Tropisms of Underground Shoots—Stolons and Rhizomes

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Abstract—The review discusses current problems in research on growth-related plant movements (phototropism and gravitropism). The existing data on physiological and molecular mechanisms of tropisms in shoots and roots are presented. Special attention is paid to underground shoots (stolons and rhizomes), which grow transversely to gravity; this phenomenon is called diagravitropism. Phytochrome control is shown to play a role in the maintenance of horizontal growth of stolons and rhizomes, and the physiological mechanisms of the phototropism and diagravitropism are discussed. The switch from diatropic to orthotropic (vertical) growth of the apexes of underground shoots was shown to be dependent on the balance of carbohydrates and phytohormones. The prospects for further studies of the mechanisms of growth orientation and morphogenesis of underground diagravitropic shoots are outlined.

PHOTOTROPISM AND GRAVITROPISM AS FUNDAMENTAL PLANT TRAITS

Light and gravitation are the main environmental factors regulating plant growth and development (Chen et al., 1999; Molas and Kiss, 2009). Light provides plants with the energy required for their vital activity and controls the processes of flowering, tuber formation, bud transition to the dormancy stage, etc. Plants developed mechanisms that help them to determine and correct their orientation toward a gravity vector. Light and gravitation allow plants to orient themselves in the environment, which allows them to optimize growth and the use of light energy, water, and mineral elements (Esmon et al., 2005). The growth movements of plants and their organs in response to a one-sided stimulus are called tropisms (Hart, 1990). In the case of a positive tropism, the response is directed towards the source of stimulus, whereas negative tropism means the response is directed from this source. Plant shoots demonstrate positive phototropism (they grow towards a light source), and negative gravitropism (they grow in a direction opposite to the center of the Earth). Roots are characterized by positive gravitropism and negative phototropism, i.e., they grow along the gravity vector. However, in some cases, the movement may be directed at an angle to the stimulus source (plagiotropism) or transversely to this source (diatropism).

The first studies of plant movements were performed in the 19th century. Studying the irritability of etiolated seedlings of canary seed (*Phalaris canariensis* L.) and oats (*Hordeum*), Darwin showed that side light was perceived only by a coleoptile tip (sensor zone), whereas phototropism-caused bending occurred in the underlying (motor) zone (Darwin, 1880). It was also found that plants have various receptor organs and tissues, such as root and coleoptile tips, tendrils, glandular hairs, and certain parts of leaves and stems. Darwin supposed that the irritated tip generated a chemical signal, which spread to a motor zone. It was later shown that this chemical signaling compound is auxin (Went, 1932; Kholodnyi, 1939).

The physiological mechanisms of tropic responses have been widely studied (Went, 1932; Kholodnyi, 1939; Wilkins, 1979; Polevoy, 1984, 1986; Hensel, 1986; Leopold, 1992; Medvedev, 1996, 2013; Chen et al., 1999; Correll and Kiss, 2005; Hopkins and Kiss, 2012; Hohm et al., 2013; Christie and Murphy, 2013; Liscum et al., 2014). The tropism phenomenon is based mainly on extension growth, though sometimes it is determined by cell division. In the case of a positive tropism, the side of an axial organ, which is distant in relation to an irritant, grows faster, so the organ bends towards the irritant. According to the Kholodnyi–Vent theory, plant phototropism and gravitropism are both based on transverse electrical polarization of their tissues, which leads to the transportation of auxin (as IAA anion) to the positively charged areas of these tissues (Went, 1932; Kholodnyi, 1939). For example, one-sided illumination causes a phototropic bending due to the concentration of auxin at the shaded side. Polar IAA transport is a key factor determining polar growth, morphogenesis, and tropisms (Polevoi, 1986; Benjamins and Scheres, 2008). It is considered that the effect of auxins (IAA) on extension growth is connected with the "acid growth effect."

IAA induces the work of an ATPase proton pump, which causes acidulation of a cell wall phase, activation of hydrolytic enzymes, and cell wall maceration. IAA indirectly stimulates proton secretion via the consecutive activation of anionic, calcium, and Ca^{2+}-dependent K^+ channels in plasmalemma (Zimmerman et al., 1994; Medvedev et al., 1998).

Of the various tropisms, *phototropism* (growth bending of plant organs caused by one-side illumination) has been studied most actively. Shoots grow towards light, demonstrating positive phototropism, whereas roots, which move from the light, show negative phototropism. Phototropism is one of few processes specifically controlled by blue light. Phototropic response has several stages: (1) blue light reception by phototropin, a membrane-bound photoreceptor; (2) light signal transduction; (3) formation of a lateral auxin gradient; (4) activation of the IAA-induced signaling; and (5) asymmetric cell stretching in the growth zone, resulting in a phototropic bending of a hypocotyl towards a light source (Hohm et al., 2013; Liscum et al., 2014).

Phototropins (PHOT1 and PHOT2) are receptors responsible only for blue light reception during phototropic response (Briggs et al., 2001). Phototropins have two absorption maxima in the blue spectral region (390 and 450 nm). *Arabidopsis* has two genes, *NPH/PHOT1* (non phototropic hypocotil1) and *NPH2/PHOT2*, that encode blue light receptors. The *NPH1/PHOT1* gene encodes flavoprotein, a phototropin, which is localized in plasmalemma and contains a serine/threonine kinase domain at the C-terminus and two so-called LOV (light, oxygen, voltage) domains (Hohm et al., 2013; Christie, 2007). These domains bind two flavinic (FMN) chromophore groups. It is considered that the NPH1 protein is phosphorylated during blue light reception that activates a Ca^{2+} channel in plasmalemma and causes Ca^{2+} uptake into the cytoplasm and activation of a calcium signaling system. Polar Ca^{2+} flows, which are formed during changes in the spatial position of a plant, influence the process of IAA polar transport (Medvedev et al., 1998).

To date there are more than ten known auxin-transporting proteins, such as PIN1−PIN8, ABCB19, AUX1, LAX2, and LAX3 (Liscum et al., 2014; Peer et al., 2011). The main transporters, which form polar IAA flows, are pin-formed proteins from the PIN family. PIN1−PIN4 and PIN7 proteins facilitate IAA transfer through plasmalemma, whereas PIN5, PIN6, and PIN8 are involved in intercellular IAA transportation. Due to the differing membrane localizations of these proteins, different IAA polar transportation directions are possible (Christie and Murphy, 2013). At all stages of plant development, PIN1 and PIN2 function as the main IAA transporters in both shoots and roots. PIN1 is localized in cells of the conducting system of shoots. The longitudinal asymmetric distri-

bution of PIN1 facilitates polar transportation of IAA from the apex to the base of a shoot. PIN2 is localized in root epidermal cells and provides IAA transportation from the shoot apex to the root extension zone (Christie and Murphy, 2013). At the same time, despite all of the achievements in the study of photoreceptor activation processes, the mechanisms of photoreceptor-mediated regulation of IAA lateral transportation, which cause phototropic bending, remain unclear.

An IAA receptor is represented by an auxin-binding protein ABP-1; it functions in the lumens of the endoplasmic reticulum (Liscum et al., 2014). There are also some other types of IAA receptors, such as the nuclear protein SKP2A (s-phase kinase-associated protein2a) and proteins of the TIR1/AFB (transport inhibitor resistant1/auxin binding f-box) family. The role of SKP2A in the phototropism is rather unclear, but both SKP2A and TIR1/AFB receptors are genetically related to the phototropic response. The further transmission and amplification of the auxin signal involves secondary mediators, such as Ca^{2+} ions, MAP-kinase cascade, G-proteins, and inositol triphosphate signalling system (Liscum et al., 2014).

The final target of the auxin signal is a genome. Auxin-regulated transcription includes six basic components:

(1) auxin response elements (AuxREs) representing specific regions in the promoter zone of primary response genes;

(2) the group of genes encoding transcription factors (auxin response factor, ARF);

(3) ARF-binding repressor proteins (AUX/ IAA);

(4) corepressor proteins TOPLESS (TPL);

(5) $SSF^{TIR1/AFB}$E3 ubiquitin-ligase complex;

(6) IAA itself.

In the presence of all required transcription factors, auxin is capable of inducing rapid (within 1 min) changes in gene transcription (Liscum et al., 2014).

Ethylene, gibberellins, and brassinosteroids, along with auxin, are also involved in the phototropic response. Ethylene may stimulate the recovery of a phototropic response in a nph4/art7-null mutant (Harper et al., 2000) via the influence on the expression of ARF genes, which function as transcription regulators (Li et al., 2006). According to some data, mutations that break the brassinosteroid signal response influence IAA-mediated phototropin-dependent phototropism (Nakamoto et al., 2006). Under conditions of low-intensive blue lighting, brassinosteroids suppress the phototropic response, whereas high-intensive blue lighting induces the opposite effect. The participation of gibberellins in the phototropic response is determined by their involvement in the regulation of NPH4/ARF7-dependent transcription (Tsuchida-Mayama et al., 2010). Gibberellins may influence the intracellular transfer of

PIN2, which positively influences root gravitropism (Willige et al., 2011).

Gravitropism is a fundamental plant feature that allows them to correct their position in relation to the gravity vector. The gravitropic response includes stimulus reception, biochemical signal formation, and early signal transduction events that result in auxin redistribution and then asymmetric growth (Hashiguchi et al., 2013; Vandenbrink et al., 2014). The reception of a gravitropic stimulus occurs in specialized root cap cells and also in endodermal cells localized between the cortex and the conducting tissue of above-ground shoots (Wyatt et al., 2013). Statoliths (starch grains), in which sedimentation on the bottom side of a cell is connected with gravity perception, play a special role in the reception of gravitropic stimuli. According to existing data, the intracellular organelle distribution and cytoskeletal state also play an important role in gravity perception. Two cell components, vacuolar membranes and actin microfilaments, are involved in amyloplast dislocation during gravitropism (Hashiguchi et al., 2013; Wyatt et al., 2013).

The mechanisms of the reception and transduction of a gravitropic signal are still not completely understood (Vandenbrink et al., 2014; Wyatt et al., 2013). The earliest gravistimulation processes are connected with the Ca^{2+} distribution and auxin flows. It is believed that amyloplasts are able to break the functioning of a microfilamentous system, so the signal is transmitted to the plasmatic membrane. As a result, the concentration of cytosolic Ca^{2+} increases, while the proton gradient level on the plasmalemma decreases, leading to auxin redistribution. Lateral auxin flows are directed to the bottom side, whereas Ca^{2+} ions are transported to the upper side of gravistimulated above-ground plant organs (Medvedev, 1996).

It is believed that the gravitropic response is regulated by the interaction of auxin, ethylene, and brassinosteroids (Vandenbussche et al., 2013; Huang et al., 2013). The enzyme (1-aminocyclopropane-1-carboxylate synthase) participating in the ethylene biosynthesis was proved to be a target for Ca^{2+}-dependent protein kinase (CDPK), which may be a signal for the gravitropic response. The results of studies in the field of gravitropism regulation indicate that the following may play a role in gravitropic signaling processes: jasmonates (Gutjahr et al., 2005); endomembrane Ca-ATPase pump and apirase (Ca-dependent membrane enzyme; Bushart et al., 2013); cytochrome P450 and flavonoids (Withers et al., 2013); and heat-shock proteins (Bai et al., 2013).

PHYTOCHROME CONTROL OF THE GROWTH ORIENTATION OF ROOTS AND SHOOTS

Plants have a perfect light perception apparatus that consists of different photoreceptor systems, such as phytochromes, cryptochromes, phototropins, and receptors of green and violet light, the nature of which is still unknown. Phytochromes are one of the most important sensor pigments; they function mainly in the red (RL, 660 nm) and far-red (FRL, 730 nm) spectral regions and regulate plant growth and development. In etiolated plants, the phytochrome presents in a physiologically inactive P_{RL} form. Being exposed to red light, it is transformed to a physiologically active P_{FRL} form. Due to the phytochrome capacity for phototransformation, plants perceive information about changes in illumination conditions and adapt to them. *Arabidopsis* has five phytochrome-encoding genes responsible for the synthesis of their protein components (PHA, PHB, PHC, PHD, PHE). Using transformed plants, Smith (1995) showed that the expression of phytochrome-encoding genes occurs in young undifferentiated stem and root tissues. These genes are localized in nuclear DNA, so they are expressed within the nucleus, while phytochrome proteins (apoproteins) are synthesized on cytoplasmic ribosomes. The phytochromes of plants that grow in the dark are localized in the cytosol. When a shoot appears from soil and become exposed to light, the photomorphogenesis program is activated. Under light, a physiologically active form of the pigment is transferred from the cytoplasm to the nucleus, where the phytochrome participates in genomic regulation processes via binding with transcription factors (Smith, 2000).

The basic phytochromes (phy) are phyA and phyB, which dominate quantitatively and functionally; they also regulate the majority of plant photomorphogenetic and photoregulatory functions (Quail, 2002; Sineshchekov, 2013). Etiolated plants mainly contain phyA, which is characterized by light lability and a high light sensitivity within the range between ultraviolet and near-infrared regions. During illumination, the pigment content sharply decreases due to its destruction (P_{FRL} proteolysis) and biosynthesis inhibition (light-mediated suppression of transcription). Due to phyA activity in the far-red spectral region, angiosperms are able to grow under a dense canopy, which provides them with some adaptive advantages. Under light, the role of the main phytochrome passes to light-stable phyB, which is involved in the light-induced phytochrome responses of plants (Sineshchekov, 2013).

Phytochromes belong to phosphoproteins and light-induced protein kinases (Ser/Thr kinases in higher plants; Sineshchekov, 2013). Kinases represent enzymes that are capable of transferring a phosphate group from ATP to a side radical of amino acid residues composed of polypeptides. They participate in

signal transduction via the regulation of enzyme activity by phosphorylation. There are several factors that interact with phytochromes and acti in both the cytoplasm and nucleus; these factors include PIF-3 (phytochrome interacting factor-3), NDPK2 (nucleotide diphosphate kinase-2), PKS1 (phytochrome kinase substrate-1), and PKS2. PIF3 is a positive regulator involved in the activation of light-regulated genes (Ni et al., 1998; Kim et al., 2003). In the absence of light, PIF3 is localized in the nucleus, where it physically interacts with a phytochrome; being exposed to light, it undergoes rapid light-induced destruction mediated by phyA, phyB, and phyD. NDPK2 is an enzyme localized in both the cytoplasm and nucleus that functionally interacts with phyA and phyB; it also acts as a transcription regulator (Choi et al., 1999; Ogura et al., 1999). PKSes (PKS1−PKS4) are membrane-bound proteins representing substrates for phytochromal kinase activity (Fankhauser et al., 1999; Lariguet et al., 2003, 2006). These proteins have a cytoplasmic localization and physically interact with phyA, which phosphorylates serine and threonine residues of PKS. As a result, phyA kinase activity is inhibited, leading to a photomorphogenesis blockage.

The photomorphogenesis program is activated when a shoot appears from the soil. Light promotes the expression of light-regulated genes, the activity of which in the dark is suppressed by special proteins. There are about ten known genes encoding repressor proteins capable of suppressing photomorphogenesis in the dark (DET—de-etiolated, COP—constitutive photomorphogenesis). In the dark or under illumination with FRL, PIF proteins in seeds activate the transcription of genes encoding gibberellin signal inhibitors, GAI (gibberellic acid insensitive), RGA (repressor of GA), and unknown X-factors (Bae and Choi, 2008). X-factors suppress gibberellin biosynthesis and activate genes controlling the biosynthesis of abscisic acid (ABA). An increased ABA content increases the level of ABA-dependent transcription factors ABI3 and ABI5 and suppresses seed germination. Under light or red light illumination, phytochrome binds with PIF proteins, resulting in their proteolysis. A decrease in the PIF content leads to a decrease in the contents of GAI, RGA, and X-factors. As a result, the gibberellin concentration increases, while the ABA concentration decreases, and these changes promote seed germination (Bae and Choi, 2008).

Along with phytochromes, red and far-red light are also perceived by two other photoreceptor types, cryptochromes and phototropins, which absorb light quanta in the blue and UV-A spectral regions (Quail, 2002; Christie, 2007). Cryptochromes (Cry1 and Cry2) may be involved in phytochrome signal transduction, since their activity increases in the case of phosphorylation with phyA (Ahmad et al., 1998), which may influence the features of the latter (Sineshchekov, 2013). In turn, the photoreceptors of red and far-red light (phytochromes A, B, C, D, and E) may repeatedly absorb blue light.

Phototropism is controlled by blue light receptors: shoots grow towards blue light, demonstrating positive phototropism. Roots show negative phototropism in relation to blue light and positive phototropism in relation to red light (Ruppel et al., 2001; Kiss et al., 2003). Shoots bend towards blue light, which improves the photosynthetic possibilities, whereas roots escape the upper soil layers, which can be penetrated by blue light. Depending on the soil type, the depth of blue light penetration may reach from 1 to 3−5 cm (Tester and Morris, 1987; Mo et al., 2015). Some light-dependent geotropic responses of roots are sensitive to low light intensity.

Red light induces positive phototropism in *Arabidopsis* roots (Kiss et al., 2003). In the case of positive phototropism, phyA and phyB play a key role in red light reception. Light reception occurs directly in these heterotrophic organs (Hopkins and Kiss, 2012). The majority of genes encoding photoreceptor proteins for blue and red light are expressed in root tissues. Phytochrome genes are expressed in the root cap, root meristem, and absorption zone (Adam et al., 1994; Somers and Quail, 1995), while the expression of genes encoding blue light receptor (PHOT1) was observed only in the absorption zone (Wan et al., 2008). Phytochromes are involved in various physiological processes occurring in *Arabidopsis* roots, such as extension growth, lateral root formation, and phototropic responses (Kiss et al., 2003; Costigan et al., 2011).

The key role in the growth orientation of the *Arabidopsis thaliana* root is played by PKS1, a membrane-bound protein that serves as a substrate for phytochrome kinase (Lariguet et al., 2003, 2006; Boccalandro et al., 2008; Molas and Kiss, 2008). PKS1 is expressed in the root extension zone; this process is induced by white, red/far-red, and blue light. It was shown that blue light−induced PKS1 expression occurs in a subapical root zone with the involvement of phyA, which repeatedly absorbs blue light; the process results in negative phototropism and positive gravitropism of this organ (Boccalandro et al., 2008). The reception of a light signal in the root apex influences the gravitropic bending of a shoot (Hopkins and Kiss, 2012). The study of the interaction of signal pathways for gravitropism and phototropism in shoots and roots is an important aspect of research in the field of tropic responses.

To date, significant progress has been achieved in the elucidation of gravitropism and phototropism mechanisms in roots and shoots, and various photoreceptors, especially phytochromes, have been shown to be involved in the regulation of these processes. Most of the current molecular and genetic data on gravitropism and phototropism were obtained on model *Arabidopsis thaliana* plants with the use of various
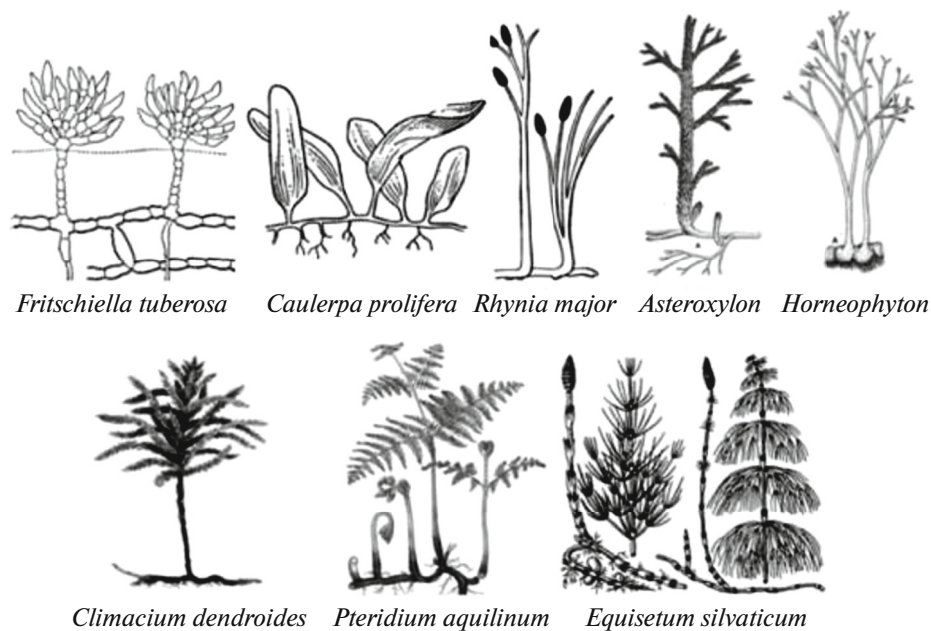
Fritschiella tuberosa   *Caulerpa prolifera*   *Rhynia major*   *Asteroxylon*   *Horneophyton*

Climacium dendroides   *Pteridium aquilinum*   *Equisetum silvaticum*

Fig. 1. Manifestation of heterogravitropism in evolutionary ancient plants. The scheme presents fossil and existing plant species forming orthotropic (vertically oriented) and diatropic (horizontally oriented) structures. Further explanation is found in the text.

mutants. In some studies, other model plants were used, such as rice (*Oryza sativa*; Kutschera et al., 1990; etc.), watercress (*Lepidium sativum*; Kutschera and Brigs, 2012), and potato (*Solanum tuberosum*; Vinterhalter et al., 2014). To reveal patterns in the regulation of phototropism and gravitropism and to understand the evolutionary transformations of these functions, it is necessary to conduct studies on both cultivated and wild plant species, including perennial plants, among which there is a wide variety of life forms and strategies.

DIAGRAVITROPISM—THE MOST ANCIENT TYPE OF GROWTH ORIENTATION

Perennial herbaceous plants that form horizontal underground (hypogeodiagravitropic) shoots, such as stolons and rhizomes, as well as creeping grasses with above-ground horizontal (epigeodiagravitropic) shoots such as stolons, tendrils, and runners, are very common in nature. In contrast to the hypocotyl and epicotyl, diatropic shoots grow horizontally above or under ground for a long time without any manifestation of phototropic or gravitropic responses (Markarov, 1996).

Diagravitropism, or a horizontal orientation of a plant growth, represents plant part growth that is transverse to gravity. In general, diagravitropism of cells, organs, or the whole organism is one of the most ancient growth orientation types (Markarov, 1996; Markarov and Golovko, 2014; Maslova, 2014; Maslova et al., 2015). It was observed even in algae of the Chlorophyta division, which are considered to be ancestors of higher plants (Takhtadzhyan, 1964;

Khohryakov, 1981; Willis and Mc Elwair, 2002). For example, the terrestrial alga *Fritschiella tuberosa* has an underground thallus consisting of cells with diagravitropic growth (Fig. 1). During vegetative reproduction, the thallus cell is divided into two daughter cells with different growth orientations in relation to the gravity vector. One of these cells is divided, forming a vertical above-ground axis, whereas the second, which has diatropic growth reaction, forms the underground part of the thallus. This underground part has a reproductive function and is better provided with water, which can be considered an adaptation of this alga to terrestrial conditions.

Diatropism as a growth process may be localized in the apical part of a plant. This situation is observed in *Caulerpa prolifera* (Forsskal) J.V. Lamouroux, which also belongs to the Chlorophyta division. The green alga *C. prolifera* consists of one giant cell and forms the creeping diatropic parts of its thalloid, reaching up to 3 m in length (Fig. 1). The rapid morphogenetic response of the diatropic *C. prolifera* rhizome to the change in its position in relation to the gravity vector is connected with the amyloplast migration to the top part of the rhizome, a process that is also typical for higher plants (Jacobs, 1993).

An underground horizontal part (rhizomoid) was also typical for ancient higher plants (Rhyniophyta) and fossil Lycopsids, horsetails, and ferns (Takhtadzhyan, 1998a). The sporophyte of the fossil *Rhynia major* formed a dichotomically branched rhizomoid with telome stems rising upward from the rhizomoid to the soil surface (Fig. 1). The diatropic rhizomoid of a fossil rhyniophyte *Horneophyton lignieri* consisted of one or
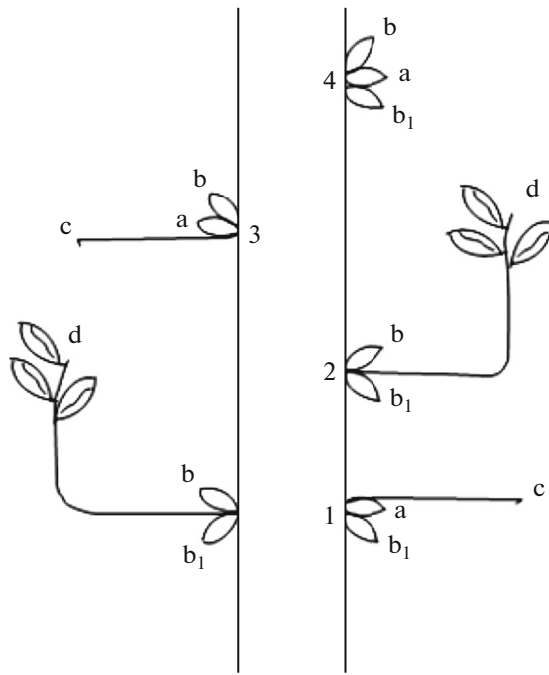
Fig. 2. Scheme of an underground metameric complex of a tuber-bearing species *Solanum demissum*. 1–4, basal metamers of an orthotropic shoot; a, second-order bud; b and b_1, third-order bud; c, stolon formation by a third-order bud; d, sarment formation by a second-order bud (Markarov and Golovko, 1995c).

Fig. 3. Sarments (a) and stolons (b) of a tuber-bearing South American potato species (*Solanum demissum*; Markarov and Golovko, 1995c).

more bulb-like structures with rhizoids. The morphological differentiation of ancient plants improved the adaptation of rhyniophytes with imperfect steles to the terrestrial conditions.

Underground horizontal rhizomes were revealed in fossil Lycopsids (*Asteroxylon*), horsetails (genus *Equisetum*), and ferns (family Cyatheaceae). The ancient *Asteroxylon*, which became extinct 400 million years ago, had an underground dichotomically branching rhizomoid characterized by monopodial growth (Fig. 1; Snigirevskaya, 1998). A well-marked underground diagravitropic rhizome is also typical for contemporary spore-bearing (Lycopsids, horsetails, and ferns) and vascular flowering plants. For example, the cosmopolite species *Pteridium aquilinum* (L.) Kuhn annually forms two "buds" on the apical part of its hypogeodiatropic rhizome. One of them (maternal bud) continues its horizontal underground growth and does not form leaves, whereas another (daughter bud) forms a shortened horizontal branch of the rhizome (Takhtadzhyan, 1998b).

Thus, diagravitropism is an evolutionary ancient function that appeared due to the adaptive evolution of plants to terrestrial conditions. Two physiological mechanisms, the maintenance of underground diagravitropic growth and the formation of a negatively gravitropic shoot, occur in the apical part of a diagravitropic rhizome. In the first case, diatropic shoot
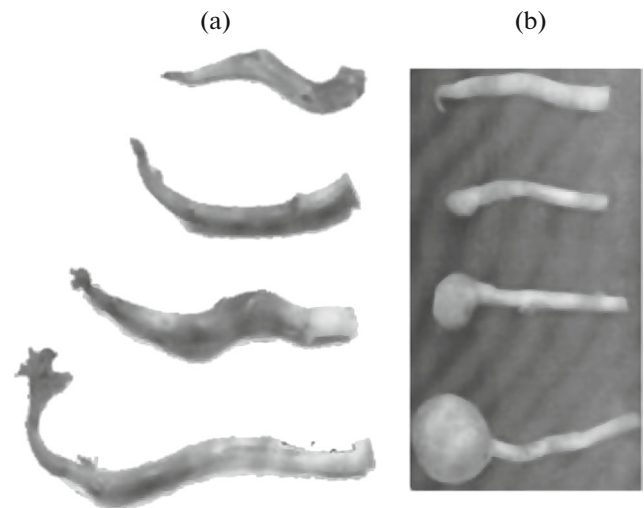
growth results in the formation of an underground pool of vegetative meristems required for plant renewal and reproduction. In the second case, a shoot appearing from the soil forms an assimilating surface for further plant reproduction. The geogravitropism of underground buds is a unique biological feature that formed in the course of phylogenetic transformation of plant life-forms.

PHYSIOLOGY OF GROWTH ORIENTATIONS OF UNDERGROUND SHOOTS

In contrast to above-ground orthotropic shoots, rhizomes and stolons grow horizontally above or under the ground and do not demonstrate any gravitropic or phototropic responses for a long period (or even permanently). The apical dome of a rhizome or stolon sometimes generates buds, which then turn to underground shoots, or sarments (Figs. 2, 3). A sarment is an underground shoot that is able to switch from a diatropic (horizontal) to an orthotropic (assimilating) above-ground shoot without any dormancy stage. During a certain period of a horizontal underground growth, the apical part of a sarment is differentiated and forms a photophilic histological complex with the further formation of green leaves (Figs. 2, 3; Markarov and Golovko, 1995c; Markarov, 1996). Sarments participate in vegetative reproduction and form juvenile plants during the vegetation season. This shoot type is generated by stolon-forming (*Solanum demissum*, *S. stoloniferum*, *Stachys siebildii*, etc.) and rhizome-forming (*Phalaroides arundinacea*, *Bromopsis inermis*, *Elytrigia repens*, *Achillea millefolium* (Fig. 4), *Tussilago farfara*, *Vaccinium myrtillus*, etc.) plant species.

Studies performed on numerous rhizome- and stolon-forming plants proved that the growth orientation of underground shoots (stolons, rhizomes, and sarments) does not depend on the photoperiod duration, phytohormone treatment, or decapitation of an above-ground shoot (Markarov and Golovko, 1995a, 1995b, 1995d; Markarov, 1996). Therefore, the apical part of the above-ground rhizome does not control growth reactions of underground shoots. Stolons and rhizomes have an autonomous mechanism of regulation of their growth orientation localized in their apical part.

Experiments arranged with the stolons of tuber-bearing oca (*Oxalis tuberosa*), South American potato (*Solanum demissum*), ulluco (*Ullucus tuberosus*) and the rhizomes of milfoil (*Achillea millefolium*), mint (*Mentha piperita*), and woundwort (*Stachys sieboldii*), showed that the growth orientation of lateral buds was not controlled by the apical bud (Markarov and Golovko, 1995b; Maslova, 2001). The response of lateral buds depends on the conditions of their formation; buds that formed in the dark or under light demonstrated negative or positive phototropism, respectively. The results of our studies provided evidence of the possibility of the simultaneous occurrence of two opposite growth reactions in an underground shoot—diatropic growth of the apical zone and orthotropic growth of a lateral bud. The autonomy of the growth reactions of underground shoots and their lateral zones is a biological feature leading to the existence of a permanent pool of underground vegetative diaspores.

It is known that the negative gravitropic and positive phototropic responses of shoot-type organs are phytochrome-dependent. Epicotyl and hypocotyl grow vertically (orthotropically) towards the soil surface and respond to exposure to natural lighting or the red spectral region by growth suppression and straightening of the apical hook. The study of light's influence on the morphogenesis of underground shoots showed that the growth orientation of stolons and rhizomes is controlled by the phytochrome system (Markarov and Golovko, 1995b; Markarov, 1996). To study the phototropism of underground shoots, their apical zones (1—2 cm) were exposed to RL (600—680 nm) or FRL (710—780 nm) with the intensity of 1 W/m^2; the exposure duration was 5 min for every night for 2 weeks. For mint (*Mentha piperita*) and milfoil (*Achillea millefolium*), FRL treatment did not influence the growth orientation of their underground shoots (Fig. 5), whereas treatment with RL or natural lighting resulted in a change in the diatropic growth orientation, such that the apical part of a rhizome grew down into the soil. A similar phytochrome-controlled response was observed for stolons of *Solanum* plants and *Oxalis tuberosa*. Therefore, the red form of phytochromes allows the maintenance of horizontal underground growth of stolons and rhizome, while its far-red form prevents the appearance of shoot apexes above the

Fig. 4. Underground shoots of a two-year long-rhizome milfoil (*Achillea millefolium*). *1*, sarments; *2*, rhizomes. Scale bar is 10 cm.

ground. It is important that regulatory functions of phytochromes are realized with respect to the processes of the apical dome formation in an underground shoot. The phytochrome system controls the growth orientation of an underground shoot during the period of photophobic development, accompanied by the formation of metamers with cataphylls; at this stage, the shoot is characterized by diagravitropism and negative phototropism. Phytochromic control stops during the photophilic period, when the apex of a horizontal shoot switches from diagravitropic to orthotropic growth; at this stage, green leaves form, and shoots demonstrate positive phototropism.

The path between the signal and effect represents a chain of consecutive events, which includes signal reception and transduction via the system of secondary mediators, the realization of received information at the genomic level, and the resulting physiological response. The activation of many genes in plant cells is induced by different compounds called morphogens, which may include phytohormones, sugars, amino acids, etc. Acting as signal molecules, these compounds may induce or block genetic programs of development and differentiation of cells and organelles.

Our studies showed that the processes of switching from diagravitropism to negative gravitropism in apical zones of rhizomes, which occur in the autumn season, take place against the background of changes in the hormonal and carbohydrate balance (Maslova et al., 2007, 2013). During this period we observed a relatively high content of cytokinins in the apical zones of underground shoots. This cytokinin accumulation may stimulate the form-building processes connected with the initial organogenesis stages in the shoot apical dome (cell divisions and tissue differentiation in lateral meristems). Cytokinins regulate cell divisions; they are also involved in plant signal systems and may influence the expression of various genes, such as early genes encoding regulatory proteins
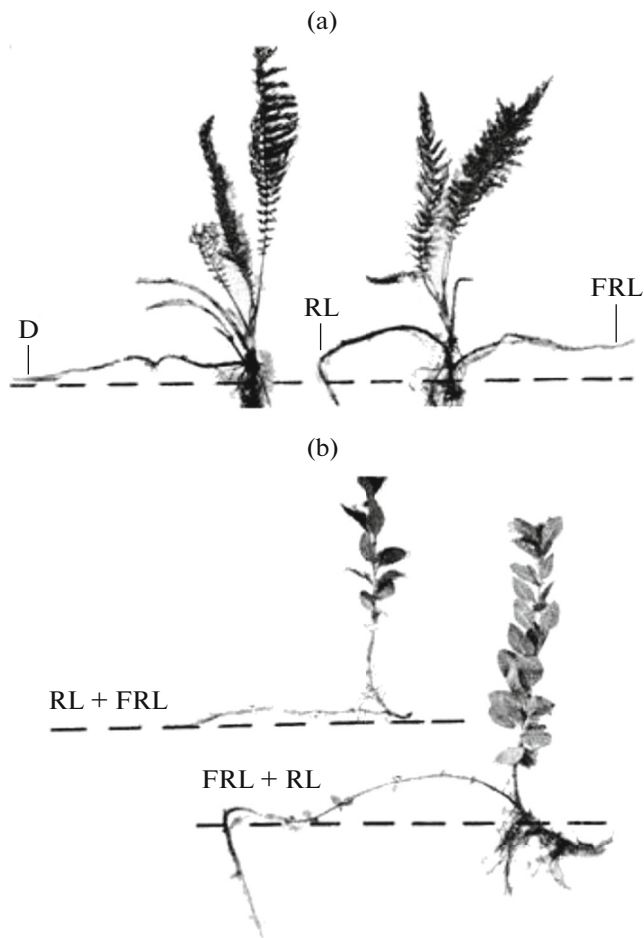
(a)

(b)

Fig. 5. Growth orientation of (a) milfoil (*Achillea millefolium*) and (b) mint (*Mentha piperita*) rhizomes in the dark (D) and in the case of illumination with far-red (FRL) or red (RL) light (Markarov and Golovko, 1995d).

(ARR5, transcription factors AP, HAT22, bHLH, Myb, proteins possessing protein kinase or phosphatase activity) and genes involved in protein proteolysis (Romanov, 2009).

Morphogenetic transformations occur in the apical parts of milfoil (*Achillea millefolium*) rhizomes against a background of an increase in the gibberellin/ABA and cytokinin/ABA ratios (Maslova et al., 2013). This phenomenon allows maintenance of the active metabolism and the growth and differentiation of cells and tissues in underground buds during the switch from diagravitropism to negative gravitropism. This rearrangement results in the subsequent-year formation of above-ground assimilating shoots.

Sugars (their composition, concentration, and flow volume) may also serve as a starting signal for the cascade expression or repression of genes in both nuclear and organelle genomes. Being a substrate for energoplastic metabolism, sugars may participate in morphogenesis regulation and enhance cell division and differentiation in meristematic zones (Hänisch

and Breteler, 1981; Veyres et al., 2008). We found that, in the course of a yearly cycle of underground shoot development, the ratio between simple and complex carbohydrates is changed. For example, tissues of young rhizomes of reed canary grass (*Phalaroides arundinacea*) in the autumn period were characterized by an increased oligosaccharide content (Maslova et al., 2007). Oligosaccharides as signal molecules may be involved in regulation of cellular division, growth, and differentiation in apical tissues of underground shoots, where the seasonal morphogenetic transformations take place in autumn.

Hormonal and trophic changes in apical tissues of rhizomes occur against the background of an active metabolism. In autumn, meristematic tissues of underground shoots are characterized by relatively high rates of respiration and heat generation (Maslova et al., 2013; Maslova, 2014). In *Phalaroides arundinacea* and *Achillea millefolium*, buds of underground shoots are able to grow and store energy during the late autumn and winter periods, when the soil temperature in the rhizome zone drops to 0°C or below. Despite the high water content in cells, the apical zones of rhizomes remain undamaged, since the ice point value within them is −8 to 9°C, which is three times lower than the temperature of soil at their location. We suppose that the maintenance of a given metabolic level in the autumn period causes some morphogenetic transformations in rhizome meristems connected with the switch from diagravitropic to negatively gravitropic growth. In this period, qualitative changes occur in the apical dome of underground shoots, and the primordia of photophilic leaves of the assimilating aboveground shoot, which grows towards the ground surface, form.

CONCLUSIONS

The study of plant tropic responses has a long history. To date, a concept of the growth movements of shoot-type organs (hypocotyl and epicotyl) has been formed. According to the existing data, the epicotyl, hypocotyl, and the shoot as a whole demonstrate positive phototropism and negative gravitropism. Significant progress has been achieved in the study of gravitropism and phototropism mechanisms in roots and shoots; various photoreceptors and their interaction in the regulation of these processes have been shown to be involved, and the role of phytochromes in gravitropism and phototropism of *Arabidopsis* shoots and roots has been identified.

In nature some plants have diagravitropic shoots (rhizomes, stolons, tendrils, and creeping shoots) that grow horizontally for a long time, either underground or on the soil surface, and do not demonstrate any phototropic or gravitropic responses. The physiological mechanisms of the growth orientations of rhizomes and stolons remained nearly unknown for a long time (Wareing and Phillips, 1981; Cline, 1991). The role of

the phytochrome system in the growth orientation of diatropic shoots (the regulatory functions of which are realized depending on the organ formation processes occurring in the apical dome of the underground shoot) was determined a little more than 25 years ago (Markarov and Golovko, 1995a, 1995b, 1995c, 1995d; Markarov, 1996). Experimental evidence showed that the exposure of apical parts of stolons and rhizomes to red or white light resulted in their growth down into the soil, whereas far-red light did not cause such bending of the subapical part of these shoots. The "red" form of phytochromes maintains a horizontal underground growth, while the "far-red" form prevents the appearance of the shoot apex above the ground. Phytochrome control stops during the photophilic period, when the shoot apex switches from diagravitropic to orthotropic growth and green leaves form.

Based on an analysis of global trends in the study of tropisms and on the results of our own research, we can consider the prospects in this field to be connected with the study of physiological, biochemical, and molecular mechanisms of heterogravitropism of underground vegetative meristems. This feature is of great biological importance, since it provides underground branching of a rhizome or stolon and the formation of above-ground assimilating shoots. To date, the problems of hormonal, trophic, and phytochrome regulation of the photo- and diagravitropism of stolons and rhizomes have been poorly investigated. We know almost nothing about the expression of genes and proteins involved in regulation of the activity of underground meristems, which control the stages of photophobic and photophilic organogenesis of apical buds of underground shoots. Little is known about the mechanisms regulating the morphogenesis of diagravitropic underground shoots.

To date, studies devoted to the identification of genes and proteins involved in the differentiation, growth, development, and metabolism of rhizomes are actively being carried out in order to identify the regulation patterns of these processes with respect to species specificity. Molecular and genetic studies of lateral underground meristems of perennial grasses from the genus *Leymus* revealed a polymorphism in the expression of genes involved in the gravitropic response of underground buds, which, depending on their growth direction, demonstrated negative gravitropism (turf grasses) or diagravitropism (rhizome grasses; Kaur et al., 2008). A study on the expression of genes and proteins involved in regulation of the activity of underground vegetative meristems showed the presence of photosynthetic genes (proteins of the photosystems I and II, chlorophyll *a*, apoprotein A1, and phototropin-2) in the apical zone of heterotrophic rhizome tissues (Ruifeng et al., 2012). The expression of these genes may occur at the photophilic stage of underground bud morphogenesis under light exposure.

In our opinion, the study of characteristics of the structural and functional organization of apical meristems in underground diagravitropic shoots at different stages of organogenesis of their apical bud is very promising. Further study of the expression of phytochrome-system genes and proteins, which control the photomorphogenesis of underground shoots during photophobic and photophilic stages of development of their apical dome, also remains relevant.

Identification of the molecular mechanisms determining the tropism of shoot-like organs and the growth orientation of diatropic shoots (rhizomes and stolons) is of both theoretical and practical significance. The spectral composition of light is one of the basic factors determining shoot generation intensity, productivity, and phytocenose stability. Under a dense canopy, the red light/far-red light ratio is shifted to the far-red light; this fact is one of the reasons for the observed suppression of shoot growth. Mowing or draining may restore this ratio to a level favorable for intensive growth and the formation of new shoots by rhizomes. Therefore, the study of the morphogenesis mechanisms and growth orientations of rhizomes and stolons is important for the development of efficient methods to control vegetative propagation, the productivity of rhizome- and stolon-forming perennial plants, and weed control.

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