Letter

Photoreceptors UVR8 and phytochrome B cooperate to optimize plant growth and defense in patchy canopies

Light is a critical source of information for plants. Plants use the phytochromes (particularly phyB) to detect light signals associated with the proximity of competitors. A low ratio of red (R) to far-red (FR) radiation (R : FR) indicates increased competition intensity, and triggers morphological responses that allow the plant to escape shading from its neighbors (the shade avoidance syndrome, SAS) (reviewed in Ballaré, 2009; Kami *et al.*, 2010; Martínez-García *et al.*, 2010; Casal, 2012; Pierik & de Wit, 2014). Recent evidence from studies on light regulation of plant immunity has suggested that plants may also use ultraviolet-B (UV-B, 290–315 nm) radiation as an indicator of competition intensity and light availability (Demkura *et al.*, 2010; Demkura & Ballaré, 2012). In addition, recent studies have shown that UV-B radiation can strongly repress SAS responses triggered by low R : FR ratios (Hayes *et al.*, 2014). Ambient UV-B radiation causes damaging effects on plants, such as DNA damage (Mazza *et al.*, 1999), and also induces adaptive photomorphogenic responses acting through a specific UV-B photoreceptor (UVR8) (Rizzini *et al.*, 2011; Christie *et al.*, 2012; Wu *et al.*, 2012) (reviewed in Heijde & Ulm, 2012; Jenkins, 2014). Therefore, the possibility exists that plants integrate information perceived by phyB and UVR8 to make decisions about growth and defense when faced with a complex light environment, such as the one that characterizes vegetation canopies. In this Letter, we address this possibility and discuss how the interplay between UV-B and R : FR signaling fine tunes plant growth and defense to optimize resource utilization in patchy canopy environments.

UV-B tempers SAS responses triggered by phyB inactivation under sunlight

In Arabidopsis seedlings grown under artificial light, moderate levels of supplemental UV-B can strongly suppress hypocotyl elongation responses to low R : FR ratio (Hayes *et al.*, 2014). However, under field conditions, phyB inactivation can trigger significant elongation responses even in plants growing under full sunlight. Perhaps the most dramatic example comes from studies with cucumber (*Cucumis sativus*), which showed that the phyB null mutant (*lh*) can grow hypocotyls as long as 30 cm even under summertime field conditions and high natural UV-B irradiance (Casal *et al.*, 1994). To further explore the interactions between phyB inactivation and natural UV-B levels, we compared the growth of *lh* and wild type cucumbers under filters that either blocked (−UV-B) or transmitted UV-B radiation (+UV-B) (see Supporting Information Methods S1). We found a dramatic effect of phyB inactivation promoting hypocotyl elongation and a modest, but significant repression of elongation by solar UV-B radiation (Fig. 1a). Less spectacular responses to partial phyB inactivation have been reported in other field studies, under solar UV-B irradiances, using other plant species exposed to lateral FR radiation (reviewed in Ballaré, 1999). Since none of these field studies involved Arabidopsis plants, we characterized SAS responses to the proximity of competitors in wild-type and *uvr8* Arabidopsis seedlings grown in the field under contrasting levels of UV-B radiation (Fig. 1b). Plants responded to the proximity of grass competitors with a rapid increase in leaf angles (hyponastic response). This hyponastic response was reduced by solar UV-B radiation, and the repressive effect of solar UV-B radiation was missing in a *uvr8* mutant (Fig. 1c). Exploration of Arabidopsis transcriptome data in microarray databases (Supporting Information Tables S1–S3) further suggest the existence of antagonistic effects of low R : FR ratio and UV-B radiation on expression of growth (auxin)-related genes (Fig. 2a). For example *YUCCA9*, *ATHB-2*, *IAA29* and *SAUR23* were all strongly upregulated by low R : FR and downregulated by UV-B radiation (Supporting Information Table S3). Significant effects of UVR8 activation reducing the expression of selected auxin-related genes have been reported recently (Vandenbussche *et al.*, 2014), particularly in plants exposed to low R : FR ratios (including *YUCCA9* and *IAA29*; Hayes *et al.*, 2014). In our meta-analysis of available microarray data, the effect of UV-B on the 'Auxin' gene ontology (GO) category appeared to be somewhat dependent on the experimental conditions (Supporting Information Fig. S1) and largely conserved in *uvr8* (Supporting Information Fig. S2). Taken together, physiological (Fig. 1) and transcriptomic (Fig. 2a; Supporting Information Table S3) results are consistent with the idea that solar UV-B radiation moderates the growth responses to neighbor proximity triggered by low R : FR ratios. The magnitude of the effect of UV-B (and UVR8) is likely to vary with the relative levels of R : FR and UV-B radiation, which emphasizes the need for using experimental approaches that cover the natural range of variation of these light signals.

UV-B and high R : FR promote plant defense under sunlight, via partially overlapping mechanisms

Solar UV-B radiation promotes plant defense against herbivorous insects and some pathogens, and here again the effects of solar UV-B are opposite to those of low R : FR ratio (Ballaré *et al.*, 2012). The positive effect of (natural) UV-B radiation on plant immunity has often been attributed to the accumulation of leaf phenolics, although enhanced signaling through the jasmonate (JA) defense pathway is also thought to play an important role (Ballaré, 2014).

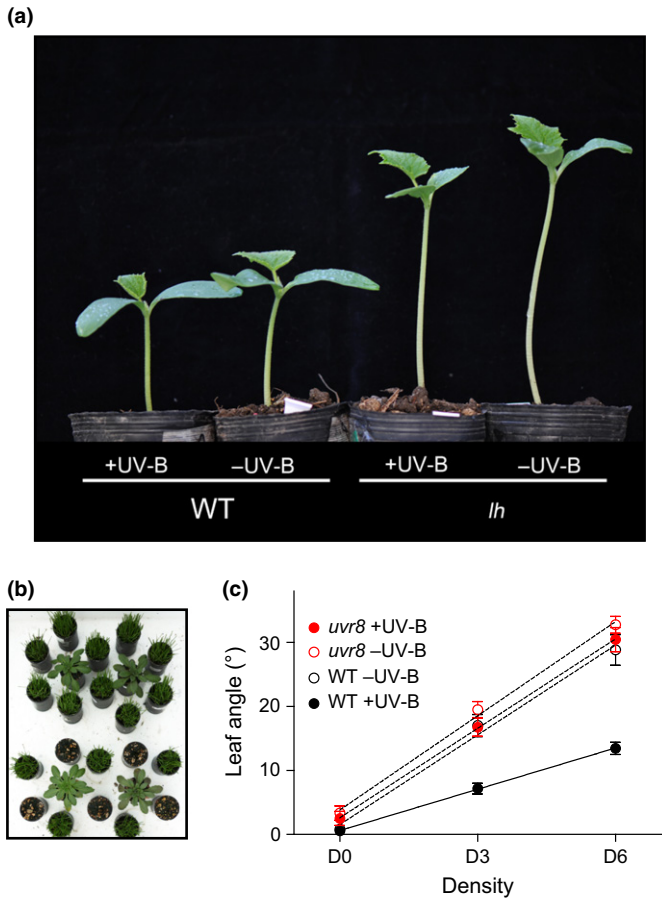

Fig. 1 The interplay between solar UV-B and phyB in shaping plant morphology under field conditions. (a) phyB inactivation in the *lh* mutant (López-Juez *et al.*, 1992) triggers a strong shade avoidance response in field grown plants, and solar UV-B represses elongation. Average hypocotyl length (cm) for wild-type (WT) plants was 5.9 (+UV-B) and 7.1 (−UV-B), and for *lh* plants 10.9 (+UV-B) and 13.0 (−UV-B); *lh* effect $P < 0.01$; UV-B effect $P = 0.05$; interaction $P = 0.56$; $n = 5$; see Supporting information Methods S1 for experimental details; filter types and configuration were as described previously (Izaguirre *et al.*, 2007; Zavala *et al.*, 2014). (b) Experimental setup used to test Arabidopsis responses to the proximity of grass neighbors in the field under contrasting levels of solar UV-B radiation. Wild-type (Col-0) and *uvr8-6* mutant (Favory *et al.*, 2009) Arabidopsis plants were surrounded by zero (D0), three (D3), or six (D6) ryegrass-containing pots [only treatments D6 (*top*, six ryegrass pots) and D3 (*bottom*, three ryegrass pots and three pots containing only soil) are shown in the picture]; the setup was replicated four times under either solar UV-B (+UV-B) or attenuated UV-B (−UV-B); see Supporting Information Methods S1 for details. (c) Arabidopsis plants respond to the proximity of grass neighbors by increasing leaf angles, and ambient UV-B tempers this response via UVR8. Bars, ± 1 standard error (SE).

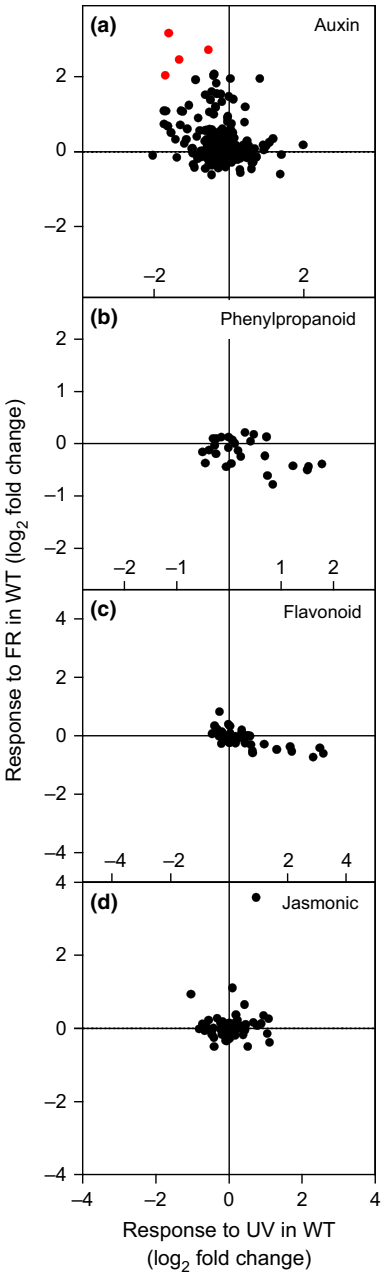

Fig. 2 Comparison of the effects of low red : far red (R : FR) and supplemental ultraviolet-B (UV-B) radiation on gene expression for genes belonging to selected gene ontology (GO) categories. Data are from public databases (see Supporting Information Methods S1 for details) and many of them have been reported in previous publications (Brown *et al.*, 2005; Tao *et al.*, 2008; Favory *et al.*, 2009; Kozuka *et al.*, 2010; Cerrudo *et al.*, 2012; Leivar *et al.*, 2012; De Wit *et al.*, 2013; Morales *et al.*, 2013; Reddy *et al.*, 2013). Data points highlighted in red (a) correspond to *YUCCA9* (At1G04180), *ATHB-2* (At4 g16780), *IAA29* (At4 g32280) and *SAUR23* (At5 g18060); see Supporting Information Table S3 for quantitative details.

Leaf phenolics

Accumulation of soluble phenolic compounds is one of the most ubiquitous responses to UV-B radiation (Searles *et al.*, 2001), which is to be expected given the key role played by these compounds in UV-photoprotection (Braun & Tevini, 1993; Mazza *et al.*, 2000). In Arabidopsis, the accumulation of both phenylpropanoids (sinapates) and flavonoids is boosted by UV-B radiation (Li *et al.*, 1993; Landry *et al.*, 1995), in a UVR8-dependent manner (Kliebenstein *et al.*, 2002; Demkura & Ballaré, 2012). Some of these compounds (sinapates) have been shown to mediate the positive effect of UV-B radiation on plant immunity against fungal pathogens (Demkura & Ballaré, 2012). In contrast to the consistent effect of UV-B, the effects of R : FR ratio on levels of soluble leaf phenolics can be quite variable (Table 1), and often not significant. These observations at the metabolite level are totally

consistent with our meta-analysis of transcriptome data in Arabidopsis: supplemental UV-B has a robust effect increasing the expression of phenylpropanoid- and flavonoid-related genes, whereas the effects of FR are generally very modest (Fig. 2b,c; Supporting Information Table S3). The effects of UV-B on phenylpropanoid- and flavonoid-related genes are mostly mediated by UVR8 (Supporting Information Fig. S2b,c).

JA signaling

Reductions in UV-B radiation and R : FR ratio may have convergent effects repressing JA signaling. Genetic evidence in Arabidopsis and *Nicotiana* indicates that some of the anti-herbivore effects of solar UV-B are missing in plants impaired in the biosynthesis of bioactive JA (Caputo *et al.*, 2006; Demkura *et al.*, 2010). Solar UV-B can increase JA synthesis or expression of JA biosynthetic genes in *Nicotiana* spp. (Izaguirre *et al.*, 2003; Đinh *et al.*, 2012), although this is not always the case (Demkura *et al.*, 2010). In species of the Solanaceae, UV-B increases plant sensitivity to JA for activation of proteinase inhibitors (Stratmann *et al.*, 2000; Demkura *et al.*, 2010). However, this enhancing effect was not detected in Arabidopsis for other markers of the JA response (Demkura & Ballaré, 2012). Available microarray data indicate that UV-B radiation increases the expression of some JA-related genes (Fig. 2d; see also Supporting Information Table S3 and Fig. S1), but this effect appears to be highly dependent on the experimental conditions (Supporting Information Fig. S1xiii–xvi), and to some extent conserved in *uvr8* mutants (Supporting Information Fig. S2d). The effects of low R : FR reducing JA sensitivity are very well documented (reviewed in Ballaré, 2014). Transcriptome data in Arabidopsis do not reveal major effects of R : FR ratio on JA-related genes in *healthy* (non-induced) plants (Fig. 2d), which is consistent with the idea that R : FR regulates JA signaling predominantly by reducing the response to the JA burst produced by the plant in response to herbivory or pathogen attack (Moreno *et al.*, 2009; Cerrudo *et al.*, 2012; De Wit *et al.*, 2013). The effect of low R : FR ratios repressing the induction of JA-dependent genes correlates with the down-regulation of specific metabolites involved in direct (Cargnel *et al.*, 2014) and indirect (Izaguirre *et al.*, 2013; Kegge *et al.*, 2013) defenses. From an ecological point of view, down-regulation of JA responses under conditions of low R : FR and UV-B irradiance is likely to help the plant to redirect resources from defense to rapid elongation, thereby increasing its ability to compete for light.

Interactions between UVR8 and phyB signaling mediated by hormonal cross-talk

Recent work on the effects of R : FR and UV-B on growth- and defense-related hormonal pathways (Hayes *et al.*, 2014; Leone *et al.*, 2014) can provide important clues to understand the mechanisms by which R : FR and UV-B signals are used by the plant to optimize resource allocation in patchy canopies (Fig. 3). Reduced JA signaling under low R : FR ratios has been attributed to increased stability of JAZ10 (Leone *et al.*, 2014) (and presumably other JAZ proteins – Chico *et al.*, 2014), and increased turnover of DELLA proteins (Leone *et al.*, 2014). JAZs are key repressors of JA signaling (Browse, 2009; Fonseca *et al.*, 2009; Kazan & Manners, 2012), and DELLA proteins, which are key repressors of gibberellin (GA) signaling (Harberd *et al.*, 2009), are known to recruit JAZs into inactive protein complexes (Hou *et al.*, 2010; Yang *et al.*, 2012). Hayes *et al.* (2014) reported that UV-B supplementation can stabilize DELLAs. Therefore, it is conceivable that changes in DELLA turnover are functionally important not only to define the balance between UV-B and low R : FR in the modulation of growth responses, but also in the regulation of JA signaling and plant immunity in canopies (Fig. 3).

Table 1 Far red (FR) provided against a background of white light to lower the red (R) to far red (R : FR) ratio has mixed effects on accumulation of soluble phenolic compounds in the leaves of de-etiolated plants

Species	Effect of supplemental FR (low R : FR ratio)	Effect of supplemental UV-B under comparable physiological conditions[1]
Betula pendula	No effect on flavonoids; marginal increase in the contents of phenolic acids, such as chlorogenic acid and cinnamic acid (Tegelberg *et al.*, 2004)	Increased falvonoids and phenolic acids (Tegelberg *et al.*, 2004)
Nicotiana longiflora	Reduced the accumulation of herbivory-induced chlorogenic acid (Izaguirre *et al.*, 2006)	Increased flavonoids and phenolic acids (Izaguirre *et al.*, 2007)
Solanum lycopersicum	Increased accumulation of flavonoids in the leaves (the opposite effect was observed for stem flavonoids and anthocyanins) (Cagnola *et al.*, 2012)	Increased flavonoid accumulation (Ballaré *et al.*, 1995)
Arabidopsis thaliana	No effect on leaf flavonoids or sinapates (Cargnel *et al.*, 2014)	Increased flavonoids and sinapates in an UVR8-dependent manner (Demkura & Ballaré, 2012)
Arabidopsis thaliana	Decreased content of anthocyanins in plants treated with methyl-jasmonate (Cerrudo *et al.*, 2012; Leone *et al.*, 2014)	Not reported

[1]Results are shown for comparison. In all the UV-B supplementation experiments listed in this column, plants were exposed to physiological levels of UV-B radiation against a background of white light.

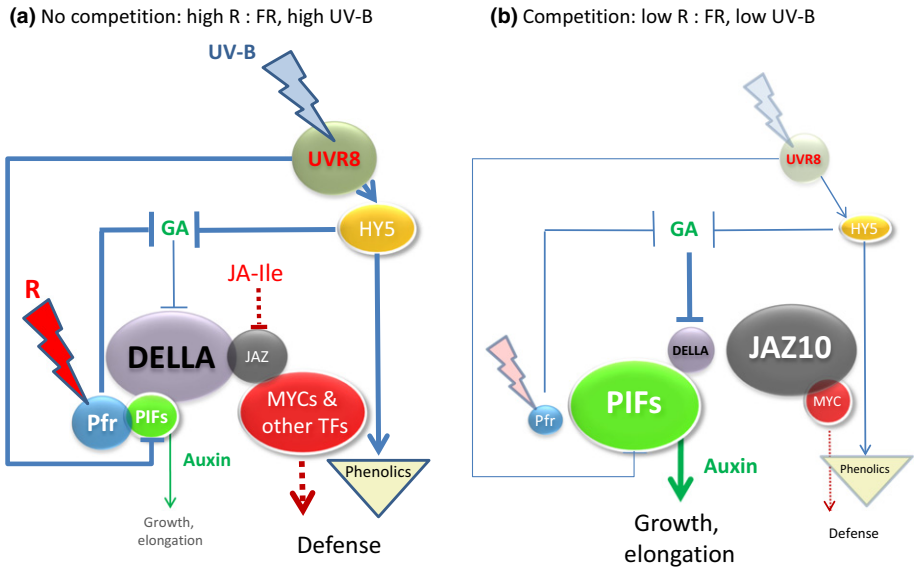

Fig. 3 UVR8 and phyB cooperatively modulate plant phenotypic plasticity in plant canopies. Hypothetical mechanism by which changes in red : far-red (R : FR), perceived by phyB, and UV-B radiation, perceived by UVR8, regulate growth and defense in response to shading and neighbor proximity. (a) In canopy gaps and when neighbors are far away, phyB Pfr levels are high, which reduce the levels and activity of f PHYTOCHROME INTERACTING FACTORS (PIFs) (Lorrain *et al.*, 2008; Hornitschek *et al.*, 2012; Li *et al.*, 2012; Park *et al.*, 2012). PIFs are also repressed by abundant DELLA proteins (Feng *et al.*, 2008; de Lucas *et al.*, 2008), which also keep JASMONATE ZIM domain (JAZ) proteins from repressing their target transcription factors, such as MYCs (Hou *et al.*, 2010). At the same time, activation of UVR8 by solar UV-B facilitates accumulation of DELLA proteins in a HY5-dependent manner (likely by increasing gibberellin (GA) degradation), and promotes PIF degradation in a HY5-independent manner (Hayes *et al.*, 2014). Under these conditions, auxin biosynthesis and elongation growth are repressed, and jasmonate (JA)-dependent defense responses can be readily activated following JA-induced JAZ protein degradation. UV-B, acting through UVR8, promotes the accumulation of soluble phenolic compounds (flavonoids and phenylpropanoids), which can contribute to increase plant defense in a JA-independent manner (Demkura & Ballaré, 2012). (b) Under shade or high density conditions, low R : FR ratios lead to phyB inactivation, increased levels and activity of PIFs, increased auxin biosynthesis (Tao *et al.*, 2008), and rapid degradation of DELLAs (Leone *et al.*, 2014), thereby promoting elongation. Low UV-B levels also reduce UVR8-induced PIF turnover and facilitate GA accumulation and degradation of DELLA proteins (Hayes *et al.*, 2014). DELLA degradation frees up JAZ proteins, which are also stabilized (Chico *et al.*, 2014; Leone *et al.*, 2014) and are therefore present and available to repress defense-activating transcription factors. Under these conditions, MYC levels can also be reduced (Chico *et al.*, 2014), which further suppresses defense responses. Arrows, promotion; blunt lines, repression/inactivation. Line thickness indicates the strength of the effect; the relative size of the ovals denotes concentration or activity , and overlap indicates an antagonistic interaction between proteins. Dashed arrows, inducible responses. JA-Ile, jasmonyl-L-isoleucine; TF, transcription factor.

Concluding remarks

UVR8 and phyB cooperatively modulate the balance between growth and defense through both convergent and parallel signaling pathways (Fig. 3). The use of common signaling elements (such as DELLA proteins), provides a simple mechanism to reinforce the response when both photoreceptors sense contingent information (e.g. under deep canopy shade or in the open), or to balance out their effects when they perceive conflicting canopy signals (e.g. during proximity perception). In the latter case, FR reflected by neighboring plants provides the plant with a key warning signal of oncoming competition when light levels are still high (Ballaré *et al.*, 1990). However, because excessive responses to low R : FR may entail fitness costs (Casal *et al.*, 1994; Dorn *et al.*, 2000; McGuire & Agrawal, 2005), moderation of these responses by UVR8 in canopy gaps (Fig. 1) may be ecologically advantageous. In addition, the use of independent signaling pathways may allow for one photoreceptor to dominate the pattern of response. This appears to be the case for accumulation of phenolic sunscreens, where UVR8 has a distinctly dominant role (Table 1; Fig. 2). Since UV-B can penetrate more in leaf canopies than longer wavelengths (Flint & Caldwell, 1998), an overriding role of the UVR8 pathway may induce adaptive UV-B photoprotection even under conditions of low R : FR. The emerging map of interactions between UVR8 and phyB signaling (Fig. 3) is revealing exciting new insights into the mechanisms used by plants to optimize growth and defense plasticity in variable light environments.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Effect of experimental conditions on the response to UV-B radiation for the GO categories discussed in this study.

Fig. S2 Effects of UVR8 in the responses to UV-B reported in Fig. 2.

Table S1 GO categories (http://geneontology.org/) used in this study

Table S2 Microarray experiments used in this study

Table S3 Effects of supplemental FR and UV-B on the Arabidopsis transcriptome

Methods S1 Additional methods on the physiological experiments and microarray meta-analysis.

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Key words: flavonoid, herbivory, jasmonate, meta-analysis, phytochrome, red : far-red ratio, UV-B, UVR8.