



Tansley insight

Light and temperature regulation of leaf morphogenesis in Arabidopsis

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Summary

Leaves are the main photosynthetic organs in plants, and their anatomy is optimized for light interception and gas exchange. Although each species has a characteristic leaf anatomy, which depends on the genotype, leaves also show a large degree of developmental plasticity. Light and temperature regulate leaf development from primordia differentiation to late stages of blade expansion. While the molecular mechanisms of light and temperature signaling have been mostly studied in seedlings, in the latest years, research has focused on leaf development. Here, I will describe the latest work carried out in the environmental regulation of Arabidopsis leaf development, comparing signaling mechanisms between leaves and seedlings, highlighting the new discoveries, and pointing out the most exciting open questions.

I. Introduction

Developmental plasticity is the capacity to adapt an organism's morphology to the prevailing environmental conditions. As sessile organisms, plants are highly dependent on this feature, and given the prominent role of leaves in light harvesting and gas exchange for photosynthesis, plasticity in leaf development has likely a substantial impact on plant survival and reproduction. In this review, I will focus on plant responses to light and temperature, two

of the most dynamic environmental factors with a strong effect on all aspects of plant physiology.

Leaf development is regulated by light intensity, light quality and light direction. In some cases, these responses are due to changes in photosynthesis and energy availability, but most frequently photosensory receptors are involved in the perception of light signals. Four families of wavelength-specific light receptors have been involved in light-regulated leaf development: phytochromes (phy; Legris *et al.*, 2019), cryptochromes (cry; Ponnu & Hoecker, 2022), phototropins (phot; Legris & Boccaccini, 2020) and UVB RESISTANCE8 (UVR8; Podolec *et al.*, 2021). For a description of the signaling mechanisms of these photoreceptors, see Box 1. Temperature perception has been mostly studied in seedlings,

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Box 1 Light signaling mechanisms regulating hypocotyl growth

Arabidopsis has five phytochromes, with phyB having the strongest role in development of light-grown plants. Phytochromes are activated by red (R) and inactivated by far-red (FR) light. This allows them to not only differentiate light from darkness, but also to perceive the presence of neighboring plants. Green tissues absorb mostly R and blue light (B) but transmit and reflect FR. Thus, in the presence of neighboring plants the red to far-red ration (R:FR) is reduced, inactivating phyB and triggering shade avoidance responses. In addition to FR, phytochromes are inactivated by a light-independent reaction, which increases with warmer temperatures. This allows phyB to perceive not only light but also temperature (Legris *et al.*, 2019). Cryptochromes (cry1 and cry2 in Arabidopsis) are activated by B. They regulate responses to the dark to light transition and contribute to shade avoidance responses perceiving changes in B intensity (Ponnu & Hoecker, 2022). UVB is perceived by UV RESISTANCE LOCUS 8 (UVR8). UVR8 not only contributes to protection against UVB damage through changes in metabolism but also regulates morphological responses (Podolec *et al.*, 2021).

These three families of photoreceptors regulate plant development mainly through changes in transcriptional regulation. Activated phytochromes, cryptochromes and UVR8 localize to the nucleus where they inhibit the E3 ligase complex CONSTITUTIVE PHOTOMORPHOGENIC 1- SUPPRESSOR OF PHYA-105 (COP1-SPA). COP1-SPA target photomorphogenesis-promoting transcription factors, which are stabilized by activated photoreceptors. In addition, phytochromes, cryptochromes and UVR8 directly interact with transcription factors regulating their activity. PHYTOCHROME INTERACTING FACTORS (PIFs) are bHLH transcription factors with a prominent role in photomorphogenesis and thermomorphogenesis. Active phytochromes and cryptochromes directly interact with PIFs, inactivating them and in many cases triggering their degradation. UVR8 also inhibits PIFs but indirectly, through its interaction with COP1.

Phototropins (phot1 and phot2 in Arabidopsis) are also activated by B and UV, but they act in different processes. In seedlings, they allow hypocotyl bending toward the light. Phototropins are plasma membrane-associated proteins with light-regulated kinase activity. Upon B perception, their kinase activity is derepressed, and they phosphorylate their targets. Among them, the most important for hypocotyl phototropism are NON-PHOTOTROPIC HYPOCOTYL 3 (NPH3), ROOT PHOTOTROPISM 2 (RPT2) and PHYTOCHROME KINASE SUBSTRATE (PKS) proteins (Legris & Boccaccini, 2020; Sullivan *et al.*, 2021; Waksman *et al.*, 2023). The specific action of these proteins in hypocotyl bending is unknown but loss of function mutants show defects in this response.

where three mechanisms have been described: phyB, the transcription factor PHYTOCHROME INTERACTING FACTOR7 (PIF7) and the transcriptional regulator EARLY FLOWERING3 change their abundance or activity in response to temperature. While their role has been described in hypocotyl elongation, it is likely that at least phyB and PIF7 also regulate leaf development in response to temperature changes, since their function in light signaling is similar in seedlings and leaves (Casal & Balasubramanian, 2019; Casal & Fankhauser, 2023). Light and/or temperature regulate all stages of leaf development, from early primordia differentiation to late leaf expansion and positioning (Roig-Villanova & Martínez-García, 2016; Fouracre & Poethig, 2020;

Box 2 Leaf development

Leaves start developing in the SAM, where the central zone provides new cells that following an auxin maxima will develop into primordia in the peripheral zone. Early in development the primordium is patterned, defining the adaxial-abaxial axis. The adaxial and abaxial domains are defined by sets of genes that antagonistically regulate those in the opposite domain, and whose expression domains are regulated by small RNAs. The establishment of the adaxial and abaxial domains is a key step to generate a flat organ and for leaf expansion. In the juxtaposition of the adaxial and abaxial domains is situated the middle domain, involved in lamina outgrowth (Nakayama *et al.*, 2022). During a short time leaf growth is driven by cell proliferation, but final leaf size and shape depends largely on cell expansion. One exception is the development of stomata, which involves cell division later in development. Stomata develop from protodermal cells that differentiate into meristemoid mother cells, a process controlled by SPEECHLESS (SPCH). These later produce meristemoids, which eventually differentiate into guard mother cells (through the action of MUTE) that divide to form guard cells (mediated by FAMA). SPCH, MUTE and FAMA are bHLH transcription factors. Two other bHLH transcription factors, SCREAM 1 (SCRM1) and SCRM2 modulate stomata development binding to the above-mentioned transcription factors and stabilizing them (Wei *et al.*, 2020).

Casal & Fankhauser, 2023). For the nonspecialist reader, a description of the steps involved in leaf morphogenesis is presented in Box 2.

Here, I will describe the effect the ways in which plants adapt leaf anatomy to the prevailing light and temperature conditions, focusing on the latest research performed in Arabidopsis. Light and temperature signaling mechanisms have been mostly studied in the context of hypocotyl elongation. So, I will compare the well-established signaling mechanisms in hypocotyls with those recently described in leaf development, highlighting the differences.

II. Early leaf development

Leaves start developing in the shoot apical meristem (SAM). Shoot apical meristem activity and leaf formation require light, which acts through photosensory receptors as well as through products of photosynthesis. Photosynthesis-derived sugars, or light perceived by phytochromes and cryptochromes can activate the expression of the homeodomain transcription factor WUSCHEL, which promotes stem cell fate. This involves the activation of the TOR kinase, which in the case of photoreceptors is mediated by inactivation of the E3 ligase CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1) (Pfeiffer *et al.*, 2017). Moreover, reducing the red to far-red ratios (R:FR) without changing the photosynthetically active radiation causes arrest of leaf primordia growth, pointing at a role of light as a developmental signal. These early effects of light on leaf development are mediated by cytokinin, which is required for cell division and is degraded in primordia in response to shade (Carabelli *et al.*, 2007; Pfeiffer *et al.*, 2017).

Another effect of light on the SAM is the regulation of vegetative phase change. Leaves of plants growing in low light (LL) resemble

juvenile leaves of plants grown in high light intensity (HL) and recent evidence suggests that the anatomical features of these types of leaves optimize photosynthesis in LL. Interestingly, this is due to a delay in vegetative phase change in LL conditions (Xu *et al.*, 2021). In LL, the expression of miR156/157 is enhanced, and their targets, the transcription factors involved in meristem transitions SPB-LIKE9 (SPL9), SPL13 and SPL15 are reduced. This response to light is mostly mediated by sugars with a minor role of photoreceptors.

Both for regulation of SAM activity, as for vegetative phase transition, the light signal is perceived in leaves, and the identity of the long-distance signal is still unclear (Pfeiffer *et al.*, 2017; Fouracre & Poethig, 2020; Xu *et al.*, 2021).

III. Petiole and blade growth

Compared with full sunlight, low R : FR caused by the presence of neighbors promotes petiole elongation and inhibits blade expansion, by inactivating phyB and allowing PIF7-mediated auxin

synthesis (Fig. 1a). The different responses in blades and petioles were related to differential auxin sensitivity (de Wit *et al.*, 2015). In deep canopies, inactivation of cry1 due to reductions in blue light also causes elongation of the petiole (Keller *et al.*, 2011; Ponnu & Hoecker, 2022).

While the response in the petiole is very similar to the responses to shade observed in hypocotyls, the analysis of leaf blade size reduction allowed to identify new signaling mechanisms. Importantly, while at a later stage of development shade only modulates cell expansion, early in development inhibition of phytochromes by end of day FR treatments inhibits cell division (Romanowski *et al.*, 2021). Transcriptomic analyses showed that phyB regulated multiple mechanisms related to cell proliferation, such as DNA replication, DNA repair and cell division. One well-described mechanism involves PIF7-mediated repression of the transcriptional regulators ANGUSTIFOLIA3 (AN3), GROWTH REGULATING FACTOR1 (GRF1), GRF3 and GRF5, which promote cell proliferation (Hussain *et al.*, 2022).

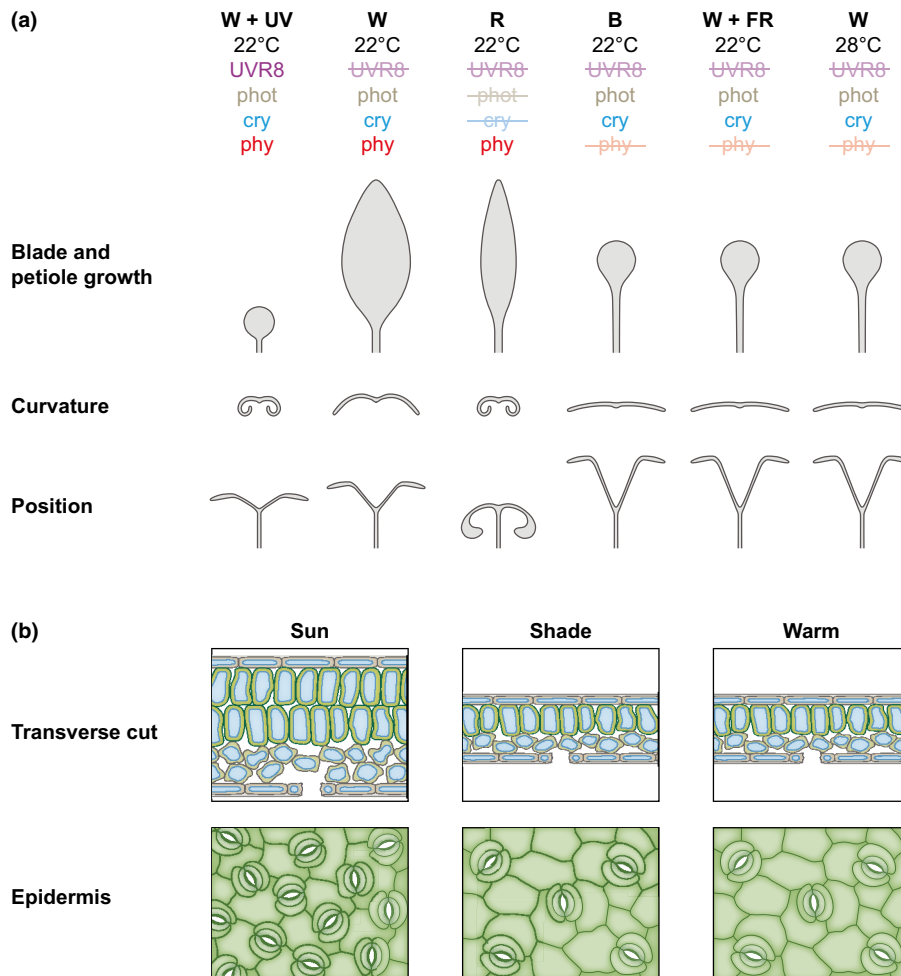


Fig. 1 Effects of light and warm temperatures on leaf development in Arabidopsis. (a) Schemes of projected leaf shape, transverse cuts and side views of Arabidopsis plants grown in various light and temperature conditions. B, blue light; cry, cryptochromes; FR, far-red light; phot, phototropins; phy, phytochromes; R, red light; UV, ultraviolet B light; UVR8, UV RESISTANCE LOCUS 8; W, white light. Strikethrough means that these receptors are inactive or less active than in other conditions. (b) Drawings of transverse cuts (upper panel) and epidermis (lower panel) of plants growing in sunlight, shade, or warm conditions, highlighting leaf thickness, palisade development and stomata development.

UVB inhibits leaf growth inhibiting cell division in a UVR8-independent manner but UVR8 contributes to sustain leaf growth in this condition by enhancing epidermal cell expansion (Wargent *et al.*, 2009; Podolec *et al.*, 2021). Phototropins also promote blade expansion, but the underlying mechanisms are not clear (de Carbonnel *et al.*, 2010).

Similar to shade signals, warm temperatures also promote petiole elongation and reduce blade expansion (Quint *et al.*, 2016). However, the molecular mechanisms described involve different factors. Blade expansion is inhibited via warm-induced PIF4 and TCP FAMILY TRANSCRIPTION FACTOR4, which regulate the cell cycle inhibitor KIP-RELATED PROTEIN1, inhibiting cell proliferation (Saini *et al.*, 2022).

IV. Stomata development

Predictably, given the strong role of stomata on photosynthesis and temperature regulation, their differentiation is under environmental control (Fig. 1b). Light promotes the formation of meristemoids and the division of guard mother cells promoting expression of key genes such as STOMAGEN, SPEECHLESS (SPCH), MUTE, FAMA, EPIDERMAL PATTERNING FACTOR2 and TOO MANY MOUTHS (Box 2; Wei *et al.*, 2020). Phytochromes and cryptochromes are involved in this response, promoting stomata development in response to light and inhibiting it in response to shade signals. Part of this response is mediated by COP1, which promotes phosphorylation and degradation of the transcription factors SPCH and SCREAM1 (SCRM1) through regulation of the MAPKKK YDA by unknown mechanisms. Moreover, COP1 interacts with SCRM1 and mediates its degradation. In addition, AN3 that is regulated by light at the transcriptional and post-transcriptional level downregulates the expression of YDA and COP1, promoting stomata development in response to light (Wei *et al.*, 2020).

As in response to shade, in warm environments, stomata development is inhibited. In this case, the described mechanism involves PIF4, which accumulates in response to warm temperatures and directly inhibits SPCH expression in stomatal precursors (Lau *et al.*, 2018). While this could reduce leaf cooling capacity, it has been shown that even in the extremely low stomatal abundance mutant *spch-5* cooling capacity was similar to the wild-type. This could be correlated with thinner leaves and larger stomata in the mutant (Pérez-Bueno *et al.*, 2022).

In addition to the photoreceptor-mediated mechanisms described, LL also regulates stomata development through a photoreceptor-independent pathway that involves changes in the photosynthetic electron transport (Zoulias *et al.*, 2021).

V. Blade thickness and curvature

Compared with plants growing in LL, plants growing in HL show thicker leaves (Fig. 1b). This is due to an increase in cell number coupled to enhanced anisotropic cell elongation in the palisade mesophyll, which increase the photosynthetic capacity in these conditions. Cryptochromes and phototropins regulate anisotropic cell elongation in an early phase after the first round of periclinal

cell division. Later, isotropic cell expansion is associated with endoreduplication and is promoted by higher sucrose levels accumulated in HL instead of photoreceptors (Hoshino *et al.*, 2019). Interestingly, although HL could be associated with warmer leaf temperatures, in warmer environments, leaves are thinner, contributing to heat dissipation (Quint *et al.*, 2016).

Finally, during the leaf expansion phase, light regulates leaf blade curvature, concomitantly affecting light interception (Fig. 1a). The main photoreceptors regulating this response are phototropins. Similar to hypocotyl phototropism, phototropins perceive light direction in the leaf, and promote blade flattening when light is perceived in the adaxial side of the blade, or curling when light is perceived in the abaxial side (Legris *et al.*, 2021). However, in contrast to their role in stems, sensitivity to light is different in the adaxial and abaxial sides of the blade, and low blue light levels perceived in the abaxial side are enough to inhibit leaf flattening. Broadly, the molecular signaling is similar to hypocotyl phototropism (see Box 1). The key phototropin signaling factors PHYTOCHROME KINASE SUBSTRATE (PKS), NON-PHOTOTROPIC HYPOCOTYL3 (NPH3) and ROOT PHOTOTROPISM2 (RPT2) are also required for the regulation of leaf curvature (Harada *et al.*, 2013; Legris *et al.*, 2021). However, PKS3 has a prominent role in leaves, while PKS1 and PKS4 are more relevant for hypocotyl phototropism. Moreover, while NPH3 is necessary for hypocotyl phototropism and leaf positioning, it is dispensable for responses to light intercepting the abaxial side of the leaf (Legris *et al.*, 2021).

In contrast to phototropins, light-activated phytochromes and UVR8 inhibit leaf flattening (Fierro *et al.*, 2015; Roig-Villanova & Martínez-García, 2016; Podolec *et al.*, 2021). However, inactivating phyB genetically or by low R : FR enhances flattening, a process that involves regulation of PIF4 and PIF5 (Roig-Villanova & Martínez-García, 2016). In addition to shade, warm temperatures also promote flattening in a phyB- and PIF4- and PIF5-dependent manner (Johansson & Hughes, 2014).

Similar to hypocotyl phototropism, leaf curvature is regulated by the spatial distribution of auxin signaling (Fierro *et al.*, 2015; Legris *et al.*, 2021). However, it is unclear whether the controlled step is auxin synthesis, transport or downstream signaling. Moreover, in leaves, changes in auxin signaling have been observed in the adaxial-abaxial, proximo-distal and medio-lateral axes, and it is not yet clear which of these changes are responsible for the changes in leaf morphology.

VI. Leaf positioning

Shade signals and warm temperatures cause an elevation in leaf angle, or hyponasty (Fig. 1a). This erect position of leaves allows reaching higher strata in the canopy and enhances cooling (Quint *et al.*, 2016; Casal & Fankhauser, 2023). Upward movement is achieved through differential cell expansion between the adaxial and abaxial sides of the petiole epidermis. While petiole elongation is triggered by low R : FR perceived locally, hyponasty occurs in response to shade perceived by phyB distally, in the tip of the leaf. This derepresses PIF7 which in turn promotes auxin synthesis via upregulation of *YUCCA8* gene expression (Casal &

Fankhauser, 2023). Auxin is then transported from the tip of the leaf to the abaxial side of the petiole, in a process that involves members of the PIN-FORMED (PIN) family of auxin efflux transporters, and plasmodesmata (Gao *et al.*, 2020; Casal & Fankhauser, 2023). In the base of the leaf, auxin is transported toward the abaxial side of the petiole in a PIN-dependent manner. Using a *pPIN3:PIN3-GFP* reporter, it was recently shown that PIN3 abundance is higher in the abaxial side of the petiole and that this difference is increased by application of auxin to the leaf tip, a treatment that mimics shade avoidance and induces hyponasty (Küpers *et al.*, 2023). This growth response requires the action of the transcriptional regulators PIF4 and PIF5, ARF6, ARF7 and ARF8. Downstream of auxin, gibberellin signaling in the abaxial side of the petiole promotes hyponasty.

Abscisic acid (ABA) also has a role in leaf hyponasty in response to shade (Michaud *et al.*, 2023). In response to low R:FR, PIFs induce ABA synthesis through upregulation of the genes coding for two rate-limiting enzymes, 9-CIS-EPOXICAROTENOID DIOXIGENASE3 (NCED3) and NCED5. To obtain a full hyponastic response, ABA signaling is required in the stomata, mesophyll and bundle sheath cells.

In deep canopy shade, reduction in blue light perceived by cry1 also induces hyponasty, in a process that requires brassinosteroids (Keller *et al.*, 2011).

Temperature-induced hyponasty shares many points with the aforementioned mechanisms of response to low R:FR. This response involves PIF4-dependent auxin synthesis in the leaf and increased auxin response in the abaxial side of the petiole (Park *et al.*, 2019). Again, site-specificity of the response is achieved through the control of PIN3 localization. In particular, PIF4 promotes the expression of PINOID (PID), a protein kinase that regulates PIN3 localization. Interestingly, the temperature-induced increase in PID expression is restricted to the abaxial side of the petiole, and this requires the leaf patterning gene ASYMMETRIC LEAVES2 (AS2; Park *et al.*, 2019).

Phototropins also regulate leaf positioning. In response to unilateral blue light, the leaf angle of the leaves facing the light is reduced, while those on the opposite site increase their elevation. Moreover, phototropin activation is required to regulate leaf angle in white light conditions. To this end, phototropins depend on NPH3 and RPT2 and PKS proteins, as well as the auxin transporter ABCB19 (de Carbonnel *et al.*, 2010; Jenness *et al.*, 2020; Sullivan *et al.*, 2021; Waksman *et al.*, 2023).

VII. Conclusions and outlook

While light and temperature signaling have been studied in depth in hypocotyls, evaluating similar responses in leaves has provided new insights into the cellular and molecular mechanisms. Hypocotyl elongation is mostly driven by cell expansion (Gendreau *et al.*, 1997). Evaluating light and temperature responses in leaves allowed to identify key components of their signaling networks affecting cell proliferation and differentiation (e.g. stomata development). Importantly, studying early leaf development allowed to identify mechanisms underlying the environmental control of the SAM. Moreover, new signaling factors downstream

receptor activation (e.g. PKS3 in phototropin signaling) or interactions with hormonal networks (e.g. light regulation of cytokinins) could be described.

Almost all aspects of leaf development are affected by light and temperature. One exception is primordia patterning, where so far, no effects of the environment have been described. Overall, our understanding of light control of SAM activity and early primordia development is scarce, and the effect of temperature remains largely unexplored. Given that meristematic activity regulates all aspects of postembryonic plant architecture, I believe that studying light and temperature signaling in this context is among the most promising research directions for the future of plant biology. Later in development, the mechanisms underlying light and temperature signaling on margin development are also unexplored. Moreover, UVB may have an effect on stomata development, but different groups have reported contradictory results, so more research is needed to clarify this point (Podolec *et al.*, 2021).

Transcriptomic approaches were instrumental for our understanding of light and temperature signaling in seedlings. Given the complex structure of leaves, with multiple domains and specialized cell types, increasing the spatial resolution of these analyses is required. In addition to localized treatments and microscopy approaches, combining the existing data with single-cell transcriptomics will allow to reach a new level of understanding of the underlying mechanisms of developmental plasticity in leaves.

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Competing interests

None declared.

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