



Editorial

Light perception, signalling and plant responses to spectral quality and photoperiod in natural and horticultural environments



1. Background

Global change and development of technology provide new challenges and opportunities for influencing plant growth processes. The warming climate will drive natural species and populations toward poles, where spectral quality and photoperiod differ from the light environment to which plant species have become adapted e.g. [Taulavuori et al. \(2010\)](#). This triggers many important questions such as how might this 'new' light environment affect the growth and development of these populations? In protected horticulture, on the other hand, active manipulation of the growth environment of plants is commonly used to optimize plant production and quality. Important factors for plant growth air temperature, humidity and CO₂-concentration are precisely controlled by computerized climate control systems, and in many greenhouses even control of photoperiod and light intensity is possible. Excess of light is screened by movable screens and shortage of light is supplemented by lamps. It is even not uncommon to apply light conditions that seldom or never occur in nature, just to achieve important goals such as precise timing of flowering or optimisation of photosynthesis required for environmental friendly and economical sustainable production ([Van Ieperen, 2012](#)). This may lead to rather extreme light climates, such as extreme long photoperiods, night breaks or even continuous light. Recent research has shown that growth of tomato under continuous light is feasible but requires inputs from the knowledge fields physiology, genetics and breeding to be fully exploited ([Velez-Ramirez et al., 2014](#)). Developments of high intensity light emitting diodes LEDs opens new avenues for optimisation of light in horticulture. To take full advantage of this technology, detailed knowledge is needed about a variety of morphological and physiological responses to light quality and their underlying signalling and metabolic pathways.

The aim of this special issue on light is to integrate the current knowledge from natural and horticultural fields through common physiological mechanisms and explore new possibilities for their application. It is emphasized that development and applications of LED systems was out of the scope of the special issue. However, their importance is to serve as an excellent insight into mechanisms in plant responses to light. One key question was: Can spectral quality be used to replace other environmental factors like temperature to induce plant responses? This special edition on light brings together 15 papers on responses to light quality at a

wide range of integration levels (from cell to host-plant symbiont relationships) and plant processes (e.g. flowering, photosynthesis, photomorphogenesis, production of secondary metabolites).

2. Reviews

This issue contains a number of reviews that summarize and update the knowledge about plant growth and functioning in response to specific wavelength ranges of light. First, [Demotes-Mainard et al. \(2016\)](#) reviewed the state-of-the-art on the perception of red (R) and far-red (FR) wavelengths, the downstream molecular responses and phenotypic results. They summarized general plant responses to R:FR ratio's that potentially can be made use of in horticulture and deduced the important knowledge gaps currently restraining its application. Secondly, [Huche-Thelier et al. \(2015\)](#) overreviewed effects of blue and UV radiation on light signalling and responses (i.e. vegetative growth, sexual reproduction) in plants, and reviewed effects on useful metabolites and plant resistance against bio-aggressors. Third, [Okello et al. \(2016\)](#) reviewed the involvement of light in the regulation of a set of cellular processes underlying plant growth: cell division, endoreduplication and cell expansion. They made an interesting attempt to separate the potential roles of light via light signalling from photo-assimilate supply, and discussed the individual importance for these cellular processes.

At the other end of the integration scale, [Markkola et al. \(2016\)](#) presented an interesting overview on host plant-symbiont (EMF) interactions in the context of global warming. They focussed on carbon economy and biomass partitioning between the autotrophic hosts and heterotrophic ectomycorrhizal fungal symbionts, reciprocally dependent on each other. They argue that the northern light environment may significantly modify competition between plant species following northward migration of southern ecotypes due to global warming, because the northern ecotypes are potentially more sensitive to changes in light quality and periodicity. They highlighted the importance as well as the lack of such studies and came up with suggestions for experimental approaches. Finally, [Warpeha and Montgomery \(2016\)](#) highlighted the key mechanistic factors and components that are especially linked to integrating responses to light and hormones during germination and the post-germinative seed-to-seedling transition. They concluded that light-/hormone-dependent mechanisms have implications for dynamics and diversity of natural plant species and communities.

3. Impact of light quality on photosynthesis

Since over half a century, it has been known that the efficiency of energy conversion of incident irradiance to chemical energy by leaves through photosynthesis is wavelength dependent (Hoover, 1937). Seminal research of McCree (1972), Inada (1976) and Evans (1987) has shown in many species that red light has by far the highest quantum yield for CO₂ fixation compared to other wavelengths in the photosynthetic active light spectrum. This high photosynthetic quantum yield of red light, combined with the high electrical efficiency of red LEDs have stimulated many researchers to use high fractions of red light to create optimal light environments for photosynthesis and growth of plants. Hogewoning et al. (2012) showed quantitatively for sun, shade and blue light spectra that leaves acclimate their photosystem composition to their growth light spectrum and how this changes the wavelength dependence of the photosystem excitation balance and quantum yield for CO₂ fixation. They proved that combining different wavelengths in growth light can enhance quantum yields substantially. Conversely, prolonged exposure to red light only can result in poor photosynthetic performance despite the usually highest photosynthetic quantum yield for monochromatic red light in leaves grown under broad-band light (Hogewoning et al., 2010). This negative effect of monochromatic red light was confirmed in this issue by Hernández and Kubota (2016) and further investigated in depth by Trouwborst et al. (2015) who used chlorophyll fluorescence in a detailed study to investigate whether the damage that occurs at photosystem level due to monochromatic red light, is permanent or can be reversed by the use of other wavelengths, such as blue. Plants do not only respond to the external light environment, but they also modify it. A well-known example is the increased fraction of FR (often characterised by a low R:FR ratio) under dense canopies (shade), which results from the wavelength-dependent absorption and reflection of natural irradiance by leaves. These spectral changes do not only occur in plant communities but also within plants. Selective absorption of wavelengths may cause spectral gradients in plant tissue. This has been recognised long before in leaves (e.g. Terashima and Saeki, 1983) and has shown to have implications for the severity of photoinhibition due to different wavelengths (Oguchi et al., 2011). In this issue Wittmann and Pfanz (2016) extended this concept to stems of woody species. Clear differences were measured in spectral composition of the light at different tissue depth, and interestingly chloroplasts in pith and wood tissue appeared to be more shade-adapted than in the cortex. Aasamaa and Aphalo (2016) studied the vegetational shade, and suggested that instead of a high stomatal regulation, shade avoiders attempt to maintain a high stomatal conductance. Vegetational shade increased the photosynthesis-mediated stomatal light response, activated an additional stomatal response through blue light receptors, and let stomata insensitive to green light. The modulation of stomatal light sensitivity participates in shade acclimation in shade-tolerating, but not in shade-avoiding deciduous tree(s).

4. Impact of light quality on photomorphogenesis and flowering

The influence of light quality on the morphology of plants comprehends multiple responses, among which those on stem elongation, leaf expansion and leaf angle are important ones. In research emphasis has long been on phytochrome related responses, traditionally discussed in the context of shade-avoidance. Today also the role of blue, perceived by cryptochromes and/or phototropins, receives considerable attention. Although variation exists between species, higher proportions of blue in growth irradiance often results in reduced stem elongation,

especially in trees (Taulavuori et al., 2005; Sarala et al., 2007, 2009, 2011). Monochromatic blue light, on the other hand, often results in increased elongation such as shown in cucumber (Hernández and Kubota, 2016) and petunia (Fukuda et al., 2016). Although monochromatic blue light drives the phytochrome photoequilibrium towards the non-activated phytochrome state (qualitative comparable to the effect of far red which usually enhances elongation), phytochrome related responses cannot explain this phenomenon because increasing fractions of blue light mostly lead to decreased elongation, despite its effect on the phytochrome equilibrium. As also pointed out by Hernandez, this phenomenon of interaction between red and blue on elongation has earlier been described as “coaction” between cryptochromes and phytochromes, and shows an interdependence of responses initiated through one photoreceptor by the other. Fernbach and Mohr (1990) demonstrated with studies on monochromatic light that also in trees hypocotyl growth is controlled by phytochrome, while the responses require also involvement of blue light. This observation on Scots pine was probably a key finding in understanding the photomorphogenic responses of trees to spectral changes. Riikonen et al. (2015) reports in this issue that physiological and morphological responses to light quality are more pronounced in shade-intolerant Scots pine than in Norway spruce seedlings. Another study on Norway spruce (Opseth et al., 2016) employing different latitudinal provenances focussed on the effects of light quality and underlying mechanisms on growth-dormancy cycling. They show that light quality and photoperiod are both involved in the control of bud set through a common pathway with FTL2 as a key factor. With respect to photoperiodic flowering, Craig and Runkle (2015) demonstrated in a set of long-day plants that night interruption with a light spectrum characterised by an intermediate phytochrome photoequilibrium optimally promotes flowering. They discussed this within an conceptual framework that flowering of long day plants could be controlled by an optimal amount of active phytochrome (P_{FR}): until a certain threshold P_{FR} promotes flowering while a greater amount of P_{FR} would inhibit flowering. Fukuda et al. (2016) investigated both elongation and flowering responses in Petunia to light quality in the context gibberellin (GA) content modulation. They observed that blue and red light caused antagonistic effects on shoot elongation and that this clearly related to GA signals. In contrast they could not demonstrate a causal relationship between light quality and flowering via GA signalling. With respect to the control of flowering in Phalaenopsis Dueck et al. (2016) suggested that the plant hormones responsible for bud break and inflorescence elongation can be stimulated by light instead of temperature. This finding is interesting, and demonstrates that light quality may provide alternative signals to replace other environmental factors.

5. Impact of phytochemical production

Blue light is reported to result in enhanced concentrations of phytochemicals in edible species (e.g. Li and Kubota 2009; Taulavuori et al., 2013). In this issue Taulavuori et al. (2016) reported that flavonoid and phenolic acid biosynthesis in plants under blue light is species dependent. Many compounds accumulated lettuce as a function of length of light manipulation period, while not in basil. There are also number of other studies indicating enhanced phytochemical production under blue light and UV radiation (see also reviews by Huche-Thelier et al. (2015) and Warpeha and Montgomery (2016)).

6. Conclusions

- The reviews altogether updated and highlighted the novel and multiple roles of light quality and photoperiod from molecular to

whole-plant level, and integrated the responses even to community and ecosystem level.

- Artificial LED lighting may result in unexpected results when monochromatic light is only used.
- Plant tissue itself is a factor modifying the spectral composition.
- There are species-specific responses to light quality both in photomorphogenesis and phytochemical production.
- The control of some mechanisms in plants may be replaced by specific light signalling.
- Both review updates and original articles provide valuable information to be applied in horticultural purposes. The findings and observations of the articles in this special issue may help agriculture, forestry and biodiversity conservation to adapt global change consequences.

References

- Aasamaa, K., Aphalo, P.J., 2016. Effect of vegetational shade and its components on stomatal responses to red, blue and green light in two deciduous tree species with different shade tolerance. *Environ. Exp. Bot.* 121, 94–101.
- Demotes-Mainard, S., Péron, T., Corot, A., Bertheloot, J., Gourrier, J., Le Travier, S., Sakr, S., 2016. Plant responses to red and far-red lights, applications in horticulture. *Environ. Exp. Bot.* 121, 4–21.
- Dueck, T., Trouwborst, G., Hogewoning, S.W., Meinen, E., 2016. Can a high red: far red ratio replace temperature-induced inflorescence development in *Phalaenopsis*? *Environ. Exp. Bot.* 121, 139–144.
- Evans, J., 1987. The dependence of quantum yield on wavelength and growth irradiance. *Aust. J. Plant Physiol.* 14, 69. doi:<http://dx.doi.org/10.1071/PP9870069>.
- Fernbach, E., Mohr, H., 1990. Coaction of blue/ultraviolet-A light and light absorbed by phytochrome in controlling growth of pine (*Pinus sylvestris* L.) seedlings. *Planta* 180 (2), 212–216. doi:<http://dx.doi.org/10.1007/BF00193998>.
- Fukuda et al. (2016). This paper did not appear online yet.
- Craig, D.S., Runkle, E.S., 2015. An intermediate phytochrome photoequilibria from night-interruption lighting optimally promotes flowering of several long-day plants. *Environ. Exp. Bot.* 121, 132–138.
- Hernández, R., Kubota, C., 2016. Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. *Environ. Exp. Bot.* 121, 66–74.
- Hogewoning, S.W., Douwstra, P., Trouwborst, G., van Ieperen, W., Harbinson, J., 2010. An artificial solar spectrum substantially alters plant development compared with usual climate room irradiance spectra. *J. Exp. Bot.* 61 (5), 1267–1276. doi:<http://dx.doi.org/10.1093/jxb/erq005>.
- Hogewoning, S.W., Wientjes, E., Douwstra, P., Trouwborst, G., van Ieperen, W., Croce, R., Harbinson, J., 2012. Photosynthetic quantum yield dynamics: from photosystems to leaves. *Plant Cell* 24 (5), 1921–1935. doi:<http://dx.doi.org/10.1105/tpc.112.097972>.
- Hoover, W.H., 1937. The dependence of carbon dioxide assimilation in a higher plant on wavelength of radiation. *Smithson. Inst. Misc. Collect.* 95, 1–13.
- Huche-Thelie et al., 2015. This paper did not appear online yet.
- Inada, K., 1976. Action spectra for photosynthesis in higher plants. *Plant Cell Physiol.* 17, 355–365.
- Li, Q., Kubota, C., 2009. Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. *Environ. Exp. Bot.* 67, 59–64.
- Markkola, A.M., Saravesi, K., Aikio, S., Taulavuori, E., Taulavuori, K., 2016. Light-driven host-symbiont interactions under hosts' range shifts caused by global warming: a review. *Environ. Exp. Bot.* 121, 48–55.
- McCree, K., 1972. Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. *Agric. Meteorol.* (10) . <http://www.sciencedirect.com/science/article/pii/0002157172900453>.
- Oguchi, R., Douwstra, P., Fujita, T., Chow, W.S., Terashima, I., 2011. Intra-leaf gradients of photoinhibition induced by different color lights: implications for the dual mechanisms of photoinhibition and for the application of conventional chlorophyll fluorometers. *New Phytol.* 191 (1), 146–159. doi:<http://dx.doi.org/10.1111/j.1469-8137.2011.03669.x>.
- Okello, R.C.O., de Visser, P.H.B., Heuvelink, E., Marcelis, L.F.M., Struik, P.C., 2016. Light mediated regulation of cell division, endoreduplication and cell expansion. *Environ. Exp. Bot.* 121, 39–47.
- Opseth, L., Holefors, A., Rosnes, A.K.R., Lee, Y., Olsen, J.E., 2016. FTL2 expression preceding bud set corresponds with timing of bud set in Norway spruce provenances under different light quality treatments. *Environ. Exp. Bot.* 121, 121–131.
- Riikonen et al., 2015. This paper did not appear online yet.
- Sarala, M., Taulavuori, K., Taulavuori, E., Karhu, J., Laine, K., 2007. Elongation of Scots pine seedlings under blue light depletion is independent of etiolation. *Environ. Exp. Bot.* 60 (3), 340–343. doi:<http://dx.doi.org/10.1016/j.envexpbot.2006.12.006>.
- Sarala, M., Taulavuori, E., Karhu, J., Savonen, E.M., Laine, K., Kubin, E., Taulavuori, K., 2009. Improved elongation of Scots pine seedlings under blue light depletion is not dependent on resource acquisition. *Funct. Plant Biol.* 36 (8), 742–751. doi:<http://dx.doi.org/10.1071/FP09012>.
- Sarala, M., Taulavuori, E., Karhu, J., Laine, K., Taulavuori, K., 2011. Growth and pigmentation of various species under blue light depletion. *Boreal Environ. Res.* 16, 381–394.
- Taulavuori, K., Sarala, M., Karhu, J., Taulavuori, E., Kubin, E., Laine, K., Pesonen, E., 2005. Elongation of Scots pine seedlings under blue light depletion. *Silva Fennica* 39 (1), 131–136.
- Taulavuori, K., Sarala, M., Taulavuori, E., 2010. Growth responses of trees to Arctic light environment. *Prog. Bot.* 71, 157–168.
- Taulavuori, K., Julkunen-Tiitto, R., Hyöky, V., Taulavuori, E., 2013. Blue mood for superfood. *Nat. Prod. Commun.* 8 (6), 791–794.
- Taulavuori, K., Hyöky, V., Oksanen, J., Taulavuori, E., Julkunen-Tiitto, R., 2016. Species-specific differences in synthesis of flavonoids and phenolic acids under increasing periods of enhanced blue light. *Environ. Exp. Bot.* 121, 145–150.
- Terashima, I., Saeki, T., 1983. Light environment within a leaf I. Optical properties of paradermal sections of *Camellia* leaves with special reference to differences in the optical properties of palisade and spongy tissues. *Plant Cell Physiol.* 24 (8), 1493–1501.
- Trouwborst, G., Hogewoning, S.W., van Kooten, O., Harbinson, J., Win, V.L., 2015. Plasticity of photosynthesis after the red light syndrome in cucumber. *Environ. Exp. Bot.*
- Van Ieperen, W., 2012. Plant Morphological and developmental responses to light quality in a horticultural context. *Acta Hort.* 956, 131–140.
- Velez-Ramirez, A.I., van Ieperen, W., Vreugdenhil, D., a, van Poppel P.M.J., Heuvelink, E., Millenaar, F.F., 2014. A single locus confers tolerance to continuous light and allows substantial yield increase in tomato. *Nat. Commun.* 5, 1–13. doi:<http://dx.doi.org/10.1038/ncomms5549>.
- Warpeha, K.M., Montgomery, B.L., 2016. Light and hormone interactions in the seed-to-seedling transition. *Environ. Exp. Bot.* 121, 56–65.
- Wittmann, C., Pfanz, H., 2016. The optical, absorptive and chlorophyll fluorescence properties of young stems of five woody species. *Environ. Exp. Bot.* 121, 83–93.

Tom Dueck (Guest editor)^a

Wim van Ieperen (Guest editor)^b

Kari Taulavuori (Guest editor)^{c,*}

^aWageningen UR, Greenhouse Horticulture, Droevendaalsesteeg 1, 6708PB Wageningen, The Netherlands

^bWageningen University, Horticulture and Product Physiology Group, PO box 630, 6700AP Wageningen, The Netherlands

^cDepartment of Ecology, University of Oulu, P.O. Box 3000, FIN-900014 Oulu, Finland

* Corresponding author. Fax: +31 358 8 553 1016.
E-mail addresses: Tom.Dueck@wur.nl (T. Dueck),
Wim.vanleperen@wur.nl (W. van Ieperen),
Kari.Taulavuori@oulu.fi (K. Taulavuori).

Available online 17 June 2015