REVIEW

Root phototropism: from dogma to the mechanism of blue light perception

Ulrich Kutschera · Winslow R. Briggs

Abstract In roots, the "hidden half" of all land plants, gravity is an important signal that determines the direction of growth in the soil. Hence, positive gravitropism has been studied in detail. However, since the 19th century, the response of roots toward unilateral light has also been analyzed. Based on studies on white mustard (*Sinapis alba*) seedlings, botanists have concluded that all roots are negatively phototropic. This "*Sinapis*-dogma" was refuted in a seminal study on root phototropism published a century ago, where it was shown that less then half of the 166 plant species investigated behave like *S. alba*, whereas 53% displayed no phototropic response at all. Here we summarize the history of research on root phototropism, discuss this phenomenon with reference to unpublished data on garden cress (*Lepidium sativum*) seedlings, and describe the effects of blue light on the negative bending response in Thale cress (*Arabidopsis thaliana*). The ecological significance of root phototropism is discussed and the relationships between gravi- and phototropism are outlined, with respect to the starch-statolith-theory of gravity perception. Finally, we present an integrative model of gravi- and blue light perception in the root tip of *Arabidopsis* seedlings. This hypothesis is based on our current view of the starch-statolith-concept and light sensing via the cytoplasmic red/blue light photoreceptor phytochrome A and the plasma membrane-associated blue light receptor phototropin-1. Open questions and possible research agendas for the future are summarized.

Keywords Auxin · Gravitropism · *Lepidium* · Phototropin · Phototropism · Root phototropism

Introduction

In 1758, the 10th edition of the famous *Systema Naturae* by Carl Linnaeus (1707–1778) was published, marking the starting point of binominal nomenclature for animals and revolutionizing taxonomy. In the same year, the French physician and botanist Henri-Louis DuHamel (1700–1782) published a little-known book on the biology of plants (DuHamel 1758). In chapter 6 of this monograph, the author concluded that the light of the sun, and not as previously thought, its warmth, elicits a positive bending response of stems and leaves. This conspicuous phenomenon was described in the 19th century as "heliotropism" (Sachs 1875; Whippo and Hangarter 2006). The knowledge that not only the sun but also artificial light sources, such as candles and incandescent bulbs, cause a similar reaction in growing plant organs, led to the introduction of the term phototropism, indicating that photons, the basic units of electromagnetic radiation, are the causative agents that elicit this physiological response (i.e., tropisms).

Charles Darwin (1809–1882), with the help of his son Francis (1848–1925), introduced the coleoptile of etiolated grass seedlings as an experimental system for the analysis of shoot phototropism under laboratory conditions (Darwin 1880). Based on these seminal studies, over subsequent decades, hundreds of papers have been published on the positive phototropic bending response of dark-grown coleoptiles (Briggs 1963a, b, 2006; Srivastava 2002;

This article is dedicated to the memory of the German plant biologist Andreas Sievers (1931–2009), a pioneer in the study of root gravitropism.

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Holland et al. 2009; Kutschera and Briggs 2009; Kutschera and Niklas 2009; Koller 2011). However, as pointed out by Hart (1990), the positive phototropic response of the above-ground organs (hypocotyl, leaves) of dicot seedlings have not received nearly as much investigation. This situation changed dramatically after the introduction of Thale cress (*Arabidopsis thaliana*) as model organism (Briggs and Spudich 2005; Laxmi et al. 2008), although the experimental work on coleoptiles was not entirely abandoned (Kutschera et al. 2010).

In both the shoot and the primary root, gravity, in addition to light, is an important signal for the direction of growth. Laboratory experiments by 19th-century botanists have shown that in seedlings of white mustard (*Sinapis alba*), the tap root displays a negative phototropic response upon unilateral illumination (Darwin 1882; Sachs 1882; Pfeffer 1904; Strasburger et al. 1911). These classic experiments led to the conclusion that "the root" displays a response that is the opposite of that of "the shoot", which always bends towards the light source.

In this article, which marks the 100th anniversary of the publication of the first systematic study on root phototropism (Schaefer 1911), we focus on this "hidden half" of land plants (embryophytes), a monophyletic clade of photoautotrophic organisms (Niklas and Kutschera 2009, 2010). We summarize the origin and development of research on root phototropism and illustrate key findings based on unpublished experiments with seedlings of garden cress (*Lepidium sativum*), a model system for the study of the response to gravity introduced by Sievers (1984) (see Bartels et al. 2011). Finally, we present a model of blue light and gravity perception in roots of *A. thaliana* that is based on a synthesis of studies published over the past decade.

The *Sinapis*-dogma and its challenge

Three pioneers of the botanical sciences, Julius Sachs (1832–1897), Wilhelm Pfeffer (1845–1920) and Eduard Strasburger (1844–1912) published in their textbooks a corresponding figure documenting that in seedlings of *S. alba*, the root is negatively phototropic. These three original drawings are juxtaposed in Fig. 1a–c. It is obvious that Sachs (1882), Pfeffer (1904), and Strasburger et al. (1911) used *S. alba* seedlings of different ages. However, the results of these qualitative experiments were the same: the hypocotyl displayed a positive and the root a negative phototropic response upon unilateral irradiation with continuous white light.

Although Darwin (1882) documented the high sensitivity of *S. alba* roots to unilateral irradiation, the first quantitative study on the root phototropism in mustard seedlings was
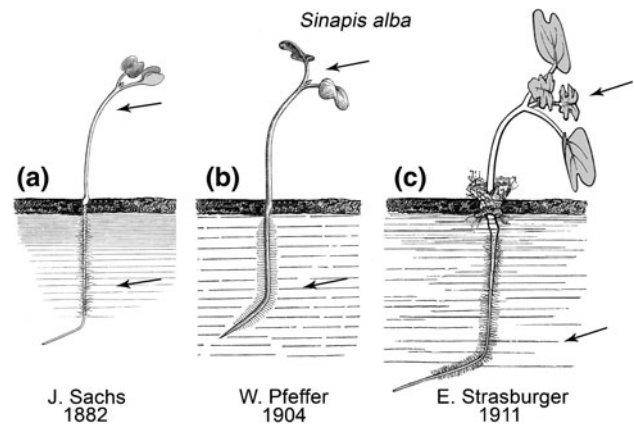

Fig. 1 Phototropic response of shoot and root to unilateral white light (*arrows*) in seedlings of White mustard (*Sinapis alba*) grown in hydroculture. Note that in all three independent experiments (**a**–**c**) the hypocotyl reacted positively, whereas the root showed a negative phototropic curvature (adapted from Sachs 1882; Pfeffer 1904; Strasburger et al. 1911)

published by Linsbauer and Vouk (1909). These authors analyzed populations of seedlings ($n = 50$) that were grown in hydroculture rather than single individuals and studied the effects of low versus high white light-treatment on the bending response. When batches of seedlings were irradiated unilaterally with light of very low intensity, ca. 60% of the individuals displayed a positive and ca. 30% a negative response (the remaining 10% did not react). However, in the presence of high-intensity irradiation, 100% of the seedlings curved away from the light source, as depicted in Fig. 1. In a subsequent study, Blaauw (1918) documented that in *Sinapis* seedlings, only the tip of the root is sensitive toward unilateral light treatment. This corroborated Charles Darwin's hypothesis that the root tip functions as a "brain" that can sense a number of stimuli, such as light, gravity and touch (Kutschera and Briggs 2009; Kutschera and Niklas 2009). Based on these and other studies, it was concluded that the seedling roots of all land plants respond like those of *S. alba*. As a result, one of the three drawings, shown in Fig. 1, was reproduced in most textbooks on the physiology of plants published over the past century (see Hubert and Funke 1937; Schopfer and Brennicke 2006), and a "central dogma of plant physiology" was deduced by the authors: "The root" always displays a negative phototropic response, whereas "the shoot" bends towards the light.

Based on the quantitative studies of Linsbauer and Vouk (1909), who in addition to that of *Sinapis*, analyzed root-bending in two other species (*Raphanus sativus*: negative curvature, *Chlorophytum* sp.: no phototropism), the German botanist Rudolf Schaefer (1884–1945?) undertook a large survey. In a little-known monograph that was published a century ago, Schaefer (1911) described root phototropism in 166 plant species, using the technique

Table 1 The occurrence of root phototropism in seed plants (angiosperms), based on data of Schaefer (1911) and Hubert and Funke (1937)

Author	Root phototropism (%)		
	+	0	−
Schaefer (1911) ($n = 166$)	5	53	42
Hubert and Funke (1937) ($n = 152$)	3	48	49

n, number of plant species investigated; +, positive; −, negative; 0, no phototropic response

shown in Fig. 1. The author confirmed the "Sinapis-dogma", but could find many examples that did not corroborate this general response. Of the 166 plant species investigated, 70 responded like *S. alba* (negative root phototropism), 8 displayed the opposite reaction (positive root phototropism), and 88 showed no response at all toward unilateral light (Schaefer 1911). Similar quantitative data were reported by Hubert and Funke (1937), who studied root phototropism in 152 plant species (Table 1). Hence, root phototropism is a species-dependent phenomenon, and the "Sinapis-textbook-dogma" had been thoroughly refuted by these investigators: only about 50% of the plant species investigated displayed the typical response shown in Fig. 1.

In the discussion of his results, Schaefer (1911) noted that the roots of garden cress (*L. sativum*) seedlings did not react to unilateral light, but the plant physiologist Julius Wiesner (1838–1916) had previously described the roots of this species as "negative phototropic" (Wiesner 1884). On the other hand, Hubert and Funke (1937) found no reproducible root bending response in this economically important plant that has been used by Sievers (1984) and other botanists for the experimental analysis of root gravitropism. These controversial findings motivated us to re-investigate the phototropic response in cress roots. Our results are summarized in the next section.

The *Lepidium*-paradox and its resolution

When grown in darkness, the primary root of garden cress (*L. sativum*) (Fig. 2a) displays a rapid positive gravitropic response that was analyzed in detail by A. Sievers and co-workers (Sievers 1984; Sievers and Hensel 1982; Sievers et al. 1989). To resolve the question whether or not this model system for the analysis of graviperception and differential organ growth is sensitive to light, we first raised seedlings of *L. sativum* in darkness and recorded the growth of hypocotyl and primary root over the subsequent 5 days. Between days 2 and 3 after sowing, both organs elongated at an approx. linear rate of ca. 0.6 mm h^{-1} (Fig. 2b).
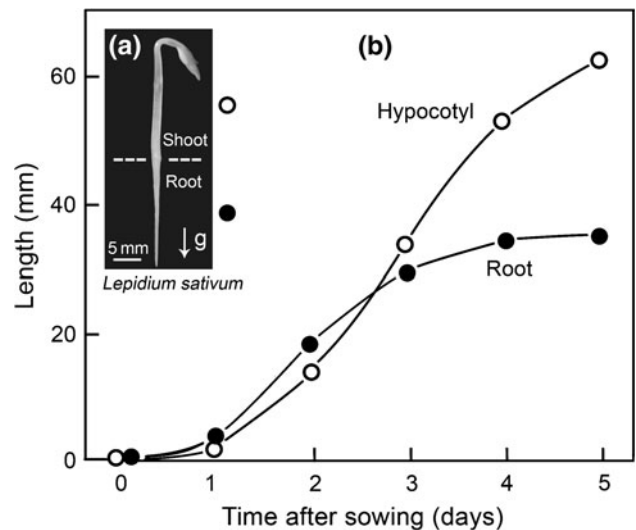

Fig. 2 a Photograph of a 2-day-old etiolated seedling of Garden cress (*Lepidium sativum*). $g =$ gravity vector; *dashed lines* indicate the onset of the root. Note that the shoot displays a negative and the root a positive gravitropic response with respect to the vector of gravity. **b** Time course of growth of root and hypocotyl in populations of seedlings raised in hydroculture in darkness (25°C). Note that between days 1 and 3 after sowing both organs elongate at approximately the same rate. The data points represent means of 50 seedlings each

In the next step, a shoot- versus root-comparison with respect to light sensitivity was performed on 2-day-old etiolated cress seedlings that were irradiated for 24 h from all sides (omnilaterally) and thereafter analyzed. In both the hypocotyl and the root, a light-induced inhibition of organ elongation was measured (Fig. 3a, c). We also determined the dry mass of the cell walls in both organs (Fig. 3b, d), using the methods described by Kutschera (1990). During growth in darkness, net accumulation of wall material did not keep pace with cell elongation so that wall thinning likely occurred. However, in white light, in both the hypocotyl and the root of *L. sativum,* the amount of wall material per organ length was more than 20% higher than in the dark control. This indicates that a thickening of the cell walls might likely have occurred. The data of Fig. 3 document that both shoot and root of *L. sativum* are sensitive to omnilateral light treatment.

In a subsequent set of experiments, we irradiated batches of 5 to 100 2-day-old etiolated *Lepidium* seedlings for 24 h with unilateral white light. In all of these experiments, the greening shoot displayed a strong positive phototropic response: the hypocotyl curved toward the light (average angle after 24 h, 61 ± 1.8 degrees, $n = 100$) and photomorphogenesis occurred (hook opening, unfolding of the cotyledons, greening, etc.). In contrast to the shoots, the roots showed a mixed response. In the representative experiment depicted in Fig. 4, three out of six roots bend away from the light source (negative response, 50%),
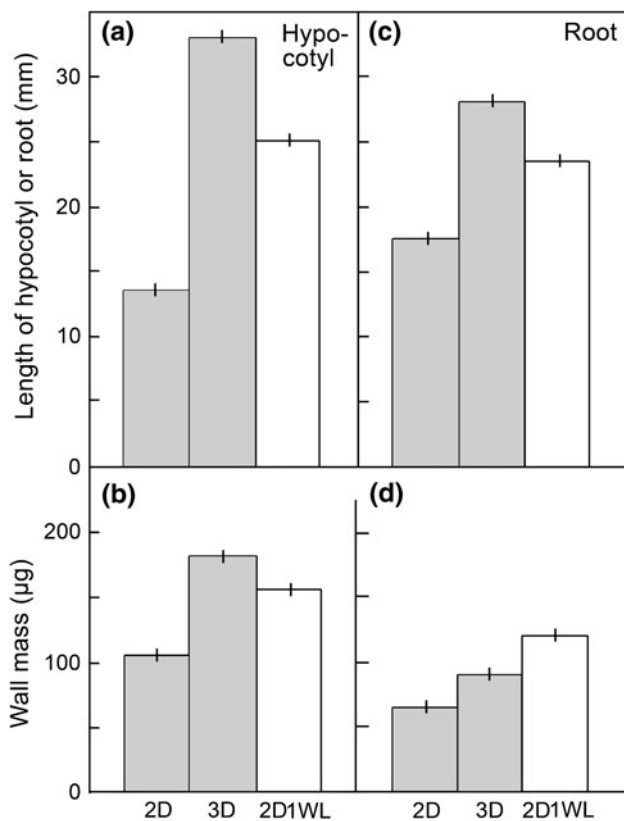
Fig. 3 Effects of omnilateral white light-treatment on length increase and the accumulation of wall dry mass in the hypocotyl (**a**, **b**) and root (**c**, **d**) of *Lepidium sativum* seedlings. *The bars* denote the standard errors of the means (SE) of 6 independent experiments. 2D, 3D = 2- and 3-day-old dark-grown seedlings, respectively. 1 WL = 1 day of white light-treatment (Osram 1316446 Halogen bulbs, photon fluence: 50 µmol m^{-2} s^{-1})

Fig. 4 Effect of unilateral white light treatment (50 µmol m^{-2} s^{-1}, see Fig. 3) on shoot and root phototropism in seedlings of *Lepidium sativum* grown in hydroculture. Two-day-old dark-grown seedlings were irradiated for 24 h before the photograph was taken. Gravity acts in the direction of the *arrow* (*g*)

Fig. 5 a Root phototropism in populations of seedlings of *Lepidium sativum* that were irradiated unilaterally with white light of three different fluence rates (for details, see Fig. 3). **b** In all three experiments, batches of 100 seedlings were analyzed (*n* = 100).+, positive; −, negative; 0, no phototropic response; *g*, gravity vector

two did not react (no response, 33%) and one grew towards the direction of irradiation (positive response, 17%). To further explore this phenomenon quantitatively, batches of 100 seedlings were analyzed as shown in Fig. 4. The results of three representative studies, expressed in the same manner as those of the earlier workers, are summarized in Fig. 5. Populations of *L. sativum* seedlings were irradiated unilaterally and the response of the roots was recorded after 24 h. In all three experiments, 52–57% of the roots displayed a negative, 29–32% no, and 12–19% a positive phototropic response. This result was independent of the photon fluence provided (10, 25, or 50 µmol m^{-2} s^{-1}, respectively) and reminiscent to that shown in Fig. 4.

In summary, our *Lepidium* studies document that, in populations of seedlings of this species, about 50–60% of the individuals react like *S. alba* (Fig. 1). This result is similar to that of Hubert and Funke (1937), who showed that ca. 50% of the primary roots of the 121 species of seedlings investigated reacted with a positive phototropic bending response. In all of these experiments, the seedlings were exposed to unilateral white light.
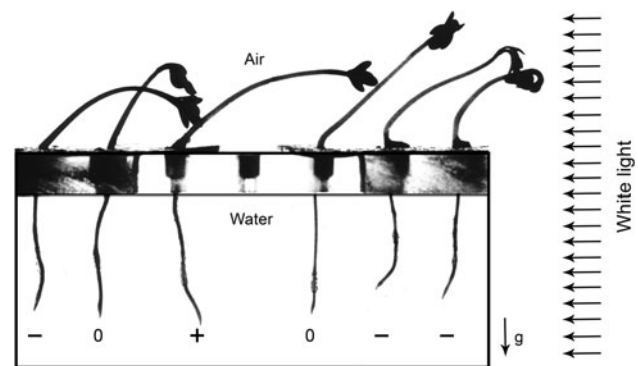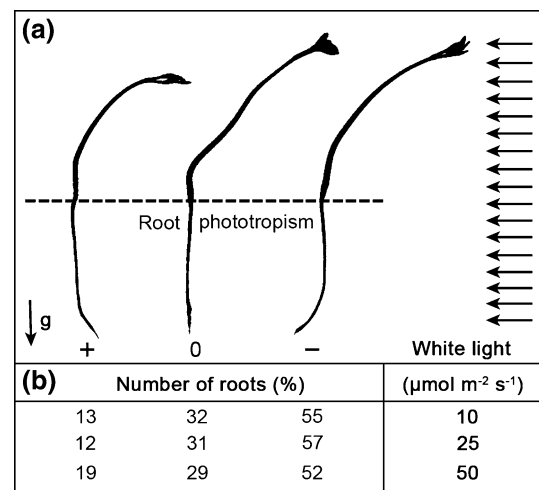
The five classes of photoreceptors in plants

To grow, develop a complex shoot- and root system, and survive/reproduce, sessile plants must constantly monitor and adapt to changes in their light environment. In the classical experiments on root phototropism (see Table 1), polychromatic white light (WL, wavelength ca. 380–800 nm), was used as photon source (Schaefer 1911; Hubert and Funke 1937), but it was already noted by these and earlier investigators that WL acts in the same manner as blue light. However, the search for specific plant signal-transducing photoreceptors only originated in 1959 with the discovery of the red/far red light absorbing phytochromes (Butler et al. 1959). Today, five classes of plant photoreceptors are known: phytochromes (class 1), cryptochromes (2), phototropins (3),

a recently described UV-B photoreceptor (4), and F-box photoreceptors (5).

Phytochromes (1), large (ca. 120 kD) cytoplasmic proteins that possess a covalently linked light-absorbing domain, a linear tetrapyrole (bilin) chromophore (phytochrombilin), were discovered six decades ago (Mohr 1972; Smith 2000; Srivastava 2002; Franklin and Quail 2010). The phytochromes A and B regulate a wide range of physiological processes, from seed germination in light-sensitive plant species, to organ senescence, and occur not only in the shoots but also in the tip (calyptra) of the root (Pratt and Coleman 1974; Schwarz and Schneider 1987; Batschauer 2003; Briggs and Spudich 2005). In addition to the phytochromes, which are responsible for sensing red/far-red wavelengths (600–750 nm), three other classes of plant photoreceptors were discovered that perceive UV-A and blue light (320–500 nm), the cryptochromes (2), the phototropins (3), and the F-box proteins (5). Cryptochrome is a name originally coined for blue light-photoreceptors that are active in cryptogams (mosses, ferns etc.). These molecules, that were "cryptic" at the time before identification (ca. 1993), are flavoproteins in plants and animals that share structural similarity to DNA photolyases, but lack this enzymatic activity (Batschauer 2003; Briggs and Spudich 2005; Schäfer and Nagy 2005).

The phototropins (3) were originally identified as photoreceptors for phototropism (Christie et al. 1998), but were later found to mediate stomatal opening, leaf expansion, rapid retardation of stem elongation, chloroplast movements, and several other blue light-activated responses (Briggs 2006, 2007; Tseng et al. 2010). The chemical structure and mode of light conversion of phototropin 1 is briefly described below.

Although the effects of UV-B (280–320 nm) on plant development has long been documented (Tong et al. 2008), the photoreceptor responsible for this damaging short wavelength-irradiation, which accounts for ca. 1.5% of the total solar energy, remained elusive. In a recent report, Rizzini et al. (2011) have shown that, in Arabidopsis seedlings, dimers of the UVR8 protein perceive UV-B, possibly via a tryptophan-based mechanism. The authors provide evidence indicating that this UV-B photoreceptor (4) may be involved in some aspects of normal plant development (Rizzini et al. 2011).

Finally, F-box proteins (5) were first demonstrated to serve as blue-light receptors one decade ago (Imaizumi et al. 2003). These photoreceptors, utilizing the same chromophore domain and photochemistry as the phototropins, are important in regulating photoperiodic responses and circadian rhythms in plants.

With respect to the root phototropism caused by unilateral white light, only the phytochromes (1) and phototropins (3) are relevant, because, these photoreceptors perceive light in the range of ca. 330–800 nm, and have been shown to occur in the "hidden half" of land plants (Pratt and Coleman 1974; Schwarz and Schneider 1987; Sakamoto and Briggs 2002). The action of blue and UV-A light (330–500 nm), on the phototropic bending response of roots, is described in the next section.

Blue light and root phototropism

Although effects of blue light on plants have been known since the early 19th century (Briggs 2006, 2010), one of the first authors to study the light quality with respect to phototropism in many different plant species systematically was Wiesner (1884). In his classic monograph, he concluded that light of short wavelength elicits the strongest phototropic response compared with other light qualities (Whippo and Hangarter 2006). Decades later, experiments with Avena coleoptiles led to the insight that blue light (wavelength ca. 450 nm) causes in fact the optimal positive phototropic response (Briggs 2006).

Naundorf (1940) analyzed the effects of blue, green, yellow and red light on the negative phototropic response of the roots of sunflower (Helianthus annuus) seedlings. As expected, blue light caused the strongest negative bending reaction, and red was ineffective. Moreover, using a bioassay for the quantification of auxin (indole-3-acetic acid, IAA), Naundorf (1940) documented that a blue light-mediated re-distribution of IAA occurs, causing an increase of this phytohormone (+41%) in the irradiated (growing) half. In the shaded (non-elongating) organ flank, no change was detected (±0%). These results are somewhat different from those reported for maize (Zea mays) coleoptiles, where unilateral blue light causes in the organ tip a rapid re-distribution of IAA (Briggs et al. 1957) with an increase in auxin on the shaded side and, in contrast to Helianthus, a compensatory decrease on the illuminated side. Based on his experimental results on the primary roots of Helianthus seedlings, Naundorf (1940) concluded that blue light leads to an enhancement in the production of IAA on the irradiated side and hence causes a phytohormone-mediated phototropic response, which is perceived in the tip of the root. In contrast, Briggs et al. (1957) concluded that there was no change in total auxin but rather a light-activated movement of the hormone away from the illuminated flank of the coleoptiles with no overall change in the amount of IAA in the auxin transport system.

Experiments with seedlings of S. alba showed that, in this classical model organism for the study of root phototropism, blue light is very effective, whereas red light causes no response (Mohr 1972). However, the systematic analysis of blue light-mediated root phototropism only gathered momentum after a new model plant, the Thale

cress (*A. thaliana*), was introduced. Like its relative *S. alba*, this member of the mustard family (Brassicaceae) displays a negative root phototropism (Fig. 1). *Arabidopsis* mutants in root phototropism were isolated and characterized (Liscum and Briggs 1995). These mutants were later shown to be deficient in the blue light photoreceptor phototropin 1 (Briggs and Christie 2002).

Phototropins are composed of a flavin mononucleotide (FMN), which acts as the light-absorbing chromophore, and a protein domain that binds to the FMN. These 110-amino acid-oligopeptides were called "LOV domains", because they were found to be similar to the domains in a wide range of otherwise entirely different signal transduction proteins that respond exclusively either to light, oxygen, or voltage. In the next step, the unique photochemistry that the FMN-LOV-domains perform upon blue light-induced photoexcitation was elucidated (see Fig. 6) (Briggs 2007; Tseng et al. 2010).

Ten years ago, Sakamoto and Briggs (2002) documented that phototropin 1 (phot 1), a Ser/Thr photoreceptor kinase that binds two molecules of FMN as chromophore, is not only distributed in the cells of the shoot but also occurs in the root. Phot 1 was shown to act as blue light photoreceptor that mediates the light-induced negative phototropic response of the root of *A. thaliana* and other plant species (Briggs and Christie 2002). However, it has been known for more than five decades that red light treatment of dark-grown seedlings can significantly alter their subsequent blue light-mediated bending response (Briggs 1963a, b). Since the red light photoreceptor phytochrome A (which also absorbs blue light) can regulate the intracellular distribution of phot 1 (Han et al. 2008), it is conceivable that these two photoreceptors interact in the root. However, phytochrome is localized in the root cap (Pratt and Coleman 1974; Schwarz and Schneider 1987), whereas phot 1 is restricted to the elongation zone of the organ (Sakamoto and Briggs 2002; Knieb et al. 2004). Thus, direct interaction seems unlikely.

In addition to the blue (and white) light-induced negative phototropism, a weak red light-mediated positive phototropic bending response was discovered in the primary root of *A. thaliana* (Kiss et al. 2003a). This physiological effect of low magnitude and unknown significance is not further discussed here.

Ecological significance of root phototropism

In the preceding sections, we have shown that the roots of three species of the mustard family (Bassicaceae), *S. alba*, *L. sativum*, and *A. thaliana*, react differently toward unilateral white light: *Sinapis* and *Arabidopsis* individuals behave as does the "textbook-example" (Fig. 1), but in *Lepidium* there is only a somewhat negative bias (Figs. 4, 5). Although the Brassicaceae is a monophyletic family of embryophytes of about 338 genera and more than 3,700 described species
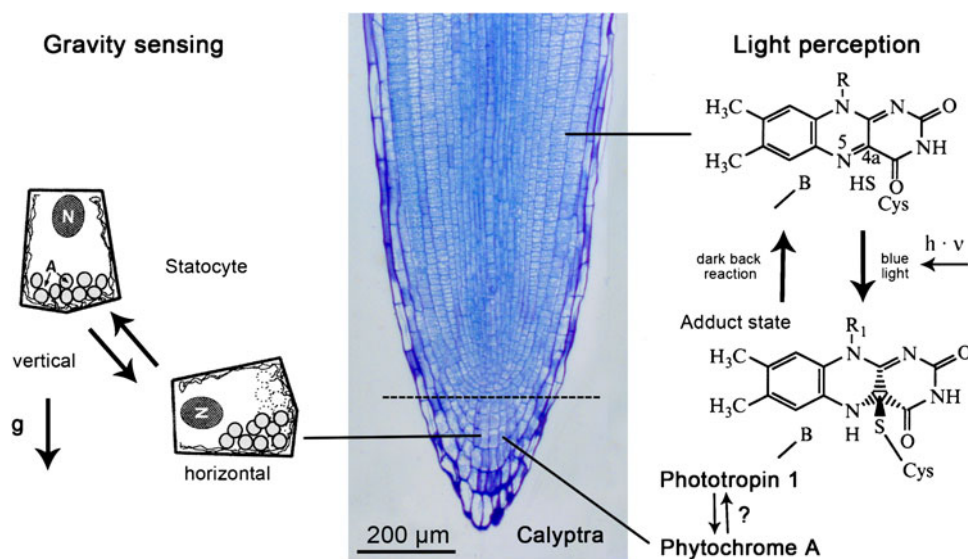

Fig. 6 Model of the perception of gravity (*g*) and light (h*v*) in the elongation zone of the root and the cap (calyptra) of a seedling (depicted is the cross-section of a 2-day-old root of *Lepidium sativum*). According to the starch-statolith-concept, gravity-dependent sedimentation of amyloplasts in statocytes of the columella (calyptra) provide directional cues and elicits the bending response. Phytochrome A is localized in the root cap, whereas phototropin 1 occurs in the growing region above the calyptra. The phototropin-1-theory of blue light-perception posits that absorption of a single photon results in the generation of an excited singlet flavin mononucleotide (FMN). The resulting FMN-cysteinyl-adduct represents the active signalling state of phot-1 ("Adduct state" of the FMN-molecule). *A* amyloplast, *g* vector of gravity, *N* nucleus (adapted from Kutschera 2001; Tseng et al. 2010)

(Al-Shehbaz et al. 2006), our three model organisms belong to separate tribes that diverged millions of years ago and are characterized today by different geographical distributions (Table 2). Hence, it is conceivable that the typical "*Sinapis–Arabidopsis*-response" represents the ancestral condition and *Lepidium* populations have lost, in part, the ability to react uniformly as white mustard. Why do most of the roots bend away from an unilateral white light source?

In his *Lectures on the physiology of plants*, Sachs (1882) concluded that "it is strange that roots, which grow below the surface of the earth, if cultivated in water or in moist air, display a heliotropic response, some a positive and others a negative one; these roots possess, via their heliotropism, a form of irritability that is, under normal living conditions, of no value for them so that it cannot be the result of a Darwinian selection process". Without reference to Sachs (1882), Schaefer (1911) speculated on the adaptive value of root phototropism and concluded that "there is no evidence that heliotropism of the roots investigated here that grew in soil or water is an adaptation". Moreover, the author pointed out that root phototropism is no uniform phenomenon, since, "not only plants from separate families, but also from the same genus behave differently" (Schaefer 1911). More recently, Kiss et al. (2003a) concluded that "The role of root phototropism is unknown, but it may serve in optimization of the orientation of the entire root system, especially in soils through which light can readily penetrate" (see Mandoli et al. 1990).

Briggs et al. (2001) documented that PHOT1, the protein that controls phototropism in seedlings, shows a wide taxonomic distribution so that it is reasonable to conclude that this blue light photoreceptor developed early in the evolution of the embryophytes, which are monophyletic (Niklas and Kutschera 2009, 2010). Moreover, Liscum and Briggs (1995) have shown that in the roots of *A. thaliana* seedlings, the later-designated PHOT1 mediates negative phototropism, possibly via weak light signals in the soil. Based on these and their own findings, Galen et al. (2004) concluded that PHOT-1 has a large effect on seedling establishment in *A. thaliana* under some environmental conditions in the field. Negative root phototropism prevented light stress in the upper layers of the soil, reduced desiccation phenomena, and enhanced seedling survival

under dry, windy conditions. In a subsequent report, Galen et al. (2006) concluded that PHOT-1 enhances performance under drought by mediating plastic increases in the efficiency of root growth near the soil surface. These studies suggest that negative root phototropism enhances the chances of seedling survival under dry conditions and hence may be of adaptive value to the developing plant.

Gravi- and phototropism of the primary root

As pointed out in the "Introduction", gravity is an important signal that directs juvenile roots to grow downward in soil, where they can elongate to take up water and dissolved mineral ions required for metabolism and expansion of all organs of the developing plant. In a classical paper, the British horticulturist Thomas A. Knight (1759–1838) analyzed populations of seedlings and documented experimentally the basic phenomenon of gravitropism, i.e., the downward bending of roots and the simultaneous upward growth of the stem (Knight 1806).

These gravity-directed growth processes (Fig. 2a) were soon found to be of significance for agriculture, since they permit crop plants to exploit the limited resources available in their environment and lead to mechanical anchorage of the organism in the soil. In addition, it became evident that through gravity-induced processes, shoots resume upward growth after prostration by the action of wind and rain (Sachs 1882; Kutschera and Niklas 2007).

Despite these insights and the clear notion that gravitropism consists of three phases (sensing, signal transduction, and the physiological bending response), the basic question remained open: how can juvenile plant organs perceive their orientation within the gravity field? In this context, the term "gravity sensing" denotes the physiological processes involved in the transformation of a physical signal (i.e., the effect of gravity upon mass) into an intracellular reaction (Barlow 1995, 2002; Chen et al. 1999; Sievers 1984; Sievers and Hensel 1982). Based on the finding that a structure at the tip of the root, the cap, is essential for gravity sensing of this organ (Darwin 1880), it was postulated in two independent reports that starch-filled amyloplasts in the root cap columella cells (i.e., statocytes),

Table 2 Systematics and geographical distribution of the three plant species from the mustard family (Brassicaceae) for which data on root phototropism are available (adapted from Al-Shehbaz et al. 2006)

Species	Tribe	Distribution
White mustard (*Sinapis alba* L.)	Brassicaceae, 46 genera, ca. 230 species	Primarily Mediterranean and southwest Asia
Garden cress (*Lepidium sativum* L.)	Lepidieae, 5 genera, ca. 250 species	All continents except Antartica
Thale cress (*Arabidopsis thaliana* L.)	Camelineae, 12 genera, ca. 240 species	Primarily Eurasia, some species in North America, Australia, New Zealand

or in corresponding tissues of the endodermis, provide directional cues to the below- and above-ground plant organs (Haberlandt 1900; Nemeć 1900). Over the past century, this so-called "starch-statolith hypothesis of gravity perception" (Fig. 6) has been critically evaluated by generations of plant biologists, using model organisms such as *L. sativum* or *Oryza sativa* (Sievers 1984; Kutschera 2001). Two lines of evidence finally confirmed the classical Haberlandt–Nemeć-model of gravity sensing via intracellular amyloplast sedimentation beyond any doubt: (1) experiments with rice (*O. sativa*) seedlings that can be "de-starched" physiologically by submergence, and (2) the analysis of starch-deficient mutants of *A. thaliana*. A series of experiments with rice seedlings, which can survive in water-logged, oxygen-depleted soil, has shown that rapidly growing submerged coleoptiles lack sedimentable amyloplasts that are present in the air-grown controls. These submerged, starch-free organs showed no graviresponse when stimulated in horizontal position (Kutschera et al. 1990; Kutschera and Hoss 1995; Kutschera 2001). Roots of *Arabidopsis* seedlings perceive gravity via sedimentation of starch-filled amyloplasts. Starch-deficient *pgm1* mutants lack the typical response to gravistimulation, and other *Arabidopsis* mutants containing intermediate levels of starch display a reduced gravitropic sensitivity (Kiss et al. 1997; Stranga et al. 2009).

Although the sedimentation of amyloplasts upon gravistimulation is well documented (Sievers 1984; Barlow 1995, 2002), the mechanism by which this physical event is transformed into an intracellular signal is still a matter of debate (Sievers et al. 1989; Stranga et al. 2009). Recent studies suggest that the translocon of outer membrane of chloroplasts (TOC) complex may play a key role in gravity signal transduction within the statocytes, but more work is required to test this hypothesis (Stranga et al. 2009).

It has long been known that root gravitropism and the phototropic response of this organ are related processes, but no clear picture of this interaction emerged over decades of research (Sachs 1882; Pfeffer 1904; Schaefer 1911; Hubert and Funke 1937; Sievers 1984). In a comparative study of blue versus red light-induced negative and positive root phototropism, respectively, Kiss et al. (2003b) discussed this problem in detail. Five years later, Boccalandro et al. (2008) proposed a scheme illustrating how light modulates gravitropism. With reference to the previous work of Vitha et al. (2000) and Correll and Kiss (2005), the authors proposed an interaction of the photoreceptors phytochrome A and phototropin 1 with respect to root gravitropism. In this model, a plasma membrane-associated protein involved in phy A signaling (PKS1) is postulated to regulate both photo- and gravitropism in the root of *Arabidopsis* seedlings (Boccalandro et al. 2008). However, the questions of how root gravitropism in dark-grown

seedlings is regulated by the red light-dependent protein PKS1 and the phytohormone auxin are open. Hence, more experimental work is also required to test this speculative model (see Laxmi et al. 2008; Li et al. 2011).

Conclusions and outlook

In the field, root tissues may be exposed to sunlight due to the penetration of solar irradiation into the upper layers of the soil (Mandoli et al. 1990). Whereas the shoots bend toward the direction of incoming blue (and white) light to optimize leaf photosynthesis, roots grow away from these light stimuli and hence avoid the stressful environment of the upper soil layers. Thus, negative root phototropism, documented for seedlings of mustard (*S. alba*) and some other plant species, became a focus of research that was summarized in the textbooks of Sachs (1882), Pfeffer (1904), Strasburger et al. (1911) and others.

One century ago, Schaefer (1911) published the first comprehensive report on the occurrence of white light-induced root phototropism in 166 species of land plants. This little-known monograph, which was supplemented and extended by a pertinent original paper of Hubert and Funke (1937), marked the origin of a research agenda into the mechanism and physiological significance of root phototropism that lasts to the present (Boccalandro et al. 2008).

A summary of our current view on gravity- and light perception in the primary root of dark-grown seedlings is shown in Fig. 6. The mechanism of gravity sensing in the statocytes (i.e., columella cells of the root cap, or calyptra that contain starch-filled amyloplasts) has been documented by Sievers (1984), Barlow (1995, 2002) and others. Statocytes are characterized by a nucleus in the upper half, an asymetrically localized peripheral endoplasmatic reticulum, and amyloplasts toward the basal end (bottom) of the cell. When the vertically growing root is placed into horizontal position, and hence gravi-stimulated, starch-filled amyloplasts are displaced toward the new physical bottom, and a signal is elicited. This not-yet clearly characterized message (a phytohormone or electrical signal) rapidly travels toward the growing region of the root, where a differential growth response occurs, leading to the downward bending of the organ (Sievers et al. 1989; Chen et al. 1999; Kutschera 2001; Esmon et al. 2005).

Whereas gravity is solely perceived in the root cap (Sievers 1984), pertinent experiments with light as the environmental signal led to conflicting results. Most investigators reported that the tip of the root senses the light signal, but critical experiments revealed that, in maize roots, phototropism still occurs after the removal of the root cap (Schneider 1965). The red/far-red light

photoreceptor phytochrome A is localized at high concentrations in the cap, and at lower levels in the cells above the tip of the organ (Pratt and Coleman 1974; Schwarz and Schneider 1987). In contrast to phytochrome, the blue light photoreceptor phototropin 1 was not detected in the calyptra, but occurs in the elongation zone of the roots (Sakamoto and Briggs 2002). Our model depicted in Fig. 6 illustrates the localization of phytochrome A and phototropin 1, as well as the blue light-mediated reaction of the LOV-domain protein within the phot 1-molecule. Upon light perception, the formation of a covalent adduct between the thiol sulfur and the carbon C4a of the light-absorbing flavin is induced, and a reversible reaction occurs in darkness (Tseng et al. 2010). Despite these insights, the mode of signal transduction from the activated phot 1 to the growing cells is unclear. Moreover, since phytochrome A also absorbs in the blue light range of the visible spectrum (Franklin and Quail 2010), it cannot be ruled out that phy A is involved or interacts with phot 1.

Finally, the relationship between the perception of gravity and light within the organ tip, and hence the interplay between gravi- and phototropism of the root, is still largely unknown. Boccalandro et al. (2008) have proposed a tentative scheme on this topic that is discussed above. Despite these insights, more work is required to further elucidate these physiological processes, which Schaefer (1911) analyzed for the first time on a large taxonomic sample of land plants that were raised in the laboratory under controlled environmental conditions.

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