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Chapter 1

Light signalling pathways during early plant development.

(General introduction)

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Abstract

For a horticultural crop such as tomato, the initial growth phase is crucial for the success of the whole production cycle. During this phase, the light requirements are relatively low, opening up possibilities to grow young plants in multi-layers that require less space and energy. Since light-emitting diodes (LEDs) make it possible to decouple light intensity from heating, building highly efficient multi-layer growth chambers is becoming more and more feasible. In order to optimise the use of LED lighting systems for vertical farming, more research has to be done on the effects of light quality on different developmental phases in multiple plant species. Moreover, by understanding the molecular mechanisms behind light-mediated plant development, we might be able to predict the effects of different wavelengths, and even circumvent possible negative effects of these wavelengths. Here we discuss the discovery, structure, and downstream signalling of plant light receptors, and new insights on early light-mediated plant development. Since these developmental processes are highly influenced by phytohormones, we also discuss the interplay between light and hormonal pathways. Finally, because this thesis is focused on the growth and development of young tomato plants, while using *Arabidopsis thaliana* (Arabidopsis) as a genetic model plant, we discuss similarities and differences in light-mediated plant development between these two species.

Keywords: LEDs, light quality, photoreceptors, photomorphogenesis, tomato, Arabidopsis

Light quality and LED technology

In the 17th century, Isaac Newton discovered that light can be broken down into different colours (Newton, 1704). The portion of the electromagnetic spectrum that is visible to the human eye, spanning a wavelength range between 400 and 700 nanometres (nm), is commonly referred to as "light". However, in the 19th century, colours outside the visible spectrum, such as infrared and ultraviolet (UV) light, were discovered and correlated to specific wavelengths and frequencies of electromagnetic radiation (Young, 1804). Spectral colours only span a narrow range of wavelengths and include red, orange, yellow, green, cyan, blue, and violet (Bruno and Svoronos, 2005) (**Table 1**), whereas unsaturated colours such as magenta are mixes of multiple wavelengths. The spectral distribution of the different wavelengths or colours within a light source is referred to as "light quality". Many artificial lights that are used in horticulture try to mimic the spectrum of sunlight by including fractions of all light colours and are commonly referred to as "white" lights. Not only does this term suggest that its spectrum consists of a single colour, but it also leads to the general misconception that all "white" lights have the same spectral quality. Therefore a more suitable term would be "multi-coloured" lights. Since different types or brands of white lights vary in light quality, it is incorrect to assume that plants will behave the same under each type or brand. Plants and algae respond to changes in light quality, mainly from colours at the end of the visible spectrum (i.e. red (R) and blue (B)), whereas the intermediate wavelengths (green and yellow) play minor roles. Moreover, land plants also respond to colours outside of the visible spectrum, being far-

Table 1: The electromagnetic radiation spectrum and its perception by land plants.
Spectral colours correspond to specific wavelengths and frequencies. This table indicates the characteristics of each colour within the plant visible spectrum and the photoreceptor families that perceive these colours. Photoreceptor families include phytochromes (PHYs), cryptochromes (CRYs), phototropins (PHOTs), Zeitlupes (ZTLs) and UV-RESISTANCE LOCUS 8 (UVR8). *Although CRYs have been reported to perceive green light, they are mainly sensitive to cyan, blue, and violet spectral ranges.

Colour	Wavelength (nm)	Frequency (THz)	Perception
Far-red	720-800	389-405	PHYs
Red	625-720	405-479	PHYs
Orange	590-625	479-508	-
Yellow	565-590	508-530	-
Green	520-565	530-576	*CRYs
Cyan	500-520	576-600	CRYs, PHOTs, ZTLs
Blue	435-500	600-689	CRYs, PHOTs, ZTLs
UV-A	315-435	689-952	CRYs, PHOTs, ZTLs
UV-B	280-315	952-1070	UVR8
UV-C	100-280	1070-3000	-

red (FR, 720-800 nm) and UV-B (280-350 nm) (Morrow, 2008). For this reason, the ratio of FR, R, B and UV-B fractions within "multi-colour" lighting systems influences the overall growth and development of plants. The development of LED technology has opened up new possibilities for more energy-efficient and economic lighting in horticulture. LEDs turn approximately 50% of the energy input directly into light. Moreover, less energy is lost in heat production, making LEDs not only more efficient, but also suitable for multi-layered growth chambers (SharathKumar et al., 2020). Because of their longer life span, additional costs for replacement and its

associated labour costs are limited. Furthermore, since LEDs lack dangerous materials such as mercury and glass casing, they are less harmful to the environment when discarded (Morrow, 2008). However, the most interesting trait of LEDs, that makes them fundamentally different from traditional lighting systems, is the possibility for spectral quality control. By matching the LED spectral output to specific light-detecting proteins and their downstream signalling pathways, optimal plant performance may be achieved without wasting energy on non-productive wavelengths (Heo et al., 2002). However, effects of these specific LED spectra have been shown to vary between species (Dougher and Bugbee, 2001). To optimise the use of LED lighting systems in horticulture, it is necessary to understand how differences in light quality influence plant development, not solely on the level of the whole organism, but also on a cellular and molecular level. In order to achieve this, we must start at the beginning of the process: the perception of light.

Light perception in land plants

As photo-autotrophic organisms, plants are capable of transforming light into chemical energy via photosynthesis by two large light-harvesting complexes consisting of proteins and pigments in chloroplasts. At the same time, plants "sense" light and translate this information into physiological and developmental responses, collectively referred to as photomorphogenesis (Arsovski et al., 2012), to optimise their stature to the light environment. Similar to the visible spectrum for human eyes, photosynthesis occurs within the spectral range of 400-700 nm. Therefore this spectral range is also referred to as photosynthetically active radiation (PAR). Photons at shorter wavelengths can be too energetic resulting in damage of cells, whereas photons

at longer wavelengths do not carry enough energy for photosynthesis (Pattison et al., 2018). Initially, the irradiance of PAR was measured in energy flux (W/m^2) which is based on the energy contained in the photons. However, for agricultural purposes it appeared to be more relevant to measure the number of photons received per area per time unit. Thus, photosynthetic photon flux (PPF), in $\mu mol/m^2/s$, was introduced as a more accurate method for measuring PAR, assuming that photons of B and R wavelengths drive the same amount of photosynthesis (McCree, 1972). Although in some cases the spectral response of photosynthesis did not follow the McCree curve (Barnes et al., 1993; Hogewoning et al., 2012; Kume, 2017), these are beyond the scope of this thesis, but are summarised in some excellent reviews (Krizek, 2004; Amthor, 2010; Wu et al., 2019). In contrast to photosynthesis, photomorphogenesis is regulated by specialised chromoproteins, or photoreceptors, that induce a downstream signal transduction cascade in response to light (Galvão and Fankhauser, 2015). Each class of photoreceptors is activated by a specific range of wavelengths (**Table 1**), and this specificity is determined by the characteristic absorption spectrum of the photosensory domain or photopigment, consisting of an amino acid sequence that binds to a chromophore (Briggs and Christie, 2002; Nagy and Schäfer, 2002; Lin and Shalitin, 2003; Li et al., 2013). Three distinct families of photoreceptors are sensitive to B light: the cryptochromes (CRYs) (Wang et al., 2018), the phototropins (PHOTs) and the Zeitlupes (ZTLs) (Suetsugu and Wada, 2013). The phytochrome (PHY) family responds mainly to R and FR light, although some sensitivity to B light has also been reported (Legris et al., 2019). Finally, the *UV RESISTANCE LOCUS8* (UVR8) photoreceptor responds to UV-B light (Yin and Ulm, 2017).

Phytochromes (PHYs)

In the early 1950s, the observation by Borthwick and colleagues that the germination of lettuce seeds was promoted by R light and inhibited or reversed by FR light (Borthwick et al., 1952) suggested the presence of a photo-reversible pigment in plants which was later isolated and identified as "phytochrome" (Sage, 1992). In the 1980s, the first *PHY* gene sequence was published (Hershey et al., 1985). Since then, members of the *PHY* family have been identified in many plant species, and even in prokaryotes and fungi (Li et al., 2015; Rockwell and Lagarias, 2020). PHYs consist of an N-terminal photosensory region that covalently binds the chromophore phytochromobilin tetrapyrrole (PΦB), and a C-terminal histidine kinase-related domain (HKRD) that is required for dimerisation (Burgie and Vierstra, 2014) (**Figure 1**). In the cytoplasm, PHYs occur in two photo-interconvertible conformations, an R-absorbing form (Pr) which is considered biologically inactive, and an FR-absorbing, biologically active form (Pfr) (Legris et al., 2019). The crystal structure of Pr shows that these conformational changes in the protein structure are a result of chromophore isomerisation (Burgie et al., 2014). This mode of action is referred to as low fluence response (LFR) and suggests that PHYs act as modular switches that are mostly activated by R light and deactivated by FR light (Franklin and Quail, 2010). PHYs can be classified into either Type I PHYs, which are activated by FR light, or Type II PHYs, which are activated by R light. Type II PHYs follow the LFR described above, whereas Type I PHYs respond to low amounts of any wavelength (very low fluence response (VLFR)) or by continuous irradiation with high intensity FR light (high irradiance response (HIR)) (Shinomura et al., 2000). In Arabidopsis, PHYA

(Type I) and PHYB-E (Type II) have roles in many developmental processes, including seed germination, de-etiolation, shade avoidance and floral transition (Galvão and Fankhauser, 2015). Many of these developmental responses are initiated by translocation of PHYs into the nucleus after their photoactivation (Kevei et al., 2007). Nuclear translocation of photoactivated PHYA requires two homologous chaperone proteins: FAR-RED ELONGATED HYPOCOTYL 1 (FHY1) and FHY1-LIKE (FHL). PHYA directly interacts with these chaperones and utilises their nuclear localisation signals (NLS) to reach the nucleus (Hiltbrunner et al., 2006). In Type II PHYs, putative NLS might be exposed after conversion of Pr to Pfr (Chen et al., 2005), but so far no canonical NLS sequences have been identified, suggesting that nuclear translocation of Type II PHYs relies on chaperone proteins as well (Pfeiffer et al., 2012). After nuclear import, PHYs accumulate into subnuclear foci called nuclear bodies (NBs) or speckles (Kircher et al., 2002). For PHYA and PHYB, interactions with the PHYTOCHROME-INTERACTING FACTOR (PIF) transcription factors are required for the formation of NBs. For PHYC-E, this process is not yet elucidated, although it is clearly independent of PIFs (Klose et al., 2015). Inside NBs, PHYA interacts with PIF1 and PIF3 (Huq et al., 2004; Al-Sady et al., 2006) whereas PHYB has been shown to interact with all members of the PIF family. These interactions lead to PIF phosphorylation and their subsequent degradation, altering gene expression, and ultimately leading to physiological responses (Pham et al., 2018) (**Figure 2**). Aside from PHY-PIF interactions, photoactivated PHYs can suppress the activities of CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and the COP9 signalosome (CSN), and thereby induce accumulation of several photomorphogenesis-promoting transcription factors, including

ELONGATED HYPOCOTYL 5 (HY5), HY5 HOMOLOGUE (HYH), LONG HYPOCOTYL IN FAR-RED (HFR1), and LONG AFTER FAR-RED LIGHT (LAF1) (Osterlund et al., 2000; Soo Seo et al., 2003; Duek et al., 2004) (**Figure 2**). Moreover, several studies also identified interactions between PIFs and COP1 or SUPPRESSOR OF PHYA1 (SPA1) repressors suggesting that regulation of gene transcription by PHYs is highly controlled and complex (Dong et al., 2014, 2015; Xu et al., 2014).

Cryptochromes (CRYs)

Shortly after the identification of PHYs, the first B light-responsive photoreceptors were described. One of these pigments was first identified in Arabidopsis as *ELONGATED HYPOTOCOTYL 4* (HY4), named after its phenotype that was specific for B light only (Ahmad and Cashmore, 1993). Based on its protein structure, HY4 was first thought to be a DNA photolyase, which catalyses B light-dependent repair of DNA lesions that result from UV damage in many other organisms. However, it was later found that HY4 lacks any photolyase activity (Malhotra et al., 1995), and instead binds to a flavin adenine dinucleotide (FAD) (Lin et al., 1995a), which strongly suggested that HY4 was in fact a CRY and thus renamed CRY1 (Lin et al., 1995b). A second CRY (*CRY2*) was identified by screening an Arabidopsis mutant population (Lin et al., 1996), and finally a third family member (CRY3) was identified through gene sequencing and phylogenetic analysis (Brudler et al., 2003; Kleine et al., 2003). In contrast to other photoreceptors, CRYs are found to be highly conserved and present across all kingdoms of life (Lin and Todo, 2005; Mei and Dvornyk, 2015).

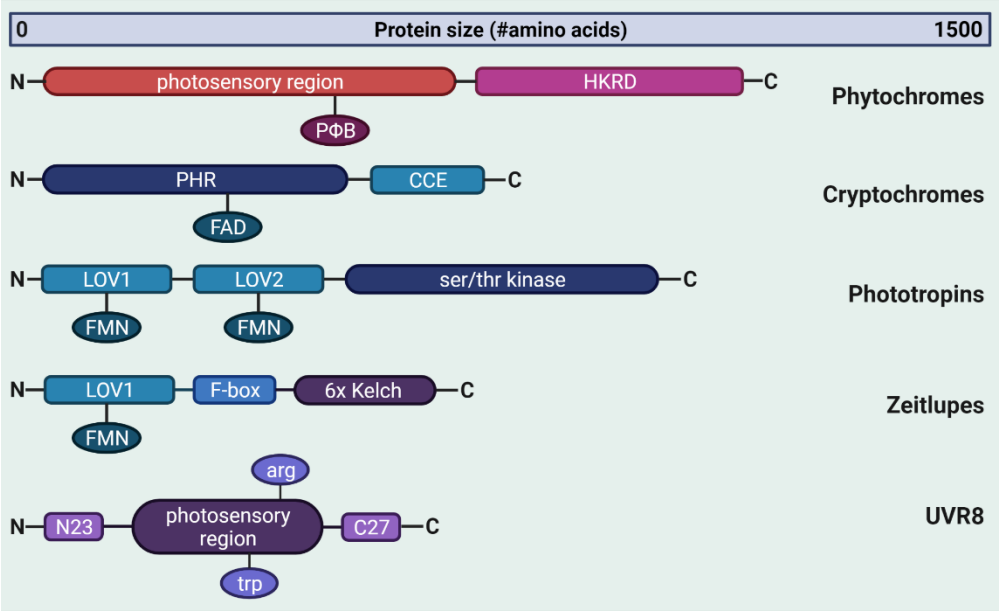


Figure 1: Protein domains in photoreceptors.
Schematic representation of the protein structures of different photoreceptor families. PHYs consist of an N-terminal photosensory region that covalently binds the PΦB chromophore, and a C-terminal histidine kinase-related signalling domain (HKRD) that is required for dimerisation and protein interactions. After photoactivation, PHYs are transported to the nucleus with the help of chaperone proteins, or via a yet to be identified nuclear localisation signal (NLS) in the active Pfr conformation. CRYs consist of an N-terminal Photolyase Homologous Region (PHR) domain bound to the fully oxidised cofactor flavin adenine dinucleotide (FAD) and a CRY C-terminal Extension (CCE) domain. The PHR domain is required for homo-dimerisation and CIB interaction, while the CCE effector domain is required for protein interactions and nuclear transport. The chromophore of PHOTs consists of two N-terminal LOV domains bound to the FMN cofactor and is linked to the C-terminal ser/thr kinase domain that phosphorylates downstream targets. Zeitlupe (ZTL) chromophores contain only one LOV-FMN domain linked to an F-box domain and to six Kelch repeats. UVR8 consists of an N-terminal NLS N23 and a C-terminal interaction domain C27. Its photosensory region comprises a chromophore consisting of three tryptophan (trp triad) residues and arginine (arg) residues for homodimerisation.

Therefore, CRYs and photolyases can be subdivided into five groups: cyclobutane pyrimidine dimer (CPD) photolyases, (6–4) pyrimidine–pyrimidone adduct [(6–4) photoproduct] photolyases, cry-DASH proteins, animal CRYs and plant CRYs (Mei and Dvornyk, 2015). Many excellent reviews about animal and prokaryotic CRYs (Losi and Gärtner, 2017; Michael et al., 2017) have been published but these are beyond the scope of this thesis. In land plants, CRY1 and CRY2 function as photoreceptors, whereas CRY3 resembles a DASH-type CRY that is thought to act as a B light-activated single-stranded DNA-repair enzyme inside mitochondria and chloroplasts (Pokorny et al., 2008). The photoreceptors CRY1 and CRY2 function as dimers (Sang et al., 2005; Yu et al., 2007) with monomers that consist of two major domains: an N-terminal Photolyase Homologous Region (PHR) domain and a diverged CRY C-terminal Extension (CCE) domain. The PHR domain binds to the fully oxidised FAD (Brautigam et al., 2004) (**Figure 1**). Upon absorption of B light, an electron transfer from tryptophan (trp) to tyrosine residues reduces the chromophore of CRY1 *in vitro,* resulting in conformational modifications in the FAD domain (Giovani et al., 2003). However, mutations of trp-triad residues in CRY2 did not decrease its photoactivation *in vivo* (Li et al., 2011), suggesting another mechanism for photoactivation of CRYs. Similar to PHYs, photoactivated CRYs can alter gene expression directly and indirectly. CRY1 interacts with SPA1, thereby mediating suppression of the COP1-dependent degradation of the photomorphogenesis-promoting transcription factors HY5, HYH, and HFR1 (Lian et al., 2011). Similarly, photoactivated CRY2 suppresses COP1-dependent protein degradation of the flowering-promoting CONSTANS (CO) (Liu et al., 2008). Moreover, the PHR domain of CRY2 binds to the N-terminal

domain of the transcription factor CRY2-INTERACTING bHLH 1 (CIB1) resulting in heterodimerisation of CIB1 with CIB3, CIB4 and CIB5 to activate *FLOWERING LOCUS T* (*FT*) transcription (Liu et al., 2013) (**Figure 2**). Aside from COP1/SPA1 complexes and CIBs, PHYs and PIFs have also been identified as CRY-binding proteins (Mas et al., 2000; Pedmale et al., 2016), suggesting synergy between R/FR and B light responses, and thus adding another layer of complexity to light signalling pathways.

Phototropins (PHOTs)

Although plant bending responses to unidirectional light were already documented by Charles Darwin in the 19th century (Darwin et al., 1880), it took more than a hundred years to identify the photoreceptors responsible for this phenomenon. While auxin, the key phytohormone in phototropism, was identified already early in the 20th century (Went, 1926), the PHOTs were only identified at the end of the 20th century. In 1989, a genetic screen in Arabidopsis for mutants defective in phototropic growth identified the *JK224* mutation (Khurana and Poff, 1989), which was later renamed to *non-phototropic hypocotyl 1* (*nph1*) (Liscum and Briggs, 1995). Cloning and sequencing of the *NPH1* gene showed that it encodes a plasma membrane-associated protein with two light, oxygen, or voltage (LOV) domains in the N-terminal half and a ser/thr protein kinase in the C-terminal half (Hanks and Hunter, 1995; Briggs et al., 2001a), suggesting that autophosphorylation was the initial step in the signalling pathway (Huala et al., 1997). When expression of the NPH1 protein in insect cells confirmed its light-dependent autophosphorylation, the protein was renamed to PHOT1 after its role in the regulation of phototropism (Christie et al., 1998, 1999). Among other loci

involved in phototropism, *NPH1-like 1* (*NPL1*) was identified in Arabidopsis with 67% similarity to *PHOT1* (Jarillo, 1998), and based on its function and the similar structure of the encoded protein the gene was renamed to *PHOT2* (Briggs et al., 2001a). The LOV domains bind the cofactor flavin mononucleotide (FMN) and together form the chromophore (Christie et al., 1999) (**Figure 1**). Photoactivation of this chromophore triggers conformational changes that liberate the C-terminal kinase domain resulting in fluence-dependent autophosphorylation of residues in both their sensory and kinase domains (Christie et al., 1998; Sakai et al., 2001). PHOTs regulate chloroplast movement and phototropism in a fluence-dependent manner, where PHOT1 is activated at both low and high light intensities, while PHOT2 only responds to high fluence rates (Inada et al., 2004). Since autophosphorylation requires more photons than are needed to induce PHOT-mediated responses, it is likely that autophosphorylation is not the main mechanism of PHOT signalling (Briggs et al., 2001b). Possibly low/intermediate fluence phosphorylation sites are important for signalling, whereas high fluence autophosphorylation sites are involved in receptor desensitisation (Salomon et al., 2003). In their inactive state, PHOTs are tightly associated with the plasma membrane. Upon photoactivation, autophosphorylation is believed to be required for plasma membrane dissociation and targeting of PHOT1 to the cytoplasm (Wan et al., 2008) and of PHOT2 to the Golgi apparatus (Kong et al., 2006). In the last decades, more and more downstream targets of PHOTs have been identified. Both Arabidopsis PHOTs have been shown to enhance cytosolic calcium increase that might act as an intermediate signalling component (Harada et al., 2003; Zhao et al., 2013). Furthermore, phototropism studies led to the discovery of PHOT1-interacting proteins: NON-PHOTOTROPIC

HYPOCOTYL 3 (NPH3), ROOT PHOTOTROPISM 2 (RTP2), and ATP-BINDING CASSETTE B19 (ABCB19) (Motchoulski and Liscum, 1999; Sakai et al., 2000; Lariguet et al., 2006; Christie et al., 2011). Moreover, RTP2 phosphorylation by PHOT1 is also required for stomatal opening (Inada et al., 2004). So far, PHOT2 has been shown to interact with PROTEIN PHOSPHATASE 2A (PP2A) and 14-3-3 λ (Tseng and Briggs, 2010; Tseng et al., 2012) (**Figure 2**). Additionally, PHOTs have been shown to interact with components of R/FR light signalling. For example, PHYA binds to PHOT1 at the plasma membrane where it likely enhances phototropic growth (Jaedicke et al., 2012), and PHYTOCHROME KINASE SUBSTRATE 1 (PKS1) and PKS2 bind PHOTs during phototropism to control leaf positioning and flattening (Lariguet et al., 2006; Boccalandro et al., 2008; de Carbonnel et al., 2010).

Other photoreceptors in land plants

Alongside the PHOTs, land plants have another family of LOV domain-containing B-light receptors: the ZEITLUPE (ZTL) family, named after its founding member. The three members of this family, *ZTL*; *FLAVIN-BINDING KELCH REPEAT 1* (*FKF1*) and *LOV KELCH PROTEIN 2* (*LKP2*), were first identified in genetic screens for period length Arabidopsis mutants (Nelson et al., 2000; Somers et al., 2000; Schultz et al., 2001) and contain one FMN-binding LOV domain for photoreception together with an F-box domain and six Kelch repeats (Ito et al., 2012) (**Figure 1**). F-box proteins are typically components of Skp, Cullin, and F-box (SCF)-type ubiquitin E3 ligases, and ZTLs were found to participate in light-regulated proteolysis of circadian clock-associated proteins including TIMING OF CAB EXPRESSION 1

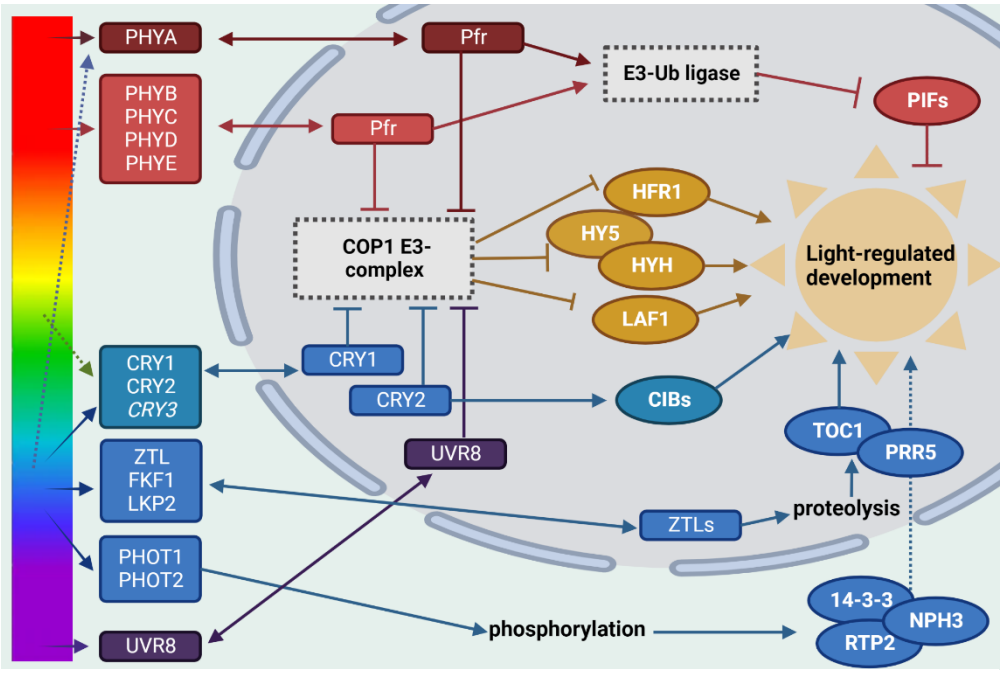


Figure 2: Signal transduction pathways of Arabidopsis photoreceptor families.

FR/R light: PHYA is activated by FR light and to some extent by B light, whereas PHYB to PHYE are activated by R light. In their active conformation, PHYs (Pfr) move to the nucleus where they inhibit the COP1 E3-complex, resulting in the accumulation of transcription factors such as HFR1, HY5 and LAF1. In addition, photoactivated PHYA and PHYB promote the ubiquitination and degradation of PIFs that repress light-regulated development. **B light:** CRYs, PHOTs, and ZTLs are all activated by B light, and CRYs to some extent by green light. Upon photoactivation, CRYs move to the nucleus where they inhibit the COP1 E3-complex to regulate photomorphogenesis. In addition, CRY2 binds to CIB transcription factors to promote flowering. PHOT signalling relies on (auto)phosphorylation. PHOTs are known to phosphorylate 14-3-3 proteins, NPH3 and RTP2 that ultimately influence phototropism and stomatal opening. Photoactivated ZTLs move to the nucleus where their F-box domains target various circadian clock proteins such as TOC1 and PRR5 for degradation by the 26S proteasome. **UV-B light:** UVR8 is activated by UV-B light. Upon its activation, UVR8 moves to the nucleus and binds COP1 to inhibit its activity, resulting in stabilisation of transcription factors such as HY5/HYH.

(TOC1) and its homolog PSEUDO-RESPONSE REGULATOR 5 (PRR5) by the 26S proteasome (Más et al., 2003; Kiba et al., 2007; Harmon et al., 2008; Gil et al., 2017) (**Figure 2**). Moreover, it has been shown that ZTL indirectly controls PRR9 protein levels, and the interaction between TOC1 and PRR3 (Fujiwara et al., 2008). By controlling protein levels, ZTLs not only regulate the timing of circadian events throughout the day, but also photoperiodic timing of flowering (Song et al., 2013; Serrano-Bueno et al., 2017). A last class of plant photoreceptors responds to UV-B radiation. UV-B (280-315 nm) is a small fraction of the solar spectrum that is potentially harmful to any organism that is exposed to sunlight. Even though solar light only contains 0.5% UV-B radiation (Blumthaler, 1993), these photons are highly energetic and can be absorbed by a number of biologically active components, including nucleic acids, ultimately leading to DNA damage. A well-known defect in animals resulting from UV-B-induced DNA damage is the induction of cancerous melanoma cells. However, plants can be exposed to UV-B radiation at substantial levels with hardly any DNA damage occurring in the cells. This UV-B tolerance is a result of a signalling pathway that is initiated when UV-B is perceived by its receptor UVR8 (Kliebenstein et al., 2002). Rather than depending on a cofactor chromophore, UVR8 uses a triad of closely packed trp residues (W233, W285 and W337) to perceive light (Di Wu et al., 2012) (**Figure 1**). At low levels of UV-B radiation, UVR8 exists as a homodimer bound by hydrogen bonds facilitated by arginine (arg286 and arg338) (Tilbrook et al., 2013). Upon UV-B exposure, these homodimers undergo rapid monomerisation, a process that depends on conformational changes in the light-perceiving trp residues (Rizzini et al., 2011). UVR8 monomers bind to the WD40 domain of COP1 to stabilise the HY5 and HYH transcription

factors, which ultimately alter gene expression (Brown and Jenkins, 2008; Favory et al., 2009; Yin et al., 2015) (**Figure 2**). These UV-B responsive genes include proteins involved in UV protection such as antioxidants and photolyases (Tilbrook et al., 2013). Furthermore, WD40-repeat proteins REPRESSOR OF UV-B PHOTOMORPHOGENESIS (RUP)1 and RUP2 are among the target genes that facilitate negative feedback of the UV-B signalling pathway by directly inactivating UVR8 (Gruber et al., 2010; Heijde and Ulm, 2013). In addition to R, FR, B, and UV-B light, it has been suggested that green sensory mechanisms monitor and adjust plant growth and development (Folta and Maruhnich, 2007; Wang and Folta, 2013). Although 10-50% of the green light is reflected by chloroplasts, the remaining photons are absorbed for photosynthesis, or for activation of CRYs or putative green light photoreceptors, suggesting that green light may be important for optimal plant performance (Terashima et al., 2009; Smith et al., 2017). Altogether, the different photoreceptor families influence many, if not all, developmental processes in land plants. Next, we discuss the interplay between light signalling and hormonal pathways during early plant development.

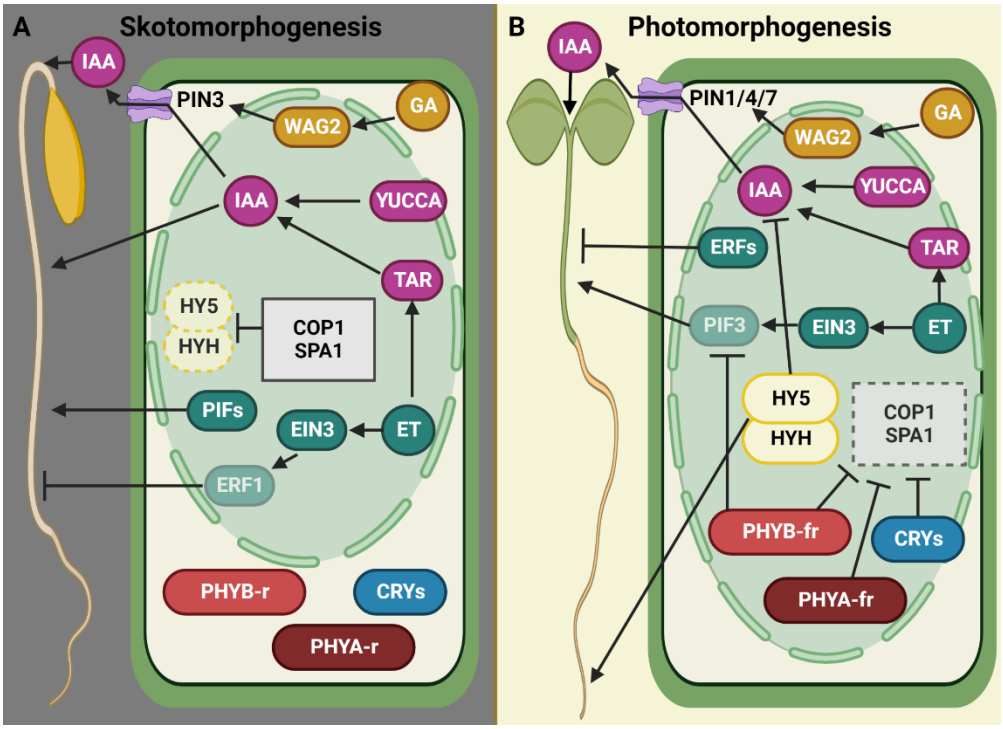
Seedling emergence: Transition from darkness to light

During seed germination, plant embryos mature from being heterotrophic (dependent on seed reserves) to fully photoautotrophic seedlings. When germination occurs in the absence of light (e.g. in the soil), seedlings undergo a developmental process that is characterised by rapid hypocotyl elongation, little root development, and the formation and maintenance of an apical hook that protects the shoot apical meristem (SAM) while the seedling shoot grows through the dark soil. These traits are collectively referred to as

skotomorphogenesis, or etiolation, and aid seedling shoots to rapidly emerge into the light (Arsovski et al., 2012; Armarego-Marriott et al., 2020). During skotomorphogenesis, the limited energy resources of the seed reserves are mainly allocated to the hypocotyl to achieve rapid seedling emergence. As a result, root development is delayed until the cotyledons have expanded and are photosynthetically active. Addition of sucrose to etiolated seedlings promotes root development in darkness, suggesting that lack of energy resources (or sugar signalling), and not direct photoreceptor signalling, is the main cause for short roots in etiolated seedlings (Kircher and Schopfer, 2012). In contrast, hypocotyl elongation and apical hook formation have been shown to be directly regulated by downstream signalling of photoreceptors (Arsovski et al., 2012; Mazzella et al., 2014). Skotomorphogenesis results from PHY- and CRY-dependent degradation of transcription factors such as HY5 and HYH via the COP1-SPA E3 ubiquitin ligase complex (Osterlund et al., 2000). As a result, HY5 and HYH no longer suppress auxin signalling, thus creating auxin maxima that enhance hypocotyl growth (Sibout et al., 2006) (**Figure 3A**). In addition, maintenance of skotomorphogenic growth is regulated by various PIFs that are stable in the dark and degraded after seedling emergence into the light (Leivar et al., 2008). During skotomorphogenesis, ethylene (ET) balances hypocotyl elongation through ETHYLENE-INSENSITIVE 3 (EIN3), which enhances expression of *ETHYLENE RESPONSE FACTOR 1* (*ERF1*) that inhibits hypocotyl growth in darkness. (Zhong et al., 2012). (**Figure 3A**). Finally, seedling emergence is enhanced by gravitropism and PHOT-mediated phototropism which aids the seedlings to efficiently direct their growth upwards and towards the light source (Masson et al., 2002; Christie and Murphy, 2013). After emergence, light exposure initiates a new developmental

program referred to as photomorphogenesis, or de-etiolation, that causes hypocotyl growth arrest, unfolding of the apical hook and induction of root development (Arsovski et al., 2012; Armarego-Marriott et al., 2020). During photomorphogenesis, COP1-dependent degradation of HY5 and other transcription factors is relieved, resulting in their accumulation (Osterlund et al., 2000). Downstream targets of HY5 include signalling components of the phytohormones auxin, cytokinin (CK), ET, brassinosteroids (BR), gibberellic acid (GA) and jasmonic acid (JA), making this transcription factor a key integrator of light signalling and hormonal pathways (Zhang et al., 2011). HY5 inhibition of auxin signalling, along with accumulation of light-stable ERFs, cause the hypocotyl growth arrest that characterises photomorphogenesis (Zhong et al., 2012). Similar to skotomorphogenic growth, ET balances the hypocotyl growth arrest via EIN3. By EIN3-mediated stabilisation of *PIF3* expression, hypocotyl growth is promoted in the light (Sibout et al., 2006; Zhong et al., 2012; de Wit et al., 2016) (**Figure 3B**). Apical hook formation, maintenance and opening rely on asymmetrical cell growth at opposite sides of the hypocotyl regulated by the phytohormone auxin (Mazzella et al., 2014). The mechanism that underlies this asymmetrical cell growth is the establishment of local auxin maxima in the cortex and epidermal cells through a combination of auxin biosynthesis and polar auxin transport (PAT) (Žádníkova et al., 2010). Mutations in auxin biosynthesis genes of the *YUCCA* (*YUC*) and *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1 / TRYPTOPHAN AMINOTRANSFERASE RELATED* (*TAA1/TAR*) families impair hook development (Zhao et al., 2001; Stepanova et al., 2005). Moreover, chemical inhibition of the PIN-FORMED (PIN) auxin transporters that drive PAT by 1-naphthylphthalamic acid (NPA) resulted in a reduced

hook, confirming that PAT is required for hook formation (Žádníkova et al., 2010). Auxin synthesised in the apical part of the seedling is transported through the stele towards the root by the PIN1 auxin efflux carriers and assisted by the AUXIN RESISTANT 1 (AUX1) auxin influx carrier. Expression studies revealed an important role for PIN3 in apical hook formation by redistributing auxin to create an auxin maximum on the inner (concave) side of the hypocotyl (**Figure 3A**). In contrast, during the transition from apical hook maintenance to opening, PIN1, PIN4 and PIN7 that are expressed at the inner cell layers of the hook redistribute auxin towards the stele (Vandenbussche et al., 2010; Žádníkova et al., 2010) (**Figure 3B**). Auxin



signalling is initiated by binding of auxin to co-receptor complexes that consist of a TRANSPORT INHIBITOR RESPONSE 1 / AUXIN BINDING F-BOX PROTEIN (TIR1/AFB) and an AUXIN / INDOLE-3-ACETIC ACID PROTEIN (AUX/IAA). This results in the subsequent ubiquitination and degradation of the AUX/IAA repressors, thereby releasing AUXIN RESPONSE FACTORs (ARFs) that activate the expression of auxin-responsive genes, ultimately leading to asymmetrical growth (Leyser, 2018). Finally, this process is enhanced by interaction with other hormonal pathways. The AGC-3 kinase WAG2 connects GA (and light) signalling to the auxin gradient. GA (and darkness) lead to PIF5 accumulation which induces *WAG2*

Figure 3: Hormonal regulation of skoto- and photomorphogenesis.
A. Skotomorphogenesis is characterised by a short root, an elongated hypocotyl, and an apical hook. Auxin signalling (pink) that results from degradation of HY5 and HYH by the COP1-SPA1 E3 complex, and dark-stable PIFs, promote hypocotyl elongation. In contrast, ET (green) inhibits hypocotyl growth in darkness through its transcriptional activation of the light-stable ERF1 via EIN3. Apical hook formation and maintenance is directly regulated by auxin biosynthesis and transport and indirectly by GA (orange) and ET signalling. Auxin efflux via PIN3, assisted by PIN4 and PIN7, results in an auxin maximum on the inner (concave) side of the hypocotyl, leading to hypocotyl bending. **B.** After exposure to light, the developmental program of photomorphogenesis is initiated, leading to inhibition of hypocotyl elongation, promotion of root growth and unfolding of the apical hook. Photoactivated PHYs and CRYs move to the nucleus where they inhibit the COP1-SPA1 E3 complex, resulting in stabilisation of the photomorphogenesis-promoting HY5 and HYH. Hypocotyl growth arrest results from HY5/HYH inhibition of auxin signalling and from light-stable ERFs that inhibit hypocotyl growth. In contrast, ET promotes hypocotyl growth in light through its transcriptional activation of the dark-stable PIF3 via EIN3. During opening of the apical hook, PIN1, PIN4 and PIN7 alleviate the asymmetric auxin distribution in the hypocotyl.

expression. By phosphorylating the central intracellular loop of PIN1, PIN3, PIN4, and PIN7 proteins, WAG2 in turn regulates PAT to maintain the apical hook (Willige et al., 2012). In addition, ET influences auxin biosynthesis and transport at the inner side of the hook by upregulation of *TAR2*, *AUX1*, *LAX1*, *PIN1*, *PIN3*, *PIN4* and *PIN7* (Vandenbussche et al., 2010; Žádníkova et al., 2010) (**Figure 3**).

Light-directed seedling development

After seedlings emerge from the soil, the apical hook unfolds, and cotyledons expand. As a result, the SAM is now exposed to light and the seedling has become fully photoautotrophic. However, when seedlings are growing under a canopy of other plants, they have to compete with these other plants for light in order to avoid overall delays in growth (Weiner, 1985). To keep up with their competition, plants channel their energy resources to apical elongation, at the expense of other tissues. In seedlings, this leads to elongated hypocotyls, hyponastic leaves, and reduced leaf lamina size, whereas older plants show elongated stems, petioles, or internodes, reduced leaf surface area and early flowering. Collectively these traits are referred to as the shade avoidance syndrome (Courbier and Pierik, 2019). The most widely studied trait of the shade avoidance syndrome is the elongated hypocotyl. Whereas hypocotyl growth during skotomorphogenesis is dependent on ET signalling, shade-induced hypocotyl elongation relies mainly on auxin. Initially, shade is detected by PHYs that monitor R:FR ratios. Sunlight reaches the top of the canopy with a high R:FR ratio where the green leaves absorb R light and reflect FR light. As a result, the R:FR ratio in the shade below the canopy is lower (Ballaré et al., 1990). The main sensor for changes in the R:FR ratio is PHYB,

while PHYC-E play minor roles in shade avoidance. In high R:FR ratios, PHYB is abundant in its active Pfr state that translocates to the nucleus where it inactivates PIF4, PIF5 and PIF7 (Buti et al., 2020) (**Figure 4A**). In contrast, in low R:FR ratios, PHYB is mainly abundant in its inactive Pr state, resulting in PIF stabilisation and subsequently into PIF-mediated changes in gene transcription. Accumulation of PIF4, PIF5 and PIF7 promotes transcription of *YUC*, *AUX/IAA* and *PIN* genes, ultimately leading to auxin-mediated hypocotyl elongation in shade (Lorrain et al., 2008; Leivar et al., 2012; Li et al., 2012a; Buti et al., 2020) (**Figure 4B**). Once the seedling has reached the top of the canopy, the SAM is fully exposed to all wavelengths within the solar spectrum. Subsequently, the SAM grows to its mature size to start the formation of new leaf primordia. During seedling development only a few first leaves are initiated in the SAM that will enhance the availability of sugars through photosynthesis. After formation of these first leaves, the higher level of available sugars activates the root apical meristem (RAM). In fact, studies with decapitated seedlings showed that cotyledon-derived sugars are essential for the initiation of root growth (Kircher and Schopfer, 2012). Furthermore, these sugars can act as shoot-to-root signals resulting in the upregulation of nutrient transporters within the root to optimise seedling growth (Lejay et al., 2008) (**Figure 4C**). However, shoot-to-root sugar signalling is a slow process since it requires both photosynthesis and sugar biosynthesis. Therefore the role of shoot-to-root signalling via sugars is likely to be subordinate to other more rapid light-induced shoot-to-root signals. Likely candidates for this are transcription factors that are downstream photoreceptor targets. Recently, HY5 was identified as a mobile signal that travels to the root upon photoreceptor activation in the shoot. Moreover, it was shown that upon arrival in the root,

HY5 promotes root growth and nitrate uptake (Chen et al., 2016) (**Figure 4C**). Aside from mobile transcription factors such as HY5, phytohormones have been shown to move from shoot-to-root to modulate root growth. Auxin that is produced in the shoot is transported to the root via the vascular cylinder in two ways: bulk transport of auxin via the phloem that is unloaded in the root apex by AUX1 (1), and auxin carrier-mediated transport that relies mainly on PIN proteins (2) (Casson and Lindsey, 2003). While *PIN1*, *PIN3* and *PIN7* are all expressed in hypocotyls, PIN1 has been shown to be the main efflux carrier for light-driven shoot-to-root auxin transport (Keuskamp et al., 2010; Sassi et al., 2012). Within the root, auxin accumulates in the quiescent centre (QC) of the RAM where primary root growth is tightly controlled by auxin and CK interplay. In the QC, auxin acts antagonistically with CK, to maintain a balanced stem cell pool. In addition, CK influences the auxin gradient to create auxin maxima that induce primary root growth. However, when the auxin levels in the RAM become too high, primary root growth is inhibited (Thimann, 1937). Next, basipetal transport of auxin (from the tip towards the base of the root) controls gravitropism and the outgrowth of lateral root primordia in the elongation zone (Rashotte et al., 2000; Casimiro et al., 2001). Within the elongation zone of the root, auxin and CK regulate the initiation and outgrowth of lateral root primordia (Jing and Strader, 2019) (**Figure 4D**). Aside from auxin, it has been reported that a biologically inactive form of GA, GA_{12}, travels from shoot to root where it is converted into the active forms GA20- and GA3-oxidases that ultimately stimulate root growth (Regnault et al., 2015). However, it remains unclear whether or not GA_{12} transport is light-dependent. In summary, mobile signals (sugars, HY5, auxin and other yet to

be identified molecules) travel from shoot-to-root to influence root development in a light-dependent manner.

Light-regulated initiation and outgrowth of lateral organs.

After the seedling stage, early plant development shifts from only apical growth to the formation of lateral organs to enhance nutrient uptake and photosynthetic capacity. In many plant species, new shoot organs are initiated in the SAM following a Fibonacci spiral pattern, which allows for optimal light capture (Strauss et al., 2020). To ensure proper phyllotaxis, a tight balance between proliferation and differentiation of meristem cells is required. Within the central zone (CZ) at the tip of the SAM, proliferation of pluripotent stem cells is tightly controlled by a feedback loop between WUSCHEL (WUS) and CLAVATA (CLV) proteins (Schoof et al., 2000). The homeobox transcription factor WUS, which is required for specification of stem cell identity, is expressed in the organizing centre (OC) within the rib zone (RZ) of the SAM (Mayer et al., 1998) (**Figure 5A, B**). WUS moves upwards to the CZ via plasmodesmata, where together with another homeobox protein SHOOT MERISTEMLESS (STM), it induces expression of the *CLV3* gene in stem cells (Brand et al., 2002; Daum et al., 2014). Subsequently, CLV3 peptides are secreted from the stem cells and are perceived by a CLV1/CLV2 receptor kinase complex in the OC to repress WUS activity, thus creating a negative feedback loop that is required for stem cell homeostasis (Brand et al., 2000) (**Figure 5B**). In addition, WUS levels are controlled by either CLV-dependent or CLV-independent CK signalling (Gordon et al., 2009). CKs and their precursors are mainly synthesised within the root and loaded by ATP-BINDING CASSETTE G14 (ABCG14) into the xylem through which they

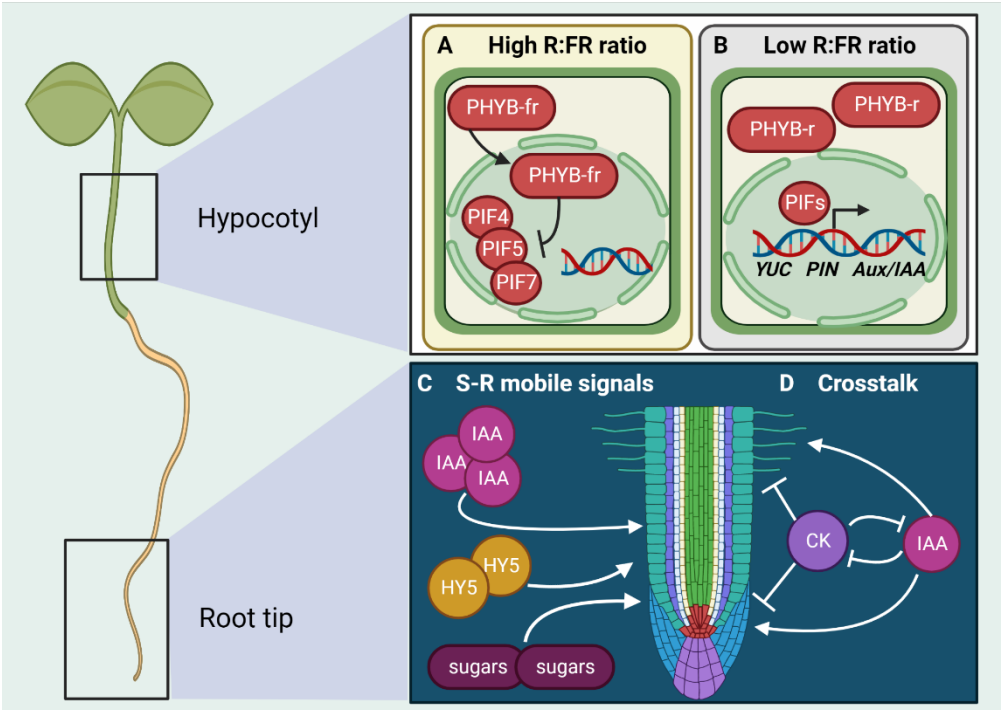
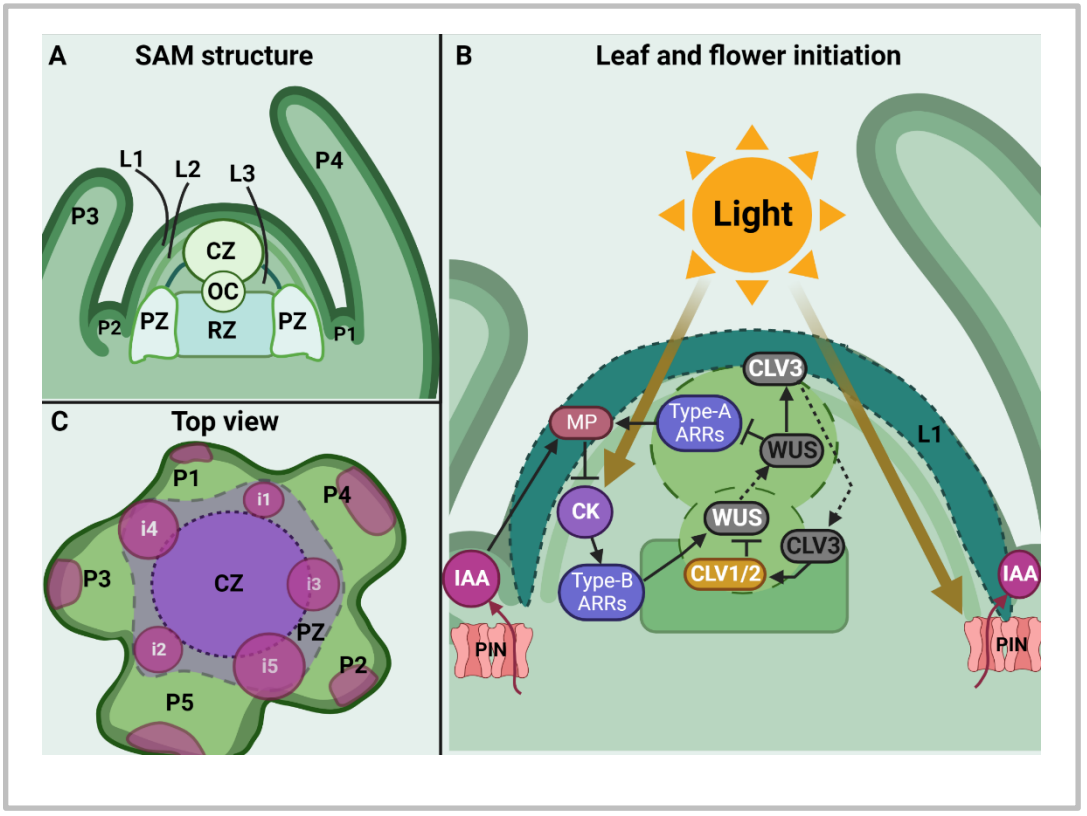


Figure 4: Light-directed hypocotyl and root development in seedlings.
In order for seedlings to optimise their photosynthetic capacity, the shoot needs to be exposed to light. **A.** In light conditions with high R:FR ratios, PHYB is activated (PHYB-fr) and moves to the nucleus where it induces the degradation of the bHLH transcription factors PIF4, PIF5 and PIF7. **B.** Shade reduces the R:FR ratio and induces the shade avoidance response. Due to the low R:FR ratio, PHYB proteins are kept in the inactive state (PHYB-r) and remain in the cytosol. This results in nuclear accumulation of PIF4, PIF5 and PIF7 that promote expression of auxin biosynthesis genes (*YUC*), transporters (*PIN*) and downstream signalling targets (*Aux/IAAs*), ultimately resulting in hypocotyl growth. **C.** Sugars available from photosynthesis in the shoot travel to the root to activate the RAM and promote root growth and nutrient uptake. Further root development depends on the shoot-to-root (S-R) transport of other mobile signals such as HY5 and auxin (IAA). Upon light detection in the shoot, both molecules travel to the root where they enhance root growth and nutrient uptake. **D.** Furthermore, auxin acts antagonistically with CK to control the size of the stem cell pool in the QC, and the formation and outgrowth of lateral root primordia.

travel to the shoot and accumulate in the OC (Ko et al., 2014; Zhang et al., 2014). Within the OC, CK signalling results in elevated *WUS* expression via type-B ARABIDOPSIS RESPONSE REGULATOR (ARR) 1, ARR10 and ARR12 (Meng et al., 2017; Xie et al., 2018). Moreover, WUS represses expression of type-A *ARR5*, *ARR6*, *ARR7* and *ARR15*, which are important for negative feedback of CK signalling, to further enhance CK-mediated stem cell proliferation (Leibfried et al., 2005) (**Figure 5B**). Finally, the interplay between WUS-CLV and CK is regulated by tissue-specific HECATE (HEC) transcription factors (Schuster et al., 2014). When stem cells divide in the CZ, their daughter cells move outwards to the peripheral zone (PZ) where new organ primordia are initiated (**Figure 5A**). Organ initiation mainly relies on PAT in the epidermis via PIN1 (Benková et al., 2003). In fact, PINs were even discovered because of their "pin-shaped" inflorescence, a result of lacking organ initiation at the inflorescence meristem (IM) (Okada et al., 1991; Gälweiler et al., 1998). Although rosette leaf formation is generally not abolished in plants that exhibit "pin-shaped" inflorescences, organ initiation by auxin is expected to rely on the same mechanisms in the SAM as well as in the IM. Studies in tomato, where the SAM is larger and more accessible than in Arabidopsis, have confirmed that leaf formation in the SAM relies on PAT via PIN1 (Reinhardt et al., 2000; Bayer et al., 2009). In the SAM, polar localisation of PIN1 in the L1 layer creates an auxin flux towards incipient primordia sites and depletion around these sites, thus generating a chemical inhibitory field (together with CK signalling) that defines the primordium boundaries (Reinhardt et al., 2003; Heisler et al., 2005; Vernoux et al., 2011; Kierzkowski et al., 2013; Besnard et al., 2014a). (**Figure 5C**). As cellular auxin levels increase at the primordium site, AUX/IAAs are targeted for



ubiquitination via TIR1/AFBs, resulting in their proteolytic degradation, and ultimately leading to the release of ARFs. MONOPTEROS (MP / ARF5), together with ETTIN (ARF3) and ARF4, regulates initiation of new primordia through activation of genes that specify cell fate (Przemeck et al., 1996; Galvan-Ampudia et al., 2020). In the SAM, MP is present at low levels in the CZ where it aids stem cell homeostasis (Luo et al., 2018), and at high levels in the PZ where it induces primordium fate by upregulation of *PIN1*, *LEAFY* (*LFY*), *AINTEGUMENTA* (*ANT*), *AINTEGUMENTA-LIKE6 / PLETHORA3* (*AIL6 / PLT3*), and *FILAMENTOUS FLOWER* (*FIL*) (Weigel et al., 1992; Elliott et al., 1996; Sawa et al., 1999; Krizek, 2009; Krogan et al., 2016).

Figure 5: Light-regulated initiation and outgrowth of lateral shoot organs. New shoot organs are initiated in the SAM, where stem cell proliferation and differentiation are tightly balanced to ensure proper phyllotaxis. **A.** The SAM consists of three layers: L1 (epidermal cell layer), L2 (subepidermal cell layer) and L3 (corpus cell layer) and can be divided into five regions: the central zone (CZ), organizing centre (OC), rib zone (RZ), peripheral zone (PZ), and outgrowing primordia (P1 to P4). **B.** To induce stem cell proliferation, *WUS* is expressed in the OC and moves to the CZ to induce *CLV3* expression in pluripotent stem cells. Subsequently, CLV3 moves to the OC to repress *WUS* via a CLV1/2 receptor kinase complex, creating a negative feedback loop that is required for stem cell homeostasis. *WUS* expression is enhanced by CK through type-B ARRs in response to light, and through a positive feedback loop via type-A ARRs that maintains CK signalling, and thus stem cell proliferation. Moreover, through MP, auxin slightly enhances *WUS* via the type-A ARR-CK feedback loop. To induce stem cell differentiation, light stabilises polar PIN protein localisation to create the auxin gradient that is required for initiation of new primordia. **C.** Incipient organs (i1 to i5) are initiated at the sites of enhanced auxin flow (pink) and are confined by chemical inhibitory fields that result from auxin depletion and cytokinin signalling (purple).

Moreover, MP has been shown to target the CK signalling inhibitor ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN 6 (AHP6) that increases the robustness of phyllotaxis by creating a secondary inhibitory field around the site of primordium initiation (Besnard et al., 2014b) (**Figure 5B, C**). Following initiation, leaf primordia undergo primary morphogenesis which is mainly regulated by *ANT* and *YABBY* genes resulting in lamina initiation and specification, and the formation of marginal structures such as serrations (Mizukami and Fischer, 2000; Sarojam et al., 2010). Finally, during secondary morphogenesis, the mature leaf is shaped by expansion, tissue differentiation and differential growth through a tight balance between CK and

GA (Achard et al., 2009; Holst et al., 2011). The newly formed leaf is part of a morphogenic unit called phytomere which also includes an internode and an axillary meristem (AM) (Galinat 1959). In Arabidopsis, the shoot meristem produces three different types of phytomers depending on the age of the plant. Type 1 phytomers form the rosette and consist of a rosette leaf, an extremely short internode, and an AM that may produce a branch. Type 2 phytomers form the inflorescence base and consist of a cauline leaf, a long internode, and an axillary branch, whereas type 3 phytomers carry the floral meristem that produces flowers instead of leaves (Schultz and Haughn, 1991). Finally, branches that arise from AMs of phytomeres can divide into second-order and third-order paraclades which can be divided between rosette paraclades that arise from type 1 phytomers, and cauline paraclades that are produced from type 2 phytomers (Talbert et al., 1995). For a long time, it was believed that stem cells in the SAM were shielded from possibly dangerous abiotic influences, and that organ formation was therefore self-regulatory (Airy, 1873). However, a first clue that light might regulate leaf initiation was found in pea plants that arrested leaf development when transferred to darkness (Low, 1971). Furthermore, microarray analysis has shown that light-regulated CK-associated genes are differentially expressed between seedlings and adult leaves, suggesting a light-dependent hormone response throughout shoot development (Ma et al., 2001). Moreover, auxin, ET, CK and GA genes are modulated in the SAM of etiolated seedlings after exposure to light. In addition, it was shown that phytochromes and cryptochromes contribute redundantly to SAM activity, possibly by modulation of these hormonal pathways (López-Juez et al., 2008). Finally, a breakthrough study by Yoshida and colleagues combined Arabidopsis and tomato research to show how light

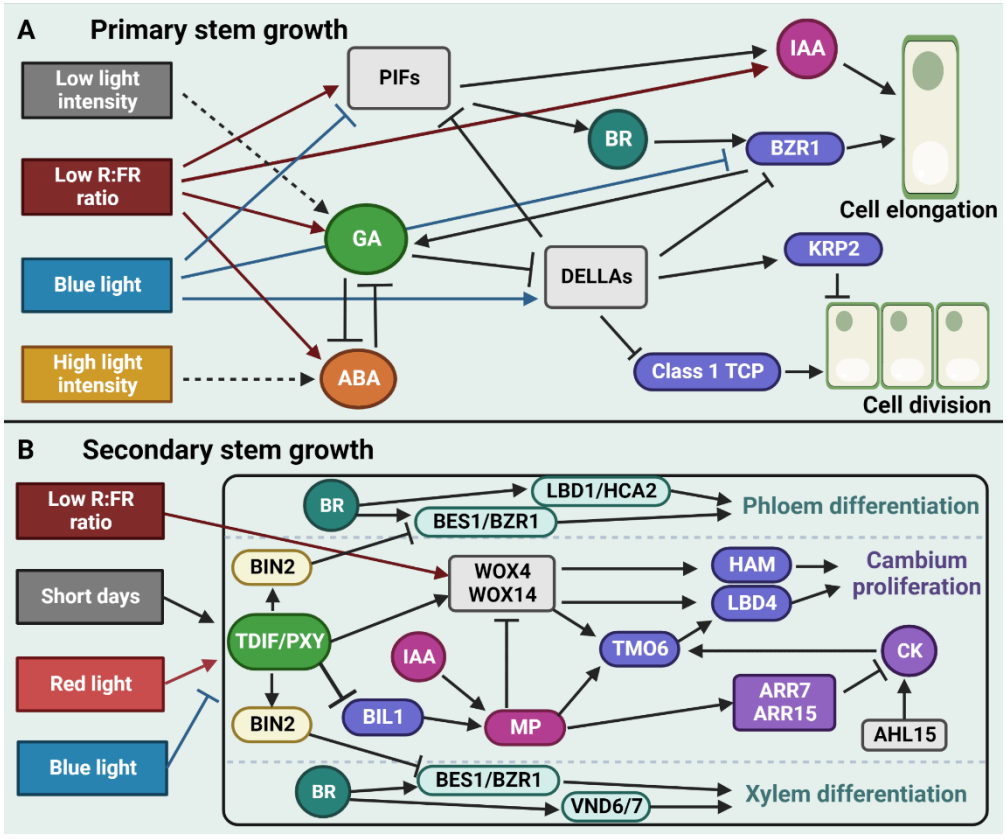
regulates SAM activity through auxin and CK. Light was shown to activate CK signalling in the SAM, which likely activates the stem cell pool via WUS-CLV. In addition, light stabilises PIN1 proteins at the plasma membrane, to establish the auxin gradient required for primordia initiation (Yoshida et al., 2011) (**Figure 5B**). A more recent study showed that light-induced SAM activation by CK coincides with elevated sugars that promote the *TARGET OF RAPAMYCIN* (*TOR*) kinase pathway, indicating the importance of metabolic in addition to hormonal signals (Pfeiffer et al., 2016). Aside from its effect on leaf initiation, light also influences leaf morphology. For example, low light intensity promotes petiole elongation and inhibits leaf blade expansion, a leaf phenotype that is well characterised as part of shade avoidance syndrome (Kozuka et al., 2005). As a response to low R:FR ratios, this altered leaf shape provides a better position for light exposure to drive photosynthesis (Tsukaya, 2004). Furthermore, darkness causes a local starvation state in the SAM that arrests cell proliferation in young primordia (Mohammed et al., 2018), and in the long term, results in leaf senescence (Weaver and Amasino, 2001). In summary, light has been shown to modulate both leaf initiation and morphology, thereby opening up many new research possibilities in identifying wavelength-specific responses and applications for horticulture.

Light-regulated primary and secondary stem growth

Similar to other shoot organs, the stem is initiated in the SAM. However, while lateral organs are initiated in the PZ, stem growth originates from the RZ of the SAM. The central region of the RZ gives rise to the pith, the peripheral regions of the RZ produces stem epidermis and cortex, and the boundary between these two regions develops the vasculature (Sachs, 1965). Elongation

of the stem relies on the interplay between GA, BR, auxin, and abscisic acid (ABA) signalling, with a key role for GA and the growth-inhibiting DELLA proteins that act downstream of the GA receptor (Ross et al., 2003; Unterholzner et al., 2015; Davière and Achard, 2016; Shu et al., 2016). The role of GA in primary growth is well characterised by the dwarfed GA biosynthesis mutants that are defective in leaf expansion and stem elongation (Thomas and Sun, 2004). GA promotes cell division in the RZ by inducing degradation of DELLAs that repress class I TCP (TEOSINTE BRANCHED 1, CYCLOIDEA, PROLIFERATING CELL FACTOR) cell cycle progression transcription factors (Davière et al., 2014). DELLAs have also been shown to directly inhibit cell division in the RZ through activation of the cell cycle inhibitor KRP2 (KIP-RELATED PROTEIN 2), thus further enhancing the role of GA in primary stem growth (Serrano-Mislata et al., 2017). In addition, DELLAs physically interact with and inhibit BRASSINAZOLE-RESISTANT 1 (BZR1) proteins, which are positive regulators of the growth-promoting BR response, suggesting that GA (partially) regulates BR-induced stem growth (Gallego-Bartolomé et al., 2012; Li et al., 2012b). However, some studies indicate that BR may also enhance stem growth by modulation of GA levels, thus highlighting the importance of both phytohormones (Tong et al., 2014; Unterholzner et al., 2015). Similarly, auxin has been shown to enhance biosynthesis of GA, and to inhibit its deactivation, to promote stem internode elongation in pea (Ross et al., 2003). Finally, to control stem growth, high levels of ABA act antagonistically on GA biosynthesis, whereas low levels of ABA promote GA biosynthesis (Seo et al., 2006; Oh et al., 2007) (**Figure 6A**). The effects of light quality and intensity on plant height are well established and have been reported in several species (Zheng et al., 2019; Paradiso and

Proietti, 2021). Low light intensity has been shown to result in increased stem elongation that is correlated to higher levels of GA in pea and *Brassica napus* (Gawronska et al., 1995; Potter et al., 1999). Stem elongation in response to low R:FR ratios is proposed to depend on a similar auxin-mediated shade avoidance mechanism that was identified in the hypocotyl and is described earlier in this chapter (**Figure 4B**). In addition, analysis of the *phyB ga1* double mutant in Arabidopsis revealed that the PHYB-mediated shade avoidance response requires functional GA signalling (Peng and Harberd, 1997), which was further supported by enhanced GA synthesis and sensitivity under low R:FR ratios (Reed et al., 1996; Hisamatsu et al., 2005). PIF stabilisation under low R:FR ratios is enhanced by GA signalling through relieving the inhibiting interaction between DELLAs and PIF1, PIF3, PIF4 and PIF6 (Feng et al., 2008; Gallego-Bartolomé et al., 2010; Lucas et al., 2008). Moreover, stabilised PIF4 promotes BR production, thus further enhancing stem elongation (Martínez et al., 2018). In contrast to shade avoidance, stem growth is inhibited by blue light via CRY1-mediated stabilisation of DELLA proteins (Yan et al., 2021), and through inhibition of PIFs and BZR1 (He et al., 2019; Ma et al., 2016). Finally, low R:FR ratios, as well as high light intensity, induce the biosynthesis and signalling of ABA to further prevent indeterminate primary growth (Huang et al., 2019; Ortiz-Alcaide et al., 2019) (**Figure 6A**). While primary (apical) stem growth depends on apical meristems, secondary (radial) stem growth depends on lateral meristems being the vascular cambium that produces xylem and phloem, and the cork cambium which gives rise to cork and phelloderm (Barra-Jiménez and Ragni, 2017). These vascular tissues provide the stem with strength and resilience, while facilitating long-range



transport of water and nutrients. In young stems, vascular tissues are organised in bundles that contain procambium, primary xylem, and primary phloem. As the plant ages, and secondary growth increases, the procambium, along with interfascicular parenchyma cells, mature into a circular vascular cambium that produces phloem towards the outside of the stem, and xylem towards the centre (Spicer and Groover, 2010; Ragni and Greb, 2018). Proliferation of cambium stem cells relies on a mechanism similar to CLV-WUS in the SAM. The

Figure 6: Regulation of primary and secondary stem growth.
Both primary (apical) and secondary (radial) stem growth respond to light. **A.** Primary stem growth relies mainly on GA inhibition of DELLA proteins that regulate cell division via KRP2 and class I TCPs, and cell elongation via BZR1. Interplay between GA and other phytohormones rely largely on PIFs, that promote cell elongation via auxin (IAA), and via BR. Additionally, ABA acts antagonistically on GA-dependent primary growth. Low R:FR ratios and low light intensities stimulate primary growth in a GA- and auxin-dependent manner. In contrast, blue light and high light intensities inhibit primary growth via ABA, or through modulation of PIFs, DELLAs and BZR1. **B.** Secondary stem growth relies on cambium proliferation, and differentiation into xylem and phloem cells. Stem cell homeostasis is regulated by proliferation-promoting WOX4/14, and by proliferation-inhibiting ARR7/15 signalling modules. The TDIF/PXY ligand-receptor complex stimulates cell division via WOX4/14 that activates HAM and LBD4 transcription factors, and through inhibition of BIL1, and its subsequent reduction in ARR7/15 via MP. TMO6 integrates CK and auxin signalling pathways to promote cambium proliferation. CK promotes cambium proliferation in an AHL15-dependent manner, while IAA stabilises ARR7/15 via MP, to inhibit cambium proliferation and promote xylem differentiation. BR stimulates xylem differentiation via VND6 and 7, and phloem differentiation via LBD1 and HCA2. In addition, BES1 and BZR1 are key factors for both xylem and phloem differentiation. R light, short days, and low R:FR ratios stimulate secondary growth, while B light represses secondary growth.

ligand-receptor complex TRACHEARY ELEMENT DIFFERENTIATION (TDIF) / PHLOEM INTERCALATED WITH XYLEM (PXY) promotes stem cell division and inhibits xylem cell differentiation via activation of the *WUSCHEL-RELATED HOMEOBOX 4* (*WOX4*) and *WOX14* transcription factors (Etchells et al., 2013, 2016). Subsequently, WOX4 and WOX14 promote stem cell proliferation through interaction with the LATERAL ORGAN BOUNDARIES DOMAIN 4 (LBD4) and HAIRY MERISTEM

(HAM) transcription factors (Suer et al., 2011; Etchells et al., 2013; Smit et al., 2020). In addition, PXY represses *BRASSINOSTEROID-INSENSITIVE 2-LIKE 1* (*BIL1*), that phosphorylates the cambium-inhibiting MP, to promote cambium proliferation via TARGET OF MONOPTEROS 6 (TMO6) (Han et al., 2018; Smit et al., 2020) (**Figure 6B**). Stem cell homeostasis relies greatly on the phytohormones auxin and CK. Auxin-dependent regulation of stem cell proliferation relies on WOX4, and its direct attenuation by MP. (Suer et al., 2011; Brackmann et al., 2018). Cambium activity and maintenance relies on CK levels that are modulated by LONELY GUY (LOG), CYTOKININ DEHYDROGENASE 2 (CKX2), and ARR7/15 (Kurakawa et al., 2007; Nieminen et al., 2008). Moreover, CK biosynthesis is promoted by the longevity-enhancing AT-HOOK MOTIF CONTAINING NUCLEAR LOCALIZED 15 (AHL15) transcriptional regulator (Rahimi et al., 2022b). Finally, TMO6 integrates auxin and CK signalling pathways to regulate cambium proliferation via LBD4 (Smit et al., 2020) (**Figure 6B**). Further towards the inside and outside of the stem, differentiation is initiated by stem cell fate identification into xylem and phloem precursors, and later on into secondary xylem and phloem cells. HIGH CAMBIAL ACTIVITY 2 (HCA2) and LATERAL ORGAN BOUNDARIES DOMAIN 1 (LBD1) have been identified as phloem-forming transcription factors (Guo et al., 2008; Yordanov et al., 2010), whereas VASCULAR-RELATED NAC-DOMAIN 6 (VND6) and VND7 are important for xylem production (Kubo et al., 2005). In addition, BRI1-EMS-SUPPRESSOR 1 (BES1) and BZR1 have been identified as key regulators of both xylem and phloem differentiation (Saito et al., 2018) (**Figure 6B**). Although the exact mechanism remains relatively unknown, BR appears to be involved in both xylem and phloem differentiation, likely via the above-

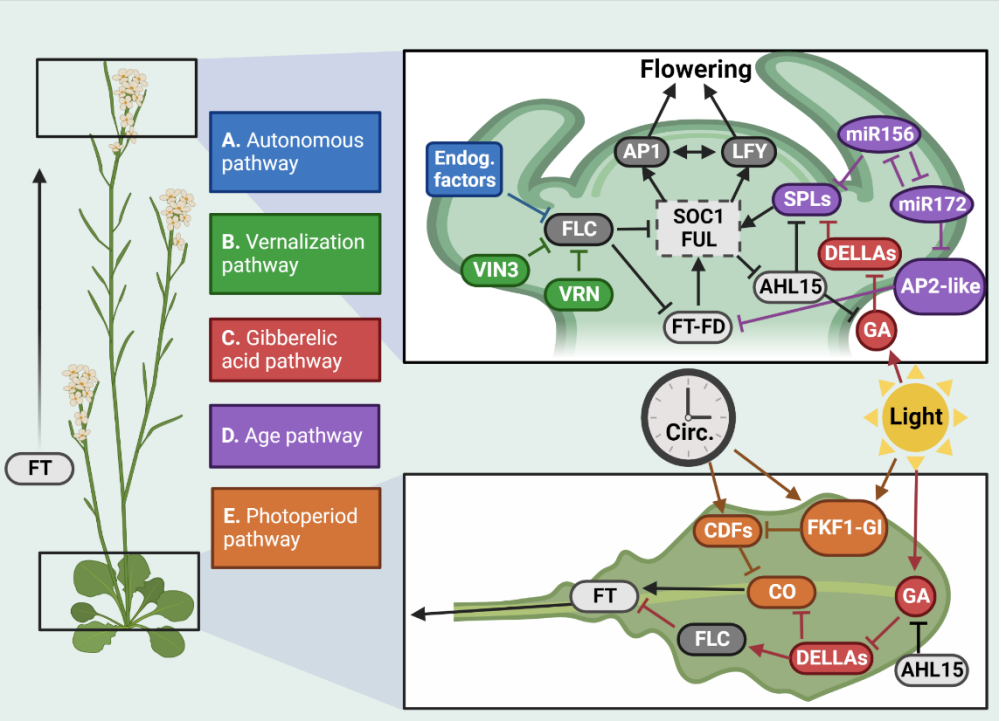
mentioned transcription factors (Miyashima et al., 2013). Light has been shown to affect secondary stem growth, mostly through intensity and day length, where shorter days (and thus less photons) result in thicker stems (MacMillan et al., 2013). In addition, low R:FR ratios have been shown to induce xylem formation in hypocotyls through activation of WOX4 (Botterweg-Paredes et al., 2020). Other light quality studies in three different plant species show that, higher fractions of (F)R light enhance stem thickness, while higher fractions of B light reduce secondary growth (Rehman et al., 2020; Cao et al., 2016; Li-Li et al., 2020) (**Figure 6B**). However, the underlying mechanisms remain to be elucidated.

Light-mediated timing of developmental phase transitions

Throughout their life cycle, plants undergo distinct developmental phases from embryonic growth all the way up to reproduction. After the formation and outgrowth of the first lateral organs, plants progress from juvenile phase to adult phase during vegetative phase change (VPC). In Arabidopsis, this transition can be easily identified by leaf heteroblasty, phyllotaxis and plastochron (Huijser and Schmid, 2011; Poethig, 2013). Conserved throughout angiosperms, the age pathway regulates developmental phase shifts including VPC (Weigel and Meyerowitz, 1993). In juvenile plants, *microRNA156* (*miR156*) levels are high, resulting in inhibition of its target genes encoding SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) transcription factors. As plants age, *miR156* levels gradually decrease, subsequently resulting in stabilisation of SPL expression. In addition, SPL levels are also promoted through GA signalling, indirectly of *miR156* (Wang et al., 2009; Jung et al., 2012; Yu et al., 2012). Six of these factors (SPL2, 9, 10, 11, 13,

and 15) regulate VPC directly via induction of leaf elongation and serration, or indirectly through activation of *miR172* (Xu et al., 2016a). As *miR172* levels gradually increase, this promotes the formation of abaxial trichomes by inhibiting *APETALA2* (*AP2*) and AP2-like genes *TARGET OF EARLY ACTIVATION TAGGED 1* (*TOE1*) and *TOE2* (Aukerman and Sakai, 2004; Chen, 2004). So far, only few publications indicate that VPC may be regulated by light. For example, VPC can be accelerated by high light intensity (Guo et al., 2017). In addition, FHY3 and FAR-RED IMPAIRED RESPONSE 1 (FAR1), that are required for PHYA signalling, have been identified recently as integrators of light and the miRNA156-SPL module of VPC (Xie et al., 2020). After acquisition of flowering competence following VPC, the SAM switches to an IM during the floral transition. A flowering hormone, or "florigen" was proposed to be synthesised in the leaves and transmitted to the SAM to acquire floral identity (Chailakhyan, 1937; Zeevaart, 1976). Later, Arabidopsis *FLOWERING LOCUS T* (*FT*) has been identified as such a leaf-to-SAM florigen that induces flowering (Corbesier et al., 2007). Moreover, *FT* homologues have been identified as florigens in several economically important, yet fundamentally different species, such as tomato, rice and apple (Lifschitz et al., 2006; Tamaki et al., 2007; Kotoda et al., 2010). Once inside the SAM, FT forms a complex with the bZIP transcription factor FD to induce floral meristem identity genes *AP1* and *LFY* via *AGAMOUS-LIKE 24* (*AGL24*), and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), *SEPALLATA3* (*SEP3*), and *FRUITFULL* (*FUL*) (Weigel et al., 1992; Abe et al., 2005; Teper-Bamnolker and Samach, 2005; Lee et al., 2008) (**Figure 7**). In contrast to FT, *TERMINAL FLOWER 1* (TFL1) acts as an "anti-florigen" that binds to FD to suppress flowering by antagonizing FT-FD

complex activity (Abe et al., 2005; Conti and Bradley, 2007). The balance between florigens and anti-florigens determines the timing of the floral transition in long-day (LD), short-day (SD) and day-neutral (DN) plant species (Higuchi, 2018). In Arabidopsis, this balance is determined via five distinct flowering pathways: (1) the autonomous pathway, (2) the vernalization pathway, (3) the GA pathway, (4) the age pathway and (5) the photoperiodic pathway. (**1**) In the autonomous pathway, endogenous factors repress the activity of the MADS-box protein FLOWERING LOCUS C (FLC), thereby relieving its inhibition of *FT* and *SOC1*, ultimately leading to flower induction (Simpson, 2004) (**Figure 7A**). (**2**) Vernalization is the requirement for exposure to long-term cold to induce flowering. Upon cold exposure, VERNALIZATION INSENSITIVE 3 (VIN3), VERNALIZATION 1 (VRN1) and VRN2 induce flowering by inhibiting *FLC* and *FLC-like* floral repressors (Kim and Sung, 2014) (**Figure 7B**). Since the autonomous and vernalization pathways are not likely to be influenced by light, we will not discuss their mechanisms in detail, and instead focus on the other three pathways that are (partially) regulated by light. (**3**) The importance of GA during floral transition was shown clearly by major flowering defects in loss of function mutants of GA biosynthesis and signalling components (Wilson et al., 1992; Jacobsen and Olszewski, 1993). Regulation of flowering by GA occurs both in the SAM and in the leaves by interacting with components of other hormonal and flowering pathways, or by direct modulation of (anti-)florigens (Bao et al., 2020). In leaves, GAs inhibit DELLA proteins that modulate the activity of a variety of transcription factors, including FT activators such as CONSTANS (CO) and WRKY75, and *FT* suppressors such as FLC and MYC3 (Li et al., 2016; Xu et



al., 2016b; Zhang et al., 2018; Bao et al., 2019). In the SAM, GA-mediated proteolysis of DELLAs leads to accumulation of *miR159*, WRKY12, NUCLEAR FACTOR Ys (NFYs) and SPLs, that activate *FUL* and *SOC1*, and subsequently *LFY* and *AP1* to promote flowering (Achard et al., 2004; Yu et al., 2012; Hou et al., 2014; Li et al., 2016b). Although most evidence for light-regulated flowering via the GA pathway depends on day length through stabilisation of the CO transcription factor, some studies also suggest

Figure 7: Light regulates flowering through GA signalling and day length. In the facultative long-day plant Arabidopsis, the floral transition is controlled via five distinct flowering pathways that rely on a group of key floral integrators and floral meristem identity genes. The florigen FT is expressed in leaves and moves to the SAM, where it forms a complex with FD to induce *SOC1* and *FUL*, among others, that subsequently enhance *AP1* and *LFY* to promote flowering. **A.** In the autonomous pathway, FLC activity is repressed by endogenous factors, resulting in relieved inhibition of *FT* and *SOC1*. **B.** The vernalization pathway is activated by exposure to long-term cold, resulting in FLC inhibition by VIN3, VRN1 and VRN2, and thus in elevation of *FT* and *SOC1*. **C.** In leaves, GA signalling induces flowering by inhibition of DELLA proteins that repress *FT* expression via CO or FLC proteins. In the SAM, GA signalling inhibits DELLAs, thereby relieving their repression of SPLs and other flower-inducing transcription factors that enhance *SOC1* and *FUL*. In both tissues, GA signalling is enhanced by light through PHY signalling, or day length. **D.** Plant ageing influences flowering depending on the balance between *miR156* and *miR172*. As plants age, *miR156* levels gradually decrease, resulting in SPL accumulation that promote flowering, while *miR172* levels increase and promote flowering through inhibition of AP2-like floral repressors. The longevity-enhancing AHL15 protein delays flowering by direct inhibition of the SPLs and through repressing GA signalling. **E.** In long-day photoperiods, FKF1, together with ZTL and LKP2, associates with the clock-associated component GI to inhibit CDFs that repress *CO* expression. Subsequently, the *CO* expression peak in the late afternoon of long days, results in enhanced *FT* expression at dusk.

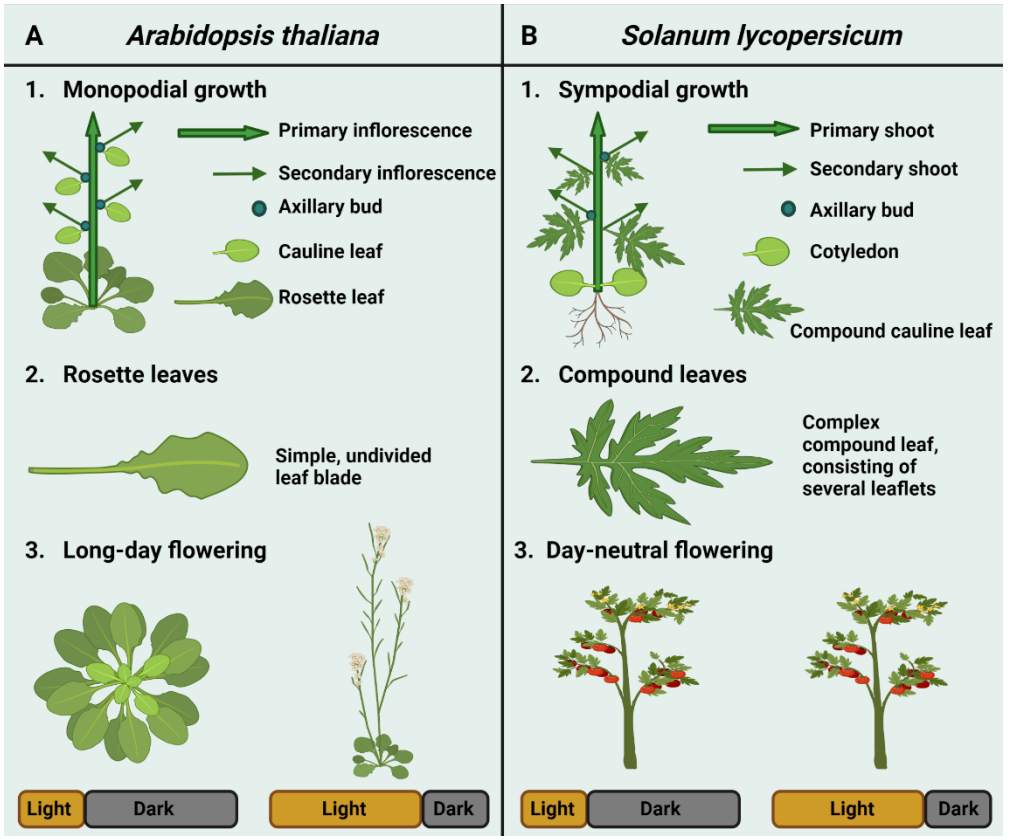
regulation of the GA pathway by light quality through PHYs and light intensity via *MYB-RELATED PROTEINs* (Hisamatsu and King, 2008; Zhao et al., 2011) (**Figure 7C**). (**4**) The age pathway mostly influences flowering through the timing of VPC as described above. As plants age and *miR172* levels increase, *AP2-like* genes that act as floral repressors are inhibited. Alleviated of its inhibition by AP2-like transcription factors, *FT* levels are elevated, ultimately leading to flowering (Teotia and Tang, 2015; Zheng et al., 2019). In addition,

higher SPL levels in adult plants activate *SOC1* transcription in the SAM, resulting in expression of *AP1* and *LFY* (Lee et al., 2008; Immink et al., 2012). To delay flowering, the longevity-promoting AHL15 protein decreases SPL levels in a *miR156*-independent manner. In addition, AHL15 has been shown to suppress GA biosynthesis, resulting in delayed flowering (Karami et al., 2020; Rahimi et al., 2022a). So far, an effect of light quality on age-dependent floral transition has not yet been identified, but some studies on VPC suggest a putative role for light in ageing (Guo et al., 2017; Xie et al., 2020) (**Figure 7D**). (**5**) Although light may influence flowering through the GA pathway and the age pathway, its main effect is through the photoperiodic pathway. This specific pathway depends on day length (photoperiod) and circadian clock components that are integrated via the light-dependent zinc-finger transcription factor CO (Samach et al., 2000; Suárez-López et al., 2001). In LD plants such as Arabidopsis, the floral transition occurs once the day length increases in late spring (Garner and Allard, 1920). During LD photoperiods, the blue-light FKF1 photoreceptor associates with the nuclear protein GIGANTEA (GI) to inhibit CYCLING DOF FACTORS (CDFs) that act as repressors of *CO* expression (Sawa et al., 2007). Its other two family members, ZTL and LKP2, both interact with FKF1 and GI to aid in the targeted degradation of CDFs (Fornara et al., 2009). The inhibition of these CDFs facilitates *CO* expression during the late afternoon resulting in a peak in *FT* expression at dusk. This FT peak promotes expression of *AP1*, *FUL*, and *CAULIFLOWER* (*CAL*) that induce the switch of the SAM to an IM (Hayama and Coupland, 2004; Abe et al., 2005; Wigge et al., 2005) (**Figure 7E**). In SD plants, such as rice, flowering occurs once daylength decreases in early autumn (Garner & Allard, 1920), and this also relies on CO-FT regulation. In rice, SD

conditions promote transcription of the florigen *Heading date 3A* (*Hd3a*, an orthologue of FT) which promotes floral transition (Tamaki et al., 2007). Similar to the GI-CO pathway in Arabidopsis, the rice orthologue of GI activates both Heading date 1 (Hd1, an orthologue of CO) and Early heading date 1 (Ehd1, a type B ARR) in response to the circadian clock (Yano et al., 2000; Hayama et al., 2003). Interestingly, Hd1 functions as an activator of *Hda3* in SD conditions and as a repressor of *Hda3* in LD conditions, indicating it is one of the main regulators of flowering in SD plants (Hayama and Coupland, 2004). Finally, in DN plants, such as tomato, flowering occurs regardless of photoperiod (Garner & Allard, 1920).

Horticultural crop versus genetic model plant: Differences between tomato and Arabidopsis.

Since this thesis focuses on Arabidopsis as a genetic model plant, and tomato as an important commercial crop, we should consider the differences and similarities between these two species. For example, germination of Arabidopsis seeds requires light, whereas tomato seeds germinate better in darkness (Mancinelli et al., 1966; Casal and Sánchez, 1998). As both species are dicots, seedling development is quite similar in Arabidopsis and tomato. However, after the seeding stage, Arabidopsis and tomato differ greatly in plant architecture, day length sensitivity, and life cycle. Differences in plant architecture between Arabidopsis and tomato are clearly visible in the shoot. Arabidopsis is an annual, monopodial plant in which the vegetative SAM produces leaves to form a spiral rosette that continues to grow until the vegetative SAM switches to a reproductive IM (Benlloch et al., 2007; Bartlett



and Thompson, 2014) (**Figure 8A**). In contrast, tomato is a semi-perennial, sympodial plant that produces 8-12 compound leaves before the vegetative SAM splits into an IM that will produce flowers, and an axillary bud that will produce new compound leaves (**Figure 8B**). After the first IM, tomato SAMs continue to split after production of three new compound leaves (Benlloch et al., 2007; Bartlett and Thompson, 2014). Not only do Arabidopsis and tomato differ in shoot meristems, they also greatly differ in leaf morphology. Rosette leaves of Arabidopsis are simple with an undivided leaf blade, whereas the

Figure 8: *Arabidopsis thaliana* versus *Solanum lycopersicum*.
Because molecular mechanisms identified in the genetic model plant *Arabidopsis thaliana* are not always conserved in important crops, the most important differences in architecture and life cycle between Arabidopsis and tomato are highlighted above. In addition, there are many differences on a genetic level resulting from mutations, duplications, and deletions. **A.** Arabidopsis is a monopodial plant that produces a spiral rosette from the vegetative SAM, until its switch to IM (1). The rosette leaves are simple, consisting of an undivided leaf blade (2). The floral transition depends greatly on day-length, with induction in long-day photoperiods (3). **B.** Tomato is a sympodial plant that produces a predetermined number of leaves before the SAM splits into an IM producing an inflorescence with flowers and an axillary bud producing a fixed set of phytomers with new leaves before it splits again in an IM and axillary bud (1). The tomato compound leaves are complex, consisting of leaflets that are separated by a bladeless region (2). As a day-neutral plant, tomato plants acquire flowering competence based on plant architecture, regardless of photoperiod (3).

compound leaves of tomato are more complex, consisting of separate subunits (leaflets) divided by a bladeless region (Bar and Ori, 2014; Du et al., 2018) (**Figure 8**). These differences in plant architecture and life cycle between Arabidopsis and tomato might be correlated to flowering competence. As a LD plant, Arabidopsis responds to changes in circadian rhythm and temperature to start flowering under increasing day length (Johansson and Staiger, 2015) (**Figure 8A**). In contrast, the DN tomato acquires flowering competence based on plant architecture (after a certain number of leaves), regardless of changes

in day length (Lifschitz and Eshed, 2006) (**Figure 8B**). Because Arabidopsis and tomato differ greatly in many aspects of plant development, photoreceptor responses most likely differ as well. All the different photoreceptor families that have been identified in Arabidopsis are also present in tomato, however evolutionary differences in photoreceptor lineage can make translation of light signalling pathways from model plant to crop quite challenging. For example, although the R/FR-sensitive PHY family in Arabidopsis consist of five members (PHYA to PHYE), this is not the case for all land plants. *PHYA* and *PHYB* lineages are greatly conserved among species. *PHYC* most likely arose from a gene duplication in the *PHYA* lineage, whereas *PHYD* and *PHYE* are a result of *PHYB* lineage duplication within *Brassicaceae* and dicots, respectively (Mathews and Sharrock, 1997). The tomato PHY family also consists of five members: *PHYA, PHYB1, PHYB2, PHYE* and *PHYF* (Van Tuinen et al., 1997; Alba et al., 2000). Tomato *PHYA, PHYE,* and *PHYF* have been identified as true orthologues of Arabidopsis *PHYA, PHYE,* and *PHYC*, respectively (Hauser et al., 1995; Alba et al., 2000). Tomato *PHYB1* and *PHYB2* however, arose from an independent duplication in *Solanaceae*, and are not exact functional orthologues of Arabidopsis *PHYB* and *PHYD* (Pratt et al., 1995). For perception of B light, the tomato CRY family consists of 4 members: *CRY1a, CRY1b, CRY2* and *CRY3.* Similar to Arabidopsis, tomato CRY3 is a DASH-type that is active in DNA repair (Facella et al., 2006). *CRY1a* and *CRY2* have been identified as homologues of Arabidopsis *CRY1* and *CRY2* (Perrotta et al., 2000). Although there are many functional similarities with their Arabidopsis counterparts, tomato *CRY1a* and *CRY2* functions differ from Arabidopsis in shoot and root elongation, circadian leaf movements and flowering (Fantini et al., 2019). Finally, tomato *CRY1b* turned

out to be a truncated copy of *CRY1a* resulting from a whole genome triplication in the common *Solanaceae* progenitor, and is likely not functional (Sato et al., 2012). Homologues of another B light-sensing receptor family, the PHOTs, have been identified as tomato *PHOT1* (Sharma & Sharma, 2007) and *PHOT2* (Sharma *et al.*, 2007). Unfortunately, functional gene studies remain limited in the tomato PHOT family. Recently, an orthologue of Arabidopsis *UVR8* has been identified to mediate acclimation to UV-B stress in tomato (Li et al., 2018). Finally, studies on the *ZTL* family in tomato are unfortunately almost non-existent. Altogether, the many differences between these two species show that translation from a genetic model plant to a horticultural crop remains challenging, and in some cases close to impossible. This indicates just how important it is to include crops in experimental studies on plant development.

Thesis outline

In this thesis, we set out to elucidate how different developmental processes during early plant development are influenced by light. In **chapter 2**, we used white TL lights to compare light and dark treatments, whereas in **chapters 3-5**, we investigated the effect of light quality on early plant development with the use of white, red, and blue LED modules. In **chapter 2**, we show that exposure of roots to light represses their primary elongation in Arabidopsis and tomato seedlings. Genetic analysis of mutants, combined with reporter lines, identified that the mechanism that regulates this phenotype depends on PHYA and PHYB that, upon their activation by FR and R light respectively, inhibit PIF transcription factors that modulate local auxin biosynthesis in the RAM. In **chapter 3**, we provide a clear and detailed overview of the early Arabidopsis and tomato phenotypes that arise when grown in red, blue, and white LED

conditions. A comparative analysis showed that primary growth responses to light quality were highly conserved between Arabidopsis and tomato. In contrast, Arabidopsis developmental phase transitions were extremely sensitive to light quality, whereas tomato phase transitions were remarkably indifferent to R or B light. In **chapter 4**, we further investigated Arabidopsis and tomato apical and radial growth responses to light quality. Microscopic and histological analyses of hypocotyls and stems throughout plant development showed that light quality can modulate both apical and primary radial growth in Arabidopsis, whereas tomato responses to R or B light are limited to apical growth. Finally, in **chapter 5**, we further analysed the major difference between Arabidopsis and tomato in light quality responses: flowering time. By combining genetic analysis of Arabidopsis plants with flowering studies in long-day and day-neutral plant species we show that B light promotes flowering through modulation of major components of the photoperiodic pathway. Moreover, we show that R light delays flowering through inhibition of important components of the age pathway. Altogether, this thesis gives a clear overview of light quality-regulated early plant development of Arabidopsis and tomato.

Author contributions

KS and RO structured the manuscript. KS wrote the manuscript and created the figures using BioRender software. All authors contributed to manuscript revision.

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