double mutants *axr1 nph4* have enhanced disruption in phototropism compared with the single mutants, indicating a possible redundant pathway between AXR1 and NPH4 (Watahiki and others 1999). However, the hypocotyls of the double mutants, *axr1 nph4,* have only a limited enhancement in the disruption in gravitropism compared with the single mutants. It will be interesting to determine if NPH4 and AXR1 act in redundant pathways of gravitropism in roots, as is suggested in the phototropic response of hypocotyls (Harper and others 2000; Watahiki and others 1999).

Another mutant that disrupts both gravitropism and phototropism in roots, described previously, is *pis1,* which is hypersensitive to specific auxin transport inhibitors (Fujita and Syōno 1997). The *PIS1* gene product appears to be a negative regulator of certain auxin transport inhibitors and acts independently of an auxin influx carrier, AUX1 (Fujita and Syōno 1997). The *AUX1* gene is expressed in a single layer of statolith-containing cells in the root columella (Bennet and others 1996; Marchant and others 1999; Swarup and others 2001; Yamamoto and Yamamoto 1998). Roots of the *aux1* mutant exhibit no gravitropic response but show normal phototropic responses (Okada and Shimura 1992). Gravitropism and phototropism are unaffected in hypocotyls *of aux1* mutants (Watahiki and others 1999). Therefore, in root gravitropism, auxin influx appears to be controlled in part by AUX1 and efflux in part by AGR.

Other mutants have been used to decipher the complex pathway involved in gravitropism. The *rhg* (*r*oot *h*ypocotyl *g*ravitropism) mutants lack gravitropic responses in roots and hypocotyls, but stems respond normally. Phototropism appears normal in *rhg* mutants (Fukaki and others 1997). Therefore,

the *RHG* gene product will be another factor that is organ-specific in the gravitropic signaling pathway. Another root gravitropic mutant *clg1* (named for the characteristic of making early coils, increased right-handed slanting, and slow gravitropic response) has recently been identified and seems to have little or no connection with the action of auxin (Ferrari and others 2000). The *clg1* mutants have increased resistance to ethylene, supporting a role of ethylene in gravitropism (Ferrari and others 2000).

Other agravitropic root mutants, *axr4/rgr1* (*r*educed root *gr*avitropism; hereafter referred to as *axr4)* and *dwf* (*dw*arf), are resistant to exogenously applied auxin, and AXR4 appears to function in a pathway separate to that of AXR1 (Hobbie and Estelle 1995; Mirza and Maher 1987; Simmons and others 1995). Thus, unlike CLG1, AXR4 and DWF appear to be auxin-dependent. There are several other genes involved in the auxin-associated pathway of gravitropism, including *AXR2/IAA17, SHY2/IAA3* (*s*hort *hy*pocotyl 2), *MSG2/IAA19, SLR/IAA14* (*sol*itary *r*oot), and *AXR3/IAA17,* and they encode proteins in the Aux/IAA family (summarized in Nagpal and others 2000). It has been suggested that Aux/IAA proteins may act by modifying transcriptional regulatory activity of auxin response factors (ARFs)(Nagpal and others 2000). When grown in the dark, *axr3, axr2,* and *shy2* mutants, in addition to exhibiting reduced gravitropism, have phenotypes similar to wild-type plants grown in the light. Thus, AXR3, AXR2, and SHY2 appear to be involved in both light and auxin-mediated development (Nagpal and others 2000). Further characterization of these Aux/IAA proteins as well as AXR4, DWF, and CLG1 may indicate other factors common between gravitropism and phototropism.

Protein phosphorylation also appears to be a controlling factor in auxin-transport in gravitropism. Roots of *rcn1* mutants (*r*oots *c*url i*n* NPA) have a reduced protein phosphatase activity, reduced gravitropic response, and increased basipetal auxin transport compared with the wild-type roots (Rashotte and others 2001). The *RCN1* gene product encodes a regulatory subunit of protein phosphatase 2A (Deruère and others 1999). When *rcn1* plants are treated with NPA, which reduces basipetal transport of auxin, gravitropism is increased (Rashotte and others 2001). Thus, it appears that phosphatase activity and precise auxin gradients are necessary for gravitropism.

Once the gravity-induced signal cascade begins, a variety of physiological events occur. In *Arabidopsis* roots, there is a cytosolic change in pH (Fasano and others 2001; Scott and Alien 1999) and auxin transport basipetally (from root apex to the base; Rashotte and others 2000). In addition, there is a strong correlation between gravitational bending and asymmetric auxin distribution (Rashotte and others 2001). Thus, it appears that the asymmetric auxin distribution can induce differential growth to direct the plant organ to grow in the appropriate direction.

Gravitropism and Phototropism Pathway Interactions

The events involved in the pathway of gravitropism and phototropism are similar: perception, transduction, and response. However, genetic studies with mutants have been used to identify steps that are unique to each (for example, sensing mechanisms, AGR, and AUX1; Figure 1). The common elements (for example, NPH4, AXR1, PIS1, Ca^{2+}, auxin, and ethylene; Figure 1) in the signal transduction pathways point to elements that may also be involved in other differential growth processes, that is, hypocotyl elongation. These overlaps in the transduction pathways represent only a part of the interactions between gravitropism and phototropism. Light can influence the gravitropic responses, and gravity can influence phototropic responses (Feldman and Briggs 1987; Hangarter 1997). Therefore, when analyzing the interactions of gravitropism and phototropism, it is necessary to evaluate the effects each tropism has on the other.

Light Effects on Gravitropism

Light is known to disrupt or enhance the gravitropic response of plants. In some cultivars, there is a light-regulated gravitropic response. For instance, in the Merit cultivar of maize, dark-grown roots grow horizontally; however, upon receiving illumination, they grow downward (Feldman and Briggs 1987; Wilkins and Goldsmith 1964). This positive gravitropic response is induced most effectively by red light, and later studies have shown phytochrome involvement in this response (Feldman and Briggs 1987; Johnson and others 1991). Red light can some enhance the gravitropic response in species (Britz and Galston 1982; Woitzik and Mohr 1988). and reduce the gravitropic response in other species (Behringer and Lomax 1999; Golan and others 1996; Liscum and Hangarter 1993; Lu and others 1996; McArther and Briggs 1979; Poppe and others 1996; Robson and Smith 1996). *Arabidopsis* seedlings, grown in the dark, have a typical orthogravitropic response (roots grow down, hy-

pocotyls grow up), however, when grown in red or far-red light, seedlings exhibit a random orientation (Fairchild and others 2000; Golan and others 1996; Liscum and Hangarter 1993; Poppe and others 1996; Robson and Smith 1996; Soh and others 1998). These red/far-red light responses suggest that phytochrome(s) plays a role in gravitropism. In *Arabidopsis,* it appears that both phyA and phyB influence the red light gravitropic response of hypocotyls (Robson and Smith 1996). In tomato, the red/far-red light reversal in the gravitropic responses is mediated by phyA, phyB1, and at least one other phytochrome (Behringer and Lomax 1999).

Phytochrome also mediates a red light repression of gravitropism in the protonemata of moss (Lamparter and others 1996). However, red light does not affect amyloplast sedimentation in the moss protonemata, suggesting that phytochrome acts downstream of sensing and in the gravitropic transduction pathway (Kern and Sack 1999). In moss protonemata, the fluence rate of the red light also appears to be a factor in regulating gravitropism. At low fluence rates (<100 nmol m^{-2} s^{-1}), gravitropism interacts with phototropism, however, at higher fluence rates (140 nmol m^{-2} s^{-1}) gravitropism is repressed (Kern and Sack 1999). Therefore, it is possible that the fluence rate of light also is a factor in regulating the gravitropism in flowering plants.

The far-red-light-induced disruption of gravitropism is eliminated in *phyA, hfr1* (long *h*ypocotyls in *f*ar-*r*ed; Fairchild and others 2000), and *fin2* (*f*ar-red *in*sensitive; Soh and others 1998) mutants. The *HFR1* gene encodes a light-regulated protein with homology to PIF3 (*p*hytochrome *i*nteracting *f*actor; Fairchild and others 2000). PIF3 is a nuclear localized protein that binds DNA and can interact with the promoters of several light-activated genes (Martínez-García and others 2000). Indeed, HFR1 can bind PIF3, and as a complex, can preferentially bind the activated forms of phytochromes A or B (Fairchild and others 2000). Therefore, it is possible that far-red light can activate phytochrome (phyA), which in turn may bind with a PIF3 and HFR1 complex to activate other genes in the gravitropic-signaling pathway (Fairchild and others 2000). Another protein involved in far-red gravitropic responses is FIN2. The *FIN2* gene is located on chromosome 3 of *Arabidopsis* and appears to function downstream of phyA in the far-red light-induced pathway (Soh and others 1998). The characterization of these proteins (HFR1, and FIN2) can serve as a starting point in determining the mechanisms involved in far-red light regulation of gravitropism.

In addition to phytochromes, blue light photoreceptors can regulate gravitropism, as is evident in studies with protonemata of the moss *Ceratodon.* Blue light reverses the gravity response from negative to positive in the protonemata (Lamparter and others 1998). This reversal of gravitropic response in blue light has not been observed in other species. Other light-activated genes in *Arabidopsis* that are involved in auxin regulation have been isolated (for example, *SHL s*eedlings *h*ypersensitive to *l*ight, *FIN219, BIG/DOC1/TIR3;* Gil and others 2001; Hsieh and others 2000; Pepper and others 2000) and future experiments to characterize their possible role in light-regulated gravitropism should be explored.

Light effects on gravity can be separated into two types of influences: vector (dependent on magnitude and direction) and tonic (illumination that causes a gravitropic response irrespective of the light direction; Grolig and others 2000). To eliminate phototropic influences on gravitropism, organisms have been grown in the dark, with bilateral illumination, or mutants with reduced or no phototropism have been used (Grolig and others 2000; Vitha and others 2000).

In the case of *Arabidopsis* roots, it was suggested that the light and gravity vectors had equal influences on the direction of root growth (Okada and Shimura 1992; 1994). However, Vitha and others (2000) demonstrated that the influence light has on gravity is dependent on the direction of illumination. For example, when the light and gravity vectors are perpendicular to each other, the vectors appear to have equal influences on the development of the root, that is the root grows at an approximate 45° angle (Okada and Shimura 1992; 1994). However, when gravity and light vectors are in opposing directions (light from below), the resulting angle is approximately 37° and not the expected 90° if light and gravity influences are equal (Vitha and others 2000). Thus, these authors concluded that gravity has a greater influence on the direction of root growth compared with light when the roots are illuminated from below. Consequentially, estimates of previously reported gravitropic responses (that is, Kiss and others 1996, 1997) may be a result of the interaction between phototropism and gravitropism (Vitha and others 2000).

The mere presence of light, regardless of direction of illumination, can influence gravitropic response, as defined by a tonic effect. The tonic effects of light on gravitropism were evaluated using the fungi *Phycomyces* sporangiospores (Grolig and others 2000). Sporangiospores, grown with bilateral illumination, still have an enhanced gravitropic response compared with sporangiospores grown in

the dark, suggesting that the light direction does not influence the response. As a first step towards resolving issues regarding tonic effects in flowering plants, approaches similar to Grolig and others (2000) should be attempted in studies of roots and stem-like organs.

Gravity Effects on Phototropism

Just as light can affect gravitropism, gravity also can influence phototropism. To reduce or eliminate the gravitational effects on phototropic studies, many methods have been used. These include using mutants with reduced gravitropism, using clinostats to reduce gravity effects, and microgravity itself (Grolig and others 2000; Kern and Sack 1999; Kraft and others 2000; Ruppel and others 2001; Vitha and others 2000).

The effects of gravity on phototropism are most evident in plants with reduced gravitropic responses. The phototropic-induced bending of *Arabidopsis* roots is exaggerated in plants with reduced gravitropic responses (Okada and Shimura 1992, 1994; Ruppel and others 2001; Vitha and others 2000). A positive red-light-induced phototropism is evident in *Arabidopisis* roots of the gravitropism-impaired mutant, *pgm*, but barely detectable in wild-type roots (Ruppel and others 2001). Thus, some phototropic responses can be masked by gravity.

In addition to mutants in elements of the gravitropism pathway, clinostats and microgravity have been used to try to mitigate gravity effects. Clinostats rotate specimens around an axis or in three dimensions (for example, random positioning machine; RPM) in an attempt to neutralize the gravitational effects (Hoson and others 1997; Salisbury 1993). The extent to which clinostats simulate true microgravity has been extensively debated. For example, only half the parameters studied in oat coleoptiles show a statistical similarity between clinostat and microgravity (Brown and others 1996). Also, in microgravity, wheat coleoptiles do not show the enhanced curvature, as predicted by clinostat studies (Heathcote and others 1995). These discrepancies could be the result of the type of clinostat used in the analyses. In the case of plastid positioning, the RPM and microgravity-grown *Arabidopsis* roots had similar results whereas plants grown in the 2-D clinostat had different plastid positioning compared with microgravity (Kraft and others 2000). Therefore, the type of clinostat and the parameter being measured are important factors in determining the extent to which the clinostat can simulate microgravity effects.

Microgravity is the most effective way to eliminate gravitational effects on phototropism. For example, in moss, a fluence dependency on the interaction between gravitropism and phototropism is only evident in microgravity (Kern and Sack 1999). The protonemata of moss grown in microgravity with high fluence rates of red light have no enhancement of phototropism, but at low fluence rates, phototropic curvature is increased. In fact, the protonemata align in the light under low irradiance rates in microgravity, but in 1*g*, this response is not detected. These researchers also observed significant gravitropism in 1*g* in low irradiance rates. It appears that in 1*g* with low irradiance rates, the protonemata tip angle results in the interaction between phototropism and gravitropism (Kern and Sack 1999). At higher irradiance rates, gravitropism is completely repressed and phototropism dominates (Kern and Sack 1999). The position of the moss protonemal apical cell prior to illumination also influences the direction to which the tip grows (that is, positive or negative phototropism; Kern and Sack 1999). Future phototropism studies in microgravity should be used to explore these issues in flowering plants as well.

The complex interaction between gravitropism and phototropism is not unique to plants. Other model systems (that is, fungi) have been used to separate these interacting influences. Fungal *Phycomyces* sporangiospores are negatively gravitropic and positively phototropic (Grolig and others 2000). When grown on a clinostat, the sporangiospores display an increase in phototropic bending, with a greater maximum angle of curvature compared with those grown at normal 1*g*. In addition, the sporangiospores grown on the clinostat also have an increased slope in the fluence response curve with a shift in the maximum phototropic action spectrum from blue light to near UV compared with plants grown at 1*g*. This shift in absorption resembles absorption spectrum of a flavin (Grolig and others 2000). Again, these issues should be explored in flowering plants through the effective use of microgravity experiments.

Conclusions

Our understanding of the phototropic and gravitropic signal cascades is just beginning to develop. As new sensing mechanisms and elements in the transduction pathways are isolated, the role they play in gravitropism and/or phototropism requires careful evaluation. Light and gravity, acting synergistically or antagonistically, can both direct plant

growth through processes that overlap. The influence of gravity and light on plant form can depend on the magnitude and direction and, in some cases, simply the presence of the other stimulus. Differences in gravity and light signal transduction among roots, hypocotyls, and stems add to the complexity of studying these tropisms. Furthermore, each transduction pathway may have redundant mechanisms to induce the same response. Due to these complexities, further research is needed to decipher these differential growth responses.

As new mutants are isolated in a particular tropic response, the effects of the mutations on other differential growth responses should be explored. In addition, these studies should carefully evaluate the rate of the tropic response in several organ types (that is, shoots, roots, and hypocotyls) at different stages of development. In the case of experiments using light, the fluence rate, wavelength, and the direction of illumination could all influence the results. Taken together, the use of mutants, clinostats, and microgravity will greatly aid in defining the interactions between gravitropism and phototropism. A future experiment in definition and development for the International Space Station (Kiss and others 2001) will attempt to separate the influences of gravity from various phototropic responses of *Arabidopsis*, perhaps identifying other interactions between gravitropism and phototropism.

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