



Tansley review

Molecular mechanisms of shade tolerance in plants

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Summary

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Shade tolerance is an ecological concept used in a wide range of disciplines, from plant physiology to landscaping or gardening. It refers to the strategy of some plants to persist and even thrive in environments with low light levels because of the shade produced by the vegetation proximity (e.g. in the understory). Shade tolerance influences the organization, structure, functioning, and dynamics of plant communities. However, little is known about its molecular and genetic basis. By contrast, there is a good understanding on how plants deal with the proximity of other plants, a divergent strategy used by most crops to respond to vegetation proximity. While generally shade-avoiding species strongly elongate in response to the proximity of other plants, shade-tolerant species do not. Here we review the molecular mechanisms that control the regulation of hypocotyl elongation in shade-avoiding species as a reference framework to understand shade tolerance. Comparative studies indicate that shade tolerance is implemented by components also known to regulate hypocotyl elongation in shade-avoiding species. These components, however, show differential molecular properties that explain how, in response to the same stimulus, shade-avoiding species elongate while shade-tolerant ones do not.

I. Introduction

Light conditions have a major impact on all stages of plant life. In nature, many seeds are covered by soil and germinate under dark or very weak light conditions. If these conditions persist once germination is initiated, the emerging seedlings follow a skotomorphogenetic development in which etiolated seedlings that elongate in search of light nourish from seed reserves and have an heterotrophic life style. Upon light exposure, a photomorphogenetic program (also termed de-etiolation) is implemented: hypocotyl elongation is inhibited, the cotyledons open and expand, and the photosynthetic apparatus is assembled and activated to use light as the source of energy to grow as autotrophic organisms (Devlin *et al.*, 2007; Legris *et al.*, 2019). Light conditions fluctuate during the day, not only in quantity (photon amount or intensity) but also in quality (wavelengths or colors). These changes might provide information of crucial ecological value for the plants. In particular, changes in the quantity and, above all, the quality of light are often associated with the structure, density, and depth of the vegetation. They therefore inform about the position that a plant occupies in relation to the surrounding vegetation (Smith, 1982; Ballare *et al.*, 1990; Casal, 2013).

In natural environments, plants may grow at low densities, that is, quite isolated or widely spaced (as they are found for instance in arid environments). It is, however, much more common to find them close to other plants from the same or different species, reaching in some cases very high densities, as in prairies or forests. In agricultural settings, in which planting density is planned by farmers, usually plants of the same species (monocultures) are sown at relatively high densities. Either way, close vegetation proximity associated with high plant density may limit the availability of light to drive photosynthesis and compromise plant growth, development, and survival (Villalobos *et al.*, 1994; Robson *et al.*, 1996; Ballare *et al.*, 1997; Libenson *et al.*, 2002).

II. A range of light signals to announce plant presence and density

Usually, the solar irradiation that reaches the ground (known as daylight or sunlight) is rather constant in quality during the day. The spectrum of sunlight used for photosynthesis is known as photosynthetic active radiation (PAR) and shows a good correspondence to that visible to the human eye (from 400 to 700 nm) (Smith, 1982), although recently, far-red light (FR, 700–750 nm) has also been shown to contribute efficiently for photosynthesis (Zhen *et al.*, 2021). Sunlight maintains a natural high ratio of red (R, *c.* 660 nm) to far-red light (FR, *c.* 725 nm) (high R : FR > 1.2). Clouds act as non-selective diffusing filters, so weather conditions do not substantially alter spectral distribution (R : FR) but do influence intensity in the visible region (a fully overcast sky might reduce light quantity by > 90%) (Smith, 1982). By contrast, the proximity of vegetation, and hence variations in plant density, changes both the quality (R : FR) and intensity of the light reaching the plant (Casal, 2012). When sunlight impacts on plant tissues, photosynthetic pigments (chlorophylls and carotenoids) absorb most of the light in the PAR region, including

blue light (B, *c.* 400–500 nm) and R, whereas FR is reflected or transmitted through plant tissues (Smith, 1982; Ballare, 1999). Consequently, different plant densities result in different profiles of light qualities (and quantities). Also, as plants take more space when growing, the light profile is dynamic and might change with time.

When a plant grows isolated (low plant density), it receives direct sunlight with a natural high R : FR (Fig. 1a). When plant density increases and/or neighboring plants grow and get closer without overshadowing, sunlight mixes with the FR reflected by the nearby plants, resulting in a reduction in the R : FR of the incident light (intermediate or low R : FR < 0.8) without lowering light intensity (Casal, 2012; Roig-Villanova & Martinez-Garcia, 2016). This so-called *vegetation proximity* is indicative of the presence of nearby non-shading vegetation and acts, therefore, as an early warning of the proximity of potentially competing vegetation (Fig. 1a). When growing in an understory, the incoming light is filtered through the plant canopy and hence not only contains less photons but it shows a reduction in B and R (used for canopy photosynthesis) accompanied by a mild reduction in FR (that is transmitted through plant tissues) (Ballare, 1999; Martinez-Garcia *et al.*, 2010; Casal, 2012, 2013). As a result, this *moderate plant shade* is characterized by a strongly reduced R : FR (very low R : FR < 0.1) as well as a lower light intensity in the PAR region (Fig. 1a). In contrast with vegetation proximity, plant shade is a warning that photosynthesis is already compromised. Indeed, in very dense canopies, the light amount arriving at the forest floor level ranges from 1% to 10% of full sunlight, resulting in *dense plant shade* (Smith, 1982; Yanovsky *et al.*, 1995; Grubb, 1998; Valladares & Niinemets, 2008; Lei *et al.*, 2016).

The term plant shade in the literature might be associated with other factors besides a reduction in R : FR and PAR, including atmospheric and substrate conditions (Valladares *et al.*, 2016; Postma *et al.*, 2021). In this review, however, we will focus mostly on those that affect only R : FR and PAR (see later). In the laboratory, vegetation proximity can be mimicked by giving pulses of FR of a few minutes at the end of the light period and immediately before the start of the dark phase of the photoperiod, a treatment known as end-of-day-FR (EOD-FR) (Fig. 1b; Downs *et al.*, 1957; Adamse *et al.*, 1988; Lopez-Juez *et al.*, 1992; Martinez-Garcia & Garcia-Martinez, 1992; Devlin *et al.*, 1996, 1998; Martinez-Garcia *et al.*, 2000). Other treatments to reproduce signals informing about the presence of nearby plants involve enriching white light (W) with FR (W + FR) either under continuous light or photoperiod regimes (Lorrain *et al.*, 2008; Martinez-Garcia *et al.*, 2014). This treatment, generally coined as *simulated shade* (Smith & Whitelam, 1997; Crocco *et al.*, 2010; Casal, 2012; Gangappa *et al.*, 2013), is more versatile and it can be used to mimic different natural situations (Fig. 1b). By changing the intensity of the applied FR, the R : FR value can reach intermediate, low (0.8–0.1), or very low (< 0.1) levels (Roig-Villanova *et al.*, 2019). For clarity, we will define the different simulated shade conditions of low R : FR as *proximity shade*, that mimics vegetation proximity, and very low R : FR as *canopy shade*, that mimics moderate plant

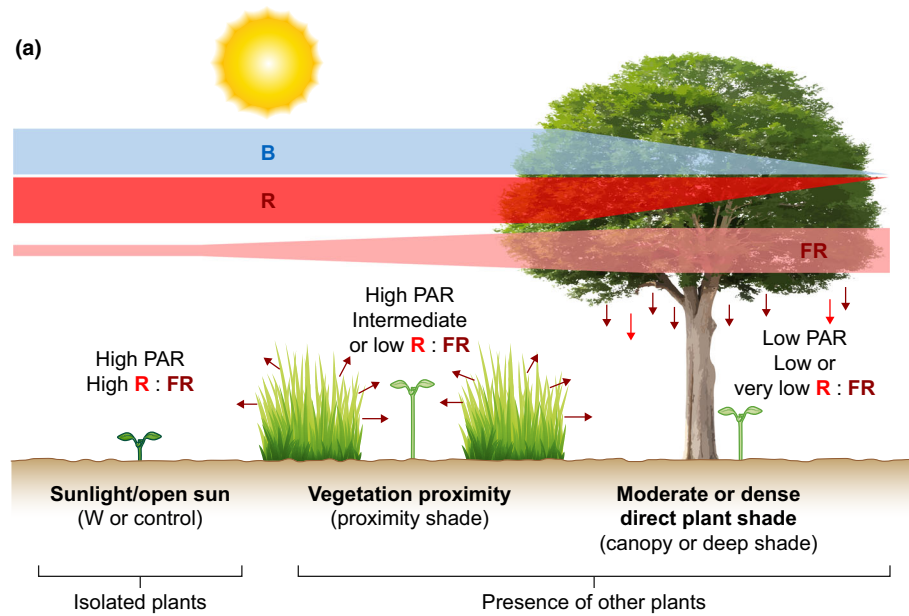


Fig. 1 Light characteristics of sunlight, vegetation proximity, and moderate or dense direct plant shade. These conditions are found in nature and can be mimicked in the laboratory. (a) Isolated plants receive sunlight that contains high amount of photosynthetic active radiation (PAR) of a high red (R) to far-red light (FR) ratio (R : FR). When vegetation density increases, sunlight is not filtered and PAR intensity (blue, B; and R) is unaffected; however, FR is reflected by neighboring vegetation, which results in an intermediate or low R : FR. We name these conditions as vegetation proximity. Under the shade of other plants, sunlight is filtered by the leaves, which lowers PAR; FR can be transmitted, which results in a low or very low R : FR. We name these conditions as moderate or dense direct plant shade. Parenthesis indicates the name of the laboratory treatments that mimic the corresponding natural condition. Red arrows, R filtered by a plant canopy; dark-red arrows, FR reflected or transmitted by vegetation. (b) Correspondence of the various conditions that can be found in nature (left column) and the light treatments that can be used in the laboratory (right column) to understand plant responses to shade. The middle columns indicate the relative R : FR and a representation of how they can be mimicked. White bulbs/rectangle, artificial illumination that provides high R : FR light; pink bulbs/rectangle, artificial FR illumination to lower the R : FR or provide an end-of-day FR treatment.

| Natural condition | Relative R : FR value | How it is mimicked | Laboratory term |
|---|--|--------------------|------------------------|
| Sunlight/open sun (unshaded) | High | | W or control |
| Vegetation proximity (close neighbors without direct shading) | Intermediate or low | | Proximity shade |
| Moderate direct plant shade | Low or very low | | Canopy shade |
| Dense direct plant shade | Very low PAR reduced | | Deep shade |
| Vegetation proximity | Very low when starting the dark period | | End-of-day FR (EOD-FR) |

shade (Fig. 1b). By additionally lowering the intensity of PAR relative to the control (e.g. by reducing the intensity of R and/or B), very dense plant shade environments can also be mimicked. We will refer to this plant shade simulation of very low R : FR and low PAR as *deep shade* (Fig. 1b). This latter condition results in stronger molecular changes and developmental phenotypes (Sessa *et al.*, 2005; Ciolfi *et al.*, 2013; de Wit *et al.*, 2016; Yang *et al.*, 2018) compared with canopy shade (Martinez-Garcia *et al.*, 2014), likely because of the combination of photoreceptor effects and/or the limited generation of photoassimilates under deep shade. Indeed, reductions in PAR (total irradiance) or just B intensity also inform about the presence of neighboring vegetation. Treatments with reduced B fluence rates (i.e. with standard W in which B is filtered out), known as low blue (low B) treatments, also induce developmental phenotypes similar to those of proximity and canopy shade (Pierik *et al.*, 2009; Keller *et al.*, 2011; Keuskamp *et al.*, 2011).

III. Avoidance and tolerance to shade: two divergent strategies to acclimate to the presence of other plants

To cope with the light gradients produced by the nearby presence of vegetation, plants have evolved two main strategies: *avoidance* (by readjusting growth and development to escape eventual shade conditions even at the expense of potentially detrimental effects on photosynthesis and defense); and *tolerance* (by adapting to grow under low light levels and adopting a conservative growth strategy). Plants that follow the first strategy are referred to as sun loving, shade intolerant or shade avoiding, and those that follow the second strategy are called shade tolerant (Valladares *et al.*, 2016).

Shade-avoiding species are those more sensitive to light starvation (Valladares & Niinemets, 2008; Valladares *et al.*, 2016). As such, typical shade-avoiding species would be one that grows normally in open spaces. If germinating in already shaded areas, or rapid growth of neighboring plants happens to

(a)

| Responses | Shade-avoidance | | | Shade-tolerance | | |
|--|-----------------|-----------------------------------|----------------------|-----------------|--|----------------------|
| | W or control | Proximity shade | Canopy or deep shade | W or control | Proximity shade | Canopy or deep shade |
| Elongation | | Strongly promoted | Promoted | | Slightly or no promoted | |
| Defense | | Reduced | | | Strong | |
| Overall performance • in high light • in low light | Good | | Poor | Stress | | Good |
| Photosynthetic performance | | High light compensation point | | | Low light | |
| Growth and resource use strategy | Rapid | High organ replacement, early DIS | | Slow | Conservative – slow organ replacement, delayed DIS | |

(b)

W W + FR W W + FR

Arabis thaliana (shade-avoiding) Cardamine hirsuta (shade-tolerant)

Fig. 2 Summary of some differential responses associated with either shade avoidance or shade tolerance strategies. (a) Plant responses known to differ between strategies are described in the various laboratory conditions used (as described in Fig. 1): white (W) or control, proximity shade and canopy or deep shade. (b) Aspect of seedlings of *Arabidopsis thaliana* and *Cardamine hirsuta* grown under W (control or unshaded) or W enriched with FR (W + FR, proximity of canopy shade) illustrating the differences in their hypocotyl length. FR, far-red light.

reduce R:FR, a shade-avoiding plant generally responds by rebalancing its growth to reach brighter areas. Indeed, following the detection of low R:FR, *Brassica rapa* seedlings allocate more carbon fixed in the cotyledons to the faster elongating hypocotyl (de Wit *et al.*, 2018). Stem elongation is one of a broader set of responses, known collectively as the *shade avoidance syndrome* (SAS), that besides changes in growth (e.g. by promoting elongation of stem-like structures and inhibiting leaf expansion) (Robson *et al.*, 1993; Kozuka *et al.*, 2005; Sasidharan *et al.*, 2010; Cagnola *et al.*, 2012; Ballare & Pierik, 2017; Romanowski *et al.*, 2021), includes adjustments in photosynthetic metabolism (by reducing the levels of photosynthetic pigments) (Casal *et al.*, 1990; Cagnola *et al.*, 2012; Patel *et al.*, 2013; Bou-Torrent *et al.*, 2015; Molina-Contreras *et al.*, 2019; Morelli *et al.*, 2021) or promotion of reproduction (by inducing flowering) (Halliday *et al.*, 1994; Cerdan & Chory, 2003; Kim *et al.*, 2008; Fig. 2). This is the case of the well-known model system *Arabidopsis thaliana*, tomato and most crops (Warnasooriya & Brutnell, 2014; Carriedo *et al.*, 2016). There are reports on other species (e.g. *Medicago sativa*) that show variations in some of these responses, such as inhibition (rather than promotion) of reproduction (Lorenzo *et al.*, 2019).

A typical shade-tolerant species would be one that normally grows very close to or under other plants, such as in prairies or forest understories. Although the reduced light levels resulting from overshading can cause light starvation in shade avoider species,

shade-tolerant plants are adapted to growth and survive under these conditions (Valladares & Niinemets, 2008).

IV. Tolerance to shade: an overview

Shade tolerance is an ecological concept that refers to the capacity of some plant species to live and thrive under low light conditions associated with high plant density environments (e.g. in the understory of forests and woodlands). This capacity can be found in both *trees* (e.g. beech and Norway spruce) (Delagrangue *et al.*, 2006; Ranade *et al.*, 2019) and *herbaceous* (e.g. the mustards *Cardamine hirsuta* or *Alliaria petiolata*, or some *Geranium* species) plants (Meekins & McCarthy, 1999; Gommers *et al.*, 2013; Morelli *et al.*, 2021; Table 1). The current view is that the strategy to tolerate shade is genetically determined. In some species, it is affected by ontogeny (it can change in different moments of their development, such as seedlings, young, and/or adult plants) and external factors (e.g. duration of the growing season or co-occurrence of multiple stresses), that might alter this capacity (Valladares & Niinemets, 2008).

V. Traits and responses associated with shade tolerance

As in shade avoidance, a large number of physiological, biochemical, and morphological traits are associated with shade

Table 1 List of shade-avoiding and shade-tolerant species mentioned in this manuscript.

| | Reference |
|--------------------------------------|--|
| Shade-avoiding species | |
| <i>Arabidopsis thaliana</i> | Molina-Contreras <i>et al.</i> (2019); Morelli <i>et al.</i> (2021) |
| <i>Capsella rubella</i> | Morelli <i>et al.</i> (2021) |
| <i>Capsella bursa-pastoris</i> | Morelli <i>et al.</i> (2021) |
| <i>Chenopodium album</i> | Morgan & Smith (1979) |
| <i>Geranium pyrenaicum</i> | Gommers <i>et al.</i> (2017) |
| <i>Medicago sativa</i> | Lorenzo <i>et al.</i> (2019) |
| <i>Pinus sylvestris</i> (Scots pine) | Ranade <i>et al.</i> (2019) |
| <i>Tradescantia sillamontana</i> | Benkov <i>et al.</i> (2019) |
| Shade-tolerant species | |
| <i>Alliaria petiolata</i> | Meekins & McCarthy (1999) |
| <i>Arabis alpina</i> | Morelli <i>et al.</i> (2021) |
| <i>Cardamine hirsuta</i> | Molina-Contreras <i>et al.</i> (2019); Morelli <i>et al.</i> (2021) |
| <i>Fagus sylvatica</i> (beech) | Delagrange <i>et al.</i> (2006) |
| <i>Geranium robertianum</i> | Gommers <i>et al.</i> (2017) |
| <i>Nasturtium officinale</i> | Morelli <i>et al.</i> (2021) |
| <i>Picea abies</i> (Norway spruce) | Ranade <i>et al.</i> (2019) |
| <i>Sysimbrium irio</i> | Morelli <i>et al.</i> (2021) |
| <i>Tradescantia fluminensis</i> | Benkov <i>et al.</i> (2019) |

tolerance. The variety of species, stages of development, experimental design, and shade conditions used in the literature, however, make it difficult to provide traits or features generally associated with shade tolerance (Valladares & Niinemets, 2008). Such shade tolerance-associated traits are expected to be opposed to those shown by shade-avoiding species (Fig. 2a). For instance, it is accepted that photoacclimation (i.e. the ability of plants to adjust their photosynthesis to changes in the incident light with specific phenotypic changes) diverges between shade-avoiding and shade-tolerant plants (Table 1). In the case of the shade-avoiding *A. thaliana* and the shade-tolerant *C. hirsuta*, a differential response to low R : FR in terms of photosynthetic pigment accumulation has been observed. Chlorophyll and carotenoid levels drop *c.* 20% in *A. thaliana* plants grown under low R : FR conditions, whereas the decrease is attenuated in *C. hirsuta* plants (Molina-Contreras *et al.*, 2019; Morelli *et al.*, 2021). In terms of light quantity, the shade-avoiding *A. thaliana*, *Capsella rubella*, and *Capsella bursa-pastoris* showed a lower capacity to acclimate to low light (low PAR) compared with the shade-tolerant species *C. hirsuta*, *Arabis alpina*, *Nasturtium officinale*, and *Sysimbrium irio*, that tolerate better the transfer to lower PAR (Morelli *et al.*, 2021). Conversely, the shade-avoiding *A. thaliana* showed a higher capacity to acclimate to intense light (high PAR) compared with the shade-tolerant *C. hirsuta* (Molina-Contreras *et al.*, 2019; Morelli *et al.*, 2021). A similar physiological behavior has been described for shade-avoiding and shade-tolerant species of the genus *Tradescantia*, a group of plants used to study the ecology of photosynthesis and the mechanisms of photoacclimation in plants (Benkov *et al.*, 2019; Ptushenko & Ptushenko, 2019; Fig. 2a). Another parameter related with the use of the light for the photosynthesis associated with shade tolerance is the light compensation point, which is the light intensity where the rate of photosynthesis (that results in CO₂

incorporation) exactly matches the rate of cellular respiration (that results in CO₂ loss). In low light, shade-tolerant species show a lower light compensation than shade-avoiding plants, reflecting the adaptation achieved by shade-tolerant plants to perform better in low light by minimizing CO₂ losses (Fig. 2a; Valladares & Niinemets, 2008). In addition, shade-tolerant plants also appear to maximize resistance to herbivore attack in the understory (Valladares & Niinemets, 2008). This is in contrast with shade-avoiding species, whose defenses are attenuated when grown in close proximity of other plants, which favors the attack of pathogens and herbivorous insects in these high-density and the low R : FR conditions associated (known as the growth–defense trade-off in high densities) (Ballare & Pierik, 2017; Pierik & Ballare, 2021). Altogether, these traits are expected to contribute to enhance survival of shade-tolerant species under low light (Fig. 2a). Consistently, seedlings of shade-tolerant species display lower mortality than those of shade-intolerant species when growing under low light (Valladares & Niinemets, 2008).

Shade-tolerant species are also found to have a conservative growth and resource use strategy. As they have slow rates of resource acquisition, these plants prioritize the preservation of existing organs over production of new ones, which results in, for instance, low leaf turnover rate (Valladares & Niinemets, 2008). A trait associated with this conservative strategy appears to be the delayed dark-induced senescence, as light deprivation caused by the dark can be considered an extreme case of shading. Indeed, *A. thaliana* is known to rapidly enter in senescence when transferred to deep shade or dark conditions (Liebsch & Keech, 2016). By contrast, DIS is delayed in the shade-tolerant *C. hirsuta* compared with the shade-avoiding *A. thaliana* (Paulisic *et al.*, 2021). A conservative strategy has also been associated with a low phenotypic plasticity to alter growth, such as elongation in response to low R : FR and/or low light, that is reduced or absent compared to shade-avoiding species (Morgan & Smith, 1979; Valladares & Niinemets, 2008; Morelli *et al.*, 2021; Fig. 2). Indeed, a negative correlation between stem elongation rate in response to low R : FR has been already reported for a range of herbaceous plants collected from various open and shade habitats (Morgan & Smith, 1979; Smith, 1982), highlighting that the elongation response to simulated shade correlates with the open or woodland habitats and, very likely, with the shade-avoidance and -tolerance habitat. In line with this negative correlation, *A. thaliana* and other species classified as shade-avoiding exhibit a range of elongation responses to low R : FR from moderate to strong, whereas *C. hirsuta* and other species classified as shade-tolerant display either no elongation or mild elongation in response to the same low R : FR treatment (Fig. 2b).

VI. Molecular regulation of shade avoidance in *A. thaliana*: a frame of reference to understand shade tolerance

Both shade-avoiding and shade-tolerance strategies involve a complex range of physiological, metabolic, and morphological responses. The molecular regulation of shade avoidance has been elucidated mostly from the studies of the model system *A. thaliana*

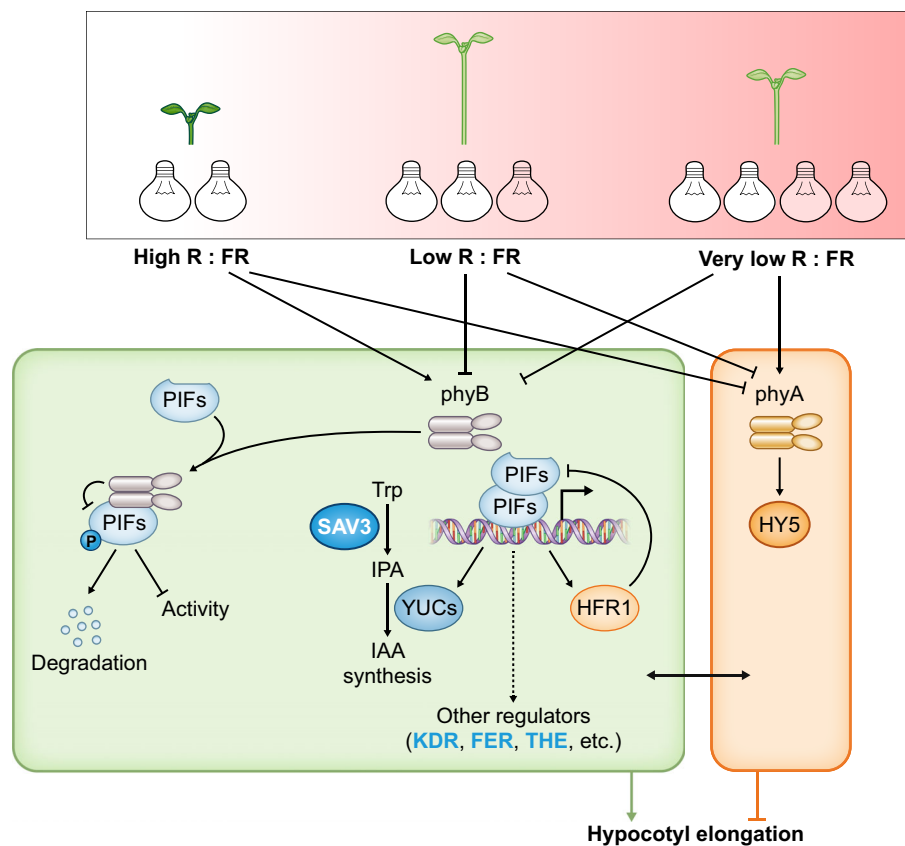


Fig. 3 Simplified cartoon of the main shade avoidance syndrome (SAS) regulatory components. These components have a role in the control of the hypocotyl elongation in response to changes in the red (R) to far-red light (FR) ratio (R : FR). In the upper panels, gradation of red color reflects the enrichment in FR and, therefore, the reductions in R : FR. Components in blue and orange/red colors refer to positively and negatively acting regulators, respectively. Arrows indicate positive regulation; blunt-ended arrows indicate negative regulation; dotted lines are interactions that involve multiple steps. HFR1, LONG HYPOCOTYL IN FAR-RED LIGHT 1; PIFs, PHYTOCHROME INTERACTING FACTORS; YUCs, YUCCAS; IAA, INDOLE-3-ACETIC ACID; IPA, INDOLE-3-PYRUVATE; phyA, PHYTOCHROME A; phyB, PHYTOCHROME B; SAV3, SHADE AVOIDANCE 3; TRP, KDR, KIDARI; FER, FERONIA; THE, THESEUS 1.

and the analyses on the effect of shade on elongation of hypocotyls, stems or petioles and, to a lower extent, the flowering regulation (Casal, 2012). From these responses, the shade-induced hypocotyl elongation of *A. thaliana* is likely the response that has better helped to understand shade-induced elongation at the genetic and molecular levels. As several reviews have extensively covered different aspects of this issue (Devlin *et al.*, 2007; Casal, 2012; Roig-Villanova & Martínez-García, 2016; Buti *et al.*, 2020a; Martínez-García & Moreno-Romero, 2020; Huber *et al.*, 2021), we will summarize the main findings to provide a frame of reference for approaching the molecular mechanisms regulating shade tolerance.

Phytochromes are the photoreceptors detecting changes in the R : FR signal. Phytochromes exist as two photoconvertible isomers, Pr and Pfr, whose relative abundance depends on the R : FR conditions. Under high R : FR (W), the photoequilibrium is displaced toward the active Pfr form and SAS responses are suppressed. Under low R : FR (W + FR), the photoequilibrium rebalances toward the inactive Pr form and SAS responses are induced (Casal, 2012, 2013; Legris *et al.*, 2019). From the five genes that encode phytochromes in *A. thaliana* (*PHYA-PHYE*), the one that encodes the photostable phyB is the major phytochrome controlling the shade-induced hypocotyl elongation response. Active phyB represses SAS responses under high R : FR conditions. The only photolabile phytochrome is phyA, that has an antagonistic role to phyB (Fig. 3). Under high R : FR and moderate or low R : FR reductions, most phyA is degraded. By contrast, under canopy or deep shade (very low R : FR) phyA accumulates to

enough levels to antagonize and prevent the excessive elongation responses triggered by the deactivation of phyB that would otherwise require a lot of energy and hence compromise survival (Martínez-García *et al.*, 2014; Yang *et al.*, 2018; Molina-Contreras *et al.*, 2019). Indeed, the elongation response of *A. thaliana* *phyA* hypocotyls ranges from similar to that of wild-type seedlings under high R : FR and proximity shade (low R : FR) to strongly enhanced under canopy or deep shade (very low R : FR) (Ciolfi *et al.*, 2013; Casal *et al.*, 2014; Martínez-García *et al.*, 2014; Yang *et al.*, 2018; Molina-Contreras *et al.*, 2019).

Active phyB interacts with PHYTOCHROME INTERACTING FACTORS (PIFs), which are members of the basic helix–loop–helix (bHLH) family of transcription factors. All eight members of the Arabidopsis PIF subfamily (PIF1–PIF8) have been shown to interact with active phyB (phyBfr), but only PIF1 and PIF3 interact with phyA (Balcerowicz, 2020). The best characterized PIFs are the so-called PIF quartet or PIFQ (PIF1, PIF3, PIF4, and PIF5) and PIF7. Whereas PIFQ are considered photolabile proteins, PIF7 is rather photostable. These PIFs collectively act as growth promoters whose activity is regulated by light conditions (Lorrain *et al.*, 2008; Li *et al.*, 2012; de Wit *et al.*, 2016; van Gelderen *et al.*, 2018). Genetic analyses indicate that only PIF7 and, to a lower extent, PIF4 and PIF5 have a central (positive) role in promoting the shade-triggered hypocotyl elongation response. Interaction of active phyB with PIFs results in their phosphorylation, which triggers PIF degradation (in the case of PIFQ) and/or inhibition of their transcriptional activity (Fig. 3). Inactivation of phyB by decreased R : FR prevents the interaction with PIFs that

are then dephosphorylated and recover their capacity to bind to their target genes. Among them, shade-activated PIFs rapidly and directly induce the expression of several *YUCCAs* (*YUCs*) (Li *et al.*, 2012; Kohnen *et al.*, 2016), which are genes encoding flavin monooxygenases enzymes involved in the production of the auxin indole-3-acetic acid (IAA), required for the shade-induced hypocotyl growth. This PIF-regulated auxin biosynthesis pathway is Trp-dependent and involves two sequential steps: the removal of the amino group from Trp by SHADE AVOIDANCE 3 (SAV3, a member of the family of transaminases) to generate indole-3-pyruvate (IPA); and the oxidative decarboxylation of IPA catalyzed by the *YUCs* to produce IAA (Fig. 3; Mashiguchi *et al.*, 2011; Zhao, 2014). Consistently, *sav3*, *pif7*, double *pif4 pif5*, and triple *pif4 pif5 pif7* mutant seedlings display attenuated elongation responses to shade.

PIFs also promote the expression of dozens of several *PHYTOCHROME RAPIDLY REGULATED (PAR)* genes (Kohnen *et al.*, 2016), such as *PAR1*, *PAR2* and *LONG HYPOCOTYL INFAR-RED LIGHT 1 (HFR1)*, which encode atypical non-DNA-binding bHLH proteins that heterodimerize with PIFs and inhibit their DNA-binding activity (Sessa *et al.*, 2005; Roig-Villanova *et al.*, 2006, 2007; Hornitschek *et al.*, 2009; Galstyan *et al.*, 2011). These atypical bHLHs function as negative SAS regulators that counteract the positive role of PIFs (Fig. 3). Other *PAR* genes encoding atypical bHLH, such as *KDR*, appear to inhibit the negative activity of the atypical *PAR1* and *PAR2* (Buti *et al.*, 2020b). Most other *PAR* genes, however, encode true transcription factors that include members of the homeodomain-leucine zipper class II (e.g. *ATHB2*, *ATHB4*) (Steindler *et al.*, 1999; Sorin *et al.*, 2009; Gallemi *et al.*, 2017), bHLH (e.g. *BIMs*, *BEEs*) (Cifuentes-Esquivel *et al.*, 2013) and B-BOX-CONTAINING (BBX) proteins (e.g. *BBX24*, *BBX25*) (Crocco *et al.*, 2010, 2015; Gangappa *et al.*, 2013), some of which are reported to act as either positive or negative SAS regulators.

PIF antagonists such as *HYPOCOTYL ELONGATED 5 (HY5)* have also been involved in the control of SAS responses. The expression of *HY5*, encoding a transcription factor of the basic-leucine zipper family that functions as a repressor of hypocotyl elongation in seedlings exposed to low or very low R:FR, has been shown to be activated by shade exposure, although changes in its expression are slower than *PAR* genes (Fig. 3; Ciolfi *et al.*, 2013). At the protein level, low and very low R:FR treatments stabilize *HY5* and promote the accumulation of this SAS repressor presumably to prevent seedlings from exhibiting excessive elongation (Pacin *et al.*, 2016; Ortiz-Alcaide *et al.*, 2019). The growth-repressing DELLAs, nuclear-pore complex components and chloroplast-derived signals also prevent an excessive response to shade, providing additional regulatory levels of this response (Djakovic-Petrovic *et al.*, 2007; Crocco *et al.*, 2015; Gallemi *et al.*, 2016; Ortiz-Alcaide *et al.*, 2019). A picture arising from the genetic characterization of this plethora of factors and their role in the control of SAS is that shade avoidance is regulated by a gas-and-brake mechanism that involves a complex balance of a network of positive and negative interactions, eventually causing hypocotyls to elongate (Buti *et al.*, 2020a,b; Fig. 3).

As mentioned, the low B signal informs about the reduction in light intensity associated with the direct plant shade (Fig. 1). In contrast with low R:FR, perceived by the phytochromes, the low B signal is perceived by the cryptochrome photoreceptors, that in *A. thaliana* are *CRY1* and *CRY2* (Pierik *et al.*, 2009; Keller *et al.*, 2011; Keuskamp *et al.*, 2011). Molecular analyses indicated that both auxin and brassinosteroids are important for the low B-enhanced hypocotyl elongation in *A. thaliana* (Keuskamp *et al.*, 2011). In contrast with the low R:FR-induced hypocotyl elongation, it does not involve changes in auxin levels or sensitivity (Pedmale *et al.*, 2016). Genetic analyses indicate that *PIF4* and *PIF5*, which bind active phyB, also interact with *CRY1* and *CRY2*. This makes these PIFs integrators of different light information associated with direct plant shade (low R:FR and low B) (Keller *et al.*, 2011; Pedmale *et al.*, 2016). The idea that the two shade-associated light signals act via different pathways is supported by transcriptomic and genetic evidence that indicate that in low R:FR, PIFs induce the expression of many anabolic processes in the hypocotyl, including sterol biosynthesis, whereas low B induces the expression of catabolic processes and promotes autophagy, which is important for hypocotyl growth promotion (Ince *et al.*, 2022).

VII. Comparative analyses to understand shade tolerance

Comparative analyses of related plants displaying diverging phenotypes, such as morphological changes caused by development or responses to the environment, have proven useful for the identification of genes that cause the phenotypic diversity. Sequencing the genetic material of the related plants has the potential to identify sequences that differentiate one organism from another. However, only a fraction of this sequence diversity is expected to contribute to phenotypic variation. Hence, an additional step would be necessary in establishing the causal relationship between the identified changes in genotype and changes in phenotype, that is, which of the identified differences in the genome cause the specific differences in the phenotype of interest (Hay *et al.*, 2014). To explore why shade-tolerant species hardly show an elongation response when exposed to shade-inducing light signals, the use of comparative analyses between related herbaceous species showing divergent elongation responses to simulated shade has proven to be a useful strategy. We will cover two case studies involving different pairs of related plant species that have improved our understanding of the molecular and genetic regulation of shade tolerance.

VIII. Comparison of two *Geranium* species: a transcriptional approach

Two wild *Geranium* species from contrasting habitats were chosen: *G. robertianum*, which grows in a wide amplitude of conditions including forest understories, and *G. pyrenaicum*, which occurs in open habitats. Seedlings from both species had non-responsive hypocotyls to simulated shade, whereas only *G. pyrenaicum* elongated the petioles of the cotyledons or true leaves (Gommers

et al., 2017, 2018). Under unshaded conditions (W), the growth rate of the second leaf petioles showed two peaks, one in the middle of the morning (ZT5–6) and another one at the beginning of the night (ZT16–18). Both species elongated their petioles soon (2 h) after simulated shade treatment. However, the shade avoider *G. pyrenaicum* enhanced the petiole growth rate toward the end of the day (after 11–12 h of the beginning of the exposure to low R : FR) and during the night, whereas the shade-tolerant *G. robertianum* suppressed it compared with W-grown plants. As a result, no net difference in growth between the high and low R : FR treatments was detected after 24 h in the shade-tolerant *G. robertianum* (Gommers *et al.*, 2017). These results indicated that: both species are able to sense and respond to reductions in the R : FR signal but; a differential growth suppression in *G. robertianum* at the end of the light period results in its lack of elongation.

Based on these results, transcriptomic analyses were done in the most responsive part of the petiole after 2 and 11.5 h of low R : FR treatment and corresponding controls grown in W (high R : FR). Both species showed strong changes in gene expression. Previously, it had been shown in shade-avoiding species that low R : FR treatments led to expression changes that promoted elongation, but also reduced defense responses against herbivorous insects and both necrotrophic and biotrophic pathogens involving jasmonic acid-(JA-) or salicylic acid-mediated signaling (de Wit *et al.*, 2013; Chico *et al.*, 2014; Ballare & Pierik, 2017). The novelty in the comparative study using *Geranium* species was that genes related to JA-mediated defense only appeared to be substantially down-regulated in the shade-responsive *G. pyrenaicum*. Consistently with these expression patterns, low R : FR treatment increased lesions caused by infection with the necrotrophic pathogen *Botrytis cinerea* in *G. pyrenaicum* but decreased them in *G. robertianum* (Gommers *et al.*, 2017).

Authors also identified *Geranium KIDARI* (*KDR*), *FERONIA* (*FER*), and *THESEUS1* (*THE1*) genes as induced in the shade-avoiding *G. pyrenaicum* but not in *G. robertianum* (Fig. 3). Functional studies in *A. thaliana* confirmed a role for the *A. thaliana* orthologs *KDR*, *FER*, and *THE1* in promoting the shade-induced elongation of petioles or hypocotyls. *KDR*, an atypical bHLH, interacts and interferes with several SAS negative regulators, including *PAR1*, *AIF2/4*, *IBH1*, and *IBL1*, but not *HFR1* (Buti *et al.*, 2020b). Importantly, no *HFR1* homologs were found in *Geranium* (Gommers *et al.*, 2017). *FER* and *THE1*, members of the family of receptor-like kinases (CrRLKs) known to regulate cell elongation (Lindner *et al.*, 2012; Wolf & Hofte, 2014), were not previously associated with photoreceptor responses. Together, these comparative approaches identified components that might suppress growth in shade-tolerant species. They also provided evidence that shade-divergent species appeared to use the same genetic components to regulate opposed responses to the proximity of vegetation (Gommers *et al.*, 2017).

IX. Comparison between two mustard species – *A. thaliana* vs *C. hirsuta*: a genetic approach

Working with species amenable for genetic analyses provides advantages when performing comparative studies. This was the

goal when selecting *C. hirsuta*, a mustard species naturally found in a broad range of habitats including shaded and semi-shaded areas (Hay *et al.*, 2014; Molina-Contreras *et al.*, 2019). The advantage of *C. hirsuta* over the other shade-tolerant species is that, like *A. thaliana*, it has been developed as a versatile experimental system. In addition to short generation time, small size, inbreeding habit, abundant progeny, and easy large-scale cultivation (Hay *et al.*, 2014), *C. hirsuta* is also a diploid species with a small genome and eight chromosomes that have been sequenced (Gan *et al.*, 2016). Very importantly, the possibility to perform genetic transformation by floral dipping and to chemically mutagenize populations, together with the availability of a dense genetic map, represent unique tools to identify the genetic components and molecular mechanisms underlying diversification of responses to a changing environment.

Despite the lack of elongation and photosynthesis responses when exposed to a range of simulated shade conditions, *C. hirsuta* seedlings are able to respond to shade by rapidly inducing the expression of typical gene markers of shade perception (e.g. the *C. hirsuta PIL1*, *ChPIL1*, or *ChATHB2* genes), which indicates that *C. hirsuta* is able to sense and respond to reductions in R : FR, like the *Geranium* species. Importantly, elongation was not compromised by other treatments such as exogenous application of growth stimulants (Hay *et al.*, 2014; Molina-Contreras *et al.*, 2019). A genetic screening for *C. hirsuta* mutants showing a hypocotyl elongation response to low R : FR exposure led to the identification of the recessive *slender in shade 1* (*sis1*) mutant that indicated that in *C. hirsuta* shade perception also triggers the promotion of hypocotyl elongation. However, the lack of shade-induced hypocotyl elongation was caused by specific components (such as *SIS1*) that suppressed the elongation in a shade-dependent manner. Because *sis1* seedlings have loss-of-function mutations in *PHYA*, it was concluded that the phyA photoreceptor was involved in the shade tolerance phenotype of *C. hirsuta* (Molina-Contreras *et al.*, 2019). Mutations of the SAS negative regulator *HFR1* in *C. hirsuta* also resulted in a *sis* phenotype (Paulisic *et al.*, 2021). These findings suggests that other SAS negative regulators are also required to implement shade tolerance.

Comparative genetic analyses indicated that *A. thaliana phyA* seedlings only showed a distinct phenotype under canopy shade conditions (very low R : FR), whereas phyA-defective *C. hirsuta sis1* seedlings displayed a mutant phenotype also under proximity shade (intermediate and low R : FR). These results suggest that *C. hirsuta phyA* (*ChphyA*) has a stronger activity than *AtphyA*, differences that might account for the attenuated shade response of *C. hirsuta* (Fig. 4; Molina-Contreras *et al.*, 2019). By contrast, phyB activity in *C. hirsuta* (*ChphyB*) seems attenuated compared with *A. thaliana*. Consistently, weak *A. thaliana phyB-4* mutant seedlings display an attenuated (though not abolished) shade-induced hypocotyl elongation (Molina-Contreras *et al.*, 2019). Whereas there are no data about the molecular basis for the attenuated *ChphyB* activity nor to its functional role for the shade tolerance implementation in *C. hirsuta*, the enhanced *ChphyA* activity appears to result from increased expression and protein abundance. In addition, complementation of the *A. thaliana phyA* mutant plants with the *ChPHYA* or *AtPHYA* genes supported the

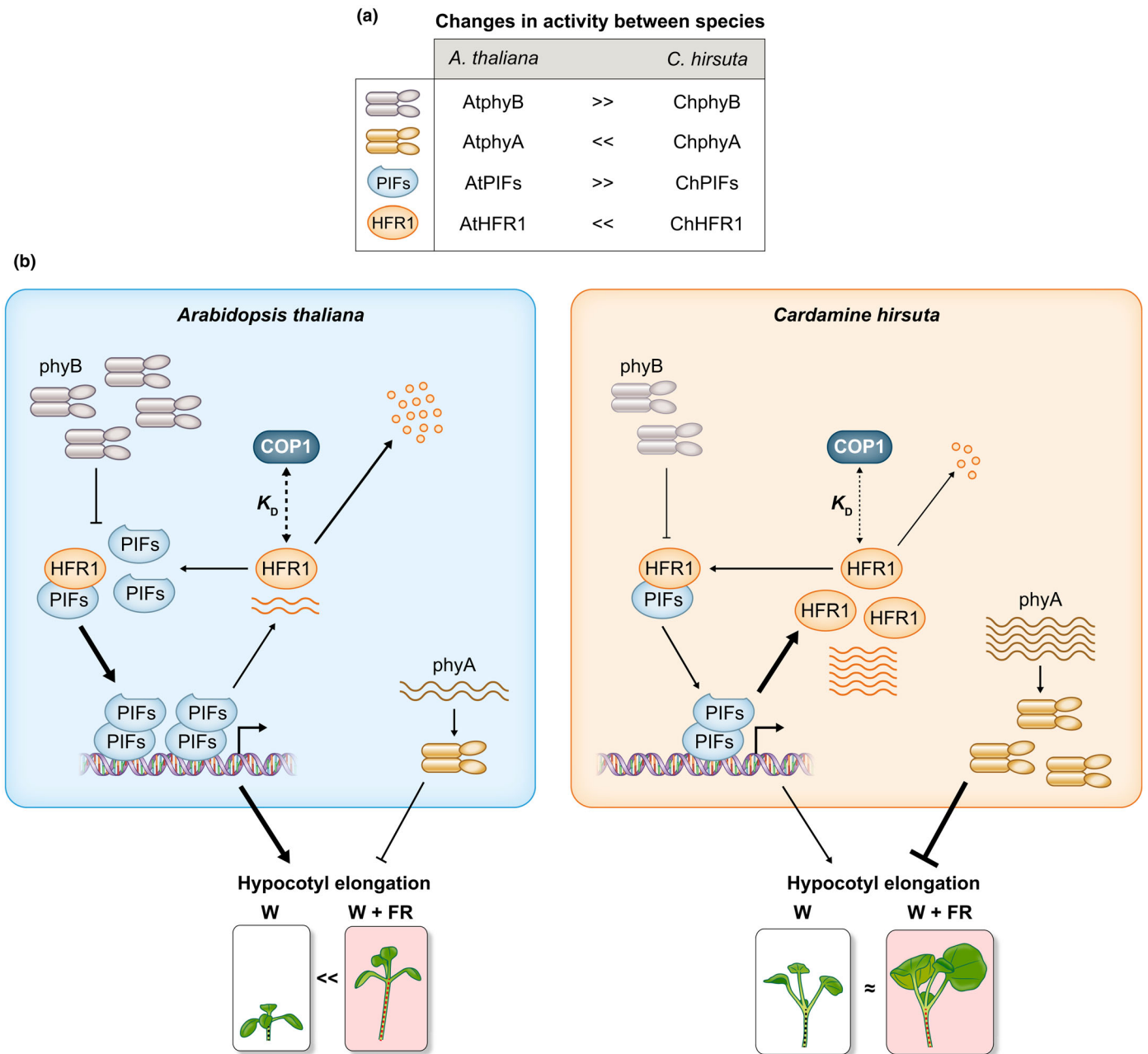


Fig. 4 Regulatory components of the shade avoidance syndrome (SAS) and molecular mechanisms currently known to have a role in the shade tolerance implementation. (a) Their role has been assessed based on the comparative studies between the shade-avoiding *Arabidopsis thaliana* and the shade-tolerant *Cardamine hirsuta*. Signs indicate whether their activity is enhanced (>>) or attenuated (<<) in *A. thaliana* compared with *C. hirsuta*. (b) Shade inhibits phytochrome B (phyB) activity by displacing phytochrome photoequilibrium toward the inactive form, allowing PHYTOCHROME INTERACTING FACTORS (PIFs) to promote the expression of shade avoidance-related genes, such as *LONG HYPOCOTYL IN FAR-RED LIGHT 1* (*HFR1*). *HFR1* heterodimerizes with PIFs and inhibits their DNA-binding ability. As a result, *HFR1* attenuates hypocotyl elongation. *HFR1* abundance is also affected by its interaction with CONSTITUTIVE PHOTOMORPHOGENIC 1 (*COP1*), that leads to its degradation. Shade allows accumulation of phytochrome A (phyA), that also inhibits hypocotyl elongation. In *A. thaliana* seedlings, the balance between these positive and negative factors results in the promotion of hypocotyl elongation in response to shade. In *C. hirsuta*, activity of phyB is attenuated compared with *A. thaliana*. Moreover, the enhanced expression, abundance, and stability of *HFR1* (by its weaker interaction with *COP1*) inhibit more effectively PIF action than in *A. thaliana*, whose activity is also attenuated in *C. hirsuta*. Both changes alter the PIF-*HFR1* balance in *C. hirsuta*, resulting in lower PIF transcriptional activity. PhyA abundance and activity is also enhanced in *C. hirsuta* compared with *A. thaliana*. As a consequence, shade-induced hypocotyl elongation is effectively suppressed in this species. Thickness of the lines connecting components reflects the strength and directionality of the activation (ending with arrowheads) or repression (ending with blunt ends). Dashed lines with two arrowheads represent the dissociation contacts (K_D) estimated for the interaction between the connected components (*COP1* and *HFR1*).

conclusion that ChphyA also has a higher intrinsic activity than AtphyA (Molina-Contreras *et al.*, 2019) which sustains the enhanced shade-induced suppression activity to implement shade tolerance (Fig. 4).

The repressor role of HFR1 in shade-unresponsive *C. hirsuta* hypocotyls also relied on an enhanced HFR1 total activity in this species caused by: an increased expression of the ChHFR1-encoding gene; and a much-enhanced ChHFR1 stability compared with that of AtHFR1. The enhanced stability of ChHFR1 was due to its lower binding affinity to CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) compared with that of AtHFR1 (Paulisic *et al.*, 2021). As HFR1 central activity is to interact with PIFs and inhibit their transcriptional activity, enhanced HFR1 activity in *C. hirsuta* (combined with an attenuated PIF activity) also results in a differently balanced PIF-HFR1 module (Fig. 4). As a consequence, reduced PIF activity also attenuates other PIF-mediated responses such as warm temperature-induced morphogenesis and dark-induced senescence (Paulisic *et al.*, 2021).

X. The implementation of a shade tolerance habit: a working model

Shade-tolerant species (as shade avoiders) carry phytochrome photoreceptors in their genomes to detect changes in R:FR conditions. Indeed, detection of this signal drives rapid changes in the expression of several well-known shade-marker genes (e.g. orthologs of *ATHB2*), confirming these species sense and respond to changes in the R:FR signal (Gommers *et al.*, 2017; Molina-Contreras *et al.*, 2019). Therefore, the molecular components that explain the differences in elongation between shade avoider and shade-tolerant species do not involve blindness to the shade signal but stronger mechanisms to repress the shade-induced promotion of elongation that, at least in *Geranium*, requires a few hours to be implemented (Gommers *et al.*, 2017). Shade avoidance and shade tolerance regulation share genetic components (up to now phyA, phyB, and the PIF-HFR1 module in mustards; and likely *KDR*, *FER*, and *THE1* in *Geranium*). These results unveil the importance of modulating photoreceptor (phyA and phyB) and downstream transducers (e.g. PIF-HFR1 module) activities to properly adapt cultivars to thrive in habitats with disparate light conditions (e.g. sunlight and shade). A simple model considers that in shade avoider species the balance of positive and negative regulators of SAS is in favor of the positive factors. In shade-tolerant plants, an enhanced activity of negative regulators would re-balance the positive and negative activities, hence resulting in no apparent SAS responses (Fig. 4b).

Shade avoidance responses were presumably acquired when shade habitats became more prevalent by the diversification of early vascular plants. Their expansion produced dense plants communities and canopies (*c.* 375–400 million years ago) (Mathews, 2006, 2010). This new environment led to select mechanisms to tolerate the proximity and shade of other plants, and allowed plants to establish in the understory and to respond appropriately by not elongating in these crowded environments. The disperse occurrence of shade tolerance traits within the Brassicaceae family tree (i.e. rather than in clusters) (Morelli *et al.*, 2021) suggests that the

genetic changes to gain a shade tolerance strategy can appear independently in evolution. This implies that: the number of molecular steps involved is low; and/or different changes can result in a shade-tolerant phenotype. In mustards, however, a relatively high number of molecular changes have been described between shade-avoiding and shade-tolerant species (e.g. differences in gene expression, phyA and phyB activities and HFR1 stability have been reported between *A. thaliana* and *C. hirsuta*). This suggests that higher-order mechanisms might coordinate the biological activity and/or abundance of several suppressors and activators of the shade-induced hypocotyl elongation. If confirmed, these mechanisms would allow plants to switch between shade avoidance and tolerance with little changes, hence easily adapting to new habitats involving different light environments.

XI. Some applications for a more sustainable food production

Agriculture in the 21st century needs to provide enough food for a growing human population while preserving our natural environment. This objective, which is at the core of the 2030 Sustainable Development Goals proposed by the United Nations, requires agriculture to develop sustainable solutions to increase food production in a climate change scenario without increasing land use. For the time being, alternative approaches such as vertical agriculture farming are still a long way from being sustainable. Current agricultural practices have a range of undesired environmental effects including the generation of *green deserts*, that is, a term coined by journalists and conservation biologists that refer to monocultured fields and orchards with a very low biodiversity and resilience (Acosta, 2011; Nakata, 2019). Understanding SAS can eventually lead to the development of productive crop varieties with attenuated SAS responses that grow well at high planting density, maximizing the land use. However, high planting density fields likely will require even a higher input of fertilizers and/or pesticides to result in high productivity, further reducing biodiversity and sustainability. Alternatively, this crop lines with attenuate SAS responses can help to obtain varieties more adequate for intercropping practices, considered to promote resilience to the effects of climate change (Faucon *et al.*, 2017; Tilman, 2020).

An additional way in making agriculture more resilient is by actively promoting biodiversity to create richer and more complex ecosystems where crops interact with wild plants, animals, and microorganisms (fungi or bacteria). With this premise, research to understand how shade tolerance is achieved might guide and contribute for agriculture transformation by applying this knowledge to beneficial weeds or *cover crops*, non-cash crops that are planted not for being harvested but to cover the soil and increase their quality. Although cover crops can be used for different purposes, such as replacing fallow, they can also be used for weed control, protecting the soil to prevent compaction, increasing soil moisture, or providing green manure, applications compatible with established cultures such a fruit orchards (Runck *et al.*, 2020; Lamichhane & Alletto, 2022). In these cases, cover crops coexist with the cash crop and, therefore, they grow shaded by the cultivated plants. Engineering of SAS components can help to

make them less shade avoiders (more shade tolerant) and enhance their growth when shaded or semi-shaded by crop plants. The types of beneficial weeds that can improve the health and resilience of our crops are mainly two: those that provide refuge to beneficial animals (e.g. predatory and parasitic insects), and those that can enhance soil quality. Legumes can fix nitrogen, hence benefiting other plants that grow closely. But many other plants can provide benefits for the soil by a different mechanism. Disease control can be improved by increasing microbial diversity in the soil, which is influenced by plants. Altogether, identifying the molecular mechanisms underpinning suppression of SAS has the potential to show how different strategies of adaptive plasticity can be regulated and inform crop-breeding programs targeted at minimizing yield losses, which are caused by wasteful carbon investments in non-harvestable stems (Carriedo *et al.*, 2016) and suppressed immunity. In summary, to provide more complex agrosystems in which food production is compatible with thriving wildlife.

XII. Important questions for the future

- (1) Do other SAS regulators (e.g. HY5, PAR1) also have a role in shade tolerance implementation?
- (2) Is shade tolerance caused by evolution changes in the activity of a broad range of suppressors and activators of elongation?
- (3) Or are there more simple mechanisms that coordinate the biological activity and/or abundance of the suppressors and activators of elongation?

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Competing interests

None declared.

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