SHADE AVOIDANCE SYNDROME: A COLOUR RATIO REGULATED GROWTH

Abstract

When plants are exposed to the shade of another plant, they exhibit a set of responses called shade avoidance syndrome (SAS). The most remarkable trait observed in plants subjected to low R:FR are an upward reorientation of leaves (leaf hyponasty) and a rapid elongation of leaves and stems. PIF (Phytochrome Interacting Factor) and DELLA gene families interact with endogenous and external signals, which are mediated by several photoreceptors including phytochrome, cryptochrome, and UVR8, and are the main regulators of molecular responses for shade signalling. Plants combine information about R: FR with a variety of signalling routes, which involve environmental elements and plant hormones such as auxin, gibberellin, ethylene, and brassinosteroid. In order to balance resource allocation between development and defence, shade also represses defence responses caused by salicylic acid and jasmonate. These molecular discoveries aidto understand the mechanisms of plant strategies such as dampening of shade-avoidance traits and optimizing growth under low light conditions to foster crop improvement and also to develop shade tolerant varieties for different agricultural ecosystems.

Keywords: Shade, Shade avoidance syndrome, phytochrome, shade tolerance, phytohormones

1. Introduction

Over the last few decades, increasing plant density and crop diversification have been key factors in improving crop yield. Amidst the current situation of swift population expansion and restricted arable land, effective farming methods may necessitate increased planting densities, intercropping, and modifications to plant design to optimise crop yields. Crop compatibility in intercropping systems depends on both the environmental conditions and crops' requirements that affect plant growth and, in turn, crop output.

Plants, which are sessile, have to constantly modify their growth and development to maximize photosynthetic activity under varying circumstances. Resources are few in an agricultural system, and individual competition frequently leads to plastic developmental responses that allow people to adapt to these resource constraints. Light is the primary environmental component that limits production under agricultural systems. Perception, transmission, and integration of many environmental cues enable this developmental plasticity.

Apart from being an essential source of energy for photosynthesis, light signals furnish plants with significant temporal and spatial information regarding their surroundings. Because of this, evolution has moulded plant systems and strategies to maximise light intake, changing the patterns of development in order to reconcile the sessile character of plants with variations in the amount of light available in their surroundings. Under natural conditions, one of the situations in which light might become scarce is in areas with canopy shade, like forests and prairies where a variety of species coexist in dense growth and might eventually result in shading which reduces the amount and quality of solar energy available for photosynthesis.Another situation is under agricultural ecosystem, where plants are cultivated communally, resulting in reduction of light quality by proximity shade. The ratio of photon irradiance in the red region of the spectrum to that in the FR region (abbreviated R: FR ratio) is the measure that is frequently used to characterise the quality of light in natural surroundings. The most used and researched light-related characteristic for plant growth and development is the R:FR ratio.

$$\mathrm{R : FR} = \frac{\text{photon irradiance between 660 and 670 nm}}{\text{photon irradiance between 725 and 735 nm}}$$

2. Shade responses:

Gommers*et al*. (2017) subjected two wild species of Geranium to FR-enriched (low R: FR = 0.2) versus control (R: FR = 1.8) white light settings. The species were found to be from contrasting environments. Petiole elongation was the reaction shown by G. *pyrenaicum*, whereas this was not seen in G. *robertianum*, suggesting that plants of the same species have distinct responses to shade.

2.1 *Shade avoidance syndrome (SAS)*

When plants are exposed to the shade of another plant, they develop a complex of reactions known as shade avoidance. It frequently involves increased apical dominance, elongation, changed flowering period, and changed resource partitioning. The shade-avoidance syndrome (SAS) is the collective term for these sets of reactions.The two most noticeable traits found in dicotyledonous plants are leaf hyponasty (Whitelam and Johnson, 1982) and rapid elongation of leaves and stem (Morgan and Smith, 1981). Franklin and Whitelam (2007) have noted similar shade responses in Brassica rapa and Arabidopsis.

With the help of these adaptations, plants are able to outcompete vegetation and increase their capacity for light-foraging in dense stands. In fact, it has been demonstrated that reflected and horizontally propagated FR radiation in the lower vegetation strata of canopies have been shown as important regulatory signals, controlling the elongation of stems in species that avoid shade (Ballare*et al*., 1990).

Reduced chlorophyll content and increased apical dominance are two additional responses to low R: FR (Smith and Whitelam, 1997). If the shade signal continues and the plant is not able to surpass the competing vegetation, it enters into reproductive phase, therefore encouraging seed set and improving the rate of reproduction (Donohue *et al*., 2001). According to Robinson *et al*., (1993), these adaptations include decreases in shoot biomass, leaf area and the size of harvestable organs.

2.2 Shade tolerance

Shade tolerance is the ability of a certain plant to withstand low light conditions. The lowest amount of light that a plant can withstand is known as shade tolerance from a physiological perspective. However, from a biological perspective, the entire plant life cycle—from early survival and growth to reproduction—must be taken into account in order to classify a species as shade tolerant. As a result, while many plants can survive at low light levels, not all of them can procreate in such environments. These include cultivars of Fuchsia, various coleus (*Solenostemonscutellarioidies*), holly (*Ilex aquifolium* L.), elephant ear (*Alocasia macrorrhiza*), and impatiens (*Impatiens balsamina*) (Valladares *et al*. 2005).

Shade tolerance is attained by a variety of responses in various species, including modifications to the physiology and biochemistry of leaves, their anatomy and morphology, and/or their architectural design. According to Valladares and Niinemets (2008), shade tolerance generally adapts to a very conservative use of resources under low light. This is typically accompanied by reduced growth rates as well as biochemical and structural changes to improve photosynthetic energy transduction efficiency and lower respiration losses. Shade-tolerant plants grow morphologically with thinner leaves, less apical dominance, more branching frequency, and less elongation response. Furthermore, under shade conditions, plants develop higher levels of chlorophyll content per leaf area or leaf dry mass (Valladares and Niinemets, 2008).

Additionally, altered source partitioning and leaf shape are typically associated with shade tolerance (Ntawuhiganayo*et al.*, 2020).

3. Photoreceptor regulation of shade avoidance

3.1 Phytochrome:

Phytochromes are photoreceptors present in algae, cyanobacteria, bacteria, fungi, and land plants, to perceive light, which differ significantly among phyla (Burgie *et al*. 2014). Phytochromes are two types of interconvertible red and far-red light receptors. The initial state is the inactive Pr state, which is transformed into the active Pfr conformation by light absorption. The Pfr conformation is then inactivated by thermal reversion or far-red (FR) light absorption.

Three kinds of phychromes—phytochrome A (phyA), phyB, and phyC—have been found in the majority of angiosperms. On the other hand, five phytochrome members (PHYA-PHYE) have been found in Arabidopsis and are divided into two subgroups, PHYA/PHYC and PHYB/PHYD/PHYE, according to sequence homology. Every phytochrome plays a distinct role, and the contributions it makes change based on the plant's developmental stage and environmental circumstances.

Activated phytochromes and blue and UV light receptors (UVR8) work together to sense inductive wavelengths and regulate a variety of physiological functions and developmental processes in plants. Active phytochromes cause germination to occur when a seed comes into contact with water (Franklin and Quail, 2009). When a seedling grows in the soil it adopts an etiolated morphology achieved through fast-growing hypocotyls and closed apical hook, inorder to maximizes its reach to the surface. Upon exposure to light, phytochromes are triggered, resulting in a reduction of de-etiolation: hypocotyl formation, followed by the opening of the apical hook, expansion of the cotyledons, and the initiation of chloroplast development in the leaves. This initial response to light occurs even in poor light conditions where blue and red light are scarce. However, because green tissues reflect FR light and absorb mostly red and blue light, the R/FR decreases in high plant density situations. Green seedlings experience decreased phytochrome activity as a result, which sets off the shade-avoidance response. Under these circumstances, plants shift their metabolism and devote more energy to developing aerial portions (Krahmer *et al*., 2018).

Plant phytochromes are dimeric, with each monomer comprising roughly 1150 amino acids covalently attached to their chromophore, phytochromobilin (PΦB), a linear tetrapyrrole.The apoprotein is composed of three structurally related domains: cGMP phosphodiesterase/adenylyl cyclase/FhlA (GAF), Period/Arnt/SIM (PAS), and a phytochrome-specific domain (PHY). The N-terminal PSM is made up of the N-terminal extension (NTE) and three structurally related domains. A histidine kinase-related domain (HKRD) and two PAS domains make up the C-terminal module (CTM).

Phytochromes go from the cytosol to the nucleus upon sensing light. This is a crucial stage that is necessary for every phytochrome response that is now understood, and it is widely maintained in both sea algae and land plants.

3.2 Cryptochrome:

Stems sense less blue light when developing beneath dense stands before leaves do (Ballaré*et al.*, 1987). Using selective spectral filters, glasshouse experiments demonstrated that removing blue wavelength light led to a noticeable elongation of the stem. Tobacco plants exposed to lower photon irradiances of blue light have also been found to exhibit enhanced leaf hyponasty (Pierik *et al*., 2004). Therefore, certain physiological reactions that are indicative of low R:FR ratio perception can be elicited by reductions in the quantity of blue light.

Cryptochromes control a variety of developmental responses and resemble DNA photolyases structurally. In Arabidopsis, two cryptochromes (CRY1 and CRY2), which vary in fluence rate and light lability, control the blue light-mediated suppression of hypocotyl. Cry1 function predominates to limit hypocotyl development under increasing photon irradiances of blue light (Lin *et al*., 1998). In situations where light is limited, CRY2 exhibits increased stability and inhibits hypocotyl growth at lower photon irradiances (< 1 μmol m−2 s−1), which increases blue light sensitivity (Lin *et al*. 1998). According to Mazzella *et al*. (2001), double mutants lacking in both photoreceptors showed more elongation than cry1 monogenic mutants, indicating the critical function of cry2 in inhibiting this response. Arabidopsis CRY1 and CRY2 interact with phytochrome-interacting factors (PIF) 4 and 5, according to Keller *et al*. (2011). The main photoreceptors that govern elongation responses to a decrease in the amount of blue light are the cryptochromes CRY1 and CRY2. Lin *et al*. (1995) noticed the reversal of Arabidopsis cry1 function in response to green light, which resulted in the identification of a green light-absorbing flavin semiquinone state of this photoreceptor.According to Padmale*et al*. (2016), cryptochromes (CRYs) in higher plants regulate growth in response to variations in blue light.When growth occurs beneath a canopy, blue light wavelengths are diminished. CRY1 and CRY2 detect this change and interact with PIF4 and PIF5, two bHLH transcription factors. These two factors are also controlled by phytochromes. But the transcriptome analyses indicated that the gene regulatory programs regulated by different wavelengths are specific (Padmale*et al***.,** 2016)

Additionally, the data showed that PIF activity can affect the CRYs signal across the genome and that these factors combine the binding of several plant photoreceptors to enable changes in growth under various light circumstances. More recently, Arabidopsis cry2 has been found to be in a semi-reduced state (Banjeree*et al*., 2007). Bouly e*t al*. (2007) states that with green light supplementation of blue and red light mixtures and under certain instance, green light had reverse cryptochrome-mediated growth inhibition. Therefore, it is possible that the inactivation of cryptochrome signalling by green light, which is mediated by light reflected from living vegetation, will amplify the consequences of decreased the quality of blue light. In Arabidopsis seedlings, cryptochrome was discovered to downregulate two XTHs, which corresponded to a reduction in hypocotyl elongation.

4. Crosstalk with hormones

The combination of phytochrome signalling with other environmental elements makes it easier to identify fluctuations in the environment. Plants integrate R:FR information through a variety of signalling routes that include plant hormones such as auxin, brassinosteroid, gibberellin, and ethylene, as well as other environmental influences.

4.1 Auxin

The YUCCA (YUC) gene family encodes the rate-limiting enzyme in TAA1-dependent auxin biosynthesis. PIF7 regulates YUCCA gene transcription, which is linked with auxin biosynthesis (Li *et al*. 2012). PIF4 and PIF5 are redundant, while PIF7 regulates YUCCA gene expression (Hornitschek*et al*., 2012). Tissue-level measurements in Brassica rapa seedlings have shown that auxin is produced in the cotyledons and transported to the hypocotyl (Procko *et al*., 2014). Tao *et al*. (2008) found that seedlings treated with an auxin transport inhibitor, such as naphthylphalamic acid (NPA), did not exhibit any shade-induced hypocotyl elongation. Pin3-3 (PIN3, auxin transporter) consistently showed a reduction in shade-induced hypocotyl elongation (Keuskamp*et al*., 2010).

Auxin sensitivity increases in the shade in addition to auxin production and transport. A group of auxin-related genes that showed up-regulation in shade responders and down-regulation in shade-tolerant tomato lines suggests that auxin has a role in the natural variation of the SAS (Shade Avoidance Syndrome). Shade response pathways involve auxin signalling components such AUX/IAAs (Procko *et al*., 2016).

Besides Arabidopsis, the function of auxin in the shade avoidance mechanism has been found in several crop species (Carriedo *et al*., 2016). Auxin levels in shade have been shown to vary in tomatoes (Kozuka *et al*., 2010) and sunflowers (Kurepin *et al*., 2007).

4.1 Gibberellin

Gibberellin (GA) production was enhanced by shade in Arabidopsis seedlings, cowpea (Vigna sinensis) epicotyls, sunflower stems (Kurepin *et al*. 2007), and bean internodes. In Arabidopsis, shade also activates the GA biosynthesis enzymes GA20ox1, GA20ox2, and GA3ox (Hisamatsu *et al*., 2005). According to Harberd*et al*. (2009) bioactive GA leads to proteasomal degradation of DELLA proteins through 26S proteosome (Harberd*et al*., 2009). Due of DELLAs' inability to directly bind DNA, they will instead connect with PIFs. This will stop PIF proteins from binding DNA and adversely affect gene expression. On the other hand, increased gibberellin production caused by shade causes the degradation of DELLA proteins. According to Djakovic-Petrovic *et al*. (2007), the GA-insensitive gai gain-of-function mutant, which possesses the GAI (DELLA) protein, had a decreased shade response, indicating that DELLA proteins restrict the SAS.

4.2 Ethylene

According to Pierik *et al*. (2009), ethylene is a positive regulator of shade-induced petiole elongation in Arabidopsis because ethylene-insensitive mutants like ein2-1 and ein3-1eil1-3 did not exhibit shade-induced petiole elongation. Yet according to Das *et al*. (2016), the ein3eil1 mutant has maintained the entire shade-induced hypocotyl response. This controversy suggests that ethylene has an organ-specific shade response. According to Shi *et al*. (2016), the ethylene signalling pathway's master transcription factor EIN3 is rapidly degraded when photoreceptor phyB is activated by light.

4.3 C*ytokinin*

Low R/FR signal triggers a rapid arrest of leaf-primordia growth by the breakdown of cytokinin by activating cytokinin oxidase. Furthermore, it has been revealed that the root-to-hypocotyl ratio is mediated by the CK receptor AHK3 under shaded conditions (Novak *et al*. 2015).This reduction of bioactive CKs ensures redirecting of source for the extension of growth under shade , reduced photosynthetic capacity and a transient arrest of leaf development

4.5 Jasmonic acid

According to Ballare (2014) low R:FR ratios down-regulate defence responses in shade-intolerant species. The shade inactivates phyBthat leads to increased susceptibility to microbial pathogens and pest. The reason for this is the decreased expression of features associated to defence, such as additional floral nectar (Izaguirre and al. 2013), glucosinolates (Cargnel*et al*., 2014), latex (Agrawal *et al*., 2012), and phenolic chemicals (Moreno *et al*., 2009).Attenuation of the two main hormonal pathways, the JA and SA signalling pathways, may also account for it (Ballaré 2014).

According to studies by Agrawal *et al*. (2012) and De Wit *et al*. (2013), shading has been demonstrated to lessen herbivory-induced JA accumulation. Likewise, inactivating phyB has been shown to reliably decrease plant susceptibility to exogenous JA.The higher turnover of DELLA proteins and the improved stability of the repressor proteins of the jasmonate ZIM domain (JAZ) attenuated the sensitivity to JA (Leone *et al*., 2014).According to Yang *et al*. (2012), the physical contact between DELLA and JAZ proteins is essential for allocating resources between immunity and growth. Thus, phyB's capacity to influence how members of these two protein families balance out is a crucial component of the defense-response chain that links shade-avoidance and defensive response (Ballaré, 2014).

Conclusion

- Light is an essential resource for plants, especially in densely populated areas where competition is high. Plants are equipped with an abundance of photoreceptors, which enable them to detect the presence of competitors and modify their growth and development accordingly.
- The dynamic and complex shade-induced transcriptional network, which is altered by both internal and external stimuli, provides the molecular foundation for the SAS responses. The dynamic and complex shade-induced transcriptional network, which is altered by both internal and external stimuli, provides the molecular foundation for the SAS responses.
- The majority of modern "Green Revolution" crops are semi-dwarfs, but they still compete for light in their monoculture system and exhibit shade avoidance responses, which is not recommended. Studies on shade tolerance will therefore become a key focus of future investigation
- Even though the majority of today's "Green Revolution" crops are semi-dwarfs, they nevertheless compete with one another for light in monoculture systems and exhibit shade avoidance characters, which is not advised.

5. Challenges and opportunity:

The main problem is to identify which all plant responses should be altered to have a significant affect on crop yield and health. For example,to counteract the impacts of light proximity signals, that diverts resources to petiole and stem elongation, at the expense of other desirable functions.For optimal light interception, however, it is equally important to retain the capacity of shoots to photo tropically locate gaps in the canopy, for the maximum light interception. Recent developments in dissecting the molecular pathways that governs the downstream of photoreceptors offer a chance to modify individual responses.

Identifying targets for crop improvement will be made easier with the development of novel model systems, genetic resources, and high-throughput sequencing technology. Recent developments in artificial lighting technologies such as development of high-output LED arrays (Demotes-Mainard *et al*., 2016), offer a wealth of opportunities to apply our knowledge of plant photobiology to increase crop productivity and quality.

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