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# Location Matters: Canopy Light Responses over Spatial Scales

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**Plants use light as a signal to determine neighbour proximity in dense vegetation. Far-red (FR) light reflected from neighbour plants elicits an array of growth responses throughout the plant. Recently, various light quality-induced signals have been discovered that travel between organs and tissue layers. These signals share upstream and downstream components, but can have opposing effects on cell growth. The question is how plants can coordinate these spatial signals into various growth responses in remote tissues. This coordination allows plants to adapt to the environment, and understanding the underlying mechanisms could allow precision engineering of crops. To achieve this understanding, plant photobiology research will need to focus increasingly on spatial signalling at the whole-plant level.**

## Highlights

Plants can convey light-quality signals through their body, allowing organs or tissues that experience different light conditions to adaptively regulate their growth and development.

Spatial light signal transduction allows roots to adapt their growth in response to leaf-derived light signals of neighbour proximity.

Within organs, photoreceptor signals can be transduced across cell layers to activate or repress downstream targets.

Spatially regulated leaf movement optimises light foraging in dense vegetation.

## Spatial Light Signal Transduction to Adapt to Heterogeneous Light Environments

Plants absorb sunlight to power photosynthesis. In addition, light is used as a signal by which plants determine neighbour proximity at high plant density. Chlorophyll preferentially absorbs blue (B: λ = 400–500 nm) and red (R: λ = 600–700 nm) light, whereas FR (λ = 700–800 nm) is reflected [1]. Reflection of FR reduces the **R:FR** ratio (see Glossary), providing an early neighbour detection signal [2] that precedes the depletion of B and R light, which together indicate canopy shade [3]. Plants use specialised photoreceptors to detect these changes in light quality and respond with extensive developmental plasticity [1] (Table 1). Seedlings elongate their hypocotyl and bend towards better light conditions [1,4]. Mature plants elongate their stems and petioles and increase leaf angles to the horizontal [5]. Collectively, these responses enhance light capture of individual plants when competing with neighbours. Since light distribution in a vegetation canopy is heterogeneous [6], different leaves of an individual plant may experience different light signals. It is generally assumed that responses to light-quality changes are coordinated at the individual organ level [7], which has been corroborated by predominantly young seedling-focussed photobiology studies. However, studies on seedlings cannot address the intrinsic developmental complexity of adult plants. Insights from a variety of studies challenge the conception that light responses would occur mostly locally.

Spatial aspects of light responses were elegantly discussed in this journal a decade ago by Martínez-García and coworkers [8] and huge progress has been made since. Petiole elongation [9], lamina (leaf blade) growth inhibition [10], and reduced indirect defence against herbivores through extrafloral nectar production [11] are **local light-signal responses** to the perception of FR enrichment within the same organ (local, Table 1). Another apparently local response to both FR [12] and B [13,14], light enrichment is hypocotyl bending (phototropism). However, phototropism may require **spatial light-signal transduction** across cell layers (intra-organ, Table 1). Other light responses to FR enrichment, such as hypocotyl elongation [15,16] and upward petiole movement (petiole hyponasty) [9,17], depend on FR perception in the

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Table 1. Spatial Aspects of Different Plant Developmental Responses to Light Quality[a]

| Light quality response | Distance of regulation | Light quality signal | Refs |
|---|---|---|---|
| Hypocotyl elongation | Inter-organ | Low R:FR cotyledons | [15,16,23–26] |
| | Intra-organ | Low R:FR hypocotyl | [23,27] |
| Hypocotyl bending | Intra-organ | Unilateral B/FR hypocotyl | [12,14] |
| Petiole elongation | Intra-organ | EODFR lamina | [28] |
| | Local | Low R:FR petiole | [9] |
| Lamina growth inhibition | Local | Low R:FR lamina | [10] |
| Reduced extrafloral nectar from leaf | Local | Low R:FR whole branch | [11] |
| Petiole hyponasty | Intra-organ | Low R:FR leaf tip | [9,17] |
| Reduced lateral root outgrowth | Inter-organ | Low R:FR shoot | [18,19,29,30] |
| Floral transition | Inter-organ | Low R:FR leaf | [31–33] |
| Reduced axillary branching | Local | Low R:FR axillary bud | [21,22] |
| | Inter-organ | Low R:FR shoot apical meristem | |

[a]Abbreviation: EODFR, end-of-day far-red treatment.

cotyledons and leaf tip, respectively, indicating spatial signalling between and within organs. Moreover, root development and flowering are regulated by low R:FR perception in the leaves, indicating true inter-organ light-quality signal transduction across the extreme ends of plants (Table 1) [18–20]. Other responses, such as reduced axillary branching in response to low R:FR, need additional work to elucidate the exact spatial aspects [21,22].

A mechanism by which light signals could move between organs would be the transduction of light itself through plant tissues. Relatively woody stems of mature arabidopsis plants and certain tree species can channel light, especially FR, through the plant tissue [34,35]. This light could then affect **phytochrome** activity in, for example, the roots [34]. Another study, using arabidopsis seedlings, found no evidence for the physiological effects of putative FR light transmission from shoot to root or vice versa [19]. Further studies are required to identify which tissues transduce light and what the ecological significance of this is. However, various recent studies have identified light-signal transmission via intermediates, such as plant hormones and mobile transcription factors.

Here, we comparatively discuss spatial light-signal transduction and responses in seedlings that comprise the embryonic tissues (i.e., cotyledons, hypocotyl, and main root), versus adult plants that also have true leaves, a complex root system, and floral organs. We discuss how light-quality signalling affects several aspects of plant development, from local cell growth to long-distance regulation of meristem outgrowth and flowering induction, and how this spatial integration helps plants optimally adjust to their dynamic environment.

## Inter-organ Signalling Regulates Hypocotyl Elongation

Early work in cucumber (*Cucumis sativus L.*) [36] and mustard (*Sinapis alba L.*) [37,38] showed that R:FR perception in the cotyledons and first leaves largely determines hypocotyl and internode elongation. It was later found that, in addition to signalling from the leaves, local low R:FR perception in the internodes themselves also regulates the elongation of this organ [2].

Inter-organ signalling between leaves and stems also occurs in arabidopsis seedlings. Seedlings perceive the horizontal reflection of FR by nearby neighbours as a low R:FR ratio, which

## Glossary

**Abaxial and adaxial side:** the two sides of an organ. Abaxial is the lower side, adaxial is the upper side. Differential growth rates between the two sides of an organ cause it to move up or down.

**Local light-signal response:** response to a light-quality signal that is perceived in the same cells; differs from spatial light-signal responses.

**Phototropin (Phot1, Phot2):** B-light-responsive photoreceptor that regulates (among others) hypocotyl bending towards B light. B-light perception results in kinase activity of this photoreceptor and phosphorylation of its targets.

**Phytochrome (PhyB, PhyA):** R- and FR-responsive photoreceptor. Phytochrome activity typically inhibits growth through repression of the downstream signalling pathway. Low R:FR light, as occurs in dense vegetation, inactivates PhyB, thereby alleviating its repression of shoot elongation.

**Red:Far Red (R:FR):** ratio between R and FR light, typically calculated as ratio between 655–665 and 725–735 nm light.

**Spatial light-signal response:** response to a light-quality signal that is perceived in different cells within the same organ (intra-organ) or in distant organs (inter-organ).

causes phytochrome-dependent induction of auxin biosynthesis [39] in the cotyledons [15,16]. Here, PhyB inactivation releases the repression of the bHLH transcription factors PHYTOCHROME INTERACTING FACTOR 4 (PIF4), PIF5, and PIF7, which in turn rapidly activate expression of YUCCA flavin monooxygenase indole-3-acetic acid (IAA) synthesis genes *YUC2*, *YUC5*, *YUC8*, and *YUC9* [40,41] (Figure 1B). YUCCAs then stimulate *de novo* IAA synthesis in low R:FR [25,42–44]. After synthesis in the cotyledons, IAA is transported to the hypocotyl by PIN-FORMED (PIN) auxin-transport proteins, where it leads to induction of auxin-responsive genes and elongation [15,16,25,26,44].

In the hypocotyl, PIN3 relocalises from a basal to a more lateral orientation in low R:FR [26], thereby allowing IAA transport from the vasculature towards the elongating epidermal cells. In the epidermis, IAA stimulates cell growth, in part through brassinosteroid-dependent signalling [23,24]. Moreover, epidermal IAA perception promotes the expression of the SMALL AUXIN UP-RNA 19 (SAUR19) subfamily of SAUR genes [23]. SAUR19 activates plasma membrane $H^+$-ATPases [45], which leads to apoplast acidification and cell growth [46] (Figure 1A). This process is reinforced by enhanced expression of cell wall-modifying enzymes, such as expansins and XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASEs (XTHs) [47], which are activated by the reduced pH [48]. Since the epidermis restricts hypocotyl growth [23,49], epidermis-specific cell elongation allows for hypocotyl elongation.

Besides inter-organ IAA transport, local auxin metabolism in the hypocotyl is also regulated by FR enrichment via repressed expression of the auxin conjugating IAA-amido synthetase *GRETCHEN HAGEN 3.17* (*GH3.17*) [27]. The resulting IAA accumulation occurs independently of IAA synthesis in the cotyledons and stimulates hypocotyl elongation. Although GH3.17-dependent modulation of auxin levels clearly happens locally in the hypocotyl, it is currently unknown whether the regulation of *GH3.17* is entirely local or if it involves inter-organ signalling from the cotyledons.

## Intra-organ Light Signalling in Hypocotyl Phototropism, Elongation, and Gravitropism

The flow of auxin from the cotyledon to the hypocotyl and then from the vasculature towards the epidermis is a great example of an intra-organ signal traversing organ boundaries and cell layers. Another example of the latter is hypocotyl phototropism, the process in which seedlings bend towards light.

Hypocotyl phototropism mainly occurs in the upper part of the hypocotyl and appears to be a local response [4]. B light is sensed by the AGC kinase **Phototropin 1** (Phot1) in the elongation zone, which triggers a more lateral distribution of PIN3 on the plasma membrane [13]. Subsequently, a relative auxin increase on the shaded compared with the illuminated side of the hypocotyl elongation zone arises, which results in uneven growth and bending (Figure 1C) [13,14].

Moreover, Phot1 signalling in the hypocotyl leads to dephosphorylation of NON-PHOTOTROPIC HYPOCOTYL3 (NPH3), which is necessary for phototropism [14,50,51]. Interestingly, epidermal PHOT1 expression causes a spread of NPH3 dephosphorylation through the entire seedling [14] (Figure 1B). Dephosphorylation causes NPH3 to dissociate from PHOT1 and the plasma membrane, a mechanism important in phototropism signalling. NPH3 is part of an E3-ligase complex that is suggested to modulate PIN3 (re)cycling [52] and the vacuolar degradation of PIN2 in the root [53]. However, the exact way in which NPH3 molecular function and dephosphorylation affects phototropism is unclear [51].

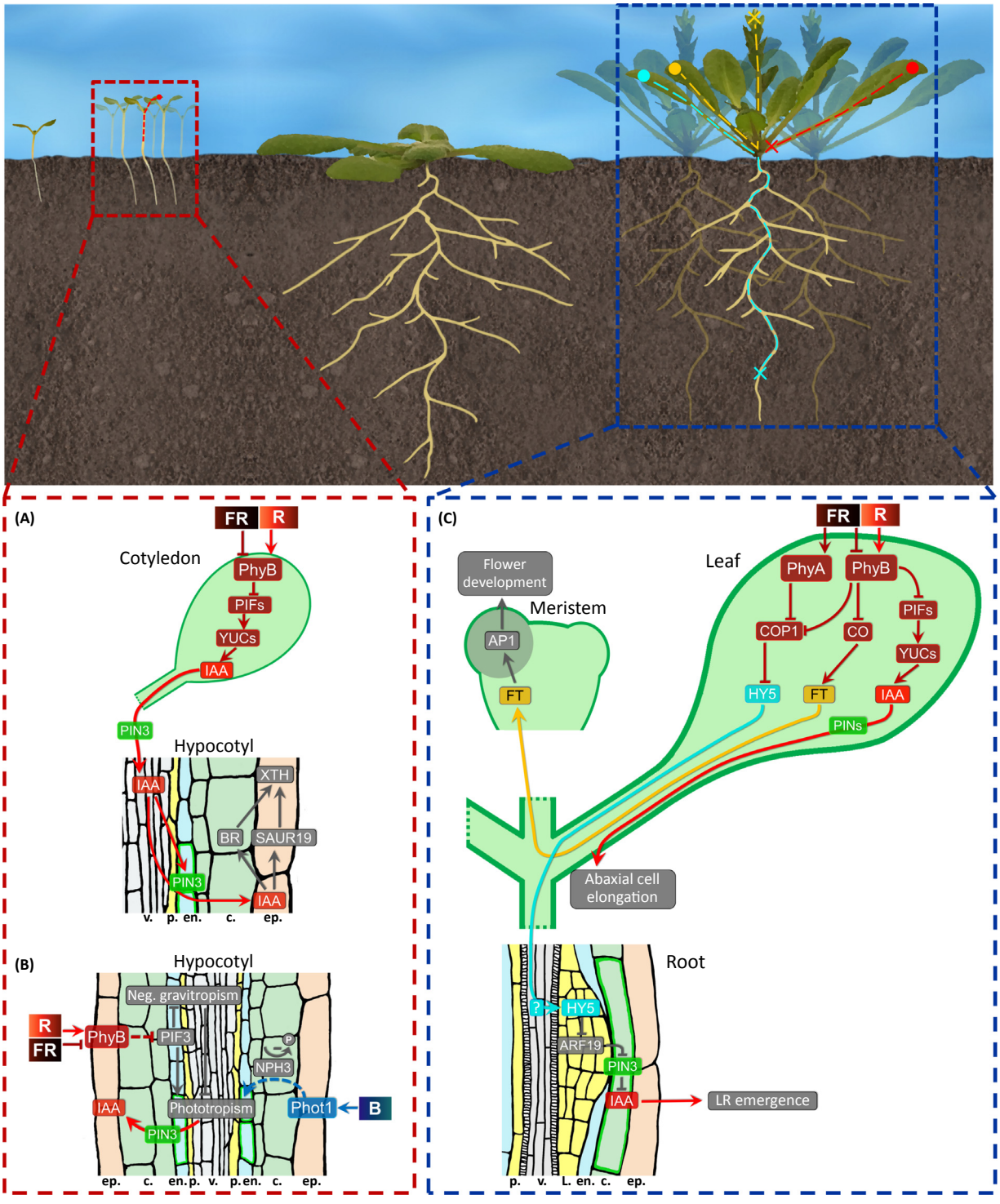


Figure 1. Spatial Light Signal Transduction in a Competitive Light Environment.

For a Figure360 author presentation of Figure 1, see the figure legend at https://doi.org/10.1016/j.tplants.2018.06.011

The top image shows arabidopsis seedlings and adult plants in (non)competitive environments and the route of spatial signals in these plants. The colours of the

*(Figure legend continued on the bottom of the next page.)*

In addition to B light, R:FR signalling also affects hypocotyl phototropism. In etiolated seedlings, PhyB activation allows phototropism by inhibiting hypocotyl negative gravitropism [54]. Gravitropism and phototropism are both bending responses of the hypocotyl. However, they are conflicting processes because they constitute growth in different directions; upward in negative gravitropism and sideways in phototropism. Negative gravitropism depends upon PIF-mediated biogenesis of gravity-sensing amyloplasts and can be supressed by R via PhyB-dependent degradation of PIFs [54,55]. It was recently shown that epidermal PhyB expression can elicit the degradation of endodermal PIFs, implying an unknown intra-organ signal that traverses cell layers (Figure 1B) [55]. When a seedling is established in light, PhyB suppresses PIFs, thereby decreasing auxin biosynthesis and growth. When such a seedling is close to competing plants, the resulting reduced R:FR relieves PIF suppression, thereby promoting auxin biosynthesis and allowing hypocotyl elongation and phototropism [12].

There are interesting signal transduction overlaps between hypocotyl elongation and phototropism. Both processes need auxin signalling in the epidermis and rely upon a redistribution of PIN3 to transport auxin sideways [13,23,26]. Moreover, both processes involve spatial intra-organ signals between endo- and epidermis that are yet to be identified and that include NPH3 dephosphorylation and PIF degradation [12,14,23,55].

## Local and Spatial FR-Signalling Responses Regulate Light Foraging in Adult Leaves

When the seedling grows to a fully fledged plant, the light environment it perceives becomes more heterogeneous over the scale of the entire organism, especially in dense stands [6]. Different parts of the shoot will experience different light qualities and it is of relevance to study the sites of light-quality perception versus response. Whole-plant exposure to low R:FR conditions promotes petiole elongation and upward leaf movement (hyponasty), which improves the competitive ability of the plant during light competition [5].

Recently, two independent studies found that upward petiole movement (hyponasty) in response to low R:FR is regulated via intra-organ signal transduction [9,17]. Localised FR irradiation revealed that hyponasty was fully induced by low R:FR perception in the very tip of the leaf, whereas FR treatment to the petiole itself failed to induce any hyponastic growth. This showed that an intra-organ signal moves from the leaf tip to the petiole base, where differential growth between the **abaxial and adaxial sides** leads to upward bending of the petiole [9,56–58]. In the leaf tip, inactivation of PhyB triggers *de novo* IAA synthesis through PIF7-dependent *YUC* transcription. IAA is subsequently transported by PIN3, PIN4, and PIN7 to the petiole base (Figure 1C) [9,17]. It is currently unknown how auxin from the leaf tip establishes differential growth in the petiole base.

long-distance signals are matched in the sections below (A–C). The red- or blue-dashed box around the plant in competition corresponds to the dashed boxes below. (A) Scheme depicting the inter-organ signal [indole-3-acetic acid (IAA), red] triggering epidermal cell and hypocotyl elongation in low red:far red (R:FR) conditions. (B) Intra-organ signalling affecting R-induced negative gravitropism and B-light (B)-induced phototropic response. The spread of PHYTOCHROME INTERACTING FACTOR3 (PIF3) degradation and NON-PHOTOTROPIC HYPOCOTYL3 (NPH3) dephosphorylation act as intra-organ epidermis-to-endodermis signals. (C) Long-distance low R:FR-induced signals in adult plants. FLOWERING LOCUS T (FT; yellow) moves from leaf to meristem to initiate early flowering, IAA (red) moves from leaf tip to petiole to induce abaxial cell elongation and leaf hyponasty and ELONGATED HYPOCOTYL5 (HY5; light blue) moves from shoot to root to reduce lateral root emergence. The tissue layers are described below the figures (c, cortex; en, endodermis; ep, epidermis; L, lateral root primordium; p, pericycle; v, vasculature). Abbreviations: AP1, APETALA1; ARF19, AUXIN RESPONSE FACTOR19; BR, Brassinosteroid; CO, CONSTANS; COP1, CONSTITUTIVE PHOTOMORPHOGENESIS1; Phot1, PHOTOTROPIN1; PhyA/B, phytochrome A/B; PIN, PIN-FORMED; SAUR19, SMALL AUXIN UP RNA 19; XTH, xyloglucan endotransglucosylase/hydrolase; YUC, YUCCA flavin monooxygenase.

Contrastingly, unidirectional petiole elongation was shown to occur in response to FR enrichment of the petiole but not by FR enrichment of the leaf tip [9]. Although this is clearly a local response, there may still be spatial signal transduction across cell layers (similar to phototropism), or perhaps from the lamina towards the petiole, as observed in an end-of-day FR study [28].

Low R:FR treatment of a single leaf had no effects on petiole elongation or hyponasty of systemic leaves that were not exposed to low R:FR [9,17], indicating that low R:FR-induced growth responses are regulated within the individual leaf. This modular response to low R:FR allows plants to meet the demands of a light environment that is heterogeneous over the scale of different organs of a single plant. Nevertheless, light quality also controls developmental responses well beyond the leaf module, all the way into the root system [19].

## Inter-organ Light Signalling Controls Root Development

When discussing spatial signal transduction over longer distances within individual plants, no distance is longer than that from shoot to root. Plants need to coordinate the growth of both organs to their respective environments to balance challenges in light and nutrient uptake [59]. Roots can detect and respond to light themselves [29,30], but low R:FR detected by the shoot can also regulate main root growth and lateral root emergence via a mobile signal that travels from shoot to root [19]. Central in this response is the light-regulated bZIP transcription factor ELONGATED HYPOCOTYL5 (HY5), which can move from shoot to root [18]. Low R:FR detected by phytochrome in the shoot leads to local *HY5* upregulation and protein stabilisation, most likely through inhibition of CONSTITUTIVE PHOTOMORPHOGENESIS1 (COP1) [19,60,61]. It was subsequently found that HY5 accumulates in the lateral root primordia, where it represses lateral root emergence by downregulating AUXIN RESPONSE FACTOR19 (ARF19) [19] (Figure 1C). This is a clear example of inter-organ, long-distance signalling, where one part of the plant detects the light and a signal is transmitted to remotely regulate development.

## Local and Inter-organ Low R:FR Signalling Regulates the Flowering Phenotype

Another adult plant response to low R:FR that involves long-distance signal transfer is accelerated flowering. Although early flowering reduces the total seed yield [15], it ensures at least some reproduction in competitive environments. The early flowering response occurs in the shoot apical meristem and is induced by PhyB inactivation in the leaves [31]. PhyB inactivation in the mesophyll releases the repression of *CONSTANS* (*CO*), which leads to enhanced *FLOWERING LOCUS T* (*FT*) transcription in the vasculature [32,33], indicating intra-organ transport of the light signal across cell layers. After translation, FT protein is transported towards the shoot apical meristem [33,62], where floral transition is stimulated through induction of *APETALA1* (*AP1*) and related floral identity genes [63] (Figure 1C). Thus, low R:FR-induced early flowering also involves long-distance inter-organ light signal transduction.

Besides flowering initiation, low R:FR can also repress the development of axillary buds to branches on the inflorescence stem. Low R:FR promotes the BRANCHED1 -dependent accumulation of abscisic acid (ABA) in the bud, thereby delaying bud outgrowth [21,64]. Although low R:FR may also regulate bud outgrowth long distance via auxin, this remains to be studied [22].

## Concluding Remarks and Future Perspectives

Here, we have discussed how several light-quality responses in both seedlings and adult plants depend on spatial transduction of light signals perceived in different parts of the plant. Although some growth responses are truly local and occur in the same cells that perceive the signal, it is becoming apparent that multiple light-induced signals travel within and between organs, allowing precise coordination of growth at the whole-organism level (Figure 1). For example, the regulation of root growth by shoot-detected low R:FR allows an organ that does not perceive light itself to adjust its growth to match the environment. Interestingly, in the shoot, both hypocotyl elongation and petiole hyponasty are largely regulated by distal light-quality signals in the cotyledons and leaf tip, respectively. The spatial separation between light perception and response in the leaves might allow plants to distinguish between shade caused by their own leaves and shade caused by neighbours. Both have the same light quality, but neighbours first shade the leaf tip, whereas the leaves of the plant itself, at least in rosette plants such as arabidopsis, first shade the petiole base [9].

Spatial light-signal transduction often occurs through transport of auxin between different cell layers and organs, for example in hypocotyl elongation, phototropism, and upward leaf movement. Additionally, small proteins, such as HY5 or FT, are involved in light-induced inter-organ long-distance signalling. Most likely there are other small proteins and hormones that can fulfil similar roles in other light responses. Indeed, gibberellic acid and ABA are candidates for intra- and inter-organ signal transduction [65,66] and future studies will likely elucidate how they control spatially explicit responses to light cues (see Outstanding Questions).

Plant responses to light quality have mostly been studied in very young seedlings under whole-seedling, homogeneous irradiation. Although this seedling model successfully aided the unravelling of shade-avoidance signalling pathways, seedlings have limited spatial and developmental complexity. Therefore, it is important to include adult plants if we are to understand plants in their full environmental and developmental complexity. This will increase the potential to contribute to challenges of global food production and efficient land use. Elucidating the exact roles of specific organs and cell types in spatial light-signal transduction will help to precisely engineer crops for optimal performance in current and future cropping systems.

### Outstanding Questions

Which organs and cell types detect specific light signals?

What other mobile signals, besides IAA, HY5, and FT, are involved in spatial light-signal transduction?

What are the mechanisms of long-distance light-signal transduction?

How are light-signal detection and downstream protein dynamics connected between tissue layers?

How do plants integrate multiple light-quality signals across the entire plant body?

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