Review Article

Canopy Light Signals and Crop Yield in Sickness and in Health

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Crop management decisions such as sowing density, row distance and orientation, choice of cultivar, and weed control define the architecture of the canopy, which in turn affects the light environment experienced by crop plants. Phytochromes, cryptochromes, phototropins, and the UV-B photoreceptor UVR8 are sensory photoreceptors able to perceive specific light signals that provide information about the dynamic status of canopy architecture. These signals include the low irradiance (indicating that not all the effects of irradiance occur via photosynthesis) and low red/far-red ratio typical of dense stands. The simulation of selected signals of canopy shade light and/or the analysis of photoreceptor mutants have revealed that canopy light signals exert significant influence on plant performance. The main effects of the photoreceptors include the control of (a) the number and position of the leaves and their consequent capacity to intercept light, via changes in stem height, leaf orientation, and branching; (b) the photosynthetic capacity of green tissues, via stomatal and nonstomatic actions; (c) the investment of captured resources into harvestable organs; and (d) the plant defences against herbivores and pathogens. Several of the effects of canopy shade-light signals appear to be negative for yield and pose the question of whether breeding and selection have optimised the magnitude of these responses in crops.

1. Light Signals in Crops

1.1. Light as a Source of Energy and Light as a Signal. The biomass produced by a crop can be accounted for by the product of three variables: the incident radiation, the efficiency to intercept the incident radiation, and radiation use efficiency (the relationship between plant dry matter and radiation intercepted), integrated for the duration of the growth cycle [1]. In turn, the yield of grain crops can be accounted for by the product of the biomass by the harvest index. Light has fundamental importance in crop yield due to its function in photosynthesis. The aim of this paper is to present an overview of the experimental evidence that supports the often neglected contribution of light as a signal (i.e., as a source of information) in crop yield. A light signal is a variable aspect of the light environment, perceived by specific sensory receptors, which affects selected plant traits. In this sense, while the action of light as a source of energy is explicit among the aforementioned components involved in biomass and yield generation, implicit in the other components there are effects of light as a source of information about the environment.

Grain crops experience two major groups of light signals: (a) light signals related to season and (b) light signals related to the status of the canopy. The first category is relatively simple; it includes photoperiod. Photoperiod changes with time of the year and also with latitude. Therefore, the photoperiods at which a crop is exposed will depend on sowing date and location, but they will change during the course of the growth period. The second category is somewhat more complex, as it includes changes in irradiance and spectral composition both in time and space. In this paper, we will focus on canopy light signals.

1.2. Plant Sensory Photoreceptors. We know the major photoreceptors present in plants, and therefore we can use the photoreceptors to unequivocally define signals; that is, there is no point in enumerating all the aspects of the light affected by the canopy, only those perceived by photoreceptors are justified. Plants have a diverse array of sensory photoreceptors that are involved (or at least predicted to be involved) in the perception of canopy light signals [2, 3]: phytochromes [4], cryptochromes [5], phototropins [6], and UVR8 [7] (Figure 1). The discovery of the UV-B photoreceptor UVR8
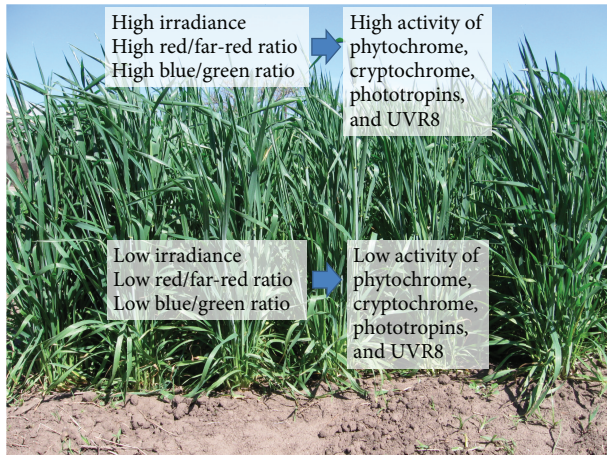
FIGURE 1: Phytochrome, cryptochrome, phototropin and the UV-B photoreceptor UVR8 perceive signals of the canopy light environment. The light incident on the canopy has high irradiance, high red/far-red ratio and high blue/green ratio. As light penetrates within the canopy, these values become reduced and the activity of the photoreceptors is also reduced.

is recent [8], and its potential role in plant adjustment to the degree of canopy shade is largely speculative. The function of a photoreceptor is to connect specific light signals to selected physiological responses via a signal transduction network. Phytochrome, cryptochrome, and phototropin molecules have an apoprotein and one or two chromophores, which are involved in light capture. In the case of UVR8, the UV-B signal is captured by selected amino acids.

Some of the photoreceptors listed above are not just a single photoreceptor but a family with several members encoded by different genes. The phytochrome apoproteins are encoded by a small family of genes involving three main clades: *PHYA*, *PHYB*, and *PHYC* [9]. In some species, the *PHYB* lineage includes different members. For instance, in *Arabidopsis thaliana*, the *PHYB* lineage includes *PHYB*, *PHYD*, and *PHYE*, and therefore, this species has five phytochromes (phytochromes A, B, C, D, and E). In tomato, the *PHYB* clade includes *PHYB*, *PHYB2*, and *PHYE*, and this species has five phytochromes (phytochromes A, B1, B2, E, and F or C) [10]. In grasses, the phytochrome gene family contains three members—*PHYA*, *PHYB*, and *PHYC*—[11, 12]. However, in maize (e.g., inbred B73), the *PHYA*, *PHYB*, and *PHYC* genes are duplicated, indicating the presence of six potentially functional phytochrome genes in this species: *PHYA1*, *PHYB1*, and *PHYC1* genes on chromosome 1, PHYA2 and PHYC2 on chromosome 5S, and *PHYB2* on chromosome 9L [13]. Maize phytochrome duplicate genes (homeologs) map to syntenic regions of the genome suggesting that these gene duplications were generated as a consequence of an ancient tetraploid event [13]. Plants have two types of cryptochromes: cryptochrome 1 and cryptochrome 2. In *Arabidopsis thaliana*, there are two cryptochrome genes: *CRY1* and *CRY2*. However, in soybean, there are six cryptochromes: four cryptochrome 1 (*GmCRY1a* to *GmCRY1d*) and two cryptochrome 2 (*GmCRY2a* and *GmCRY2b*) [14].

This pattern can be accounted for by the paleotetraploid nature of soybean [14]. These are only some examples of the wider available knowledge concerning different photoreceptor families, which should help those who are not experts in the field to understand the literature on the species of their own interest.

If we consider the occurrence of different types (families) of photoreceptors and of different members within a photoreceptor family, it is clear that plants have a surprising multiplicity of photoreceptors. There is some degree of redundancy but also functional specificity. Photoreceptors connect specific light signals to selected physiological responses via signal transduction networks; different photoreceptors perceive different signals and/or control different processes. For instance, the action of phytochromes, cryptochromes, phototropins, and UVR8 is irradiance dependent; therefore, in principle, all these photoreceptors could perceive changes in irradiance associated to the degree of canopy shade (Figure 1). In some cases, whether the range of irradiance dependence of the photoreceptor matches the range of canopy-induced changes in irradiance remains to be elucidated, but given the daily variations in incoming radiation it is likely that at some point the different degrees of canopy shade will affect irradiance in the range of photoreceptor sensitivity. Plants respond to the range of canopy red/far-red ratios (see below), with fine sensitivity to small drops beneath the ratios provided by unfiltered sunlight in open places [15]. Based on the analysis of mutants in *Brassica rapa* [16], *Arabidopsis thaliana* [17], maize [18], sorghum [19], rice [20], and barley [21], it is possible to conclude that the responses to the red/far-red ratio is mediated mainly by phytochrome B. In some cases, various members of the phytochrome B clade contribute to mediate responses to the red/far-red ratio [22]. Phytochrome A also participates in the control of plant responses to canopy shade but apparently by perceiving irradiance, rather than red/far-red ratio [3, 23]. Phytochrome can perceive the red/far-red ratio because it has two forms: Pr, with maximum absorbance at 660 nm (i.e., red light), and Pfr, with maximum absorbance at 730 nm (i.e., far-red light). Upon excitation, Pr is photo-transformed to Pfr and Pfr is photo-transformed to Pr. Therefore, under natural radiation, the two forms reach a steady state that favours Pfr if the red/far-red ratio is high (open places) and Pr if the ratio is low (dense canopies). Only the Pfr form is biologically active, and therefore, phytochrome activity depends on the ratio between red and far-red light. These features correspond to all phytochromes, but in the case of phytochrome A, there are other processes [24] that make of it a good sensor of irradiance but not of red/far-red ratio.

At the other end of the function of photoreceptors are the target processes that they control, and at this point there is also redundancy and specificity. For instance, phytochrome B is the most important in shade-avoidance responses, cryptochromes are important to regulate the investment in photoprotective mechanisms, phototropins are crucial for the rapid and reversible positional adjustments of chloroplasts and leaves, and UVR8 is important in the control of UV-B screens [3]. In maize, the analysis of mutants of *PHYB1* or *PHYB2* genes has revealed some degree of subfunctionalization of these phytochromes because they show some differences
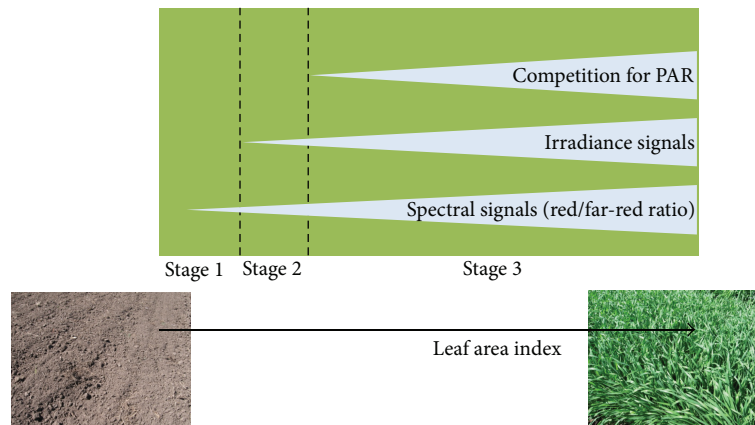
FIGURE 2: Intensity of the canopy shade-light signals and competition for PAR as affected by leaf area index. Three stages are distinguished: at low leaf area indexes (typically lower than 1), stage 1 is characterised by the presence of light signals involving spectral changes (mainly a reduction in the red/far-red ratio). At stage 2, the leaves shade the stem of neighbours, which receive low red/far-red ratios and low irradiance, but leaves do not shade mutually. At stage 3, mutual shading among leaves is established, and therefore the plants receive light signals (both spectral and irradiance signals) and compete for PAR.

in their respective contribution to different light responses [18].

1.3. Canopy Light Signals Are Dynamic. Canopy light signals depend on light attenuation patterns within the canopy and on the optical properties of the leaves. Canopy light attenuation depends on canopy architecture, which can be defined as the size, shape, and orientation of shoot components [25]. The leaf-area index, the arrangement of the plants within the crop (i.e., the relative distance between plants within the rows and between rows, the orientation of rows), and the more erectophile or planophile growth habit of the plants affect light attenuation within canopies and the degree of mutual shading among plants. The photosynthetic pigments (chlorophyll, carotenoids) present in leaves and other green organs absorb a large proportion of the photosynthetically active radiation (PAR, i.e., the radiation between 400 and 700 nm) that they intercept, whereas a small proportion, enriched in the green waveband, is transmitted and reflected. Wavebands out of the 400–700 nm range are also important in the generation of canopy light signals and green leaves absorb strongly in the UV range but much weakly in the far-red range (700–800 nm). Canopy signals of increasing intensity result from two types of changes of the light environment that can be perceived by sensory photoreceptors: (a) the attenuation of irradiance and (b) the change in spectral composition. The latter involves a decrease in the red/far-red ratio and a decrease of blue/green ratio. Phytochrome, cryptochrome, and UVR8 perceive changes in irradiance levels (mainly in the red plus far-red, blue plus UV-A, and UV-B regions of the spectrum, resp.). Phytochrome B perceives the red/far-red ratio [16–21]. Cryptochromes apparently also perceive the blue/green ratio [23, 26, 27]. Very often, plant responses to irradiance (in particular plant responses to PAR) are considered to be mediated by photosynthesis, and only the response to red/far-red is conceptually assigned the category of informational signals. This idea is not entirely correct

because the effects of irradiance can in part be mediated by photosensory receptors.

Figure 2 shows a diagrammatic representation of the dynamics of light signals and competition for PAR in a growing canopy, where three main stages can be distinguished. Canopy light signals anticipate competition for PAR as, at the first stage, before mutual shading among plants is established, selective reflection on green organs alters the spectral distribution of the light (mainly the red/far-red ratio) of the vertically oriented organs (e.g., stems). At this stage, plants surrounded by sparse neighbours receive more far-red light than fully isolated plans [15, 28–30]. At the second stage, the upper leaves project their shade on the stems of neighbours, and therefore they do not seriously affect the ability of neighbour leaves to capture PAR but canopy light signals become more intense. At the third stage, competition for PAR is established when there is mutual shading among leaves. The red/far-red ratio is in itself a very reliable signal of the status of a canopy [31]. In wheat, for instance, the red/far-red ratio measured at the base of the canopy decreases almost linearly with the leaf area index between 0 and 10 [32].

1.4. Canopy Light Signals in the Context of Other Effects of Neighbours. Canopy architecture affects different aspects of the environment, which go beyond changes in the light environment itself to include, for instance, the impact of wind (Figure 3). Actually, differences in canopy architecture can also be associated to differences in the availability of soil resources (water, nutrients). In turn, each one of these aspects of the environment can affect diverse physiological processes (Figure 3). For instance, if we focus on the light environment, increasing mutual shading in more developed or more densely sown crop canopies or as a result of the presence of weeds increases the magnitude of shade-light signals, enhances the competition for PAR, reduces the chances of damage caused either by excessive light absorption by photosynthetic pigments or by UV radiation, lowers plant
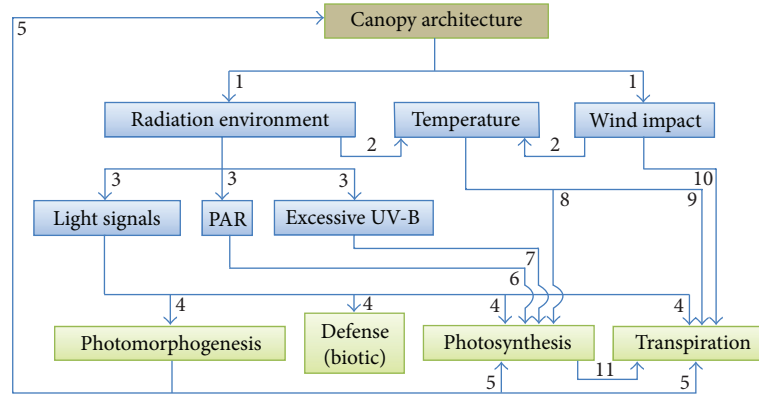
FIGURE 3: Canopy architecture affects multiple aspects of the environment experienced by the shoot, which in turn impact on multiple aspects of plant physiology. Environmental features are shown in blue, and plant processes are shown in green. Arrowheads indicate the direction of the effect. The model represents a simplification of the real world. Canopy architecture affects the sunlight radiation and wind impact received by each plant (1); these features of the environment in turn affect tissue temperature (2). The radiation environment involves three functional categories: the light signals (perceived by sensory receptors), PAR, and damaging UV-B (3). These categories overlap in terms of spectral wavebands (e.g., some wavebands are active both photosynthetically and as a signal). Light signals control plant form (photomorphogenesis), the status of defences against pathogens and herbivores, and stomatal aperture, which modulates the rates of carbon and water vapour exchange (photosynthesis, respiration) (4). Photosynthesis and transpiration are also affected by photomorphogenesis (e.g., via changes in in stomatal density) (5). The altered photomorphogenesis also modifies canopy architecture (e.g., by changes in stem height, leaf position, etc.) (5). Both PAR (as the source of energy) (6) and UV-B (via its damaging effect) (7) affect photosynthesis, which also depends on temperature (8). Temperature (9), wind impact (10), and photosynthesis (via effects on carbon dioxide concentration and stomatal conductance) (11) affect transpiration rates.

tissue temperature by lowering the radiation load, and so forth (Figure 3).

Given the complex modification of the environment caused by increasing canopy density, estimating the exact quantitative contribution of the light signals perceived by photoreceptors can be cumbersome. Ideally, achieving this goal would require independent simulation of all the changes and their combinations, which is impossible at least with current techniques. However, the literature offers a very wide list of examples, where even suboptimal light signals cause significant effects on plant traits, demonstrating that light signals play a key role in crop performance. For a more detailed analysis of the methods to simulate canopy shade signals, we refer to previous publications [2, 33]. However, some discussion is useful here to illustrate the point. Very often, the low red/far-red ratios of canopy shade are simulated by adding varying amounts of far-red light to a common source of PAR. This procedure prevents confounding effects via photosynthesis, but it does not simulate the lower irradiance signal also perceived by photoreceptors under dense canopies. Rather, increasing far-red lowers the red/far-red ratio, but it increases irradiance, and this can generate a signal typical of open, rather than shaded places, partially counteracting the impact of lower red/far-red.

1.5. Plant Responses to Canopy Light Signals. Canopy light signals perceived by sensory photoreceptors control several aspects of plant morphology and physiology. Shade signals initiate the so-called shade-avoidance responses (e.g., increased stem growth) that tend to alleviate the degree of shade. In addition, open-canopy versus shade signals perceived by sensory photoreceptors, also help to acclimate plants to the conditions that they cannot avoid. These responses are often context dependent. There is inter- and intraspecific genetic variation and other aspects of the environment (e.g., temperature and PAR) can strongly interact with the signals perceived by photoreceptors.

2. Stem Morphology and Physiology in Response to Canopy Light Signals

2.1. Canopy Shade-Light Signals Promote Stem Growth, but Not Always. One of the most obvious and widespread responses to canopy shade-light signals is the promotion of stem growth. In pioneer phytochrome studies, Downs et al. [34] used brief pulses of red or far-red light given at the end of the white light photoperiod (the so-called end-of-day light pulses) to, respectively, establish high or low levels of the active form of phytochrome (Pfr) and observed stem promotion in end-of-day far-red light-treated beans. The same methodology reported similar results in numerous species including tobacco (*Nicotiana tabacum*) [35] and tomato (*Solanum lycopersicon*) [36]. Adding far-red light to a source of white light to lower the daytime red/far-red ratio keeping similar levels of PAR has also been shown to promote the stem in many species, including mustard (*Sinapis alba*) [37], *Chenopodium album* [38], and cucumber (*Cucumis sativus*) [39]. Lowering only the red/far-red ratio reaching the stem (i.e., keeping the leaves at a high red/far-red ratio) either by adding far-red light or by reducing red light is effective to promote stem growth in *Sinapis alba* [37], *Datura ferox* [40], and sunflower (*Helianthus annuus*) [41], but the response is more persistent if also the leaves receive a low red/far-red ratio [42]. Stem growth also responds to selective reductions

in irradiance in the blue light or red plus far-red light regions of the spectrum [40, 43, 44], which are signals, respectively, perceived by cryptochromes and phytochromes.

Although the promotion of stem growth by shade-light signals is well documented, not all the species have this response. In wheat, low red/far-red ratios may promote the growth of the basal internodes [45]. Although this effect can be significant in relative terms, these internodes remain short and make little contribution to overall plant height. However, the extension of the uppermost internode (peduncle) is delayed (rather than accelerated) by low red/far-red ratios [45, 46].

Stem growth can in principle affect crop yield in different ways: the stem may compete for resources with other parts of the plant, including harvestable organs [47], shorter stems can be more resistant to lodging [48], shorter stems can impair light interception [49], and so forth.

2.2. Stem Length and Stem Dry Matter Accumulation.
In addition to increase stem length, low red/far-red ratios often increase stem dry matter accumulation [35, 50, 51], but this is not necessarily always the case. In mustard (*Sinapis alba* L.), low red/far-red ratios reaching only the stem (a signal typical of sparse canopies) increase stem length but not its dry weight [51]. When both the leaves and the stem of mustard plants are exposed to low red/far-red ratios, the stem does increase its dry weight [52], but this in part is caused by an increased capacity of the leaves to export carbon thanks to the higher activity of the sucrose-phosphate synthase [53]. The case is different in sunflower, where lowering the stem red/far-red ratio is enough to increase its dry weight proportionally to its length increment [51]. In the latter species, if stem extension is physically blocked, the stem recovery of labelled carbon fed to the leaves is also reduced, indicating that increased dry weight would be the consequence of increased stem extension growth [51].

Compared to the wildtype, in the *lh* mutant of cucumber (*Cucumis sativus*), deficient in phytochrome B, stem length is more strongly enhanced than stem dry matter accumulation, and therefore, the *lh* mutant shows a lower dry matter/length ratio and a lower diameter [54]. Anatomical inspection revealed reduced cell diameter, reduced area occupied by load bearing tissues, and reduced number and diameter of xylem vessels in the stem of the *lh* mutant [54]. In turn, these anatomical differences showed functional implications for the *lh* mutant, including reduced field survival due to stem susceptibility to wind impact and reduced stem water conductivity [54].

2.3. Stem Growth Direction.
Stem phototropism is a response that has been extensively investigated under controlled conditions but less considered in field experiments. The blue-light gradient is perceived by phototropin [55]. *Arabidopsis* mutants deficient in phototropin show reduced survival under dense canopies [56]. The red/far-red ratio of the canopy, perceived by phytochrome B, can condition the stem phototropic response [57]. The phototropic response would help to colonise patchy canopies by directing the foliage to less crowded areas [58].

2.4. The Stem Metabolome in Response to Canopy Light Signals.
In sunflower, many metabolites (including reducing sugars and cell-wall carbohydrates) conserve their stem concentration despite the growth promotion of this organ caused by low red/far-red ratios selectively applied to the stem. However, some metabolites do change their concentration in response to low red/far-red ratios [51]. The levels of sucrose, tetradecanoic acid, pentadecanoic acid, and octadecanoic acid decrease in the upper and lower sections of the first internode, while the levels of asparagine 3 and octadecanol decrease only in the upper section. Conversely, the levels of galacturonate, glutarate, saccharate, fructose, and inositol increase in the upper and lower sections of the internode in response to low red/far-red ratios, and the levels of glutamate, pyroglutamate, hexadecanol, and campesterol increase only in the lower section [51].

2.5. Mechanisms Involved in the Control of Stem Growth by Light.
The molecular and cellular mechanisms involved in the promotion of stem growth by shade-light signals have been reviewed recently [3] and are beyond the scope of this paper. However, a brief summary of the current models is informative. The proteins that bind DNA and modify the rate of transcription of the nearby genes are called transcription factors. Many signals modify different aspects of plant physiology by altering the activity of selected transcription factors. The active form (Pfr) of phytochrome B is able to bind different members of the bHLH transcription factors called PHYTOCHROME INTERACTING FACTORS (PIF) in the nucleus. Binding by phytochrome B causes PIF phosphorylation, reduces the ability of PIFs to bind their DNA targets, and causes the labelling for destruction of some members of the PIF family. The low red/far-red signal indicative of shade shifts the steady state of phytochrome B from the active to the inactive (Pr) form, which migrates to the cytoplasm. Released from the negative regulation imposed by Pfr, PIFs bind the promoter region of their target genes, which include auxin synthesis genes. The levels of auxin are increased and stem growth becomes promoted. Connected to this short and simple set of signalling events, there is a complex set of regulatory networks linking light signalling to other hormones such as gibberellins and brassinosteroids.

Despite recent advances in *Arabidopsis thaliana*, the knowledge is more scant in other species and there might be differences. For instance, rice PIF-like protein OsPIL1, which is phylogenetically related to *Arabidopsis* PIF4 and PIF5, promotes growth in rice as PIF4 and PIF5 do in *Arabidopsis*. However, OsPIL1 does not interact with rice phytochrome B and might not be involved in the response to canopy signals [59]. Conversely, OsPIL1 expression is inhibited under drought stress leading to reduced stature [59].

One of the key elements of the "Green Revolution" was the introduction of dwarfing genes. Reduced stem growth reduced the risk of lodging and allowed the incorporation of Nitrogen fertilisation to wheat plants. In addition, these plants with reduced stem growth divert a higher proportion of their photoassimilates to the spike, rather than to the stem. Wheat dwarfing genes were shown many years later to encode DELLA proteins [60]. DELLA proteins are present in

the nucleus, where they bind PIFs impeding their binding to DNA and therefore their ability to control transcription [61, 62]. In the presence of the growth-promoting hormone gibberellins, DELLAs are bound by a protein complex involving the activated receptor of gibberellins, and as a result of this, DELLAs become targeted for degradation [60]. DELLA degradation releases PIFs, which then can activate transcription of growth-promoting genes. The dwarfing genes introduced into elite wheat cultivars were mutant alleles of DELLA genes, which produce a mutant protein able to bind PIF but not recognised by the active receptor of gibberellins (the mutation specifically affects the domain of the DELLA proteins that is recognised by the receptor complex). Therefore, these mutant DELLA proteins arrest PIFs and growth even in the presence of gibberellins, causing dwarfism. Dwarfing alleles of DELLA genes reduce the responses to canopy shade signals in *Arabidopsis* [63].

2.6. The Energetic Cost of Enhanced Stem Growth in Response to Canopy Shade-Light Signals. The analysis of the stem-specific changes in the transcriptome of tomato plants transferred from white light to white light plus supplementary far-red light under controlled conditions revealed both rapid and persistent responses [64]. Not unexpectedly, given the strong promotion of stem growth by low red/far-red ratios, the treatment enhanced the expression of genes involved in auxin signalling and cell-wall carbohydrate metabolism. Noteworthy, low red/far red also reduced the expression of genes involved in flavonoid synthesis, isoprenoid metabolism, and dark reactions of photosynthesis. These changes in gene expression were reflected on stem-specific reductions in the levels of flavonoids (anthocyanin, quercetin, and kaempferol) and selected isoprenoid derivatives (chlorophyll and carotenoids) and in photosynthetic capacity. Changes in the levels of jasmonic acid could be involved in these responses. The rate of stem respiration was also strongly reduced in low red/far-red-treated plants. Therefore, by downsizing the stem photosynthetic apparatus and the levels of photoprotective pigments in response to shade-light signals, tomato plants reduce the energetic cost of shade avoidance responses [64]. This is important because shade-avoidance responses can coexist with limited availability of PAR due to mutual shading.

3. Branching in Response to Canopy Light Signals

3.1. Canopy Light Signals Reduce Branching. Low red/far-red ratios reduce tillering in cereals such as wheat [46, 65–67], barley [68], sorghum (*Sorghum bicolor*) [69], teosinte [70], and maize [71]. In maize, the effect is dependent on the cultivar [71]. A mutant of sorghum deficient in phytochrome B shows reduced bud outgrowth even under high red/far-red ratios [69]. Based on the analysis of spring wheat plants grown at three plant population densities with or without neutral shading, Evers et al. [67] have proposed that cessation of tillering is induced when the proportion of PAR intercepted by the canopy exceeds 40–45% and the red/far-red ratio is below 0.35–0.40. Similar responses to

low red/far-red ratios have been observed in forage grasses such as *Lolium multiflorum* [72]. The enrichment of red light beneath the canopy of a natural grasslands promoted tillering in *Paspalum dilatatum* and *Sporobolus indicus* plants [73]. Reduced branching in response to low red/far-red has also been reported for many eudicots, including tobacco [35], tomato [74], and *Trifolium repens* [75]. Tillering is important for grain yield in many crop conditions [76].

3.2. Mechanisms Involved in the Control of Tillering by Canopy Shade-Light Signals. Differences in tillering between maize (*Zea mays* sp. *mays*) and teosinte (*Zea mays* sp. *parviglumis*) can largely be accounted for by the higher (two-fold higher) expression of the *teosinte branched1* (*TB1*) gene in maize than in teosinte [77]. *TB1* encodes a putative basic helix-loop-helix transcription factor that represses the growth of axillary buds and enables the formation of female inflorescences [77]. In sorghum (*Sorghum bicolor*), supplementary far-red light represses bud outgrowth and promotes the expression of *TB1* in the buds [69]. The mutation of the gene encoding phytochrome B has the same consequence. These observations suggest a sequence of signalling events where low red/far-red ratios reduce phytochrome B activity and represses bud outgrowth by promoting the expression of *TB1*.

Another genetic variant in maize with defects in floral development and increased tiller number (six to seven compared to no tillers in the wildtype of the same genetic background) is the *grassy tillers1* (*gt1*) mutant [70]. The *GT1* gene encodes a transcription factor of the type named class I homeodomain leucine zipper (HD-Zip). This gene is expressed in shoot axillary buds, among other organs, and the protein can be found in the nucleus, as expected for a transcription factor [70]. Therefore, the GT1 protein is expected to act in the buds to repress their outgrowth; the *gt1* mutation releases this inhibition, increasing tillering. Teosinte and sorghum plants branch prolifically when grown without signals of neighbours. Lowering the red/far-red ratio promotes the expression of the *GT1* gene and lowers tillering in teosinte. A mutant of phytochrome B in sorghum shows enhanced expression of *GT1* and reduced tillering. Both, *TB1* and *GT1* are involved in the local control bud outgrowth and respond to red/far red. To investigate their functional relationship, the expression of each one of the two genes was investigated in plants mutant for the other. The expression of *TB1* was unaffected by the *gt1* mutation, but the expression of *GT1* was reduced in a *tb1* mutant compared to the wildtype [70]. Taken together, these observations suggest a model where low red/far-red ratios reduce the activity of phytochrome B favouring enhanced expression of *TB1*, which would lead to enhanced *GT1* expression and repression of bud outgrowth [70]. How phytochrome B controls *TB1* expression remains to be elucidated.

3.3. Tiller Death. In field experiments with wheat plants grown at different densities and with different Nitrogen availabilities, the start of tiller death was closely related to the red/far-red ratio reaching the base of the canopy, not to the PAR available per shoot or to Nitrogen levels. This result has been interpreted in terms of a critical red/far-red

ratio for the initiation of tiller death in winter wheat [78].

4. Leaf Morphology and Physiology in Response to Canopy Light Signals

4.1. Leaf Position in Response to Canopy Signals. Many crops are sown in rows with a short distance between contiguous plants within the row and wider distances between adjacent rows. This rectangular pattern generates a heterogeneous red/far-red ratio environment, with high values towards the interrow spaces and low values within the row. In maize, these differences appear early in the ontogeny of the crop and persist to flowering [71]. Isolated maize plants grown in the field next to filters reflecting far-red light placed their leaves mainly perpendicular to the direction of the incoming reflected far red (i.e., parallel to the filters). Control plants with filters that did not lower the red/far-red ratio randomly oriented their leaves on the horizontal plane [71]. The ability to reorient leaf growth according to the light signals is cultivar specific and correlates with the ability to reorient leaf growth in response to rectangular sowing arrangements in the field. Maize leaves did not change the position of origin in the meristem. Rather, when far-red light was directed by means of fibre optics to the position where a leaf was expected to appear, the leaf growth turned away from the predicted direction towards any of the sides [71]. The ability to respond to the red/far-red signals reduced mutual shading among leaves, increasing their efficiency to intercept PAR [71].

The vertical angle of the leaves can also respond to canopy signals. Under low red/far-red ratios, the leaves often adopt a more erect position, particularly in rosette plants such as *Arabidopsis* (see [2], for references) but also in other species. Solar tracking by the upper leaves of sunflower cultivars is reduced when the plants are grown under low red/far-red ratios [79]. In some wheat cultivars, low red/far-red ratios induce a more erect position of the tillers [80].

4.2. Leaf Expansion in Response to Canopy Light Signals. The red/far-red ratio has normally large effects on stem growth but weak effects on leaf growth in eudicots. In sunflower, for instance, low red/far-red ratios reduce the early rate of leaf growth and promote leaf growth at later stages, largely not affecting the final size of the leaf [79]. There are, however, cases where leaf area is increased or decreased in response to low red/far-red ratios [81]. In grasses, including *Lolium multiflorum*, *Paspalum dilatatum*, and barley (*Hordeum vulgare*), low red/far-red [68, 82] or low blue light [83] promotes leaf sheath growth. This is a stem-like response that helps to place leaf lamina at higher strata within the canopy.

4.3. Leaf Senescence in Response to Canopy Shade-Light Signals. In dense sunflower crops, the senescence of basal leaves can anticipate anthesis. The beginning of senescence of target leaves of sunflower plants grown in the field at a very low density was advanced both by lowering PAR with the aid of neutral filters and by lowering the red/far-red ratio with the aid of mirrors placed beneath the leaves to selectively reflect far-red light [84]. Conversely, increasing the red/far-red ratio

received by basal leaves of plants grown at high density by means of red-light emitting diodes delayed senescence compared to non-irradiated controls. The effect of red-light enrichment was not photosynthetic as it increased the daily PAR integral in approximately 4%, and a 5% enrichment of PAR with green light had no significant effects [85].

4.4. Stomatal Conductance in Photoreceptor Mutants. The blue-light photoreceptors phototropins and cryptochromes affect stomatal conductance although via different pathways. Phototropins mediate the well-established promotion of stomatal aperture induced by blue light [86]. Contrary to the expectations, mutants of phototropins in *Arabidopsis* have demonstrated that these photoreceptors are important for full stomatal opening even at midday [87]. The effect of cryptochromes appears to be indirect; rather than perceiving the light stimulus causing immediate stomatal opening, cryptochromes would perceive the general status of the blue-light environment, reduce the levels of abscisic acid, and hence condition the subsequent response of stomatal opening to either blue or red light [87]. As for phototropins, the effects of mutations at cryptochrome genes reduces stomatal conductance more strongly at the high irradiances of midday [87]. As a result of these stomatal responses, both phototropins and cryptochromes increase transpiration at the time of the day when atmospheric water demand is maximal. The idea is that the action of these photoreceptors rather than saving water would help to reduce eventual midday limitations of photosynthesis by carbon dioxide availability, with their concomitant risk of diverting the energy captured by photosynthetic pigments to the generation of reactive oxygen species. The irradiance dependency of these responses argues in favour of their role in response to canopy shade [87].

The low red/far red [88] or low irradiances [89] perceived by phytochrome B reduce stomatal density and stomata index in *Arabidopsis*. This reduces stomatal conductance and transpiration and increases long-term water-use efficiency estimated by the analysis of isotopic discrimination against $^{13}CO_2$ [88]. In agreement with the results in *Arabidopsis*, rice mutants deficient in phytochrome B exhibit reduced stomatal density [90]. The enhanced transpiration caused by phytochrome B in open places would be detrimental for the plant water status, but this effect can be compensated by a reduction in leaf area [88] and a higher sensitivity of stomatal conductance to abscisic acid [91]. As discussed above for the effects of phototropin and cryptochrome, enhanced stomatal conductance would reduce the risk of generation of reactive oxygen species. In the case of rice, the phytochrome B mutants exhibited reduced total leaf area per plant, contributing to the lower rates of transpiration, and the root system showed no obvious differences [90].

4.5. Leaf Photosynthesis in Photoreceptor Mutants. Phototropins mediate the adjustment of chloroplast position to maximise the efficient use of PAR. Under high irradiance, the chloroplasts move to the anticlinal wall of palisade cells [92–94], decreasing light absorption and the risk of damage of the photosynthetic by excess excitation [95]. Under low irradiance, the chloroplasts accumulate at the periclinal

wall of palisade cells [94], increasing efficient light capture [96].

The mutants lacking phototropins or cryptochromes have reduced photosynthesis in the field [87]. This is caused mainly by nonstomatic effects. The phytochrome B mutant also has reduced photosynthesis but these effects result from a combination of stomatic and nonstomatic limitations [88]. Rice phytochrome mutants also show reduced photosynthesis [90].

5. Root Responses to Canopy Light Signals

5.1. Root Growth. Root growth can be affected by canopy light signals. For instance, low red/far-red ratios reduce root growth in tobacco [35] and *Vigna unguiculata* [97], the number of rooted phytomers in *Trifolium repens* [75], and lateral root formation in *Arabidopsis thaliana* [98]. Some mutants deficient in phytochrome B show reduced root growth as it is the case in cucumber [54], *Lotus japonicus* [99], and *Arabidopsis thaliana* [98]. In *Arabidopsis*, shoot-localised phytochrome B is able to affect the flux of auxin to the root and control the growth of this organ. There are many cases, however, where red/far-red treatments [72] or phytochrome B mutations [90, 91] did not show obvious effects on root biomass accumulation.

5.2. Nodulation. Kasperbauer and Hunt [97] inoculated seeds of southern pea (*Vigna unguiculata* (L.) Walp.) with *Bradyrhizobium japonicum* and grew the plants in pots under photoperiods of 12 h of white light terminated with five minutes of red or far-red light to establish either high or low levels of active phytochrome at the beginning of the night. The far-red light treatment promoted stem elongation, but it reduced root growth and nodule number. Suzuki et al. [99] compared two mutants of *Lotus japonicus* deficient in phytochrome B to the wildtype MG20 grown under white light. The mutants showed approximately the same stature as the wildtype, but they produced less shoot biomass, root biomass, chlorophyll, and number of nodules. When the plants were grown under low red/far-red ratios, the number of nodules decreased in the wildtype and remained low in the mutants (at the same levels observed under high red/far-red ratios). In grafting experiments, the use of the phytochrome B mutant as the scion reduced the number of nodules regardless of the wildtype or mutant rootstocks, whereas the use of MG20 as a scion resulted in wildtype nodule number regardless of the rootstock genotype. These results indicate that phytochrome B in the shoot either stimulates the production of a signal that migrates to the root to promote nodule formation or reduces the production of a signal that migrates to the root to repress nodule formation. The endogenous levels of jasmonoyl isoleucine (the active jasmonic acid derivate) were reduced in the roots of the phytochrome mutant, compared to the MG20 wildtype of *Lotus japonicus* [99]. As expected, adding jasmonic acid at appropriate concentrations increased nodule number in the wildtype under low red/far-red ratios and in the phytochrome mutant grown under high red far-red ratios. Taken together, these observations indicate that plants of *Lotus japonicus* use phytochrome B

to monitor the red/far-red ratio reaching its shoot, and this signal controls the levels of jasmonoyl isoleucine in the root, which in turn controls nodulation. The suppression of nodule development in response to shade-light signals would be part of the mechanisms of autoregulation of nodulation, in this case favouring shade-avoidance over nitrogen fixation under increasing competition for PAR.

6. Reproductive Responses to Canopy Light Signals

6.1. Flowering Time. Low red/far-red accelerate flowering in barley [100] and *Lolium multiflorum* [101]. In soybean, low red/far-red ratios have been shown to correlate with delayed flowering, but since the experimental setting compared incandescent versus fluorescent lighting, other aspects of the light environments were also affected by the treatments [102]. In wheat, the red/far-red ratio has normally no effect on the final number of leaves on the main shoot [45, 46]. In *Arabidopsis*, low red/far-red ratios accelerate flowering by enhancing the expression of *FLOWERING LOCUS T (FT)* [103, 104], that is, the gene encoding the "florigen" involved in the induction of flowering by long days [104]. Consistently with this observation, in the long-day plant *Arabidopsis*, the acceleration of flowering under simulated shade light is maximal when the days are short [105].

6.2. Grain Number per Shoot. Libenson et al. [41] placed selective plastic filters around the stem of sunflower plants grown in large pots arranged at low densities in the field, to reduce the red/far-red ratio reaching the stem, without affecting PAR reaching the leaves. Compared to the controls bearing clear plastic filters, lowering the red/far-red ratio reaching the stem promoted the growth of this organ (both in terms of length and dry matter accumulation) and reduced grain number and grain yield per plant [41]. The promotion of stem growth by the light environment typical of dense commercial stands could reduce the resources available for grain yield in sunflower crops [41].

Heindl and Brun [106] used fluorescent tubes to enrich the red-light environment of the lower part of a soybean canopy during three weeks late in flowering. The treatment had no effects on the flowers produced per node, but it reduced flower abscision and increased seed yield per node [106]. Since field-grown plants were grown at high PAR levels, the effect of supplementary red light could be mediated by increased red/far-red ratios perceived by phytochrome, rather than by increased photosynthesis.

In wheat, the growth of the spike and its developmental progression are delayed by low red/far-red ratios achieved by supplementing sunlight with far-red light during the final hours of the photoperiod [46]. This treatment also delays the growth of the peduncle. Increasing plant densities reduces the total number of floret primordial initiated, increases the rate of floret abortion, and reduces the number of kernels per spike in wheat crops [107]. Similarly, low red/far-red ratios also reduce the number of florets at anthesis and the subsequent number of grains (and grain yield) as a result of reduced floret initiation and increased rate of floret

decay [46]. This light signal accelerates the developmental progression of the florets but it causes the subsequent interruption of this progression, which is predicted to result in floret death before anthesis [46]. In these experiments, low red/far-red ratios did not increase wheat plant stature, and therefore it is not possible to account for the reduction of grain number on the basis of resources diverted to the growth of other organs. A more direct action of red/far-red ratio on the development of the spike has been proposed, consistently with the observed associated effects on the expression of developmental genes in the ear [46]. The analysis of the kinetic of spike and stem growth also suggests that floret death involves a developmental decision and is not just the consequence of scarcity of photoassimilates [108]. In rice, the triple *phyA phyB phyC* mutant shows reduced seed production, but this is mainly caused by impaired dehiscence of the anther wall and poor pollination [109].

7. Defence Status in Response to Canopy Light Signals

It is becoming clear that the light signals of dense canopies reduce the defences against biotic agents. These responses are not just the consequence of the morphological responses to canopy light signals. Rather, they are caused mainly by the action of photoreceptors on key points of the defence signalling networks (see [110] for a recent review).

7.1. Defence against Herbivores. Caterpillars of *Manduca sexta* show a higher mass increment when fed on plants of wild tobacco (*Nicotiana longiflora*) exposed to sunlight plus supplementary far-red light than on leaves grown under sunlight with a high red/far-red ratio [111]. Caterpillars of *Spodoptera eridania* grow better on mutant tomato plants lacking phytochromes B1 and B2 than in the isogenic wildtype [111]. The phytochrome B1 and B2 mutant of tomato is also more susceptible to damage by thrips (*Caliothrips phaseoli*), which show preference for the mutant leaves. Plants of *Arabidopsis thaliana* grown in pots at high density or at low density but with supplemental far-red light to provide a signal of neighbours produced leaf tissue that favours weight gain of *Spodoptera frugiperda* caterpillars [112]. In wild tobacco and *Arabidopsis thaliana*, low red/far-red ratio alters the expression of defence-related genes and inhibits the accumulation of herbivore-induced phenolic compounds [111, 112]. A priori, the reduced antiherbivore defences as a result of reduced phytochrome B activity caused by neighbour signals could be either the indirect consequence of shade-avoidance responses or the result of a more direct control of the defence signalling network by phytochrome. In favour of the second interpretation, the *sav3* mutant of *Arabidopsis thaliana*, deficient in auxin synthesis, shows impaired shade avoidance but retains downregulation of defences in response to low red/far-red ratios [112]. Plants grown under low red/far-red ratios show reduced sensitivity to jasmonate, a key hormone in the induction of antiherbivore defences [112]. The *lh* mutant of cucumber, deficient in phytochrome B, showed stronger damage by herbivores in the field, but actual shade had no effect [113].

There are several examples showing the effects of UV-B radiation on plant-herbivore interactions. The intensity of leaf tissue damage caused by phytophagous insects in young seedlings of *Datura ferox* grown in the field decreased with increasing UV-B between 0% and 100% of sunlight values [114]. Comparable differences were observed if UV-B was restricted at the time of insect exposure indicating that the UV-B effect is at least partially on the plant itself. However, in addition to plant responses, phytophagous insects can perceive and avoid UV-B [115]. Similar results were obtained in soybean crops [116] and natural ecosystems [114]. UV-B also reduced the growth of *Manduca sexta* caterpillars on plants of *Nicotiana longiflora* or *N. attenuate* [117]. Plant perception of UV-B causing enhanced resistance to insect herbivores could be mediated by UVR8, but testing this idea awaits evaluation of mutant plants lacking this photoreceptor. Meanwhile, it is not strictly possible to exclude that enhanced resistance derives from UV-B damage.

7.2. Defence against Pathogens. When sprayed with a conidia suspension of the blast fungus *Magnaporthe grisea,* wildtype seedlings of rice developed symptoms in the youngest but not in the oldest leaves. When exposed to the latter treatment, the *phyA phyB phyC* mutant of rice (lacking all phytochromes) shows wildtype density of lesions in young leaves, but it exhibits more than two lesions per cm^2 even in old leaves [118]. When inoculated with *Magnaporthe grisea* or when treated with the defence-related hormones jasmonate or salicylic acid, the wildtype shows enhanced accumulation of the pathogenesis-related class 1 (PR1) protein in old leaves 20 or 24 h later [118]. In young leaves, PR1 accumulation is observed to some degree 48 h after inoculation and reaches the level observed in old leaves at 72 h. In the *phyA phyB phyC* triple mutant, PR1 accumulation is observed only in old leaves but 72 h after inoculation. These observations indicate that in wildtype rice, the leaves develop an age- and phytochrome-dependent ability to respond to fungal infection (and to downstream signals), which is related to the levels of PR1. In addition to the reduced induction of PR1, the triple mutant also had reduced basal levels of PR1 [118].

Wildtype plants of *Arabidopsis* exposed to low red/far-red ratios or mutant for phytochrome B grown at high red/far-red ratios develop more intense disease symptoms than the wildtype grown under high red/far-red ratios when inoculated with a spore suspension of gray mould pathogen *Botrytis cinerea* [110]. The increased susceptibility to *B. cinerea* as a result of reduced phytochrome B activity (either by the light condition or the mutation) is apparently not the consequence of the morphological responses induced by lowering phytochrome B activity. In fact, a mutant deficient in auxin synthesis is severely impaired in morphological responses to low red/far-red ratios while it retains normal defence responses to low red/far-red ratios [110].

Low levels of UV-B enhance the resistance of glasshouse-grown plants of *Arabidopsis* to *B. cinerea*. The level of lesions observed in the mutant lacking UVR8 was similar to that of wildtype plants in the minus UV-B controls, but this mutant failed to respond to UV-B [110]. These observations indicate that UVR8-mediated perception of UV-B enhances

resistance to *B. cinerea*, which is therefore not an indirect effect of UV-B-induced damage. The mechanism of action could involve the control of the levels of sinapates by UVR8 [110]. Canopy shade could therefore reduce plant defences by reducing UVR8 activity [110].

Plants of *Arabidopsis* lacking phytochrome B show enhanced growth of incompatible strains of *Pseudomonas syringae* [119, 120]. A screening for plants with defects in shade-avoidance responses helped to identify the *constitutive shade avoidance* (*csa*) mutant affected in the TOLL/ INTERLEUKIN1 RECEPTOR-NUCLEOTIDE BINDING SITE-LEUCINE-RICH REPEAT (TIR-NBS-LRR) gene [120]. TIR-NBS-LRR proteins had previously been implicated in defence responses, indicating an intimate link between the control of plant growth and development by light and plant defences.

8. Early Responses to Canopy Light Signals Impact Subsequent Crop Performance

In growing canopies, phytochrome perception of low red/far-red ratios caused by far-red light reflected on neighbours anticipates mutual shading among plants [15] (Figure 2). These reductions in red/far-red ratio are small but enough to cause plant responses. For instance, seedlings of *Datura ferox*, *Sinapis alba,* or *Chenopodium album* showed enhanced stem growth (i.e., a typical shade-avoidance response) when exposed to far-red light reflected either on selective mirrors or on green neighbours placed opposite to the side of incoming sunlight (to avoid shading), compared to the controls with senescent (nongreen) neighbours or red plus far-red reflecting mirrors [15].

Markham and Stoltenberg [121] have proposed that the early season red/far-red ratio is important for subsequent grain yield under field conditions. They conducted field experiments, where equidistantly spaced corn plants were grown at 107,600, 53,800, and 3000 plants ha^{-1} from emergence to canopy closure (V7), when all the treatments were thinned to 3000 plants ha^{-1}. The red/far-red ratio decreased with plant density and apparently caused a reduction in the number of tillers per plant, which was associated with a lower per-plant grain yield at a later stage. The availability of PAR, the gravimetric soil water content, and the soil nitrate-nitrogen, phosphorus, or potassium contents were not affected by the early plant density treatments, and therefore cannot account for the observed differences in yield.

The critical period of weed control defines the number of weeks after emergence during which the crop must be weed-free in order to prevent crop yield losses beyond an acceptable amount [122]. This empirical concept is useful in weed management, but in the absence of a deeper understanding of the underlying processes controlling the susceptibility of the crop to the presence of weeds, the values are difficult to extrapolate [122]. One of the obvious mechanisms by which weeds can reduce crop yield is by capturing resources that then become scant for the crop plant. Consistently with the latter interpretation, the presence of weeds in maize crops can anticipate the development of water-deficit or Nitrogen-deficiency symptoms, as well as reduce the interception of PAR [122].

However, the effects of weeds on the crop often appear more strongly linked to a reduced capacity of the crop plant to increase root and leaf area surface to capture resources than to an actual scarcity of resources [122]. Therefore, signals and not just resources, could be important in the interactions between weed and crop plants. The impact of red/far-red light signals produced by weeds on the growth of maize plants was investigated in a series of experiments, where maize plants were grown in a field fertigation system at a low plant density, with or without the presence of neighbours weeds (a mix of *Lolium perenne* L. and *Poa pratensis* L., *L. peremne* alone, or *Amaranthus retroflexus* plants). The weeds were grown in separate pots, fed by separate fertigation lines (ensuring no water movement between root systems) and maintained by manual clipping to prevent direct shading of maize seedlings. Therefore, the weeds did not compete for PAR, water, or nutrients with the crop, but they reduced the red/far-red ratio received by maize plants due to reflected far-red light. Maize plants developing in the weedy environment displayed increased plant height, reduced leaf area, and a transiently increased shoot/root ratio caused by a reduced number of nodal roots and reduced root biomass [123, 124]. Compared with maize growing in the weed-free treatment, the presence of weeds until silking caused a 20% reduction in ear dry weight and most of the effect was caused by the presence of weeds beyond the 8-leaf tip stage [125], but even when weed neighbours were removed 30 days after emergence of the maize crop, reduced kernel number per plant and harvest index were observed in weedy compared to weed-free plants at maturity [123]. The experimental support for the idea of long-term consequences of early weed signals is not limited to maize. A comparable experimental setting demonstrated increased soybean internode elongation, reduced branching, and decreased yield per plant in response to the upwards reflection of far-red light by neighbouring weeds, compared to weed-free controls with high red/far-red ratios [126].

The early low red/far-red ratio signals caused by the presence of weeds can also affect the ability of crop plants to cope with abiotic stress. In some of the maize experiments described in the previous paragraph, after the neighbours were eliminated, fertigation was interrupted 3–5 d in half of the plants of each previous neighbour condition to create a moderate abiotic stress. Maize grain yield and kernel number per plant at maturity were influenced by interactions of early neighbour treatments and stress. The apparent synergy of stresses indicates that early shade avoidance can reduce the tolerance of maize plants to subsequent stressors [123].

9. Genetic Modification of the Impact of Canopy Light Signals

Some (but not all) of the responses to the light signals of dense canopies appear detrimental for yield, but it is not possible to reduce these signals in most commercial crops. However, it would be feasible to search for genotypes with optimised responses to canopy light signals. In this section, we address three issues related to the genetic variability in plant responses to the light signals of dense canopies. First, we will analyse the use of transgenic plants with increased levels

of photoreceptors. Second, we will consider whether breeding and selection for yield are leading to cultivars less responsive to the light signals of dense canopies. Third, we will argue the possibility of nonadverted choice of strong or weak plant responses to canopy light signals with the conscious choice of cycle duration.

9.1. Transgenic Plants. Increased interference among plant shoots reduces the activity of photoreceptors (Figure 1). If, due to transgenic expression, plants have elevated levels of photoreceptor molecules, a higher absolute amount would remain active even under shade, and this could result in the reduction of plant responses to canopy density. This idea has been tested in several crops.

Robson et al. [127] cultivated transgenic tobacco plants expressing the gene of phytochrome A (*PHYA*) from *Avena sativa* in the field. High levels of phytochrome A impaired the promotion of stem growth normally caused by the canopy light signals of increasing plant densities. Actually, the presence of neighbours reduced plant stature instead of the normal growth promotion, likely because the transgenic plants responded to far-red light reflected on neighbours as more light rather than as a lower red/far-red ratio. In wildtype crops of tobacco, increasing plant densities have only a moderate influence on plant inequalities because shorter plants become more intensely shaded and induce a stronger shade-avoidance response that tends to compensate the differences [128]. This is not the case in transgenic crops with elevated levels of phytochrome A, unable to respond normally to canopy shade signals, where small plants become rapidly suppressed by their taller neighbours [128]. Therefore, shade-avoidance reactions can contribute to crop yield by reducing the chances of occurrence of very small plants that capture some resources but do not generate yield [129].

Expression of the *Arabidopsis* phytochrome B (*PHYB*) gene in transgenic potato plants increased tuber number and tuber yield in field crops planted at high densities [130]. High phytochrome B levels reduced the decay of maximum photosynthesis normally observed in older leaves, which are more intensively shaded due to their basal position [130]. The higher rates of maximum photosynthesis were related to increased stomatal conductance, largely due to increased aperture of the stomatal pore, rather than increased stomatal density. In glasshouse experiments, these transgenics showed delayed leaf senescence, lower carbohydrate, and higher Nitrogen levels in leaf and stem tissue, leaf photosynthesis, and conductance [131]. However, in contrast to the field experiments, increased conductance was caused by a higher stomatal density. Furthermore, measurements of intercellular leaf CO_2 partial pressure point to nonstomatic limitations of photosynthesis [131]. Although the transgenics bearing high levels of phytochrome B had higher photosynthesis per unit leaf area, they showed reduced ability to cover the soil, underscoring the importance of adequate sensing the canopy light signals to optimally accommodate the leaves, reducing mutual interference [130]. The simplest interpretation of these results is that in dense canopies, plants with higher levels of photoreceptors due to transgenic expression maintain a higher absolute number of active photoreceptor molecules

than the wildtype. As a result of this, some of the effects of increased canopy densities are attenuated. In addition, it is important to note that transgenic modification of photoreceptor levels not only alters the perception of the light environment, but it also modifies the environment itself [130]. In effect, increased photoreceptor levels lead to a shorter, bushier morphology and reduced shading among plants in different rows. In addition, since these plants had a reduced ability to project their foliage towards shade-free areas, the degree of shading within the row was increased [130].

Transgenic japonica rice cv. Nakdong plants expressing *Arabidopsis* phytochrome A grown under sunlight showed reductions in the length of the culm, panicle and leaves, and increments in grain weight and size, which depended on the strength of phytochrome expression [132]. However, transgenic plants showed smaller tiller number and low grain fertility compared to wildtype plants causing yield reductions. Transgenic expression of phytochrome in the indica rice variety Pusa Basmati-1 also reduced plant stature and slightly increased grain weight, but it increased panicle number and grain yield per plant [133]. The different results might reflect differences between the cultivars.

9.2. Breeding and Selection. We have presented examples from different crops where canopy shade-light signals tend to reduce yield potential or yield-related traits. One might therefore expect breeding and selection for yield to reduce the impact of these signals on yield per plant. To test this hypothesis, Ugarte et al. [46] compared the response of tillering, grain yield, grain number, and weight of 1000 grains to red/far-red ratio in ten cultivars released to the Argentinean market at different times of the 20th century. Against the expectations, the most modern cultivars of the series did not respond less than the oldest. Actually, some traits showed the opposite pattern. Thus, breeding and selection for yield are not reducing the impact of the negative control of yield by low red/far-red ratios. One of the scenarios that could account for this pattern is that in commercial crops the low red/far-red ratio could initiate an early adjustment of yield potential that the plant would otherwise experience afterwards, when more intense mutual plant shading occurs. In the field, the red/far-red ratio and the subsequent availability of resources would be correlated and the signal could not seriously reduce yield below the potential. In the low density plants used by Ugarte et al. [46], the low red/far-red treatments would reduce the generation of yield components below the potential because the plants did not mutually shade each other at a later stage; that is, under these conditions, the low red/far-red signal would not correlate with a subsequent scarcity of resources due to mutual shading.

9.3. Does Selection for Cycle Length Affect the Responses to Canopy Shade-Light Signals? The photoperiodic regulation of flowering helps to adjust the duration of crop cycle to the ecological conditions and agricultural needs. The perception of daylength requires the action of photoreceptors to distinguish between light and darkness, and the action of the circadian clock to restrict the sensitivity to light to a given portion of the day [134]. The photoreceptors involved
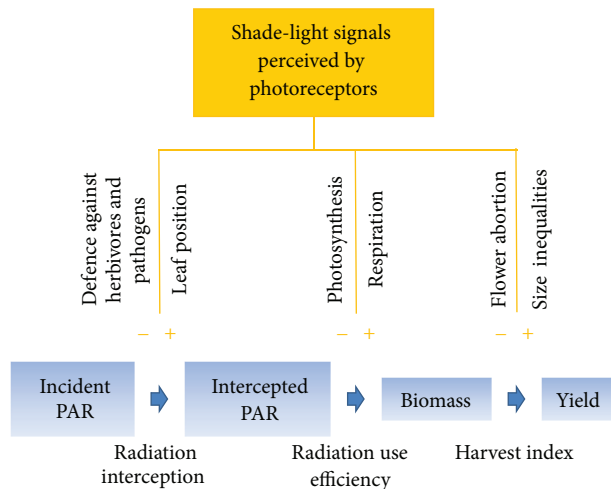
FIGURE 4: Canopy light signals impact on crop yield. Incident radiation is intercepted by the canopy with an efficiency that depends on canopy architecture; intercepted radiation is transformed into biomass with an efficiency that depends on the processes that fix (photosynthesis) and release (mitochondrial respiration, photorespiration) carbon dioxide; part of the biomass is allocated to harvestable organs. The light signals of dense canopies have both positive and negative effects on these processes, and selected examples of the processes that impact on PAR interception, radiation use efficiency, and harvest index are included.

in daylength perception often control other aspects of plant growth and development such as the stem growth response to shade signals. In soybean, the abundance of cryptochrome 1 shows a circadian rhythm controlled by photoperiod and correlates with photoperiodic flowering and latitudinal distribution of soybean cultivars [14]. When expressed in transgenic *Arabidopsis* seedlings under the control of a constitutive promoter, soybean cryptochrome 1 inhibited hypocotyl growth in response to blue light and rescued the long hypocotyl phenotype of the *Arabidopsis* mutant deficient in cryptochrome 1 [14]. In soybean, nine maturity loci (E1 to E8 and J) have been identified, and the E3 and E4 genes encode copies of phytochrome A genes (*GmPHYA3* and *GmPHYA2*) [135]. These observations suggest that selection for different daylength responses and cycle lengths could be driving selection for different degrees of response to shade.

10. Concluding Remarks

Coming back to the beginning of this paper, crop yield is the integral for the growth period of the product of the incident PAR, PAR interception, radiation use efficiency, and harvest index [1], and canopy light signals can affect these terms (Figure 4). Canopy light signals can increase PAR interception, for instance, by guiding leaf and stem growth direction towards the gaps within the canopy. However, canopy light signals can reduce PAR interception by reducing the number and/or area (at least the photosynthetically effective area) of the leaves as a consequence of reduced branching and defences against herbivores and pathogens. Canopy signals could reduce radiation use efficiency by reducing photosynthesis per unit leaf

area via stomatic and/or nonstomatic responses. However, canopy light signals could increase radiation use efficiency by lowering the rate of respiration of selected organs. Canopy signals can reduce harvest index, for instance, by enhancing floret abortion. However, canopy signals can reduce size inequalities and the chance of occurrence of small plants that capture resources but fail to efficiently translate them into yield. Finally, in some crops, canopy light signals can shorten the duration of the cycle by accelerating flowering. The available evidence clearly support supports the strong influence of canopy light signals on crop yield, but we are far from predicting the balance among the positive and negative forces.
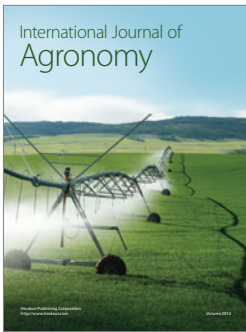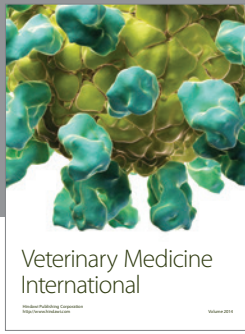
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