

Light signal perception in *Arabidopsis* rosettes

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Highlights: Light signals are important signals for future and present competition. We used an architectural model of *Arabidopsis* development to show that vertical growth of neighboring vegetation is more important than proximity for early detection of competition. Self-signaling is greatly enhanced when own organs grow more vertically, and signal strength differs between signal perception at the apex compared to the leaves.

Keywords: *Arabidopsis*, light signaling, shade avoidance, competition

INTRODUCTION

Plants are able to adapt their development to the level of competition for light with neighboring plants, by increased height growth (Franklin and Whitelam, 2005), increased hyponasty (leaf angle) (De Wit et al., 2012, Vandenbussche et al., 2005) and reduced branching (Finlayson et al., 2010, Casal et al., 1987) among others. These responses are termed the shade avoidance syndrome (SAS), and together they result in allocation of biomass in regions of the canopy where competition for light is minimal. In order to accurately judge the intensity and timing of future and present competition for light, plants are equipped with an array of neighbor-sensing mechanisms. Next to mechanisms based on gaseous ethylene perception (Pierik et al., 2003) and physical touching (De Wit et al., 2012), plants use light signals such as the red/far-red ratio (R:FR) (Ballaré et al., 1990) and blue light intensity (Pierik et al., 2004). Light reflected or transmitted by plant organs have a low R:FR and blue intensity (red and blue light are mostly absorbed by green tissues whereas far-red light is mostly scattered) which makes them suitable to be interpreted as signals for competition. To do so plants are equipped with photoreceptors such as phytochromes and cryptochromes (Franklin, 2008) that translate the strength of the light signal into a physiological state, enabling the plant to respond accordingly.

Photoreceptors are generally found throughout the plant body, but there are still many questions regarding the location of signal perception in relation to their orientation in the canopy. In gramineous species, vertically oriented organs such as the stem base and young elongating leaf blades are sensitive to low R:FR (Skinner and Simmons, 1993) as light travelling more or less parallel to the soil surface is most likely to have been scattered by surrounding vegetation. Indeed, in *Arabidopsis* (*Arabidopsis thaliana*) the vertical orientation of leaves heavily determines R:FR signal strength (De Wit et al., 2012). In other dicots, both internodes, leaves and axillary buds have been reported to be sites of R:FR perception (Girault et al., 2008, Casal and Smith, 1988, Morgan et al., 1980). In both dicots and monocots the phytochrome and cryptochrome receptor genes show expression in all organs, but the link between the individual photoreceptor signaling pathways and other processes like hormone synthesis may differ between organs (Evers et al., Submitted). No information is available to date about what are the sites of perception for low blue light-induced shade avoidance.

Also, the extent to which a plant is exposed and reacts to light signals created by its own leaves and stems is unclear. The light that influences plant development is a combination of sky light, light reflected from neighboring structures and from the plant's own organs, but the proportion self-signaling to total signaling in relation to the vegetation density is unknown. Plant simulation models are suitable to address such questions

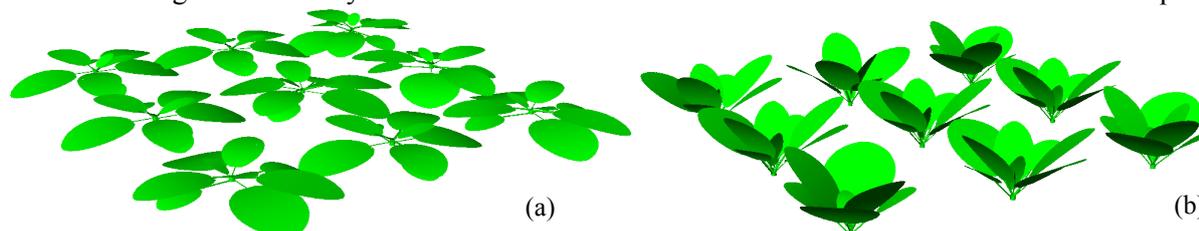


Fig. 1. Example of the visual output of the *Arabidopsis* rosette model showing virtual canopies after 225 hours at a plant distance of 2 cm; (a) normal leaf inclination, (b) 50% increased leaf inclination.

Table 1: Canopy composition and leaf angle in the simulated treatments

Treatment		Leaf angle increase focal plant	Leaf angle increase border plant
1	Single plant	0 %	-
2	Plot	0 %	0 %
3	Plot	0 %	50 %
4	Single	50 %	-
5	Plot	50 %	50 %

related to signal perception. The purpose of this simulation study was to assess to what extent different plant components of Arabidopsis rosettes receive R:FR and blue light signals in relation to the density and structure of neighboring vegetation and to their own plant structure.

SIMULATIONS

We used a descriptive simulation model of Arabidopsis rosette development (Evers et al., Submitted, De Wit et al., 2012), which was constructed using the simulation platform GroIMP v1.4.1 (Hemmerling et al., 2008). Simulation of the light environment was done using the GroIMP radiation model. All rosette organs were provided with values for reflectance, transmittance and absorbance of red, far-red and blue light based on measured data from greenhouse-grown Arabidopsis plants using a Perkin Elmer Lambda 9 Spectrometer (Perkin Elmer, Waltham, USA). Light signal perception was defined for leaf blades as well as for the shoot apex (represented by an invisible spherical sensor in the center of the rosette).

Arabidopsis plants were simulated individually as well as in stands of nine plants in a 3×3 square grid at 2, 4 and 6 cm plant distance (Fig. 1), of which the middle plant (the focal plant) was used for analysis. Due to model stochasticity, simulations were done five times. Orientation in the x-y plane of simulated plants was chosen at random for each plant. To assess the effect of hyponasty on light signaling, in a second set of simulations the inclination of all leaves was increased by 50% (Fig. 1b). Finally, a third set of simulations of nine plants was done in which the focal plant were non-hyponastic and the border plants had 50% increased leaf inclination (table 1). R:FR of the incoming light was 1.2. For the range 150 to 250 hours, R:FR and blue light levels at the apex and on all leaf blades were recorded and averaged.

RESULTS AND DISCUSSION

The apex perceived lower R:FR values than the leaves across treatments (Fig. 2a) due to the shielded location of the apex in the rosette, receiving mostly light scattered from its own leaves. R:FR perceived at the apex and on the leaves decreased with the addition of non-hyponastic neighbors, and decreased further in case neighbors were hyponastic (i.e. had more vertically oriented leaves). A more pronounced drop occurred

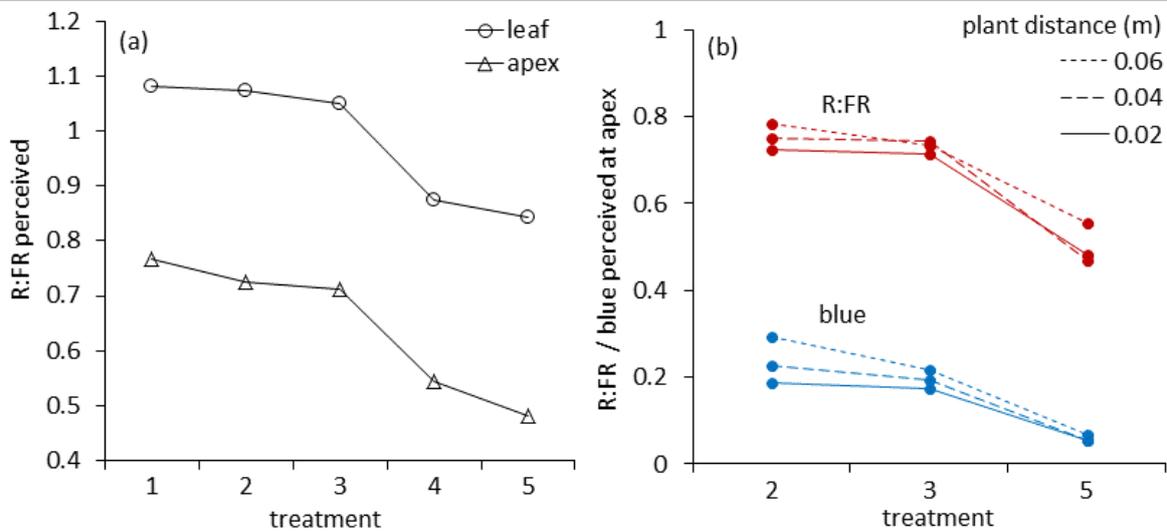


Fig. 2. (a) R:FR perceived by the leaves (circles) and the apex (triangles) in treatments 1 to 5. Treatments sorted with decreasing value of R:FR perceived. (b) R:FR and blue light (expressed as a fraction of incoming blue light intensity) perceived by the apex in treatments 2, 3 and 5 at three plant distances.

when the focal plant itself was hyponastic and largest decrease in R:FR occurred at the combination of both hyponastic focal and border plants. Hyponasty in the focal plant clearly had a much larger effect on R:FR perceived by both apex (34.1%) and leaves (64.1%) than adding neighbors. Adding neighbors never contributed more than 9.1% in case neighbor and focal plant leaf angle were identical. Adding hyponastic neighbors to a non-hyponastic focal plant provided an additional R:FR drop up to 22.1%, showing the relevance of vertical growth for R:FR signaling. This trend was observed for all plant distances (Fig. 2b). Plant distance hardly affected R:FR perceived by the apex. Blue light signaling was only affected in non-hyponastic situations: blue light fractions ranged from 0.19 to 0.29 when increasing plant distance from 0.02 to 0.06 m). In a fully hyponastic canopy, blue light signaling at the apex was not affected by plant distance.

This exercise highlights the relative importance of vertical neighbor growth in plant competition. Even if competitors are relatively close, they will not be noticed through light signaling if they do not show significant vertical growth. This strengthens the conclusions of De Wit *et al.* (2012) that touch rather than light signals provide the strongest early signals for competition in ‘flat’ canopies such as those composed by Arabidopsis rosettes. Furthermore, the observed differences in light signal perception between apex and leaves gives interesting questions regarding signal integration and site of perception. For example, increased petiole extension leading to local exploration of space is a local response to R:FR perception by the attached blade (Kozuka *et al.*, 2010), for which relatively mild drops in R:FR may be sufficient (Fig. 2a). However shoot branching regulation by auxin (Domagalska and Leyser, 2011) may be modulated at least partly by R:FR at the apex, since leaf blades do not respond to low R:FR in terms of auxin activity (Evers *et al.*, Submitted), in which case our model predicts more severe drops in R:FR are required. Further experimental and simulation studies will be conducted to assess how the different signals act in concert to give rise to the various responses in the shade avoidance syndrome.

LITERATURE CITED

- Ballaré CL, Scopel AL, Sánchez RA. 1990.** Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science*, **247**: 329-332.
- Casal JJ, Sánchez RA, Deregibus VA. 1987.** Tillering responses of *Lolium multiflorum* plants to changes of red/far-red ratio typical of sparse canopies. *Journal of Experimental Botany*, **38**: 1432-1439.
- Casal JJ, Smith H. 1988.** Persistent effects of changes in phytochrome status on internode growth in light-grown mustard: occurrence, kinetics and locus of perception. *Planta*, **175**: 214-220.
- De Wit M, Kegge W, Evers JB, Vergeer-van Eijk MH, Gankema P, Voeselek LACJ, Pierik R. 2012.** Plant neighbor detection through touching leaf tips precedes phytochrome signals. *Proceedings of the National Academy of Sciences*, **109**: 14705-14710.
- Domagalska MA, Leyser O. 2011.** Signal integration in the control of shoot branching. *Nature Reviews Molecular Cell Biology*, **12**: 211-221.
- Evers JB, Vos J, Bouwmeester H, Van der Krol AR. Submitted.** Light signalling in hormone-regulated shoot branching.
- Finlayson SA, Krishnareddy SR, Kebrom TH, Casal JJ. 2010.** Phytochrome regulation of branching in Arabidopsis. *Plant Physiology*, **152**: 1914-1927.
- Franklin KA. 2008.** Shade avoidance. *New Phytologist*, **179**: 930-944.
- Franklin KA, Whitelam GC. 2005.** Phytochromes and shade-avoidance responses in plants. *Annals of Botany*, **96**: 169-175.
- Girault T, Bergougnoux V, Combes D, Viemont JD, Leduc N. 2008.** Light controls shoot meristem organogenic activity and leaf primordia growth during bud burst in *Rosa* sp. *Plant, Cell and Environment*, **31**: 1534-1544.
- Hemmerling R, Kniemeyer O, Lanwert D, Kurth W, Buck-Sorlin GH. 2008.** The rule-based language XL and the modelling environment GroIMP illustrated with simulated tree competition. *Functional Plant Biology*, **35**: 739-750.
- Kozuka T, Kobayashi J, Horiguchi G, Demura T, Sakakibara H, Tsukaya H, Nagatani A. 2010.** Involvement of auxin and brassinosteroid in the regulation of petiole elongation under the shade. *Plant Physiology*, **153**: 1608-1618.
- Morgan DC, O'Brien T, Smith H. 1980.** Rapid photomodulation of stem extension in light-grown *Sinapis alba* L. *Planta*, **150**: 95-101.
- Pierik R, Visser EJW, de Kroon H, Voeselek LACJ. 2003.** Ethylene is required in tobacco to successfully compete with proximate neighbours. *Plant, Cell & Environment*, **26**: 1229-1234.
- Pierik R, Whitelam GC, Voeselek LACJ, De Kroon H, Visser EJW. 2004.** Canopy studies on ethylene-insensitive tobacco identify ethylene as a novel element in blue light and plant-plant signalling. *Plant Journal*, **38**: 310-319.
- Skinner RH, Simmons SR. 1993.** Modulation of leaf elongation, tiller appearance and tiller senescence in spring barley by far-red light. *Plant, Cell & Environment*, **16**: 555-562.
- Vandenbussche F, Pierik R, Millenaar FF, Voeselek LACJ, Van der Straeten D. 2005.** Reaching out of the shade. *Current Opinion in Plant Biology*, **8**: 462-468.