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Control of early plant development by light quality

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Summary



Young horticultural plants such as *Solanum lycopersicum* (tomato) are relatively small and require less light, thus opening up possibilities to be grown in multi-layers that require less space and energy. Since light-emitting diodes (LEDs) decouple light intensity from heating, they can be applied in such “vertical farming” growth systems. Moreover, LEDs offer spectral quality control that may be used to steer plant development. To achieve this, the effect of light quality on growth and developmental processes via the different light-sensing “photoreceptors” must be revealed. The photoreceptor families respond to different wavelengths (colours) within the spectrum: phytochromes (PHYs) are sensitive to red and far-red light, phototropins (PHOTs), cryptochromes (CRYs), and Zeitlupes (ZTLs) respond to blue light, and the UV-RESISTANCE LOCUS 8 (UVR8) receptor is activated by UV-B light.

Chapter 1 reviews the discovery and protein structures of, and signalling pathways triggered by, the different photoreceptors in land plants. Next, we discuss the role of each photoreceptor during different phases of plant development, and their interplay with major hormonal signalling pathways. After seed germination, the embryo matures from heterotrophic to fully photoautotrophic, and at this stage, light becomes a requirement for further development. Following seed germination, darkness promotes apical hypocotyl growth in seedlings to ensure rapid emergence from the soil. After emergence, light activates PHYs and CRYs to inhibit hypocotyl elongation and promote apical hook opening, thereby exposing the shoot apical meristem (SAM). Subsequently, the SAM responds to light by producing leaves and by initiating signalling cascades that modulate the architecture of the root. A widely-studied example of light-regulated plant growth is shade avoidance, where PHY signalling results in apical dominance, hyponastic leaves, and

early flowering, in response to low light intensity or low red: far-red ratios. Aside from the light responses that are described above, plants also monitor changes in light intensity and quality to become reproductive. For long-day (LD) plants, such as the genetic model dicot *Arabidopsis thaliana* (*Arabidopsis*), flowering is promoted in late spring through connections between ZTL photoreceptors and the circadian clock. In contrast, day-neutral (DN) plants, such as tomato, flower in response to other autonomous and hormonal pathways, regardless of day length. Therefore, at the end of **chapter 1**, we also discuss the major differences in light-associated genes and phenotypes between the genetic model dicot *Arabidopsis* and the horticultural crop tomato. In **chapter 2** we investigated how direct exposure of roots to light alters primary root growth of seedlings. We introduced a system to grow *Arabidopsis* and tomato seedlings in a “more natural” *in vitro* environment: the dark-grown roots (DGR) condition. Compared to traditional *in vitro* conditions with light-grown roots (LGR), DGR seedlings showed a better developed root system. Further analysis showed that red light activates root-localised PHYB proteins, that subsequently inhibit PHYTOCHROME INTERACTING FACTOR (PIF) 4, an activator of the auxin biosynthesis gene *YUCCA 6*. In a similar way, PHYA was found to inhibit PIF1, an activator of *YUCCA 4* and *YUCCA 6*, in response to far-red light. Subsequently this results in a suboptimal auxin concentration in the root apical meristem of LGR seedlings, ultimately leading to shorter roots. In DGR seedlings, PHYA- and PHYB-mediated inhibition of auxin biosynthesis does not occur, thereby creating optimal auxin levels for root growth. Proof-of-principle experiments in tomato suggested that the mechanism is at least partially conserved in plants. In **chapter 3**, *Arabidopsis* and tomato plants were grown in three different light



Summary

conditions: white light (control), monochromatic red light, and monochromatic blue light. Monochromatic red light promoted apical growth, resulting in longer hypocotyls and stems, and a higher shoot/root ratio in *Arabidopsis* and tomato plants. In contrast, monochromatic blue light resulted in shorter hypocotyls and stems, and a lower shoot/root ratio. Adult *Arabidopsis* plants developed a large rosette, flowered extremely late, and showed enhanced branching in the red LED condition, whereas blue light-grown plants flowered extremely early and developed only very few rosette leaves and branches. Interestingly, lateral organ formation and flowering of tomato plants appeared to be remarkably indifferent to the LED conditions, highlighting once more that responses in horticultural crops can greatly differ from what is observed in the genetic model plant *Arabidopsis*. In **chapter 4** we further investigated the hypocotyl and stem phenotypes that were observed in the different LED treatments. We showed that monochromatic red light promotes apical hypocotyl growth in seedlings, while decreasing its primary radial growth in both *Arabidopsis* and tomato seedlings. In contrast, treatment with monochromatic blue light resulted in shorter and thicker hypocotyls, when compared to white light. Histological and microscopic analysis revealed that these phenotypes were caused by changes in epidermal and pith cell sizes, suggesting that light quality affects cell wall loosening and vacuolar expansion to regulate hypocotyl growth. Interestingly, we observed that primary radial growth of adult tomato plants was completely indifferent to red and blue light, similar to leaf production and flowering. In contrast, primary radial growth of adult *Arabidopsis* plants was affected by light quality, resulting in thick stems in monochromatic red light, and thin stems in monochromatic blue light. These phenotypes were correlated to changes in primary xylem width and the number

of vascular bundles. Finally, analysis of *Arabidopsis* photoreceptor mutants suggested that CRYs and PHYs play an important role in light-regulated apical and primary radial growth. **Chapter 5** explores the leaf and flowering phenotypes that were observed in the different LED treatments in more detail. In monochromatic red light, an increase in *Arabidopsis* SAM size and an extended vegetative phase resulted in the production of an extremely big rosette, while the blue LED condition had an opposite effect. Interestingly, tomato SAMs were indifferent to light quality, resulting in the same number of leaves and flowering time in the different LED conditions. This suggested that light-regulated flowering of LD *Arabidopsis* plants was correlated to daylength sensitivity. Mutant and gene expression analysis confirmed that the photoperiodic pathway is only activated by light spectra that contain blue light,









	Red Light		Blue Light	
	Arabidopsis	Tomato	Arabidopsis	Tomato
	 <p>Long, thin hypocotyl</p> <p>Short root, few lateral roots</p>	 <p>Long, thin hypocotyl</p> <p>Normal root length</p>	 <p>Short, thick hypocotyl</p> <p>Short root, many lateral roots</p>	 <p>Short, thick hypocotyl</p> <p>Short root</p>
	 <p>Big rosette, late flowering</p> <p>Long, thick stems with many branches</p>	 <p>Normal flowering time</p> <p>Long stems with normal thickness</p>	 <p>Small rosette, early flowering</p> <p>Short, thin stems with few branches</p>	 <p>Normal flowering time</p> <p>Long stems with normal thickness</p>

Figure 1: Growth and development of *Arabidopsis* and tomato plants grown in red or blue light.

Summary of the *Arabidopsis* and tomato phenotypes that were observed in monochromatic red light (left) or monochromatic blue light (right), when compared to white light. “normal” indicates that the phenotype does not deviate from what was observed in white light.



while only spectra that contain red light activate the age pathway. Additional gene expression and *phy* mutant analysis showed that PHYB-mediated inhibition of the age pathway delays flowering in response to red light. This explains why Arabidopsis and lettuce plants flowered early in the blue LED condition that lacks red light, thus leaving PHYB in its inactive Pr conformation. Based on the work presented in this thesis we can conclude that red and blue light often act antagonistically during many aspects of plant growth and development. In addition, by including both Arabidopsis and tomato plants in our studies, we showed that light quality responses are not necessarily conserved between species, thus highlighting the importance of crop research in addition to the use of genetic model plants (**Figure 1**).

