

# Turning plant interactions upside down: Light signals from below matter

## 1 | LOOKING DOWN ON NEIGHBOURS: LIGHT SIGNALS FROM BELOW MATTER IN PLANT-PLANT INTERACTIONS

Plants in nature and agriculture growing in dense stands compete with their neighbours for resources such as light. To maximize survival and to optimize performance, plants have evolved the ability to perceive and interpret light cues indicating prevailing and future competition. Plant tissues preferentially absorb light energy in specific wavebands (e.g., red and blue) and transmit and reflect light in other wavebands (e.g., far-red) (Smith, Casal, & Jackson, 1990). As a result, spectral composition of the light reflected off plants is dramatically different from that of incident light. Those changes are potentially important light signals used by plants as an indicator of neighbour proximity. Plants respond to such light signals by, for example, increasing internode and petiole length and leaf inclination angle, collectively known as shade-avoidance responses (Ballaré & Pierik, 2017; Smith, 1982).

The physiological mechanisms underlying shade avoidance and its ecological consequences for plant performance have been extensively studied. These studies often focus on the light spectrum of incident light or reflected light from the sides, implicitly assuming the presence of an overhead canopy or similarly sized neighbours (e.g., Ballaré, Sánchez, Scopel, Casal, & Ghera, 1987; Holmes & Smith, 1977). However, in many natural and agricultural systems, plants are surrounded by other smaller plants. Those smaller plants also affect the canopy light environment by reflecting light upwards which may be sensed by the larger plants. For example, the presence of small weeds reduces red to far-red ratio (R:FR) in light reflected upwards; this increases maize plant height and shoot: root ratio, even though there may be no threat of light competition (Rajcan, Chandler, & Swanton, 2004). This suggests that light signals from below caused by smaller neighbours are not necessarily reliable cues for light competition, yet plants may still respond to such signals. In contrast to the vast number of studies quantifying ecological consequences of shade-avoidance response for plant performance, very few studies focus on plant responses to light signals from below (Rajcan et al., 2004; Zhang et al., 2020).

Here, we propose that light signals from below should not be ignored in studies on light-mediated plant interactions, as their potential consequences for plant performance differ among ecological situations and crop settings. In general, light signals from below perceived by a plant organ could come from either smaller neighbours or from lower parts of that same plant. In the latter case, the signals do not predict future competition. Signals originating from smaller neighbours might predict future competition depending on the type of neighbours: some smaller neighbours may be small simply because they emerge late but could potentially grow tall and become competitors, whereas other smaller neighbours may stay small during their whole life. In this paper we describe the type of adaptive responses to light signals from below in these different situations and discuss possible mechanisms that evolved in plants to optimize responses to light signals from below in different situations. We discuss the relevance of light signals from below in crop systems. We propose to use 3D plant simulation models to quantify the strength and relevance of light signals from below and to explore plant responses to light signals depending on the system they grow in.

## 2 | LIGHT SIGNALS FROM BELOW: A WARNING OR A FRIENDLY CALL?

Many plants grow in vegetation stands where they, at least to some extent, compete for light. In these situations, shade-avoidance responses may improve access to light but also come with costs. These costs can be in terms of invested resources (Ballaré, Scopel, & Sánchez, 1991; Givnish, 1982), hydrological effects (e.g., elongated plants may experience higher evaporation loads due to more direct radiation and stronger winds at higher canopy strata, Huber et al., 2004), lower mechanical safety factors (Anten, von Wettberg, Pawlowski, & Huber, 2009), or reduced defence (De Vries, Poelman, Anten, & Evers, 2018; Leone, Keller, Cerrudo, & Ballaré, 2014). Optimizing performance requires plants to balance between the benefits and costs of shade avoidance. Too little shade avoidance may result in being outcompeted. But too much shade avoidance may also be detrimental, which is evident from the frequently observed height convergence in plant communities: plants maintain similar height

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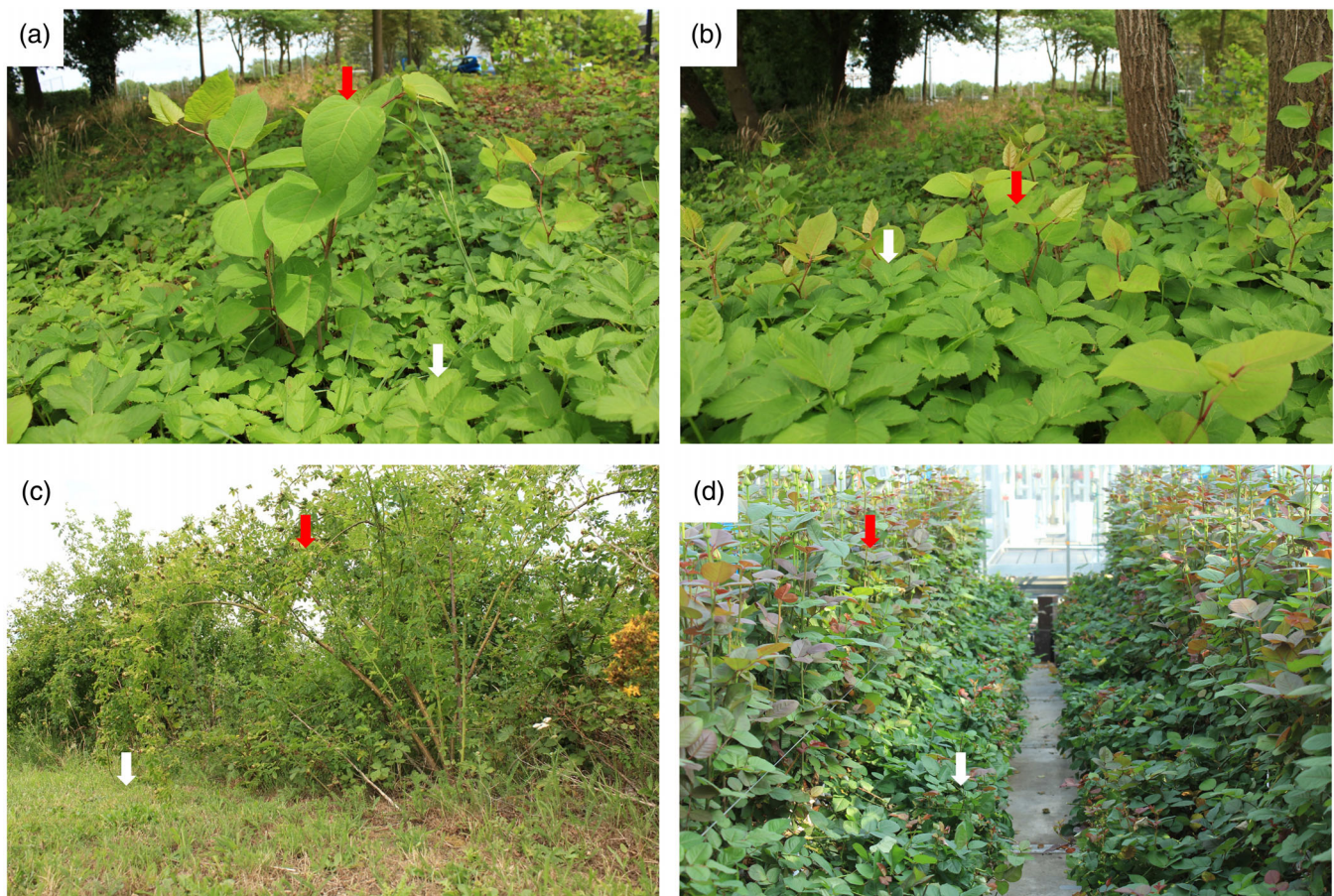
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with their neighbours even when they are able to grow taller for more light capture (Vermeulen, Anten, Schieving, Werger, & During, 2008). This involves regulations by both light signals and mechanical stimuli (Nagashima & Hikosaka, 2012). Maintaining similar height enables plants to avoid overtopping and being exposed to stronger winds than their neighbours, and thus lowers the risk of stem buckling (Nagashima & Hikosaka, 2011). Then, how should plants interpret light signals from below and respond to such signals appropriately?

## 2.1 | Light signals from smaller neighbours that can grow tall: Better to respond

Light signals perceived by a plant from below may be given off by smaller neighbours that have the potential to grow tall and even outgrow the plant (Figure 1a, b). This can happen between different species, as well as between the same species. For example, in tall-grass meadows, C3 plants occupy higher canopy strata in spring,

while C4 grasses are initially shorter but become dominant in summer (Anten & Hirose, 1999). Similar dynamics tend to occur during forest succession where later successional species emerge at some earlier stage as initially smaller individuals and eventually take over. In mono-species stands, light signals from below could be caused by differences in timing of seed emergence; the later-emerging plant is smaller than the earlier-emerging one at the beginning but can potentially grow taller if it grows on a more favourable spot. In such cases, light signals from below are reliable cues for light competition. Showing shade-avoidance responses upon perception of signals from below could enable plants to better compete with neighbours in the future and capture as much light as possible. The benefits of shade avoidance, however, would depend on plant developmental stages. At later stages of a growth cycle, shade-avoidance responses may not be so beneficial as light capture is not very important for fitness anymore. In contrast, if plants are still in a stage where light capture is crucial for fitness, it is better for plants to respond to light signals from below by shade avoidance. This is extremely important when neighbours have a genetically determined large size or when



**FIGURE 1** Examples of situations where light signals from below are involved. A,B: *Reynoutria japonica* (indicated by red arrows) grows with *Aegopodium podagraria* (indicated by white arrows) that is initially small (a) but can potentially grow tall at its later developmental stage (b). (c) *Rosa rubiginosa* (indicated by red arrow) grows with *Hypochaeris glabra* (indicated by white arrow) that has inherently short stature. (d) Greenhouse roses (*Rosa hybrida*) with complex canopy structure consisting of upper (indicated by red arrow) and lower (indicated by white arrow) canopy parts

they are very strong shade-avoiders, as plants would likely lose light competition when such neighbours grow tall. Hence, timely responding to signals from below when neighbours are still small allows plants to maximize light capture before neighbours outgrow and shade those plants.

## 2.2 | Light signals from smaller neighbours that stay small: Better to ignore

Plants may also interact with neighbours that have inherently shorter stature (Figure 1c). For instance, in many forest and agroforestry systems, adult trees or large woody species interact with smaller herbaceous plants or grasses. Although such neighbours also affect the surrounding light environment by absorbing and reflecting light, they are not real light competitors. This means light signals from such smaller neighbours are not reliable cues for light competition. Responding to such signals by shade avoidance is unnecessary and may even be detrimental, in the sense that resource, mechanical or hydrological costs incurred are not compensated by improved light acquisition. Hence, when neighbours are staying small and non-competitive, it is better for plants to not respond to light signals from below and avoid unnecessary shade-avoidance responses.

Plants may avoid unnecessary responses through a feedback whereby plants allocate resources to competitive responses only when they lead to continuous benefits (Novoplansky, 2009). Thus, plants may initially show shade-avoidance responses to light signals from below regardless of the type of neighbours, but only sustain such responses when continuously avoiding shade is required. For instances, shade-induced petiole and internode elongation will be stronger when these responses improve leaf placement and result in enhanced light harvesting (Leefflang, During, & Werger, 1998; Weijschedé, Martinková, De Kroon, & Huber, 2006). The rate of internode elongation also differs depending on plant size (e.g., small weeds vs. medium-sized soybean or large maize plants, Weinig, 2000) or on vertical growth rate (Vermeulen et al., 2008) of neighbours. When growing with smaller neighbours that stay small, plants may respond to light signals from below at the beginning but may not respond to such signals later on when responses do not lead to benefits in light capture.

## 2.3 | Light signals from lower parts of the same plant: Better to optimize

For plants with a complex canopy structure, light signals from below may be generated by lower parts of the plant's own canopy, that is, self-signals (Figure 1d). Competition within the same plant could be ecologically and evolutionarily costly and potentially damaging (Novoplansky, 2009). When light signals from below are self-signals, it is better for plants to adopt a growth strategy that reduces self-competition to optimize canopy performance. In greenhouse rose

systems, lower parts of the canopy reflect substantial amounts of far-red and thus reduce R:FR in light reflected from below; this signal was shown to induce steeper leaf angles in the upper canopy, which allowed more light to penetrate to lower canopy and enhances whole-canopy photosynthesis (Zhang et al., 2020). It is not yet clear whether such canopy optimization induced by light signals from below is a general phenomenon in other situations than in greenhouse rose systems. Light-mediated canopy optimization is generally found to be induced by light signals reflected from horizontal and is genotype-dependent (Crepé & Casal, 2015; Maddonni, Otegui, Andrieu, Chelle, & Casal, 2002; Pereira, Sadras, Batista, Casal, & Hall, 2017). Nevertheless, if optimization induced by light signals from below results in increased canopy performance, such a response would likely be a general response in most plant species.

A similar situation as self-interaction here is that plants grow with kin neighbours. Plants may grow with a kin neighbour that is initially small due to late emergence, causing light signals from below. In this case, light signals from below can be regarded as self-signals as well, and responses to such signals should reduce competition with kin and increase group performance. *Arabidopsis* plants exhibited less competitive responses to light signals when interacting with kin than with non-kin (Crepé & Casal, 2015). Such kin recognition involves phenotype matching by which individuals may be able to discriminate kin neighbours based on their phenotypic and genetic similarities (Lacy & Sherman, 1983). As kin plants are genetically linked and thus have similar architecture, light reflected by kin plants shows a similar profile that enables indirect kin recognition (Crepé & Casal, 2015). However, if a kin neighbour is smaller due to late emergence, plants would likely fail in phenotype matching via light cues. In this case, plants may still recognise kin by root signalling (Chen, Doring, & Anten, 2012), and crosstalk between aboveground- and belowground cues may enable plants to show less competitive responses to light signals from below caused by smaller kin neighbours.

## 2.4 | Can plants tailor their response to the nature of their neighbours?

It is clear that optimal plant responses to light signals from below depend on the origin of the signal. In case light signals from below come from potential light competitors, showing shade-avoidance responses are likely beneficial for plant performance. Otherwise, plants should either ignore the signal or adopt a strategy of canopy optimization. This requires plants to be able to discriminate the nature of vegetation that produces the light signals from below, for example, self- versus nonself-signal, or a signal caused by potential light competitors vs. non-competitive neighbours. It is unlikely that plants can identify the nature of their neighbours only by light signals from below. Plants may however be able to tailor their response to light signals from below by combining their message with other types of signals.

First, physical connections between plant parts may be an important signal for plants to discriminate self- and nonself-signals. Lower

plant parts that cause light signals are physically connected with upper plant parts, whereas independent neighbour plants are not physically connected (Zhang et al., 2020). Second, root signals (e.g., exudates, see review by Chen et al., 2012) and/or volatiles (Karban, Yang, & Edwards, 2014) may enable plants to determine the genetic relatedness of a neighbour. Third, the way light signals change over time may provide information on the nature of neighbours. Signals from neighbours that remain short may simply dilute over time as the focal plant grows but the neighbour does not (i.e., the height difference between focal plant and neighbour becomes larger). If neighbours grow taller during their development, direction and strength of light signals caused by those neighbours also change dynamically. The dynamics of light signals integrated over a time period may provide information for plants to tailor their responses to neighbours. Last, plants may have adopted a given response to light signals from below through natural selection (Dudley & Schmitt, 1995). For instance, if in the habitat of a plant, light signals from below are predominantly from non-self neighbours that do not pose a competitive threat, over generations such plants may evolve to not respond to light signals from below. There are many studies on divergent evolution of shade avoidance, which shows differentiation in plasticity to low R:FR between ecotypes from different shade habitats (Anten et al., 2009; Donohue, Messiqua, Pyle, Heschel, & Schmitt, 2000; Dudley & Schmitt, 1995; Huber et al., 2004). Similarly, plant responses to light signals from below may also differ between ecotypes.

### 3 | THE RELEVANCE OF LIGHT SIGNALS FROM BELOW IN CROP SYSTEMS

Light signals from below in crop systems could result from coexistence of weeds (in weed-infested systems, Ballaré & Casal, 2000), larger crops inter-planted with other smaller ones (in intercropping systems, Li et al., 2020), manipulations of canopy structure (e.g., shoot bending in cut-rose production, Ohkawa & Suematsu, 1997), the use of artificial lighting in the greenhouse (e.g., inter-lighting, Trouwborst, Oosterkamp, Hogewoning, Harbinson, & van Ieperen, 2010), and the application of soil mulches or ground covers in many agricultural and horticultural systems (Decoteau, Kasperbauer, Daniels, & Hunt, 1988; Decoteau, Kasperbauer, & Hunt, 1990; Kasperbauer, 1994). To optimize crop production in these systems, one cannot ignore the consequences of responding to light signals from below.

Ideal crop responses to light signals from below depend on the type of crop systems and should either lead to suppression or cooperation. When light signals from below are caused by weeds, under-sown species, mulches, other ground covers, or any object that does not contribute to yield production, ideal crop responses to such signals should enable crop plants to capture as much as possible light and prevent light to penetrate to weeds or ground. This suppresses weed development and reduces waste of light energy. Such responses of maximizing light capture are comparable with competitive responses described in the previous section, but only some of the competitive responses are desirable in crop systems. In general, responses that enhance leaf

growth for higher light capture are desirable (e.g., higher shoot:root ratio) in crop systems, whereas responses that aim at increasing vertical growth (e.g., increasing internode length and leaf angles) are less favourable, as in this case, putting leaves at higher positions hardly brings benefits in light capture of the crop and may even entail costs (e.g., crop lodging). However, competitive responses diverting energy for resource harvesting may come at the cost of seed production, which is not favourable for crops aiming at grain yield. Hence, crop plant responses should ideally be such that the distribution of light within the crop canopy is optimally efficient but hardly any light passes through to the soil, considering the trade-off between allocating resource for light harvesting versus seed production.

For crop systems with a heterogeneous canopy structure, light signals from below could be caused by lower parts of the canopy of the crop stand. The lower canopy could be either a lower part of the same plant, or a lower part of other plants belonging to the same genotype, or smaller crops of an intercropping system. In such cases, desirable crop responses should lead to cooperation between different plant parts or between plants and neighbours to optimize canopy performance. In an intercropping system, there are two or more species with different statures coexisting for the whole or part of the growth cycle (Li et al., 2020). Complementary traits of different species are important for maximizing resource-use efficiency (Duchene, Vian, & Celette, 2017). To maximize light-use efficiency of an intercropping system, it is important that the large crop cooperates with the small crop. In this regard, ideal crop responses to light signals from below should improve light distribution in the whole system, even if this may require reducing light capture by large crops to allow more light to penetrate to small crops.

Generally, the objective in agriculture is to maximize community level performance of the crop. Given the potential conflict between individual- and group performance, the idea of selecting genotypes with high group performance is gaining interest (Anten & Vermeulen, 2016; Denison, Kiers, & West, 2003; Weiner, 2019). This would favour selection for crop types that respond to light signals from below in a way that optimizes performance of the whole crop system. This is especially important for crop systems with mixed species (e.g., intercropping and agroforestry systems) where size differences between individuals tend to be larger. In terms of crop-weed interactions, selection for responses to light signals from below depends on specific situations. If there is high weed pressure and strong restriction for using herbicides, and thus weed suppression becomes the breeding objective, trait selection should go for competitive responses that maximize light capture. In case seed production would be the main breeding objective, responses to light signals from below that divert energy to resource harvesting would not be favourable, and selection should aim at balancing weed suppression and seed production.

### 4 | FUTURE DIRECTIONS

The light environment in plant canopies is highly heterogeneous and entails many light signals for plants to detect their neighbours.

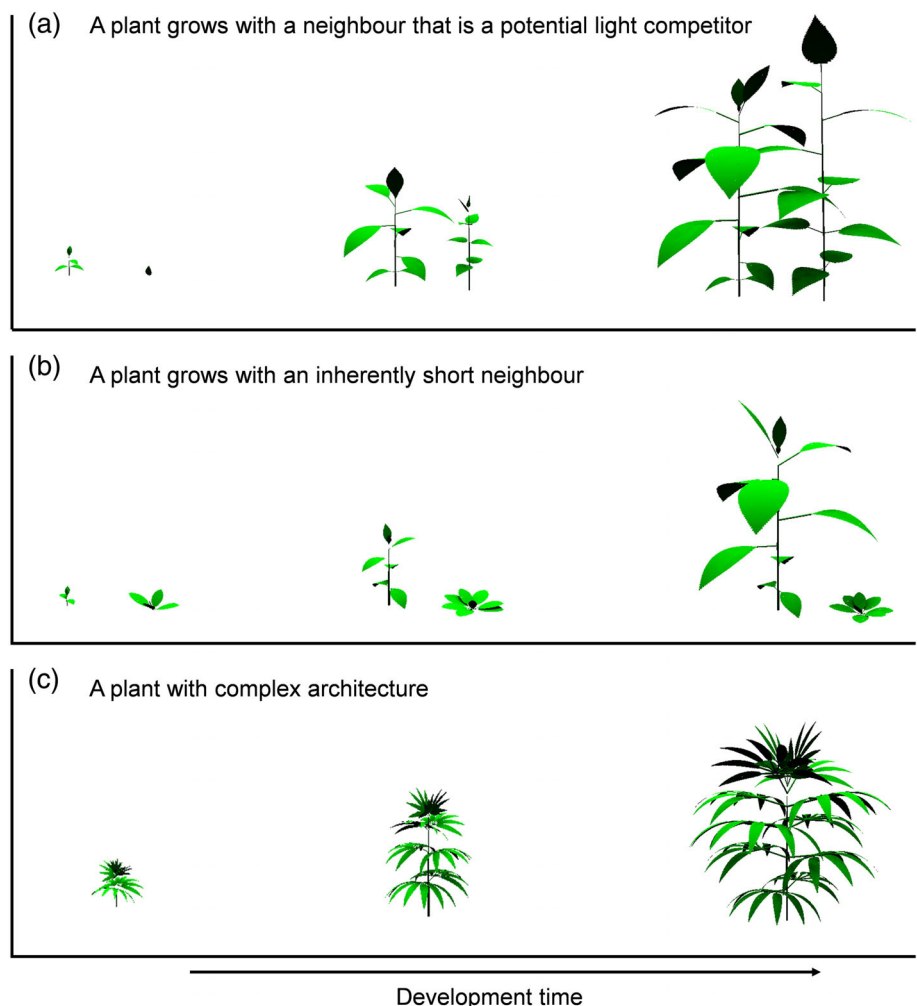
Although neighbours that are tall are often a strong competitor for light, it is time to look downwards to small neighbours that reflect light upwards. Plant responses to light signals from below result in different consequences depending on the origin of the signal. We argue that (a) when light signals from below are given off by small neighbours that can grow tall and are thus potential competitors, optimal plant responses should lead to competition, (b) when light signals from below come from small neighbours that stay small, it is better for plants to not respond to such signals, and (c) when light signals are from lower parts of the same canopy or ramets from the same genetic individual, optimal responses should lead to canopy optimization. A high performing crop, however, should show suppressive responses to signals from below when they are from objects that do not contribute to yield production, but should be cooperative when signals from below are given off by lower canopy that is part of the crop system.

#### 4.1 | Linking light models to plant models to quantify light-plant-plant interactions

Quantifying the performance value (e.g., implications for fitness or crop yield) of a give response to directional light signals, such as light

signals from below, is highly challenging. Plants are sensitive to both strength and direction of light signals that themselves are the result of a complex interplay between light and plant architecture. This entails a complex feedback whereby light signals induce changes in plant architecture, which in turn affects the strength and direction of these light signals. Unrevealing these dynamics thus requires a modelling approach that captures both physiological drivers of plant responses and 3D representations of light distribution and plant architecture. Functional-structural plant (FSP) models simulate plant growth and development over time in three dimensions as a function of underlying processes driven by environmental variables like light, water and nutrients (Vos et al., 2010). Given the explicitly described plant architecture in 3D, FSP models can capture any difference between individual plants and different parts within a plant and simulate their interactions (Figure 2). Spatial variation in environmental conditions can be captured by such models, as well as their feedback relationships with plant growth.

To quantify plant responses to light signals from below, an FSP model should at least include two components: (a) a light model that simulates the 3D distribution of light intensity and spectrum affected by the optical properties of any objects in the simulated scene, and (b) a plant model that simulates plant growth, development and



**FIGURE 2** Virtual plants simulated by a functional-structural plant model (Evers & Bastiaans, 2016). (a) A hypothetical dicot species grows with sunflower that is initially small, but can grow tall and even outgrow the dicot species at later developmental stage. (b) A hypothetical dicot species grows with *Arabidopsis* that stays small during its life cycle. (c) A hemp plant with complex architecture which may entail light signals from lower parts of its own foliage [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

architectural changes regulated by light signals perceived by individual plant parts. Thus, any feedbacks between changes in the strength of light signals from different directions and plant responses to those light signals can be captured. Recently, light models that allow the representation of a full spectrum instead of monochromatic or white light are developed and implemented into FSP models (Henke & Buck-Sorlin, 2017; Hitz, Henke, Graeff-Hönninger, & Munz, 2019). With virtual light sensors in the FSP model, light intensity and spectral composition of light from different directions can be quantified (Hitz et al., 2019; Zhang et al., 2020). However, plant responses to light signals as a function of the origin of the signal are not yet included in FSP models (Zhang et al., 2020), as there are still several gaps in our understanding of the perception and integration of, and responses to light signals from different directions, especially from below. These knowledge gaps (discussed below) should be addressed to design more complete modelling tools that can be used to expand our understanding of light-mediated plant interactions.

## 4.2 | Knowledge gaps in light-mediated plant interactions

First, which plant tissue is sensitive to light signals from below? Plants need to detect light signals at the optimal location to allow timely responses. For example, *Arabidopsis* plants first detect low R:FR at the leaf tips, which optimizes the timing of leaf movement in response to neighbours and prevent hyponasty induced by self-shading (Pantazopoulou et al., 2017). It is possible that only specific organs or part of the organ may be sensitive to signals from below to enable appropriate responses.

Second, how does the plant integrate light signals from various directions with different strengths? No matter which organ or part of the organ is responsible for detecting light signals from below, it will likely receive additional light signals from other directions as well, which may even contain a different message on competition. How plants perceive the spatial distribution of light signals in 3D and integrate their embedded information is largely unknown. Plants may either respond to an average signal from all directions, or respond to the strongest of the incoming signal, or separately respond to signals from different directions. Some plant responses are induced by local signal perception, whereas other responses are induced by integrating signals from the whole plant (Domagalska & Leyser, 2011; Pantazopoulou et al., 2017). How plants integrate light signals from all directions and what role light signals from below may play in the integration is a major unsolved question.

Third, what type of responses can be induced by signals from below? Some early studies revealed that the type of responses induced by low R:FR reflected upwards, such as increasing internode length and shoot: root ratio, seem to be typical shade-avoidance responses that can also be induced by low R:FR from other directions (Decoteau et al., 1988; Kasperbauer, 1994; Rajcan et al., 2004). However, we found that low R:FR from above induced both stem elongation and steeper leaf angle in rose, whereas low R:FR from below only

induced steeper leaf angle while internode length was not affected (Zhang et al., 2020; Zhang, van Westreenen, Anten, Evers, & Marcelis, 2019). Given the contrasting consequences of responding to light signals from below in different situations, the type of responses may also differ between specific situations.

Finally, do light signals from below predict competition for other resources than light? A small neighbour that causes light signals from below may not be a light competitor aboveground, but may still pose a threat for resource competition belowground. Given that plants use light signals as an indicator of neighbour proximity, those light signals may also play an important role in shaping plant behaviour belowground (Gundel, Pierik, Mommer, & Ballaré, 2014). Phytochromes are found to regulate belowground processes such as phosphorus uptake and lateral root development (Sakuraba et al., 2018; van Gelderen et al., 2018). Whether and how plants use light signals from below to regulate belowground competition, especially when such signals do not predict light competition aboveground, is another important piece of the puzzle in terms of light-mediated plant interactions.

In conclusion, light signals from below require attention if the role of plant responses to competition and the ecological or agronomical consequences are to be fully understood.

## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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