

Competing neighbors: light perception and root function

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Abstract Plant responses to competition have often been described as passive consequences of reduced resource availability. However, plants have mechanisms to forage for favorable conditions and anticipate competition scenarios. Despite the progresses made in understanding the role of light signaling in modulating plant–plant interactions, little is known about how plants use and integrate information gathered by their photoreceptors aboveground to regulate performance belowground. Given that the phytochrome family of photoreceptors plays a key role in the acquisition of information about the proximity of neighbors and canopy cover, it is tempting to speculate that changes in the red:far-red (R:FR) ratio perceived by aboveground plant

parts have important implications shaping plant behavior belowground. Exploring data from published experiments, we assess the neglected role of light signaling in the control of root function. The available evidence indicates that plant exposure to low R:FR ratios affects root growth and morphology, root exudate profiles, and interactions with beneficial soil microorganisms. Although dependent on species identity, signals perceived aboveground are likely to affect root-to-root interactions. Root systems could also be guided to deploy new growth predominantly in open areas by light signals perceived by the shoots. Studying interactions between above- and belowground plant–plant signaling is expected to improve our understanding of the mechanisms of plant competition.

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Introduction

Plant competition has been a major research topic in various disciplines because of its implications for species coexistence in natural ecosystems and crop yield in agriculture. Traditionally, plant growth and plant responses to competition have been viewed as being primarily dictated by changes in the availability of resources (light, nutrients and water) and modulated by regulators (e.g., temperature, photoperiod). However, plants are not passive organisms that simply tolerate the limitations that their environment imposes on them. They have sophisticated mechanisms to sense and integrate environmental signals, which allow them to forage for more favorable conditions and anticipate changes in the supply of environmental resources, including those imposed by the proximity of competitors

(reviewed in Ballaré 2009; Novoplansky 2009; Pierik et al. 2013). For example, changes in light quality and quantity caused by the proximity of competitors induce shade-avoidance responses, such as stem elongation and leaf hyponasty, which allow the plant to outgrow neighbors and improve competitive performance (Aphalo and Ballaré 1995; Schmitt et al. 1995). In addition to light, other non-resource signals can modulate competitive responses of plants, including those derived from touching of leaves (de Wit et al. 2012), volatile compounds (Kegge and Pierik 2010), root exudates (Bais et al. 2006), and soil microorganisms (Hendriks et al. 2013).

The strategies used by terrestrial plants to forage for light and avoid being shaded by other plants have attracted attention in a broad cross-section of disciplines, from ecology to molecular biology. The role of photoreceptors of the phytochrome family in providing information about the proximity of neighbors has been investigated in detail (reviewed in Schmitt et al. 1995; Ballaré 2009). In the last decade, plant responses to shade have been extensively studied in the reference plant *Arabidopsis thaliana*, and the pathways that connect perception of light signals by phytochrome with the expression of the shade-avoidance syndrome (SAS) phenotype have been mapped in considerable detail (Hornitschek et al. 2012; Li et al. 2012; see reviews in Martínez-García et al. 2010; Casal 2013; Gommers et al. 2013).

Compared with aboveground responses, root responses to the proximity of neighboring plants have been less intensively studied at the mechanistic level, and their adaptive significance is not well understood. Most research on the belowground compartment of plant function has focused on responses to changes in the availability of nutrients and water rather than on root-to-root signaling, as often a single plant (or a low number of interacting individuals) has been studied in pot experiments (Gersani et al. 1998; Kembel and Cahill 2005; Hodge 2009; Mommer et al. 2011, 2012). Root competition has been notoriously difficult to study, as roots are hidden by the soil, and species are difficult to recognize from belowground organs. However, in the last few years, substantial progress has been made in the development of imaging-analysis software and molecular tools (e.g., DNA barcoding), which have led to advances in the field of root ecology (Mommer et al. 2008, 2011; Kesanakurti et al. 2011; Lobet et al. 2011). These advances have motivated new attempts to understand the belowground complexity of plant communities in natural, species-rich systems (Cahill et al. 2010; Frank et al. 2010; Jones et al. 2011).

Despite recent advances in the description of mechanisms of plant–plant interactions, studies aiming to understand how plants use and integrate information gathered above- and belowground are scarce. In this article, we

first provide a brief overview of (1) the role of light signals in the perception of competition aboveground, and (2) the controls of root growth and behavior. Other recent reviews have separately covered light signaling (see e.g., Martínez-García et al. 2010; Ruberti et al. 2012; Casal 2013) and root interactions (see e.g., Schenk 2006; Cahill and McNickle 2011). Next, we review the literature related to the role of the photoreceptor phytochrome as a modulator of root behavior and ecology. We propose that aboveground perception of neighbors via changes in light quality has important implications for plant behavior belowground. We hope these considerations will stimulate discussion on signal integration, and promote experimentation on mechanisms of plant competition.

Light signals mediate ecological interactions between plants

Solar radiation is the essential source of energy for photoautotrophic organisms. Plants have evolved complex information-acquiring systems that allow them to adjust their phenotype as a function of light signals that indicate present or future competition with neighboring plants for access to solar radiation (reviewed in Aphalo and Ballaré 1995; Franklin 2008; Ballaré 2009). This information is gathered and processed by several dedicated photoreceptors such as phytochromes, cryptochromes and phototropins, which are sensitive to specific wavelengths of the solar spectrum (reviewed in Chen et al. 2004; Franklin 2008; Ballaré 2009; Gommers et al. 2013). Differential absorption by chlorophyll reduces red (R) light relative to far-red (FR) radiation, and this reduction provides information about the proximity of neighboring plants. Thus, R:FR ratios between 1 and 1.2 are indicative of direct sunlight (Fig. 1), whereas lower values indicate some degree of shading (Holmes and Smith 1977) or the proximity of potential competitors (Ballaré et al. 1990). Phytochromes are responsible for the perception of changes in the R:FR ratio. These photoreceptors have two photo-interconvertible forms: Pr (R-absorbing form and bio-inactive) and Pfr (FR-absorbing form and bio-active) (Smith 2000; Bae and Choi 2008). The *A. thaliana* genome has five phytochrome genes (*PHYA-E*) but many angiosperms have three (*PHYA-C*) (Franklin and Quail 2010). Of the five *Arabidopsis* phytochromes, *phyA* and *phyB* are the best characterized, and especially *phyB* is well known to play a central role in determining plant responses to changes in the R:FR ratio caused by the proximity of other plants (Franklin 2008; Ballaré 2009; Gommers et al. 2013).

Light signals perceived by phytochromes control almost every aspect of plant life, from seed germination to flowering. Seed germination in many plant species is sensitive

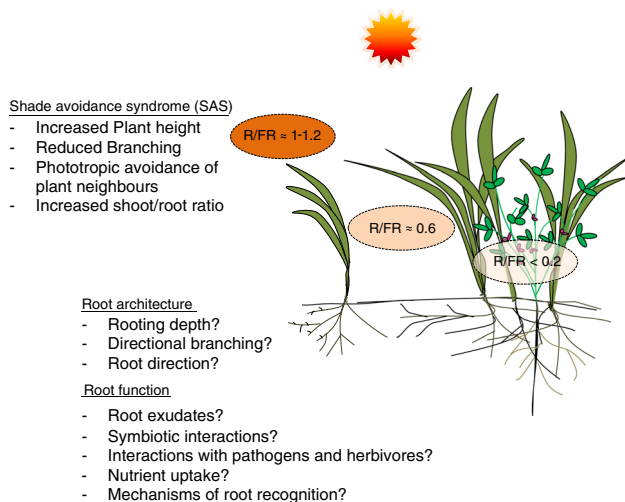


Fig. 1 Schematic representation of the effects of informational signals perceived by phytochrome in the shoots on root growth and function. Shade-avoidance syndrome responses triggered by low red:far red ($R:FR$) ratio have been well documented (*upper part*), whereas the consequences of light signaling on root behavior and performance under competition are not well understood, as indicated by *question marks (bottom part)*

to light signals sensed by phytochromes; this link between phytochrome and the termination of seed dormancy increases the likelihood that the seed germinates under conditions of reduced competition [e.g., canopy gaps, recently disturbed soil, etc. (Benech-Arnold et al. 2000)]. Once the plant establishes itself at the point of seed germination, it continuously adjusts its phenotype to the prevailing conditions in the light environment, avoiding shade from other plants and optimizing light interception. These morphological adjustments, collectively referred to as SAS, are triggered by light-quality signals (particularly a low $R:FR$ ratio; Fig. 1), although depletion of blue light and UV radiation, perceived by other photoreceptors, including the cryptochromes, phototropins, and UV resistance locus 8, also play an important role under certain canopy conditions (Pierik et al. 2004a; Keller et al. 2011; Keuskamp et al. 2011; reviews in Casal 2013; Ballaré 2014). Components of the SAS include elongation of the hypocotyl, stems and petioles, bending of shoots and leaves away from the shade and towards the light (phototropism), and increased apical dominance (reviewed in Franklin 2008; Ballaré 2009; Martínez-García et al. 2010; Ruberti et al. 2012; Casal 2013; Gommers et al. 2013). Light that is horizontally reflected by neighboring vegetation is enriched in FR radiation (low $R:FR$ ratio) and carries information about the proximity of neighbors and their spatial distribution relative to the receiving plant. Therefore, reflected FR radiation plays a major role in early detection of neighboring plants, stimulating stem growth away from the direction of potential

competitors (Ballaré et al. 1990; Ballaré 2009). Phototropins (Briggs and Christi 2002) control phototropic movements of plant shoots, which are an important component of the mechanisms that allow plants to forage for light in patchy canopies. Summarizing, phytochromes and other informational photoreceptors have been found to play a central role controlling critical phenological switches and driving adaptive changes of shoot morphology in relation to competition. In contrast, very little is known about the role of photoreceptors in controlling root growth, architecture and functionality.

Root behavior: patterns of growth and interaction between individuals

Knowledge about the signals that control root growth is essential for the understanding of belowground interactions among plants. Besides anchoring the plant to the substrate, the main function of roots is the uptake of nutrients and water. Therefore, it is hardly surprising that research on the mechanisms of root-to-root interaction has focused primarily on root responses to these two belowground resources (de Kroon et al. 2003; Schenk 2006; Cahill and McNickle 2011). In general, plant growth is reduced in nutrient-poor soils, but the relative allocation of carbon to roots (i.e., root/shoot ratio) usually increases in response to nutrient deprivation (Poorter et al. 2012). Root responses to spatial variation of nutrients in the soil has received substantial attention, from ecologists investigating competitive consequences of root growth toward nutrient hotspots (Farley and Fitter 1999; Kembel and Cahill 2005; Hodge 2009; Mommer et al. 2011, 2012), to molecular biologists studying the signal transduction mechanisms that control local root proliferation (Forde and Walch-Liu 2009; Araya et al. 2014). Molecular biologists successfully described a nitrate sensor and transporter in *Arabidopsis* (e.g., Ho et al. 2009), as well as receptors for other nutrients (reviewed in Ho and Tsay 2010).

Several papers in the last decade have supported the notion that belowground interactions may involve more than just competition for the uptake of belowground resources (Semchenko et al. 2007; Cahill et al. 2010; Mommer et al. 2010; Fang et al. 2013; Pierik et al. 2013). Interest in research on root-to-root interaction as “more than nutrients” was promoted by the papers by Mahall and Callaway (1991, 1992), who showed that the interaction between two desert shrub species was markedly affected by allelochemical compounds. These papers sparked interest in the idea that roots are able to discriminate self from non-self roots, kin from non-kin individuals, and con- from hetero-specific roots (e.g., Gersani et al. 2001; Maina et al. 2002; Gruntman and Novoplansky 2004; O’Brien et al. 2005; Dudley

and File 2007; Murphy and Dudley 2007, 2009; Biedrzycki et al. 2010; Fang et al. 2013). The conclusions drawn from some of these studies have been challenged (Schenk 2006; Hess and de Kroon 2007; Klemens 2008), in part because some of the results may have been affected by the variation in pot size, which affects both rooting volume and nutrient availability simultaneously (i.e., split-root design). Nonetheless, in experiments where the soil volume available for each plant was controlled, root responses that were not necessarily related to nutrient availability were demonstrated (Maina et al. 2002; Semchenko et al. 2007; Biedrzycki et al. 2010; Cahill et al. 2010; Mommer et al. 2010; Fang et al. 2013; Hendriks et al. 2013).

Different growth patterns have been described in the response of one root system to the presence of a neighboring root system. The “avoidance” term (or “undermixing” or “segregation”) describes a pattern in which the growth of a root system is inhibited by the presence of a neighboring root system. In turn, this inhibition in one side can be compensated for (“compensatory”) or not (“non-compensatory”) by growing toward the opposite side of the neighbor position. In overlapping root systems, the terms “intrusive” (other alternative terms: “over-mixing”, or “aggregation” or “over-proliferation”) or “unresponsive” (other alternative terms: “random mixing” or “no response”) are used to refer, respectively, to situations in which the growth of a focal root system is either increased or unaffected by the presence of neighboring roots (Brisson and Reynolds 1994; Gersani et al. 2001; Maina et al. 2002; Falik et al. 2003; Semchenko et al. 2007; Cahill and McNickle 2011). A recent review revealed that avoidance is one of the most frequently reported root growth patterns (Cahill and McNickle 2011). However, the underlying mechanisms are elusive. For example, the avoidance pattern in roots of *Abutilon theophrasti* induced by the presence of a neighboring plant was tentatively attributed to a (non-identified) belowground cue (Cahill et al. 2010). However, a potential role of aboveground signals could not be ruled out in these experiments. Summarizing, root ecology and physiology have become very active fields of research and important questions have emerged regarding the signals that control root growth and function in plant communities.

Effects of light-quality signals perceived aboveground on root growth and function

General patterns

Some insights into the effects of neighbor-proximity signals on root growth patterns can be gained from agronomic studies exploring the effects of variation in planting density on crop plant morphology. Although these studies have

mostly focused on aboveground plant parts, some effects of density on the spatial orientation of roots and the vertical profiles of root systems have been documented. For example, planting apple trees (*Malus* sp.) at high density increased root growth into deeper soil layers, but not horizontal expansion in upper layers (Atkinson et al. 1976). Qualitatively similar results were reported for cotton (*Gossypium hirsutum*) crops (Grimes et al. 1975). In sunflower (*Helianthus annuus*), the rate of root growth was higher within-row than in the inter-row spaces, and crops sown at high density showed earlier exploration of deeper soil layers compared with crops sown at low density (Sadras et al. 1989). Row spacing had no effect on maximum root depth in soybean (*Glycine max*) crops, but root length density increased when plants were grown in narrow rows (Mason et al. 1982). Roots of two cultivars of *Trifolium subterraneum* responded to increased plant density not by growing in depth, but by increasing in density (length per volume of soil), a pattern observed beneath the row but not in the inter-rows (Pearson and Jacobs 1985). Therefore, the evidence from agricultural experiments suggests that plant density can result in changes in the vertical distribution of roots and sometimes in the horizontal growth pattern. These effects of plant proximity on root growth and development could have significant effects on the efficiency with which crop plants capture resources from the soil. From an adaptive point of view, increased exploration of deep soil layers in response to crowding might increase, in some soil environments, the likelihood of maintaining adequate rates of water supply even in the presence of a high number of competitors.

The causes of these morphological responses of root systems to crowding are not understood, but could conceivably involve signals derived from photoreceptors in the shoots. In fact, effects of mutations in photoreceptor genes or genes involved in photoreceptor signal transduction on root gravitropism (Galen et al. 2006; Bocalandro et al. 2008) and root development (Salisbury et al. 2007) are well documented in controlled-environment studies using the reference plant *A. thaliana*. Of course, under field conditions, the responses of root systems to population density could be triggered by multiple factors besides changes in the light environment, including the level of below- and aboveground resources. However, attempts to separate effects of aboveground signals (e.g., low R:FR ratio) from above- and belowground resource competition (see e.g., Dorn et al. 2000; Murphy and Dudley 2007, 2009) have been limited.

phyB and root growth and morphology

Since the photoreceptor phyB plays a principal role in acquiring information about the proximity of potential

competitors and canopy cover, we scrutinized results from experiments that have addressed the effects of phytochrome manipulations (either by changes in the R:FR ratio or mutation of the *PHYB* photoreceptor gene) on root-related traits. A recent meta-analysis suggested that reductions in the R:FR ratio often increase stem biomass with few effects on root growth (Poorter et al. 2012). However, the analysis of individual cases reveals important variation in the response of roots to the R:FR ratio. In many studies that explored the effects of reducing the R:FR ratio on plant biomass allocation, a promotion of biomass allocation to shoots, at the expense of roots, has been demonstrated. These reports include experiments with *Raphanus sativus* (Keiller and Smith 1989), *G. hirsutum* (Kasperbauer and Hunt 1992), *Zea mays* seedlings (Kasperbauer and Karlen 1994; Rajcan et al. 2004; Liu et al. 2009; Page et al. 2009), *Phaseolus vulgaris* (Hoddinott and Hall 1982), *Sinapis alba* (Cowan and Reekie 2008) and *Pinus sylvestris* (de la Rosa et al. 1998). Other studies have failed to find effects of light quality on plant biomass partitioning in *Amaranthus quitensis* (Ballaré et al. 1991) and *Plantago lanceolata* (van Hinsberg and van Tienderen 1997) and variations among species have often been reported (Corré 1983; Mitchell and Woodward 1988; Dale and Causton 1992; Tinoco-Ojanguren and Pearcy 1995; Hoddinott and Rickey 1996; Lee et al. 1996; McKendrick 1996; Pattison et al. 1998; Stuefer and Huber 1998).

The response of root biomass to changes in phyB status may depend on habitat-specific adaptations, ontogenic stage, and complex interactions with other environmental factors. For shade-avoiding species, it would appear that phyB inactivation by low R:FR ratios or the *phyB* mutation (which leads to constitutive expression of the SAS phenotype), typically cause a reduction in root biomass, and it may also negatively affect the initiation of seminal, adventitious and lateral roots (Morgan and Smith 1979; Keiller and Smith 1989; Lambers and Poorter 1992; Newton et al. 1996; Lötscher and Nösberger 1997; Smith and Whitelam 1997; Pechácková 1999; Rajcan et al. 2004; Salisbury et al. 2007). However, effects of low R:FR ratios reducing root mass and the root/shoot ratio may depend on plant ontogeny (Liu et al. 2009; Page et al. 2009; Green-Tracewicz et al. 2012). Part of the variation in the responses of root/shoot ratio to phyB manipulations may also be explained by interactions with other factors of the above- and below-ground environments. Increased allocation to aboveground structures with a concomitant reduction in root biomass was expressed in seedlings of *Rumex obtusifolius* and *P. lanceolata* exposed to low R:FR ratios only when grown at high irradiance (McLaren and Smith 1978; van Hinsberg 1997). In *Impatiens* spp., reductions in the root/shoot ratio in response to low R:FR ratio were only apparent when neighboring plants shared a common soil substrate,

but not when their root systems were experimentally isolated (Murphy and Dudley 2009). In *P. sylvestris*, low R:FR ratios resulted in a reduced root/shoot ratio only under high nutrient availability (de la Rosa et al. 1998, 1999; but see also Aphalo and Lehto 2001). Beyond the potential effect of species-specific, idiosyncratic factors, results suggest that not only the nutrient status of the soil, but also competition for aboveground resources and the presence of neighboring roots may play a role in modulating morphological responses of root systems to changes in the R:FR ratio.

We did not find papers that explicitly investigated the effects of R:FR on root spatial architecture (directional branching, root bending, etc.). However, based on the observations that (1) plant population density affects root growth patterns, (2) the effects of density on shoot architecture are often mediated by variations in R:FR, and (3) mutations of plant photoreceptors also affect key elements of root physiology, we speculate that root systems could be guided to deploy new growth predominantly in open areas by light signals perceived by the shoots. This would be an attractive hypothesis because of the well-documented effects of light signals on shoot architecture, including directional growth away from neighbors, and the fact that changes in the R:FR ratio can provide an early signal of the proximity of potential competitors (Fig. 1). A hypothetical mechanism for the effects of changes in the R:FR ratio on root architecture might involve the plant hormone auxin. Auxin regulates shade avoidance and phototropic bending by tightly controlled localization of auxin transport carriers and auxin biosynthesis (Tao et al. 2008; Keuskamp et al. 2010; Ding et al. 2011; Hornitschek et al. 2012; Li et al. 2012). If the resulting auxin gradients established in the shoot by the proximity of other plants persist into the root system, they might induce directional root growth, away from potential competitors. Indeed, auxin is a well-known regulator of root development (Blilou et al. 2005), architecture (Peret et al. 2009) and plasticity (Krouk et al. 2010) and has been suggested to mediate phytochrome effects on root development in *Arabidopsis* (Salisbury et al. 2007).

phyB and root exudates

Changes in the R:FR ratio can have strong effects on plant secondary chemistry (Tegelberg et al. 2004; Engelen-Eigles et al. 2006; Izaguirre et al. 2006; Agrawal et al. 2012; Cerudo et al. 2012; reviewed in Ballaré 2014) and on the quality and quantity of compounds that plants emit or secrete (Finlayson et al. 1998; Pierik et al. 2004b; Izaguirre et al. 2013; Kegge et al. 2013; reviewed in Pierik et al. 2014). However, most studies to date have focused on the chemistry of aerial plant parts, particularly in connection to plant defense against pathogens and herbivores (Ballaré 2014). Light quality perceived by the shoots could affect the

quality of root exudates, with potential consequences for below-ground interactions, but this possibility has received little experimental attention. Lateral irradiation of plants with FR radiation changed the profile of root exudates in seedlings of *Avena fatua*, increasing some compounds with a potential allelopathic effect (e.g., sesquiterpenes) (Pomilio et al. 2000). The authors suggested that these compounds might increase the ability of *A. fatua* plants to interfere with competitors (Pomilio et al. 2000). The architecture of root systems can be affected by exudates released by roots of the same plant or by roots that belong to other plants (Caffaro et al. 2011, 2013). Root exudates also appear to be important for the recognition of neighboring roots (Biedrzycki et al. 2010; Cahill et al. 2010; Caffaro et al. 2013; Fang et al. 2013); therefore, changes in exudate profiles induced by variations in light quality might affect plant–plant interactions belowground. Finally, given that exudates play an important role in the interaction between roots and soil microorganisms (Bais et al. 2006), changes in light quality perceived by phytochrome and other informational photoreceptors may affect plant–microorganism interactions in the rhizosphere (see below).

phyB and root interactions with symbionts

Symbiotic associations between roots and soil microorganisms can be affected by low R:FR ratios perceived aboveground. Early studies showed that legumes such as *G. max* and *Vigna unguiculata* exposed to light treatments enriched with FR radiation had fewer nodules of their symbiotic nitrogen-fixing bacteria than plants that received light with a high R:FR ratio (Kasperbauer et al. 1984; Kasperbauer and Hunt 1994). Studies on mycorrhizal fungi detected a reduction in root colonization of *Festuca rubra* plants exposed to a low R:FR ratio compared to plants obtained from the same clones under a high R:FR ratio (Skálová and Vosátka 1998; Pechácková 1999). Similarly, a negative effect of low R:FR ratios was observed on root length and mycorrhization of plantlets of *P. sylvestris* (de la Rosa et al. 1998). These effects could result from within-plant competition for resources (e.g., competition for carbohydrates between shoots and roots) or most likely, be brought about by phytochrome-mediated changes in patterns of hormone distribution. A recent study demonstrated that exposure to low R:FR conditions significantly reduced the *Lotus japonicus* association with nitrogen-fixing bacteria (Suzuki et al. 2011). The evidence is consistent with the idea that phyB modulates the interaction between plants and belowground symbionts by altering plant sensitivity to jasmonate (JA), a central hormone involved in plant developments and defense. In fact, the effect of low R:FR ratios reducing plant sensitivity to JA is a well-documented phenomenon (Ballaré 2011), with profound consequences on plant

resistance to leaf pathogens and herbivores (Moreno et al. 2009; Cerrudo et al. 2012; de Wit et al. 2013; Izaguirre et al. 2013; Kegge et al. 2013). The effects of changes in JA signaling brought about by variations in the R:FR ratio on root interactions with pathogenic soil microorganisms have not been investigated.

Another mechanism by which light perceived by photoreceptors in the shoot could affect root interactions with symbiotic organisms is via changes in the profiles of root exudates. Phenolic compounds are involved as important signaling molecules in the interactions between plant roots and symbiotic microorganisms, and have been particularly studied in the symbioses between legumes and rhizobia (Zhang et al. 2009), and mycorrhizal plants and mycorrhizal fungi (Abdel-Lateif et al. 2012). Since sunlight has been found to affect the levels of phenolic compounds in plant shoots (e.g., Ballaré 2014), including flavonoids and isoflavonoids in legumes (Zavala et al. 2014), it may potentially regulate flavonoid levels in root exudates, with consequences for signaling with symbionts in the rhizosphere. In the same vein, strigolactones, which play a central role as plant host-recognition signals for parasitic and symbiotic organisms (Akiyama et al. 2005), are thought to be regulated by phyB (Brewer et al. 2013) and known to interact with a key element of light-signaling pathways (Tsuchiya et al. 2010; Ruyter-Spira et al. 2013). Therefore, light might affect signaling processes in the rhizosphere by altering strigolactone homeostasis. Clearly, there is tremendous potential for new discoveries in the area of modulation of the root microbiome by light signals perceived by the aerial parts.

Concluding remarks and future perspectives

R:FR signaling through phytochromes appears to dominate various aspects of plant development and behavior in canopies, including adaptive stem elongation and directional shoot growth (Franklin 2008; Ballaré 2009; Martínez-García et al. 2010; Ruberti et al. 2012; Casal 2013; Gommers et al. 2013), leaf growth (Carabelli et al. 2007), flowering time (Cerdán and Chory 2003) and modulation of plant immunity against herbivores and pathogens (Ballaré et al. 2012; Ballaré 2014). The evidence discussed in this article strongly suggests that light quality perceived aboveground also affects belowground plant behavior. The best-documented effects of the R:FR ratio on root function include changes in biomass allocation to roots and modification of interactions between roots and microbial symbionts. However, the number of factors that have been found to affect root behavior is strikingly high, including levels of soil resources, rooting volume, presence/absence of neighbors, symbionts, and pathogens. An important

challenge is to find out the hierarchy of their action and the magnitude of their effects. A combination of physiological and genetic approaches using model organisms will provide a fast way forward to separate the effects of different factors and cues, but ultimately, field experiments under realistic conditions will be required to understand the mechanisms that control root behavior in nature. We propose that neighbor perception through changes in light quality mediated by phyB has important potential implications for root growth and function under natural conditions (Fig. 1). Many studies in which root-to-root interactions have been tested may have included the influence of aboveground signals in their reported patterns, since neighboring-roots or “no-neighboring-roots treatments usually involve neighboring shoots as well. The phyB-mediated detection of neighboring plants, which has been shown to have strong implications for architectural plasticity aboveground, has yet to be explored for its consequences belowground.

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