Environmental and Experimental Botany 121 (2016) 4–21

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Plant responses to red and far-red lights, applications in horticulture

Sabine Demotes-Mainard[a,b,*], Thomas Péron[a,b], Adrien Corot[b,c], Jessica Bertheloot[a,b], José Le Gourrierec[b,c], Sandrine Pelleschi-Travier[b,c], Laurent Crespel[b,d], Philippe Morel[a,b], Lydie Huché-Thélier[a,b], Rachid Boumaza[b,d], Alain Vian[b,c], Vincent Guérin[a,b], Nathalie Leduc[b,c], Soulaiman Sakr[b,d]

[a] INRA (Institut National de la Recherche Agronomique), Unité Mixte de Recherche 1345 IRHS (Institut de Recherche en Horticulture et Semences), Beaucouzé F-49071, France
[b] SFR (Structure Fédérative de Recherche) 4207 Qualité et Santé des Plantes (Plant Quality and Health), Angers F-49000, France
[c] Université d'Angers, Université Nantes Angers Le Mans, Unité Mixte de Recherche 1345 IRHS (Institut de Recherche en Horticulture et Semences), Angers F-49000, France
[d] Agrocampus-Ouest, Unité Mixte de Recherche 1345 IRHS (Institut de Recherche en Horticulture et Semences), Angers F-49000, France

ARTICLE INFO

Article history:
Received 24 February 2015
Received in revised form 21 May 2015
Accepted 23 May 2015
Available online 28 May 2015

Keywords:
Phytochrome
phyB
R:FR ratio
Light signaling
Photomorphogenesis
Light emitting diode

ABSTRACT

Light drives plant growth and development, so its control is increasingly used as an environment-friendly tool to manage horticultural crops. However, this implies a comprehensive view of the main physiological processes under light control, and bridging knowledge gaps. This review presents the state of the art in (i) perception of red (R) and far-red (FR) wavelengths and of the R:FR ratio by plants, (ii) phenotypic plant responses, and (iii) the molecular mechanisms related to these responses. Changes in red or far red radiation and R:FR ratios are perceived by phytochromes. Phytochrome-mediated regulation is complex and specific to each physiological process. Our review presents the effects of red and far-red lights on germination, aerial architectural development, flowering, photosynthesis and plant nutrition. It also addresses how red and far-red radiations interact with tolerance to drought, pathogens and herbivores. Current knowledge about the mechanisms whereby red, far-red and R:FR regulate these different processes is presented. The specific actors of light signal transduction are better known for germination or flowering than for other processes such as internode elongation or bud outgrowth. The phenotypic response to red, far-red and R:FR can vary among species, but also with growing conditions. The mechanisms underlying these differences in plant responses still need to be unveiled. Current knowledge about plants' response to light is being applied in horticulture to improve crop yield and quality. To that purpose, it is now possible to manipulate light quality thanks to recent technological evolutions such as the development of photo-selective films and light-emitting diodes.

1. Introduction

Plants perceive signals from their environment that enable them to adapt and modify their biological cycle. Specific light wavelengths are among such signals. Plants perceive changes in light quality through different types of photoreceptors, including phytochromes (see Galvão and Fankhauser, 2015; Huché-Thélier et al., 2016 this issue, for reviews). Phytochromes can be either in an inactive or active form. The equilibrium between the two forms dynamically changes with the composition of the light spectrum within the 300–800 nm range, and is strongly correlated with R/FR proportions in incident radiation (Holmes and Smith, 1977a; Sager et al., 1988). The R:FR ratio is often used to quantify spectral photon flux distribution in the R and FR wavelengths. In sunlight, the R:FR ratio is low (about 0.6) at the beginning and end of the

* Corresponding author at: INRA (Institut National de la Recherche Agronomique), Unité Mixte de Recherche 1345 IRHS (Institut de Recherche en Horticulture et Semences), 42 rue Georges Morel, Beaucouzé F-49071, France.
Tel.: +33 241 22 56 46.
E-mail addresses: sabine.demotes@angers.inra.fr (S. Demotes-Mainard), thomas.peron@angers.inra.fr (T. Péron), adrien.corot@etud.univ-angers.fr (A. Corot), jessica.bertheloot@angers.inra.fr (J. Bertheloot), jose.gentilhomme@univ-angers.fr (J. Le Gourrierec), sandrine.travier@univ-angers.fr (S. Pelleschi-Travier), laurent.crespel@agrocampus-ouest.fr (L. Crespel), philippe.morel@angers.inra.fr (P. Morel), lydie.thelier@angers.inra.fr (L. Huché-Thélier), Rachid.Boumaza@agrocampus-ouest.fr (R. Boumaza), Alain.vian@univ-angers.fr (A. Vian), vincent.guerin@angers.inra.fr (V. Guérin), nathalie.leduc@univ-angers.fr (N. Leduc), soulaiman.sakr@agrocampus-ouest.fr (S. Sakr).

http://dx.doi.org/10.1016/j.envexpbot.2015.05.010
0098-8472/

photoperiod, compared to its value at solar noon (about 1.0 to 1.3) (Holmes and Smith, 1977a). The R:FR ratio slightly varies with cloud covering and is little sensitive to seasonal variation (Holmes and Smith, 1975; Turnbull and Yates, 1993; Hertel et al., 2011). But the R:FR ratio is markedly reduced in canopies, (0.033 under a sugar-beet canopy for example) (Holmes and Smith, 1975). In canopies the R:FR ratio perceived by plant organs varies spatiotemporally in a range within which slight R:FR variation causes large variation in phytochrome photoequilibrium (Smith and Holmes, 1977; Chelle et al., 2007).

Phytochromes regulate different processes through the plant life cycle, including induction of seed germination, seedling de-etiolation, flowering time (Franklin and Quail, 2010; Strasser et al., 2010), fruit quality (González et al., 2015), root elongation (Salisbury et al., 2007; Costigan et al., 2011) and tolerance to biotic and abiotic stressors (Ballaré et al., 2012). Shade avoidance syndrome (SAS) is regulated by phytochromes, but also cryptochromes, and possibly by phototropins and UVR8 as it involves perceiving not only R and FR, but also blue and UV and the equilibrium between blue and green (for reviews on SAS, see Franklin, 2008; Casal, 2012; Ruberti et al., 2012).

Farmers and horticulturists have long been lacking means to avoid undesired plant responses to R:FR decrease following canopy closure. Their most efficient levers were genotype and plant density. The recent launch of light emitting diodes (LEDs) and films now enables horticulturists to manipulate light quality efficiently. The use of such tools is particularly adapted to horticultural productions under greenhouse. Thus, evaluating how new data about plant physiological responses to R and FR light can be applied to improve ornamental and vegetable horticulture to supplement or replace more conventional factors as temperature or growth regulators is a true challenge.

In this review, we describe the phenotypic effects of R and FR lights, as well as the mechanisms underlying them, on different developmental processes crucial for plant development and survival: germination, aerial architecture development (stem elongation, leaf growth, bud outgrowth), and flowering. We also describe how R and FR radiations affect photosynthesis, mineral nutrition and plant responses to abiotic and biotic factors. The last section shows how knowledge about plants' response to R and FR radiations can be used in ornamental and vegetable horticulture.

2. Phytochromes

Phytochromes were the first light-sensing molecules discovered in plants and then identified in a broad spectrum of eukaryotic and prokaryotic phyla (Duanmu et al., 2014; Quail, 2010). The phytochrome molecule is a 240-kDa apoprotein synthesized in the cytosol, where it is covalently linked to a plastid-derived tetrapyrrole (billin) chromophore (Montgomery and Lagarias, 2002). Prediction of its three-dimensional structure indicates that each monomer is composed of two functionally and structurally distinctive domains (Sharrock, 2008; Nagatani, 2010). Phytochromes are encoded by a small multigene family in many species. There are five members in *Arabidopsis* and tomato (Sharrock and Quail, 1989; Clack et al., 1994, 2009; Hauser et al., 1997; Azari et al., 2010), 3 members in sorghum, black cottonwood and rice (Basu et al., 2000; Childs et al., 1997; Dehesh et al., 1991; Howe et al., 1998; Takano et al., 2009; Weller et al., 1997), and two in pea (Weller et al., 1997). PhyA and PhyB are conserved across all angiosperms investigated to date (Franklin and Quail, 2010; Kami et al., 2010), and form two subfamilies originating from a single ancestral phytochrome (Duanmu et al., 2014). Sensor functions of phytochromes resides in billin photoisomerization that quickly triggers photoconversion of the two phytochrome forms: the R light-absorbing form (Pr) is the inactive form that switches to the active FR light absorbing form (Pfr) in response to red (Nagatani, 2010; Quail, 2010). This latter translocates into the nucleus to trigger downstream signaling events (Galvão and Fankhauser, 2015; Sheerin et al., 2015) and is converted back to Pr when exposed to FR. Molecular mechanisms behind PhyA and PhyB translocation into nucleus have been well documented (For review see, Casal et al., 2014; Fankhauser and Chen, 2008; Possart et al., 2014).

Photomorphogenesis responses are categorized into three types: VLFR (Very Low Fluence Response) and FR-HIR (Far-Red High-Irradiance Response) (Schäfer and Bowler, 2002), that are mainly mediated by PHYA and LFR (Low Fluence Response) that is mainly ensured by PHYB (Casal et al., 2014; Rausenberger et al., 2011; Possart et al., 2014).

Phytochromes also contribute to blue light-dependent regulation redundantly or synergistically with others photoreceptors cryptochromes. For example, PhyB and cryptochromes (cry1a and cry1b) act cooperatively but independently to inhibit leaf sheath elongation in rice seedlings (Hirose et al., 2012). Photoreceptors UVR8 (UV RESISTANCE LOCUS 8) and phytochrome B cooperate to optimize plant growth and defense in patchy canopies (Mazza and Ballaré, 2015). Furthermore, physical interactions between CRY1 and PHYA proteins (Ahmad et al., 1998) and between CRY2 and PHYB (Más et al., 2000) have been reported in *Arabidopsis*. More recently, a potential role of PhyB in low PAR perception has been proposed (Trupkin et al., 2014), further supporting its major role in the monitoring of various light cues.

3. Germination

Seed germination is a crucial event in plant life. It is highly regulated by environmental factors. Among them, temperature and light are of particular importance to ensure a successful process. Seed germination is prevented by a light-sensitive mechanism based on the relative abundance of red and far-red perceived by phytochromes. PHYB and PHYA are present in the endosperm and the embryo, and are strongly involved in the photocontrol of seed germination (Lee and Lopez-Molina, 2012; Lee et al., 2012). In open areas, light is rich in R, so PHYB is the main phytochrome involved in the control of germination through the LFR that takes place right after seed imbibition. By contrast, under dense canopies, FR light is abundant, and PHYB-dependent germination is blocked: FR activates *PHYA* and allows for germination in negatively photoblastic seeds (Takaki, 2001; Lee and Lopez-Molina, 2012). PHYA is primarily implied in the VLFR, which allows seeds to respond to very low amounts of light (Casal et al., 2014). Alternatively, PHYA-dependent seed germination under canopy light conditions (low intensity and FR-rich spectrum) might inhibit PHYB signaling, and lead to so-called explosive germination due to the disruption of intact testa by embryonic growth (Lee et al., 2012). Takaki (2001) proposed to leave aside the notion of photoblastism and rather mention control of germination by phytochromes: PHYB for germination of positively photoblastic seeds (through the LFR response), and PHYA for germination of insensitive seeds (through VLFR) and negatively photoblastic seed germination through HIR.

When a seedling emerges from the seed coat, it is located underground. When it protrudes from the ground, it gains access to light. Then a de-etiolation process rapidly takes place, mainly under the dependence of PHYB through the LFR pathway when R light is abundant (Franklin and Quail, 2010). However, the first steps of this process are quite often dependent on the VLFR pathway. This pathway is sensitive to low amounts of light and PHYA-related, particularly when litter alters light penetration, a situation commonly encountered in woods and natural conditions, but rare in crop cultures (Casal et al., 2014). PHYB-related LFR operates the de-etiolation process in open areas. PHYB is also implied in its termination when the seedling emerges from the

litter, except under very dense canopies. In that case, the PHYA-related HIR pathway mainly completes the de-etiolation process (Casal et al., 2014). The implication of other phytochromes was investigated by Dechaine et al. (2009). A model for the roles and interactions of phytochromes in seed germination was recently proposed: single and multiple-mutant approaches showed that PHYD and PHYE stimulated germination under low R:FR ratios in relation with PHYA (Arana et al., 2014).

PHYA and PHYB act by inhibiting the activity of the constitutively present transcription factor PIL5, also known as PIF1 (Phytochrome Interacting Factor). The central inhibiting role of PIF1 on seed germination was highlighted using *pif-1* mutant plants that do not require light for seed germination (Oh et al., 2004). PIF1 acts on several targets that prevent germination (reviewed in Leivar and Quail, 2011) and includes an inhibition of gibberellic acid (GA) metabolism probably via a stimulation of the SOMNUS transcription factor (Kim et al., 2008), a stimulation of abscisic acid (ABA) biosynthesis and the expression of *DELLA* genes that all repress germination (Cao et al., 2005). Light transforms phytochromes into the Pfr active form that moves to the nucleus and binds to PIF1, leading to its rapid (1–2 min) inactivation by phosphorylation and proteolytic degradation (Shen et al., 2008). Lower amounts of PIF1 open the way for GA biosynthesis and repression of ABA, allowing for the induction of seed germination (Fig. 1). *PIF1* transcriptional activity (rather than protein level) is also inactivated when PIF1 is complexed with the light-induced LONG HYPOCOTYL IN FAR-RED1 (HFR1) factor (Fairchild et al., 2000). HFR1 prevents PIF1 binding to DNA (Shi et al., 2013), and acts as a positive regulator in PHYB-mediated seed germination. Epigenetic regulation also occurs through histone arginine demethylation mediated by JMJ20/22, whose activation enhances *GA3ox1* and *GA3ox2* expression to promote germination (Cho et al., 2012). A possible implication of PIL6 in seed germination was also proposed by (Penfield et al., 2010).

4. Development of the vegetative architecture

4.1. Stem elongation

Promotion of stem elongation by low R:FR either during daytime or only at the end of the day (EOD) is widespread among dicotyledonous and ornamental species, and also concerns the inflorescence stem of *Arabidopsis* (Table 1). Stem elongation sensitivity to low R:FR appears weaker at the end of the day than during daytime (Morgan and Smith, 1978; Casal et al., 1997 for review) and varies depending on the variety and species (Maddonni et al., 2002; Cerny et al., 2003). Shade-tolerant woodland species displayed little or no response to a decrease in the R:FR ratio (Morgan and Smith, 1979; Von Wettberg and Schmitt, 2005) and it was suggested that the ability to respond to R:FR may not provide a competitive advantage over neighbors in the natural habitat of these species.

Stimulation of stem elongation by low R:FR is due to greater internode elongation rather than a greater number of internodes (Franklin and Quail, 2010; Casal, 2013 for review) (Table 1). The internode itself can perceive its R:FR environment and displays strong sensitivity and quick response to FR (Morgan et al., 1980; Child and Smith, 1987; Ballaré et al., 1991; Libenson et al., 2002). The leaf is also a major component in the control of internode elongation by R:FR, but the sensitivity to FR exposure is lower when the leaf is illuminated rather than the internode (Morgan et al., 1980; Casal and Smith, 1988, 1989). Perception of blue light by the leaves is necessary and enhances perception of R:FR by the internodes (Casal and Smith, 1988).

As PHYB represses different SAS phenotypes, it is regarded as the main player in R-mediated repression of internode elongation. A similar repressive role is assigned to PHYA when the R:FR ratio is very low (i.e., under extreme canopy shade; see Possart et al., 2014 for a review). It has been proposed that both PHYA and PHYB inhibit elongation, with peaks in R for PHYB (inducing LFR) and in FR for PHYA (inducing FR-HIR). By contrast to hypocotyl (Casal, 2013), only few studies have focused on the molecular processes regulating internode elongation in response to reduced R:FR. In sunflower internodes, low R:FR induced high levels of two phytohormones (Gibberellin GA1 and auxin IAA), supporting that these hormones act in concert as causal growth-effectors in this process (Kurepin et al., 2007). Additional experiments are required to disentangle the exact roles of plant hormones and identify the players connecting light perception to the molecular basis of internode elongation.

4.2. Leaf development

4.2.1. Petiole extension

In dicotyledonous species, petiole elongation is stimulated by low R:FR (Table 1). This response depends on PhyB (Nagatani et al., 1991; Kozuka et al., 2005; Pierik et al., 2009) and involves a cooperative effect of auxin and brassinosteroid (BR) signaling

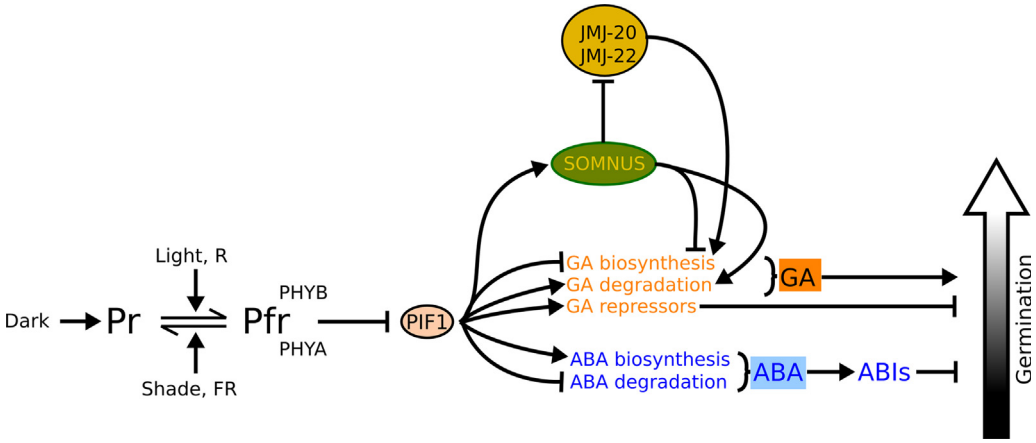

Fig. 1. Schematic representation of the network involved in the regulation of germination by phytochromes.
The Pfr active form of the phytochrome moves into the nucleus and binds to PIF1 to inactivate it. As a result, higher levels of gibberellic acid (GA) and lower levels of ABA favor germination. The two histone arginine demethylases JMJ20/22 are activated through the PHYB pathway; they positively regulate germination by increasing GA biosynthesis. They are blocked by SOMNUS. PIF-1 is a transcription factor that prevents seed germination by keeping GA levels low (it stimulates GA degradation and represses its synthesis) and promoting ABA accumulation (it stimulates ABA synthesis and represses its degradation). Elevated levels of ABA inhibit germination through ABI transcription factors.

Table 1
Effects of low R:FR or *PHYB* reduced expression on plant vegetative development, bud outgrowth, flowering, photosynthesis, mineral nutrition, pathogen–pest–drought tolerance (Ballaré et al., 1987; Barreiro et al., 1992; Boccalandro et al., 2003, 2009; Bradbeer, 1971; Deitzer et al., 1979; Girault et al., 2008; Halliday et al., 1994; Heraut-Bron et al., 1999; Holmes and Smith, 1977b; Johnson, 1976; Kasperbauer, 1971; Kebrom et al., 2006; Linkosalo and Lechowicz, 2006; Lötscher and Nösberger, 1997; Mor and Halevy, 1984; O'Carrigan et al., 2014; Ouedraogo and Hubac, 1982; Ouedraogo et al., 1984; Rajapakse and Kelly, 1994; Rajasekhar et al., 1988; De la Rosa et al., 1998; Sakamoto et al., 1990; Schuerger and Brown, 1997; Seith et al., 1994; Shibuya et al., 2010, 2011; De Simone et al., 2000a,b; Stagnari et al., 2014; Su et al., 2011; Teller and Appenroth, 1994; Tezuka and Yamamoto, 1975; Wan and Sosebee, 1998; Whitelam and Johnson, 1982; Williamson et al., 2012).

Process	Variables	Effect of low R:FR or of *PHYB* reduced expression	Quantification	Species / disease	WT or mutant	Light conditions			References
						R:FR	PPFD (µmol m^{-2} s^{-1})	Supplemental information	
Vegetative development	Stem length	↑	+241%	*Nicotiana tabacum*	WT			White light, except 5 min each day at the end of the photoperiod with red light (360 µW cm^{-2} over 600-700 nm) or far red light (360 µW cm^{-2} over 700-770 nm)	Kasperbauer, 1971
			+22%	*Arabidopsis*	*phyB* vs WT				Reed et al., 1993
			ca +17%		WT	0.05 vs 2.98	175		Finlayson et al., 2010
			ca +13%/+35%/+12%	*Chenopodium album*		From 1.09 to 3.97 vs from 0.16 to 0.23	100		Morgan and Smith, 1978
			+35%	*Zinnia elegans*		0.77 vs 1.51		Daily light integral: from 9 to 10 µmol m^{-2} d^{-1}	Cerny et al., 2003
			+14%	*Cosmos bipinnatus*					
			+17%	*Dendranthema x grandiflorum*					
			+10%	*Anthirrhinummajus*					
			+14%	*Petunia x hybrida*				Daily light integral: 25 µmol m^{-2} d^{-1}	
		=		*Rosa hydrida*(cv Cherry Cupida)		0.77 vs 1.51		Daily light integral: from 9 to 10 µmol m^{-2} d^{-1}	
	Internode length	↑	*ca* +800%	*Impatiens multiflora*		0.1 vs 0.68	13	White light	Whitelam and Johnson, 1982
			ca +54%	*Sinapis alba*		0.55 vs 0.94	NA	Green vs yellowish fences	Ballaré et al., 1987
			+27%	*Daturaferox*		0.62 vs 0.80		Mirrors reflecting, FR vs R	Ballaré et al., 1987
			+94%	*Sinapis alba*		0.57 vs 0.93			
			+35%	*C. album*		NA			
			ca +55%	*Helianthus annuus*		0.3 vs 1.1			Libenson et al., 2002
			From +4% to +178%	*Tageteserecta*		NA	90	Fluorescent lamps + supplemental FR vs fluorescent lamps only	Heo et al., 2002
			From +108% to +219%, depending on internode rank	*Salvia spendens*					
			From +21% to +38%, depending on season	*Rosa hydrida*(cv Meijikatar)		1.1 vs 5.8	675, 850 or 875	PPFD depending on season	Rajapakse and Kelly, 1994
			ca +43%	*Arabidopsis*		0.25 vs 1.2	140	White light	Djakovic-Petrovic et al., 2007
	Petiole length	↑	*ca* +25%						Sasidharan et al., 2010
			+121%		*phyB* vs WT		50	Red light	Kozuka et al., 2005
			NA	*Impatiens multiflora*	WT	0.1 vs 0.68	13		Whitelam and Johnson, 1982
			+110%	*Cucurbita pepo* L.		0.03 vs 2.16	195 (WL)	White light.Supplemental FR vs R during the last 10 min of the photoperiod (85 µmol m^{-2} s^{-1})	Holmes and Smith, 1977b
	Leaf length	↑	+100% for 1st sheath	*Lolium multiflorum*					Casal et al., 1987a
			+33% for 2nd sheath						
			+27% for blade				NA	Daylight + EOD. Supplemental R (PAR=5 µmol m^{-2} s^{-1} between 600 and 800 nm) or supplemental FR (PAR=23 µmol m^{-2} s^{-1} between 600 and 800 nm).	
			+13% for selected sheath	*Paspalum*		0.89 vs 1.54	145	White light	
			+24% for sheath above						
			+9.3% sheath	*Hordeum vulgare*			450	White light. FR specifically applied on the exposed portion of the elongating	Skinner and Simmons, 1993
			+4.5% blade						

								leaf blade (fibre-optic light guide supplying 250 µmol m^{-2} s^{-1})	
	Angle between the soil and the leaf	↑	*ca* +163%	*Arabidopsis*		0.24 vs 0.68		White light	Tao et al., 2008
			ca+147%		*phyB* vs WT	0.68			
			NA	*Impatiens multiflora*	WT	0.1 vs 0.68	13		Whitelam and Johnson, 1982
	Leaf mass area	↓	-20% (cotyledon)	*Cucumis sativus* /Powdery mildew (PM)		1.1 vs 7.0	300	Fluorescent lamps	Shibuya et al., 2011
			-17% (first leaf)						
			-9% (seedling)			1.2 vs 7.0		Metal-halidelamps vs. fluorescent lamps	Shibuya et al., 2010
	Leafnumber	↓	-43%	*Solanum lycopersicon*		NA	300 (white light) vs 100 (red light)	Greenhouse	O'Carrigan et al., 2014
	Leafthickness	↓	-7.8 %	*Phaseolus vulgaris*		0.7 vs 1.3	300		Barreiro et al., 1992
			-11.2%				800		
	Leaf duration	↓	-5d.	*Helianthus annuus*				Natural light vs natural light supplemented with R light (8.33 µmol m^{-2} s^{-1})	Rousseaux, 2000
	Stomatal density	↓	*ca* - 40%	*Arabidopsis thaliana*	*phyB* vs WT	4.1	250		Boccalandro et al., 2009
			ca -31%		WT	4.1 vs 4.1 with EOD=0.04			
			-11%	*Citrus × insitorum*	WT vs phyB-OEM[a]	NA	NA	Natural light conditions in greenhouse	Distefano et al., 2013
			ca -14%	*Oryza sativa*	*phyB* vs WT	NA	270 (at noon on sunny days)	Natural light conditions in greenhouse, after 2 days of water shortage	Liu et al., 2012
	Stomatal length	↓	*ca* -8.6%						
	Number of mesophyll cell per leaf section	↓	-7.4 % for palisade cell	*Phaseolus vulgaris*	WT	0.7 vs 1.3	800		Barreiro et al., 1992
			-12.5% for spongy cell						
	Palisade cell length	↓	-16 to -23% depending on mutation	*Solanum tuberosum*	WT vs phyB-OEM[a]		From 150 to 500	Natural light conditions in greenhouse	Thiele et al., 1999
	Root hair density	↓	*ca* -93% - R light	*Lactuca sativa*	WT	only FR (2.3 W m^{-2}) vs only R (1.7 W m^{-2})		Light treatments : 9h after dark period Fluence of 2 kJ m^{-2}	De Simone et al., 2000b
			ca -95% - Blue light			only FR (2.3 W m^{-2}) vs blue (2.1 W m^{-2})			
			ca -60% with FR light	*Arabidopsis thaliana*	*phyA*	only FR (1.3 Wm^{-2}) vs dark		After 3 days lighting	De Simone et al., 2000a
			ca +390% with R light			only R (1.9 Wm^{-2}) vs dark			
	Root ramification	↓	*ca* -13%	*Arabidopsis thaliana*					Salisbury et al., 2007
			ca -20%		*phyA* vs WT		100		
			ca -30%		*phyE* vs WT *phyB* vs WT				
			ca -27%		WT (Col accession)	high (NA) vs low (0.126)	70		
			ca -38%		WT (L*er* accession)				
	Root length	↓	-30%		*phyB* vs WT	NA	NA	Natural light conditions in greenhouse	Reed et al., 1993
	root biomass	↓	-28.6% roots (root + nodule)	*Glycine max*	WT	EOD FR (5min, 3.6W/m²) vs EOD R (5min, 3.6W/m²)	520		Kasperbauer, 1987
	Shoot biomass	↑	+13.8% for shoot (stem + petiole, not leaf)						
		↓	-71%	*Solanum lycopersicon*		NA	300 (white light) vs 100 (red light)	Greenhouse	O'Carrigan et al., 2014
	Plant height	↓	-47%						
Bud outgrowth	Percentage of sprouted buds	↓	-17% (top 3 buds)	*Rosa hybrida*	WT	1.1 vs 4.8	200		Mor and Halevy, 1984
			-100%	*Rosa hybrida*		0.25 vs 4.4	2.7		Girault et al., 2008
			ca -10%	*Koeleria macrantha*		0.2 vs 1.4	NA	similar PPFD for the two R:FR treatments	Williamson et al., 2012
			ca -15%	*Elymus canadensis*					
			ca -10%	*Panicum virgatum*					
			ca -10%	*Schizachyrium scoparium*					
			ca -37 to -67% depending on branch type and	*Trifolium repens*		0.32 vs 1.12	175		Lötscher and Nösberger, 1997

			phytomer(no effect on phytomers formed on parent axis before light treatment)						
			ca -15%	*Lolium multiflorum*		0.8 vs 1.6	107		Casal et al., 1985
		=		*Dichanthelium oligosanthes*		0.2 vs 1.4	NA	similar PPFD for the two R:FR treatments	Williamson et al., 2012
				Andropogon gerardii					
	Standardized primary rosette branches	↓	*ca* -35%	*Arabidopsis thaliana*		0.05 vs 2.98	175	R:FR=2.98 until day7 then application of lower R:FR treatment	Finlayson et al., 2010
			ca -30%		*phyB* vs WT	2.08	180		
	Bud length	↓	*ca* -54% 9 days after planting	*Sorghum bicolor*	WT		600	R:FR=3.0 until day7, then R:FR=3.0+FR supplementation (resulting R:FR not available) vs R:FR=3.0	Kebrom et al., 2006
			ca -50% 9 days after planting		*phyB* vs WT	3.0	600		
	Timing of bud outgrowth	Advanced	-4 days	*Betula pendula*		0.58 vs 1.3 during twilight	From 72 to 85 during twilight	Rest of the day: R:FR=1.3, PPFD =180 µmol $m^{-2}s^{-1}$	Linkosalo and Lechowicz, 2006
			-1.03 day top rosette bud (=n)	*Arabidopsis thaliana*		0.05 vs 2.98	175	R:FR=2.98 until day7 then application of lower R:FR treatment	Finlayson et al., 2010
		Delayed	From *ca* +0.7 to + 5.5 days, depending on branch type and phytomer	*Trifolium repens*	WT	0.32 vs 1.12	175		Lötscher and Nösberger, 1997
			NQ	*Eragrostis curvula*		0.59 vs 1.1	69		Wan and Sosebee, 1998
			NQ	*Triticum aestivum*		0.6 vs 1.2 (two hours before sunset)	NA	Natural light supplemented with FR vs R (10 µmol $m^{-2}s^{-1}$) during 4h in the afternoon to beginning of full darkness.	Ugarte et al., 2010
			+2.91 days bud n-2	*Arabidopsis thaliana*		0.05 vs 2.98	175	R:FR=2.98 until day7 then application of lower R:FR treatment	Finlayson et al., 2010
			From +1.45 to + 2.47d.top 3 rosette buds	*Arabidopsis thaliana*	*phyB* vs WT	2.08	180		
		=	bud n-1	*Arabidopsis thaliana*	WT	0.05 vs 2.98	175	R:FR=2.98 until day7 then application of lower R:FR treatment	Finlayson et al., 2010
Flowering	Time to flower (days)	↓	- 5 d.	*Arabidopsis thaliana*	WT	0.13 vs 6.81	100		Halliday et al., 1994
			-13 d.	*Hordeum vulgare*		0.45 vs 5.6	428	Photoperiod: 12h	Deitzer et al., 1979
			-3.1 d.	*Petunia hybrida*			450	FR light vs R light,12h photoperiod	Ilias and Rajapakse, 2012
			-1 d.	*Zinnia elegans*		0.77 vs 1.51		Daily light integral=9 to 10 mol m^{-2} d^{-1}	Cerny et al., 2003
			-2 d.	*Dendranthema × grandiflorum*					
			-9 d.	*Antirrhinum majus*					
			From -1 to -12 d. Depending on photoperiod	*Petunia ×hybrida*		0.77 vs 1.51		Same daily light integral and photoperiod between treatments. Photoperiod varying from 10-11 to 13-14.5 h d^{-1} and daily light integral varying from 9-10 to 25 mol m^{-2} d^{-1}	
		=		*Cosmos bipinnatus* *Rosa hybrida*		0.77 vs 1.51		daily light integral=9 to 10 mol m^{-2} d^{-1}	
Photosynthesis	CO_2 stomatal conductance	↓	*ca* -35%	*Solanum tuberosum*	WT vsphyB-OEM[a]			Natural light conditions in field	Boccalandro et al., 2003
			ca -20%	*Arabidopsis thaliana*	*phyB* vs WT	3.8	185		Gonzalez et al., 2012
		↑	+19%	*Citrus × insitorum*	WT vs phyB-OEM[a]	NA	NA	Natural light conditions in greenhouse	Distefano et al., 2013
	Enzyme activity of Calvin cycle	↓	RBC[b]: -71%	*Phaseolus vulgaris*	WT	FR vs WL	150 (FR) vs 400 (WL)	Dark conditions, with brief exposure to FR (20 min) vs	Bradbeer, 1971
			PK[b]: -60%						

			GDD[b]: -63% T[b]: -76%				(µW cm^{-2})	white light (5 min)	
	Chlorophyll content	↓	-20% chl a -23% chl b	*Citrus × insitorum*	WT vs phyB-OEM[a]	NA	NA	Natural light conditions in greenhouse	Distefano et al., 2013
			ca -32%	*Solanum tuberosum*			From 150 to 500	Natural light conditions in greenhouse	Thiele et al., 1999
			ca -40%			Value NA, stable	300, 600 or 900		Schittenhelm et al., 2004
			-15.9%	*Trifolium repens*	WT	0.4 vs 2.4	320		Heraut-Bron et al, 1999
			-10.3%				110		
			-24%	*Solanum lycopersicon*		EOD FR (5min, 0.99 Wm^{-2}) vs no FR	5W m^{-2} white light		Tucker, 1981
			-40%	*Cucumis sativus*					
	Net assimilation rate	↓	-10 to -21%	*Phaseolusvulgaris*		0.7 vs 1.3	300	Measurements performed under a range of PPFD from 100 to 850 µmol m^{-2} s^{-1}	Barreiro et al., 1992
			-42 to -88%				800		
			ca -40%	*Oryza sativa*	*phyB* vs WT		270 (at noon on sunny days)	Natural light conditions in greenhouse	Liu et al., 2012
			ca -40%	*Arabidopsis thaliana*	*phyB* vs WT (L*er* accession)	4.1	250		Boccalandro et al., 2009
			-19%	*Solanum tuberosum*	WT vs phyB-OEM[a]		From 150 to 500	Natural light conditions in greenhouse	Thiele et al., 1999
			-30 to -55% depending on foliar stratum					Natural light conditions in the field	Boccalandro et al., 2003
			-13 to -19% depending on PPFD, average on plant cycle			Value NA, stable	300, 600 or 900		Schittenhelm et al., 2004
		↑	+13%	*Citrus × insitorum*	WT vs phyB-OEM[a]	NA	NA	Natural light conditions in greenhouse	Distefano et al., 2013
		=		*Trifolium repens*	WT	0.4 vs 2.4	110 or 320		Heraut-Bron et al., 2000
				Arabidopsis thaliana	*phyB* vs WT (Col accession)	11.7	160 or 280		Su et al., 2011
Mineral nutrition	Mycorhize formation	↓	-27%	*Pinus sylvestris*	WT	0.39 vs 1.3	200		De la Rosa et al., 1998
	Nodule formation (nb.plant^{-1})	↓	-80%	*Lotus japonicus*		low (0.1) vs high (∞)	100		Suzuki et al., 2011
			-60%		*phyB* vs WT				
	Ion content	↑	N content in stems : +16 %	*Pinus sylvestris*	WT	0.39 vs 1.3	200		De la Rosa et al., 1998
			Concentrations in tuberous roots K :+125% P: +44% Mg: +217% Fe: +87% Zn: +77% Mn:+21% Ca: +10%	*Beta vulgaris*		Green film (R:FR=0.43) vs natural light	NA	Natural light conditions in greenhouse with photo-selective films	Stagnari et al., 2014
			Stem contents : *ca* +255% K *ca* +111% P	*Phaseolus aureus*		NA	FR = 4500 vs R = 800 (erg cm^{-2} s^{-1})	Only FR vs only R light	Tezuka and Yamamoto, 1975
		=	N, P, K contents in needles	*Pinus sylvestris*		0.39 vs 1.3	200		De la Rosa et al., 1998
		↓	Contents in roots N : -27% P: -31%						
			Concentrations in leaves Fe : -28% B : -23% Mn: -35% Cu: -42%	*Solanum lycopersicon*		NA	300 (WL) vs 100 (R)	After 8 weeks of greenhouse	O'Carrigan et al., 2014

			Zn : -72% Ni : -27%						
	Protein content	↓	-41%			NA	WL: 5W m²	white light + EOD FR (5min, 0.99 Wm²)	Tucker, 1981
			-32%	*Cucumis sativus*					
	NR gene expression	↓	ca -73%	*Cucurbita maxima*				FR light pulses (5min, 0.003Wm^{-2}) vs R light pulses (5 min, 0.45W m²)	Rajasekhar et al., 1988
	NR activity	↓	-50%	*Sinapis alba*			NA	FR light (12h, value not available) vs white light (12h) after darkness	Johnson, 1976
			-60%	*Cucurbita maxima*				FR light pulses (5min, 0.003Wm²) vs R light pulses (5 min, 0.45W m²)	Rajasekhar et al., 1988
	NiRactivity	↓	-37%	*Hordeum vulgare*				FR light pulses (3x5min, 3.5Wm^{-2}) vs R light pulses (3x5 min, 6.8W m^{-2})	Seith et al., 1994
	GS gene expression	↓	High inhibition, NQ	*Lactuca sativa*				FR pulse (2min) vs R pulse (2min)	Sakamoto et al 1990
	GS activity	↓	-16%	*Spirodella polyrhiza*				FR light (3.5W m^{-2}) vs R light (6.8W m^{-2})	Teller and Appenroth 1994
	N Allocation	↑	+18.5% in aerial organs in 5 days	*Pinus sylvestris*		0.39 vs 1.3	200		De la Rosa et al., 1998
Drought	Tolerance	↑	days of plant survival under water stress: *ca* +108%	*Gossypium hirsutum*			100	EOD FR (30min, 12.5W m^{-2} s^{-1}) vs no EOD FR	Ouedraogo and Hubac, 1982
			+80% of plants recovered after being re-watered	*Oryza sativa*	*phyB* vs WT	NA	270 (at noon on sunny days)	Natural light conditions in greenhouse	Liu et al., 2012
		↓	NQ	*Arabidopsis thaliana*					
	ABA sensitivity	↓	ABA signaling genes: *ABCG22: ca*-71% *PYL5: ca* -72% *HAB1:ca* - 95%			3.8	185		Gonzalez et al., 2012
	Stomatal resistance	↑	+273%	*Gossypium hirsutum*	WT		100	EOD FR (30min, 12.5 W m^{-2} s^{-1}) vs no EOD FR	Ouedraogo and Hubac, 1982
	Water loss	↓	*ca* from -14% to -23% depending on modality of FR application						
			ca -33%	*Oryza sativa*	*phyB* vs WT			Natural light conditions in greenhouse, after 2 days of water shortage	Liu et al., 2012
	Gene expression	↑	ERECTA family: x 1.8 EXPANSIN family: x 2.0						
	Osmotic potential	↑	+32%	*Gossypium hirsutum*	WT	NA	100W m^{-2} s^{-1}	EOD FR (30min, 12.5 W m^{-2}) vs no EOD FR, after 7 days of water shortage	Ouedraogo et al., 1984
	Osmoprotectant content	↑	Proline: *ca* +25%	*Oryza sativa*	*phyB* vs WT	NA	270 (at noon on sunny days)	Natural light conditions in greenhouse, after 2 days of water shortage	Liu et al., 2012
			Osmolites: *ca* +18%	*Arabidopsis thaliana*		3.8	185	After 7 days of water shortage	Gonzalez et al., 2012
Pathogens and herbivore resistance	Number of pathogen colonies	↑	+25% (cotyledon)	*Cucumis sativus*/Powdery mildew	WT	1.1 vs 7.0	300	Fluorescent lamps	Shibuya et al., 2011
			+61% (first leaf)						
			+115% (leaf)			5.1 vs 99	330	LED (660/735)	Schuerger and Brown, 1997
			+78% (seedling)	*Cucumissativus* /Sweetpotato Whitefly		1.2 vs 7.0	350	Metal-halidelamps vs. fluorescent lamps	Shibuya et al., 2010
	Area of necrosis /inoculum droplet	↑	Around +600%	Broad bean/*Botrytis cinerea*		NA	328 vs 287 (μW m^{-2})	Pre-treatment of detached leaf under fluorescent lamps during 24h before inoculation. Max. wavelength 740 vs 650 nm	Islam et al., 1998

↑: significant increase, ↓: significant decrease, =: no significant effect

[a] phyB-OEM: phyB-overexpressing mutant.

[b] Ribulose biphosphate carboxylase, Phosphoglycerate kinase, Glyceraldehyde phosphate deshydrogenase, Transkelotase.

pathways in *Arabidopsis* (Kozuka et al., 2010). The photoperceptive site is the leaf blade rather than the petiole itself (Kozuka et al., 2010), with a minor contribution of PIF4 and PIF5 (Keller et al., 2011). GA and ethylene could also be implied in low R:FR ratio mediated petiole elongation (Djakovic-Petrovic et al., 2007; Pierik et al., 2009; Iwamoto et al., 2011). In rice, the three phytochromes (PhyA, PhyB and PhyC) contribute to multiple steps in the control of internode elongation, such as expression of the GA biosynthesis gene *OsGA3ox2* and the ethylene biosynthesis gene *ACO1*, and onset of internode elongation (Iwamoto et al., 2011). Reducing R:FR enhances petiole length by stimulating the activity of xyloglucan endotransglucosylase/hydrolases (XTHs), a major protein family involved in cell wall loosening (Sasidharan et al., 2010): XTH activity increased and five *XTH* genes (*XTH9*, –15, –16, –17, and –19) were upregulated after 24 h of exposure to low R:FR. However, no link has been established so far between auxin and BR signaling on the one hand and *XTH* regulation on the other hand.

4.2.2. Leaf expansion

In grasses like *Lolium multiflorum, Paspalum dilatatum* or barley, leaf length can be increased by low R:FR ratios during daytime or by EOD supplemental FR (Table 1). Stronger increases were

observed in sheaths than in laminae (Casal et al., 1987a). In barley, leaf elongation rate rather than elongation duration is stimulated by low R:FR, and elongating laminae (but not mature ones) are involved in light perception (Skinner and Simmons, 1993). In grasses, height mainly depends on sheath growth, so low R:FR leads to longer shoots (Casal et al., 1985 for wheat; Skinner and Simmons, 1993 for barley). The resulting phenotype is similar to that of dicotyledonous species.

Among dicotyledonous species, the leaf growth response to R:FR significantly varies, ranging from inhibition to promotion (see Casal and Smith, 1989 for a review). This effect is dependent on the activity of PHYB and PHYD, whose mutants (*phyB* and *phyBphyD*) displayed a reduced leaf area (Reed et al., 1993; Devlin et al., 1998; Kozuka et al., 2005). This inhibitory effect of FR on leaf expansion may in part result from competition for resources with the stem, the growth of which is stimulated under FR (Casal et al., 1987b). Alternatively, such reduction could also be due to auxin-induced cytokinin breakdown in leaf primordia, leading to reduced leaf cell proliferation and thereby promoting redirection of carbon sources to growing petioles under low R:FR.

4.2.3. Leaf hyponasty and phototropism

In *Arabidopsis*, lower R:FR irradiance causes leaves to bend upward by modifying the petiole angle (Table 1). This response is called hyponasty and was also observed in *I. pasiflora*. In *Arabidopsis*, the hyponastic response to low R:FR was severely reduced in the auxin biosynthesis mutant *sav3* and in the auxin transport mutant *pin3* (Tao et al., 2008; Moreno et al., 2009; Keuskamp et al., 2010). Therefore, hyponasty requires intact auxin synthesis, polar transport and signaling. Combining experiments and modelling, De Wit et al. (2012) showed that physical contact between leaves of neighboring plants, was the earliest signal triggering leaf hyponasty in *Arabidopsis*, and therefore low R:FR is the consequence rather than the cause of leaf hyponasty. This response is not associated with the induction of mechano-stimulation-related genes (i.e., *TOUCH* genes,), but rather involves BR signaling (De Wit et al., 2012). In the same vein, Maddonni et al. (2002) did not observe obvious changes in the angle of maize leaves on a vertical plane in response to R:FR irradiation simulating neighboring plants.

Plants also display a negative phototropic response to FR. Maize leaves grow away from low R:FR signals (Maddonni et al., 2002), and low R:FR reduces solar tracking by sunflower leaves (Casal and Sadras, 1987). The photoptropic behavior is not specific to the leaves and was observed for *Cucumis sativus* shoots, which modify node spatial distribution toward sites with high R:FR (Ballaré et al., 1995), as well as for tillers of *Lolium multiflorum,* which adopt a more erectophile position in response to low R:FR (Casal et al., 1990). However, positive phototropism toward FR has been documented in the parasite *Cuscuta* sp., which probably uses FR to remotely detect the proximity of prospective plant hosts (Orr et al., 1996).

4.3. Bud outgrowth

Inhibition of bud outgrowth under low R:FR has been reported in many species and leads to reduced branching (Table 1). The timing of bud outgrowth is either advanced or delayed under low R:FR according to species (Table 1). The R:FR perception sites involved in bud outgrowth regulation have been little investigated. In *Trifolium repens,* indirect evidence suggests that bud outgrowth is sensitive to the R:FR ratio perceived by the subtending leaf when still unfolded (Robin et al., 1994a,b). In several grass species, the base of the plants could be a perception site regulating tillering in response to R:FR (Deregibus et al., 1985; Casal et al., 1987c; Evers et al., 2006).

Bud outgrowth is under the control of a well-described hormonal network implying synthesis of and signaling by the hormones auxin, strigolactones (SLs), and cytokinins (CKs). Auxin and SLs prevent branching, while CKs promote it (Domagalska and Leyser, 2011). Recent studies have tried to elucidate how R:FR interacts with the different actors that control bud outgrowth.

Auxin levels are increased by low R:FR ratios in various species, organs, and developmental stages, but not all (see Casal, 2013 for a review). But little is known about the role of auxin in bud outgrowth regulation by PHYB. AUXIN RESISTANT1 (AXR1) is implied in auxin signaling; it acts downstream of PHYB to regulate bud outgrowth frequency (Finlayson et al., 2010). In *Arabidopsis* buds grown in vitro, bud outgrowth was more sensitive to auxin in *phyB* mutant than in wild type (Reddy and Finlayson, 2014). In addition, several auxin-responsive genes were more expressed in *phyB* than in the wild type, attesting that auxin signalling was elevated in *phyB* compared to the wild type. This suggests that PHYB suppresses auxin signaling to promote branching. Besides, auxin is known to inhibit CKs biosynthesis and to stimulate CKs catabolism and SLs synthesis (see Domagalska and Leyser, 2011 for a review).

Little is known about the role of CKs in bud outgrowth regulation in response to R:FR. In *Arabidopsis* seedlings, expression of *CYTOKININ OXIDASE* (*CKX*) genes (involved in CKs catabolism) is stimulated by low R:FR and ARR4, a negative response regulator of CKs signaling, interacts with PHYB (Carabelli et al., 2007; Hornitschek et al., 2012; Sweere, 2001). These results suggest a cross-talk between these two pathways, but it remains to demonstrate whether CKs are involved in the control of branching by PHY.

SLs inhibit branching, and also seem to be involved in bud outgrowth regulation by PHY, as *phyB* mutation affects bud outgrowth only if *Arabidopsis MORE AXILLARY GROWTH* (*MAX*) genes *MAX2* (involved in SLs inhibitory effect) and *MAX4* (involved in SLs biosynthesis) are functional (Finlayson et al., 2010). Consistently, in sorghum axillary buds, expression of *SbMAX2* (a homolog of *Arabidopsis MAX2)* was promoted both in *phyB-1* mutant and by FR supplementation in wild-type plants when seedling buds became dormant (Kebrom et al., 2010; Table 1).

Inside axillary buds, *Teosinte branched1 (tb1)*-like genes, in monocots, and *BRANCHED1* (*BRC1*)-like genes, in dicots, act as integrators of different factors, including the hormones cited above, to repress outgrowth (Aguilar-Martinez et al., 2007; Minakuchi et al., 2010). They could be involved in the low R:FR-induced response of branch suppression, and seem to act downstream of PHYB (see Leduc et al., 2014 for a review). Thus, there are many cues indicating that the hormonal network upstream of BRC1 is involved in bud outgrowth regulation by PHYB, but whether BRC1 is directly regulated by PHYB or only indirectly via auxin, SLs and CKs remains unknown.

ABA is another hormone that appears to be involved in bud outgrowth regulation by R:FR. ABA biosynthesis is needed for bud outgrowth inhibition by low R:FR and many ABA-responsive genes are induced under low R:FR, suggesting that ABA signaling plays an important role in the control of axillary bud arrest (Gonzalez-Grandio et al., 2013; Reddy et al., 2013). Besides, *BRC1,* which seems to be required to maintain ABA signaling, could positively regulate key ABA transcription factors (Gonzalez-Grandio and Cubas, 2014). The mechanisms whereby: (i) ABA inhibits bud outgrowth; (ii) ABA inside the bud interacts with the network formed by auxin, SLs and CKs to regulate bud outgrowth in response to R:FR; are as yet unknown.

During the growth-to-dormancy transition within buds, cells become quiescent at checkpoints before the S (Synthesis) and M (Mitotic) phases (Devitt and Stafstrom, 1995; Kebrom et al., 2010). Cell cycle phase transitions and progress during a given phase are

largely controlled by cyclin dependent kinases (CDKs) (Nigg, 1995). The effects of light quality on cell division are mediated through various transcription factors (upstream of CDKs) that are key regulators of cell cycle: BRC1 might negatively control the expression of some cell cycle related genes either directly or by competing with TCP transcriptional activators (Gonzalez-Grandio et al., 2013). This research field deserves to be deeply addressed to improve our understanding of the molecular mechanisms behind the response of cell division activity to light quality and to disentangle the exact role of BRC1 in this process.

Fig. 2 presents a working model of how PHYB interacts with some actors involved in bud outgrowth regulation.

5. Flowering

Accelerated flowering is observed in many crops in response to low R:FR ratios (Table 1). The flowering process consists of two phases: (i) floral transition includes flower induction, floral evocation and flower initiation, and (ii) flower development consists in floral differentiation and anthesis. Flower induction occurs in leaves, while floral evocation occurs in shoot apical meristems and modifies the shape of meristems prior to floral initiation (Samach and Smith, 2013). By contrast, some plants remain insensitive as regards flowering time in response to low R:FR: in wheat, anthesis time was affected rather than apex transition time to the reproductive stage (Ugarte et al., 2010).

Flower induction, which is the first crucial step of floral transition, requires the integration of environmental and endogenous cues through six genetic pathways: the photoperiod, vernalization, autonomous, gibberellin, age, and warm temperature pathways (Bäurle and Dean, 2006; Srikanth and Schmid, 2011). In these different pathways, light quality – especially low R:FR (shade) and/or EOD-FR – leads to accelerated flowering in many long-day (LD) plants including *Arabidopsis thaliana, Campanula carpatica* and *Gypsophila paniculata* (Kristiansen, 1988; Kim et al., 2008; Nishidate et al., 2012). All these pathways converge to the floral integrator genes *FLOWERING LOCUS T* (*FT*) and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) (Putterill et al., 2004). In the photoperiodic pathway of flowering induction, red and far-red lights are perceived in leaves where they act both at the transcriptional (through circadian clock) and post-transcriptional levels (mediated by photoreceptors) to control CONSTANS (CO), a central floral regulator. CO in turn induces *FT* (florigen gene) in leaf vascular bundles (Suárez-López et al., 2001; An et al., 2004). FT moves from the leaves to the apex where it interacts with FLOWERING LOCUS D (FD) to activate *APETALA 1* (*AP1*) and *SOC1* (Abe et al., 2005; Corbesier et al., 2007). In Arabidopsis, a long day plants, PHYB and PHYA are major photoreceptors that control

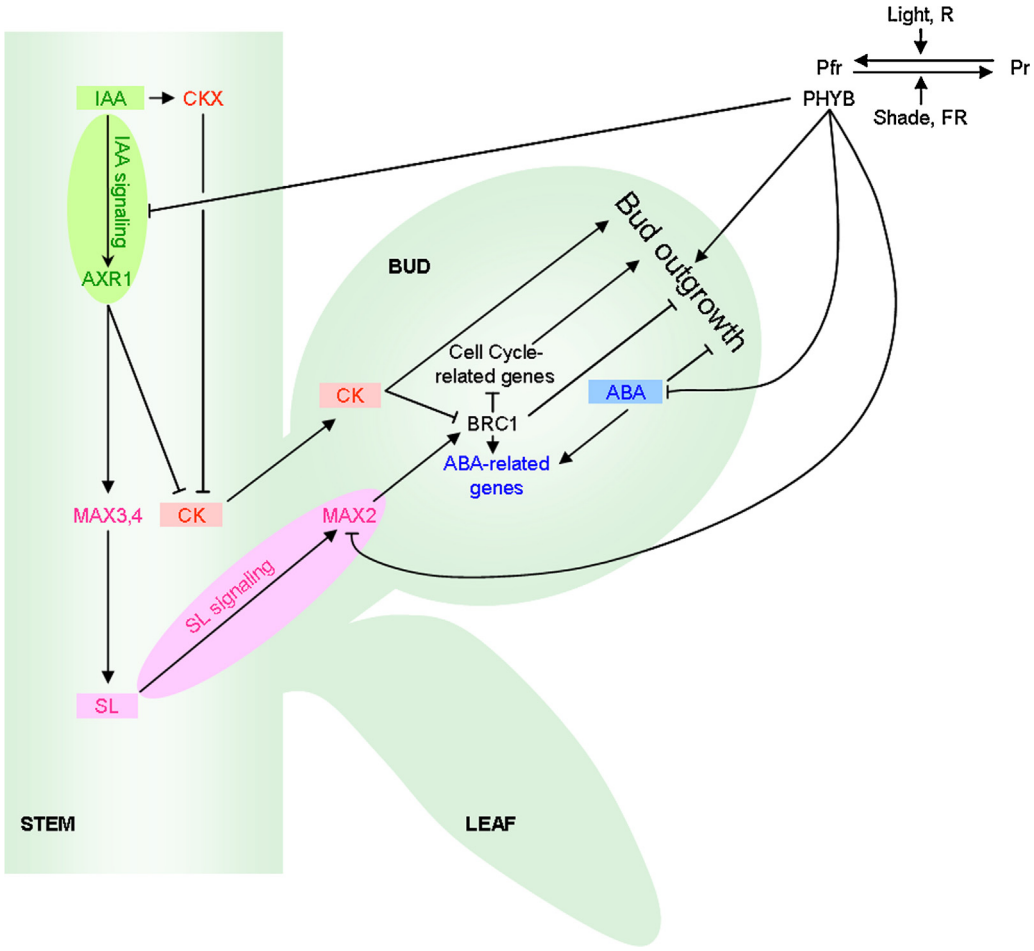

Fig. 2. Schematic representation of the network involved in bud outgrowth regulation by PHYB.
PHYB is considered as a major light integrator that positively regulates bud outgrowth, due at least partly to its negative action on the auxin (IAA) signaling pathway, with possible consequences on strigolactone (SL) and cytokinine (CK) synthesis. Additionally, a direct link between PHYB and SL is probable via inhibition of *MAX* genes. BRC1 also seems to act downstream of PHYB as a hormonal integrator: its gene is induced by auxin and SL signaling and repressed by CK, so PHYB can indirectly regulate BRC1 via its action on the auxin and/or SL signaling pathways. BRC1 can inhibit bud outgrowth by repressing the expression of cell-cycle-related genes and/or by inducing the expression of ABA-related genes. This is in line with the fact that ABA was recently found implied in the inhibition of bud outgrowth in response to low R:FR.

flowering under R and FR lights (Mockler et al., 2003). In the morning in long and short day conditions, R light delays flowering by promoting CO degradation mediated by PHYB in a COP1-independent pathway. Antagonistically, in LD late afternoon (EOD-FR) PHYA inhibits the COP1-SPA1 complex suppressing COP1 activity and accelerating flowering through stabilization of CO (Valverde et al., 2004; Andrés and Coupland, 2012). Although PHYB is the most important photoreceptor mediating low R:FR, acceleration of flowering in response to low R:FR and EOD FR might also be mediated by PHYB, D, and E in a functionally redundant manner (Franklin et al., 2003). Endo et al. (2013) recently reported that mutation in the *PHYTOCHROME-DEPENDENT LATE FLOWERING* (*PHL*) gene caused a late flowering phenotype, while this phenotype was abolished in the *phyB phl* double mutant. They concluded that PHL functioned as a suppressor of CO degradation by PHYB in a red light-dependent manner through a PHL/PHYB/CO tripartite complex (Fig. 3).

PHYTOCHROME AND FLOWERING TIME 1 (PFT1), previously identified as a downstream actor of PHYB signaling, is considered as the MED25 subunit of the plant mediator complex (Cerdán and Chory, 2003; Bäckström et al., 2007). This mediator complex, first identified in yeast, plays a central role as a transcriptional co-regulator in all higher eukaryotes. In response to shade (and EOD-FR), PFT1 (MED25) promotes flowering through activation of *CO* transcription and also of *FT* transcription in a CO-independent manner (Franklin et al., 2003). In contrast, in rice, a short day plant, two daylength pathways are involved in floral induction (CO homolog HEADING DATE 1 (HD1)- FT-like HEADING DATE 3a (HD3a) and GRAIN NUMBER PLANT HEIGHT AND HEADING DATE 7 (GHD7)- EARLY HEADING DATE 1 (EHD1)-HD3a) (Song et al., 2015). In this pathway, PHYA is required to promote expression of *GHD7*, encoding a floral repressor of the flowering inducer *EHD1* in LD conditions (Casal et al., 2014). In LD afternoon, red light converts HD1 activity from activating to repressing *HD3a* expression via PHYB (Song et al., 2015).

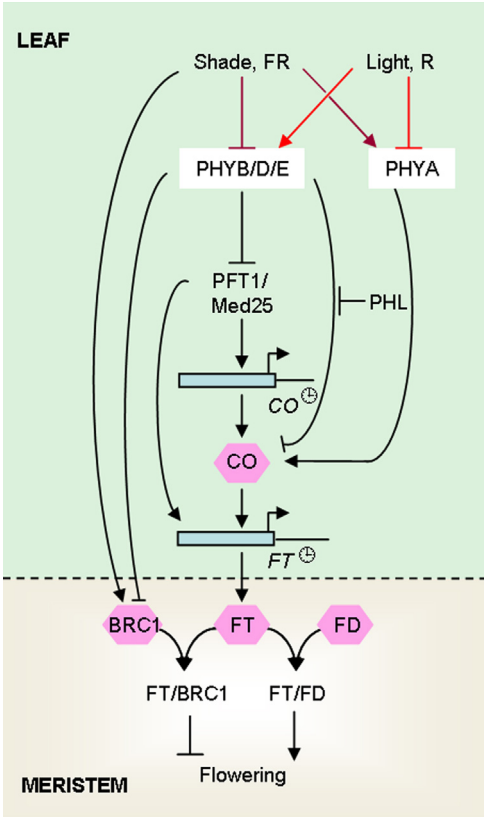

Fig. 3. Schematic representation of the network involved in the regulation of flowering by phytochromes.
In leaves, red light perceived by PHYB/D/E triggers CONSTANS (CO) degradation, whereas far-red light perceived by PHYA stabilizes it. *PHYTOCHROME-DEPENDENT LATE FLOWERING* (PHL) suppresses the inhibitory effect of PHYB, and in turn promotes flowering in response to red light. Downstream of PHYB/D/E, the mediator complex PHYTOCHROME AND FLOWERING TIME 1 (PFT1) subunit promotes flowering by activating the *CO* and *FLOWERING LOCUS T* (*FT*) circadian-clock genes. CO activates *FLOWERING LOCUS T* (*FT*) transcription, and the small FT protein moves through the phloem to the meristem, where the FT-FD (FLOWERING LOCUS D) complex initiates flowering. Antagonistically, in response to shade, BRANCHED1 (BRC1) interacts with FT to repress axillary bud flowering and give priority to floral transition in the meristem of the main shoot.

Although the effect of low R:FR on timing of floral induction is well studied in the literature, less is known on axillary bud and flower development. *brc1-2* exhibited early floral transition in axillary shoots, so BRC1 may not only inhibit axillary bud outgrowth, but also suppress floral transition in axillary buds of *Arabidopsis thaliana* through its direct interaction with FT (Niwa et al., 2013) (Fig 3). These authors suggest a balance between BRC1 and FT in response to low R:FR, whereby BRC1 restricts the scope of FT on floral transition in the shoot apical meristem to the main shoot only. In *Petunia*, there was in average 0.96 supplemental flower under FR light compared to R light (Ilias and Rajapakse, 2012). Under low R:FR treatment, reduced flower diameter has been reported in *Paeonia lactiflora,* as well as reduced petal and pistil lengths in *Brassica* (Weinig, 2002; Zhao et al., 2012).

6. Photosynthesis

Through its effect on branching, leaf area and leaf orientation (see Section 4), the R:FR ratio can indirectly change photosynthesis at the scale of the whole plant. In this section we will focus on the direct effects of R and FR on photosynthesis.

Various traits involved in photosynthesis are regulated by phyB and R and FR lights. *PhyB* and phyB-overexpressing mutants showed that reduced expression of *PHYB* decreases stomatal opening, and can either decrease or increase CO_2 stomatal conductance (Table 1). FR light down regulates the activity of some enzymes of the Calvin cycle (Table 1). *PHYB* also regulates photosynthesis through anatomical changes. Thus, low R:FR or *PHYB* reduced expression often decreases leaf mass per area, with a decrease in the number and length of palisade mesophyll cells, it also decreases stomatal density (Table 1, see Vegetative development). In *Arabidopsis thaliana,* stomatal maturation is promoted by PHYB in response to R light, and by PHYA in response to FR light (Kang et al., 2009). Stomatal development in young leaves is regulated by white light perceived by mature leaves (Casson and Hetherington, 2014). However, PHYB does not seem to affect stomatal development in *Oryza sativa* (Liu et al., 2012). Chloroplast development was found under the control of PHYB (Thiele et al., 1999), and so were thylakoid structure and protein composition changes under R or FR exposure (Frado and Stern, 1982; Eskins and Duysen, 1984). Low R:FR or reduced expression of *PHYB* decreases foliar chlorophyll content *per* unit area in many species (Table 1).

However, there is a large variability among studies in the specific net assimilation rate responses to R:FR, *phyB* mutation or *PHYB* overexpression. Thus, in various species the specific net assimilation rate decreases in response to low R:FR or *PHYB* reduced expression (Table 1). By contrast, specific net assimilation rate was higher in wild type *Citrus* × *insitorum* than in phyB-overexpressing mutants, this could be due to a higher CO_2 stomatal conductance in the wild type (Distefano et al., 2013). Moreover, specific net assimilation rate was unaffected by low R:FR or *phyB* mutation in *Trifolium repens* and in *Arabidopsis* (Table 1). Thus, the regulation of net assimilation rate by R:FR and *PHYB* expression is

not clear; the different and sometime contrasted responses between studies may reflect variability between species and genotypes, and/or variability in the growing conditions used. Indeed, PHYB effects on specific net assimilation rate notably depend on PPFD and plant age (Schittenhelm et al., 2004).

7. Mineral nutrition

The R:FR ratio affects different steps of plant nutrition: absorption, assimilation under organic form, and allocation to plant organs.

7.1. Absorption

Root efficiency is of prime importance to allow significant water and mineral element uptake. In *Arabidopsis*,PhyA, E and D mainly contribute to the maintenance of a branched root (Table 1, see Vegetative development). FR has a negative effect on root hair density that is under the unique dependence of PhyA, while R light strongly favors this process (Table 1, see Vegetative development). In *Glycine max* EOD FR light significantly increases shoot relatively to root biomass while no variation occurred under light supplemented with EOD R light (Kasperbauer, 1987) (Table 1, see Vegetative development). Red light (vs white light), likely through phyB pathway, strongly decreases aerial plant biomass, plant height and leaf number suggesting a complex array of regulations (Table 1, see Vegetative development).

Moreover, mycorrhiza formation is strongly inhibited by FR which affects mineral nutrition, particularly N and P absorption (Table 1, see Mineral nutrition), but the effect on P metabolism is not documented. The number of nodules strongly decreases in *phyB* mutants, and in wild plants under low R:FR (Table 1). In parallel, grafting experiments showed that the stem genotype is the determining parameter of nodule formation in roots, suggesting the existence of a stem-to-root signal that drives nodule differentiation (Suzuki et al., 2011).

The direct impact of the R:FR ratio on mineral absorption, and more specifically ion transporters, is not documented. However, FR light negatively affects ATP formation, and may thus lower the capacity of these transporters (Dedonder et al., 1992). FR illumination appears to affect global ion contents (N, P, K) in all vegetative organs with a decrease in root and an increase in aerial organs, but tubers (Table 1). R illumination stimulated micronutrient absorption in *Solanum lycopersicon*, yet in an unclear way (Table 1). A reduced R:FR ratio can decrease leaf duration by increasing loss of chlorophyll and photosynthesis-related proteins (Tucker, 1981; Rousseaux et al., 2000) (Table 1, see Vegetative development). This effect is independent of the seasons as R:FR ratio is only slightly affected by seasonal daylight variation (Turnbull and Yates, 1993). Moreover a low R:FR ratio decreases the accumulation of a storage protein in *Populus* bark (Zhu and Coleman, 2001). These results suggest that nutrient recycling at least partly depends on phytochromes.

7.2. Assimilation and allocation

Nitrogen assimilation is down-regulated by low R:FR ratio that affects the key enzymes such as nitrate reductase (NR), nitrite reductase (NiR) and glutamine synthetase (GS). (i) NR activity and gene expression were decreased by phytochromes under FR light pulses (Table 1). Due to NR central role in amino-acids synthesis (Johnson and Smith, 1978), R:FR may impact overall cell metabolism. (ii) NiR activity was also decreased by FR pulses in comparison with R light pulses (Table 1). (iii) GS gene expression, and activity, is decreased under FR light (Table 1).

A low R:FR ratio increased allocation of nutrients (N,P,K) to aerial organs (Table 1), resulting in a rapid increase in size and dry matter of these organs at the expense of the roots. In *Glycine max*, this dry matter distribution causes a reduction in N_2 assimilation through reduced nodule formation (Kasperbauer, 1987).

8. Red and far-red lights and their interactions with drought and biotic factors

8.1. Drought

FR light or *phyB* mutation can either dampen or promote drought tolerance, according to species (Table 1). Moreover, *Arabidopsis phyB* mutants were less tolerant to drought than wild-types although they displayed lower stomatal conductance in well-watered conditions (González et al., 2012). Therefore, plants' responses in well-watered conditions cannot be extrapolated to assess drought tolerance.

In *Arabidopsis thaliana PHYB* reduced expression decreases drought tolerance by delaying the drop of stomatal conductance under a reduction in soil water availability (González et al., 2012). Delayed stomatal closure is due to a decreased sensitivity to ABA in *phyB* mutants, through the down-regulation of early ABA signaling genes (González et al., 2012, Table 1). On the opposite, FR or *phyB* mutation could increase plant tolerance to drought by increasing stomatal resistance under drought conditions, and was likely responsible for a decreased water loss in *Gossypium* and *Oryza* (Table 1). In *Oryza sativa phyB* plants, stomatal length and density are lower than in wild type plants; lower stomatal density is in turn due to increased epidermal cell expansion, that probably results from higher expression of *ERECTA* and *EXPANSIN* family genes (Liu et al., 2012, Table 1).

Under drought conditions, *PHYB* inactivation increased concentrations in osmoprotectants and osmotic potential (Table 1). However, in *Arabidopsis thaliana*, this higher osmolite concentration was not sufficient to acquire drought tolerance (González et al., 2012). R:FR ratio may also influence drought tolerance as a consequence of aerial morphological responses (changes in plant leaf area and hyponasty can affect total leaf transpiration and soil covering) (see Section 4).

Additional works are needed to disentangle how FR or phyB mutation can either promote or reduce drought tolerance according to species. A comprehensive view of all phyB-dependent mechanisms related to drought tolerance is needed, followed by a careful examination to determine which ones are dampened or promoted in both drought-sensitive and -tolerant species. Firstly, additional investigations are required to unravel the exact role of the osmotic adjustment caused by *PHYB* inactivation under drought. Secondly, we need to know if ABA sensitivity changes with R:FR in the species in which FR or phyB mutation promote drought tolerance. Besides, the different steps between the light signal and the anatomical response also need to be further elucidated.

8.2. Pathogens and herbivores

Plant infection by a range of pathogens as well as pest attack and propagation can be affected by the light environment of the host before or during infection (see Ballaré et al., 2012; Ballaré, 2014; Roberts and Paul, 2006 for reviews). Shading or high population density frequently increase both the infection by pathogens and the severity of plant diseases (see Burdon and Chilvers, 1982; Roberts and Paul, 2006 for reviews). Likewise, plants exposed to low R:FR ratios (<1) or *phyB* mutants express increased sensitivity to insects or pathogens (Table 1) (Islam et al., 1998; Kazan and Manners, 2011; Ballaré et al., 2012; Cerrudo et al., 2012)

This enhanced sensitivity to pathogens and herbivores, though *PHYB* inactivation by low R:FR ratios, has been correlated to (i) changes in leaf morphological characteristics such as a thinner epidermal tissue (Table 1, see Vegetative development) or a pale color due to a lower chlorophyll content (Table 1, see Photosynthesis), and to (ii) down-regulation of the jasmonate (JA) and salicylic acid (SA) signaling pathways (Wang et al., 2010; Moreno et al., 2013; Ballaré, 2014). The SA pathway is activated predominantly to fend off biotrophic microbial pathogens, whereas the JA pathway is mainly activated in response to attacks by necrotrophic pathogens or chewing insects (Reymond et al., 2000; Glazebrook, 2005). Little is known on the mechanisms implied in the repression of SA-induced genes by low R:FR ratios or by *PHYB* inactivation. It could be mediated via the repression of NPR1 (Non expressor of Pathogenesis-Related genes) phosphorylation, as NPR1 monomers are essential for full expression of SA-induced genes (Spoel et al., 2009; De Wit et al., 2013).

Inactivation of *PHYB* rapidly reduces DELLA protein abundance and stabilizes JAZ10 (JASMONATE ZIM DOMAIN), a protein required for the inhibitory effect of low R:FR ratios on JA (Cerrudo et al., 2012; Leone et al., 2014). Low R:FR ratios also represse the accumulation of metabolites covering the whole spectrum of JA-induced plant defenses, i.e., soluble phenolics, anthocyanins, glucosinolates, terpenoids (Ballaré, 2014). Down-regulation of the JA signaling pathway may also be mediated through Gibberellin (GA) levels. Low R:FR ratios often increase GA levels, which in turn increases DELLA protein degradation (Kurepin et al., 2007; Hou et al., 2010). So under conditions of competition for light, down-regulation of JA responses reduces allocation of resources to defense pathways, and this can help the plant to invest in rapid elongation to increase individual exposure to light resources. This is a typical SAS response (Leone et al., 2014).

9. Use of R and FR lights in ornamental and vegetable horticulture

As mentioned above, light quality, in particular the R:FR ratio, impacts on plant development and functioning during its life cycle. Stem elongation and foliar expansion are often promoted by low R:FR, whereas branching is generally dampened. Flowering is often accelerated under low R:FR ratios. These responses open prospects onto interesting applications for ornamental and vegetable plants grown under the greenhouse, where light can be monitored by artificial lighting to supplement natural light, or by the use of light filters that modify the natural light spectrum.

In ornamental horticulture, the shape of pot plants is one of the essential components of their visual quality, therefore of the commercial value of the products (Boumaza et al., 2010). This shape results from architectural construction, and especially depends on stem elongation and branching. For plants marketed in flower, commercial value also depends on the flowering process, including flowering date and duration, and number of floral buds. It is thus necessary for horticulturists to control branching, stem elongation and flowering in order to obtain products adapted to the current market demand. In Western Europe, there is presently a high demand for branched, compact potted plants. Rational management of light quality is one of the levers available to horticulturists, in particular by acting on the R:FR ratio. Two methods are currently used and/or tested to manipulate light quality: modifying the natural light spectrum by the use of absorbing FR films, and using artificial lighting supplemented in R (and Blue, B), using either fluorescent lamps, or more recently LEDs. These methods are particularly adapted to greenhouses, and represent an environment-friendly alternative to the use of chemical growth regulators.

FR-absorbing plastic films make it possible to limit stem length to some extent. Solatrol® film modified the R:FR ratio from 1.0 in natural light to more than 3.8. Its use reduced plant height by 30% in *Petunia x hybrida,* and 19% in *Impatiens walleriana*, compared to a standard polyethylene film. On the other hand, flowering was delayed for one to two days in *Petunia x hybrida* (Fletcher et al., 2005). Similar observations were made on plant height in *Euphorbia pulcherrima* with an even more absorbing FR film (R:FR ratio = 5.7) (Mata and Botto, 2009). In that study, plant branching was not modified. However, in the same species, a 25.8% increase in the number of axillary stems was observed under another absorbing FR plastic film (R:FR ratio = 1.74) (Clifford et al., 2004).

In greenhouse under natural light, supplemental R (and B) LED lighting limits stem length. Thus, in *Euphorbia pulcherrima*, R (80%) and B (20%) LED lighting applied 10 h a day reduced stem length by 34% compared to supplemental photosynthetic lighting provided by high-pressure sodium lamps (HPS) (Islam et al., 2012). In culture chamber, with white fluorescent lamp lighting, the height of *Tagetes erecta* (marigold) seedlings was not modified by supplemental R LED lighting, but increased by 78% with supplemental FR; for the latter condition, a 50% reduction in the number of floral buds compared to white fluorescent lamps was also observed (Heo et al., 2002).

To control the flowering of photoperiod-sensitive plants, the incandescent lamps usually used in greenhouse (R:FR ratio = 0.59) can be replaced by LEDs. Thus, flowering was earlier in *Petunia multiflora*, whereas it was delayed in *Tagetes erecta* (marigold) using LED lighting (R:FR ratio higher than 0.66), compared to incandescent lamp lighting (Craig and Runkle, 2012).

In vegetable horticulture, the two essential components of the commercial yield of a crop are biomass production and product quality, i.e., its visual aspect and its nutritional value. Biomass production directly depends on photosynthesis, therefore on the quantity of photosynthetically active radiation received by the leaves, while product quality depends much on the wavelengths perceived by the plant, in particular B light and the R:FR ratio. To simultaneously increase biomass and improve quality, the light spectrum can be modified using spectrum conversion films or LEDs, or more conventional lighting (fluorescence, HPS . . .) to supplement natural light. Thus, the light spectrum can be modified to obtain a higher R:FR ratio using plastic films converting the least effective wavelengths for photosynthesis (green) into R. In cucumber (*Cucumis sativus*), this kind of film allowed a 39.1%, gain in fruit yield thanks to a 44.6%, increase in fruit number despite a 3.6% reduction in average fruit weight (Nishimura et al., 2012).

In greenhouse production, tomato (*Lycopersicon esculentum*) and cucumber (*Cucumis sativus*) seedlings were cultivated under three types of lighting provided by (i) HPS lamps, (ii) B:R LEDs (15% B:85%R), (iii) B:R:FR LEDs (15%B:85%R + FR), as a supplement to natural light. Under B:R LEDs, the plants were more compact but did not produce more dry matter than under the HPS control, while plants under B:R:FR lighting exhibited the highest dry matter weight, with +21% for cucumber and +15% for tomato. These results can be explained by a different orientation of the leaves under B:R:FR LED lighting, improving light interception, while no significant difference was observed for leaf area or for photosynthetic activity *per* unit leaf area. This increase in biomass was located primarily at the stem level (Hogewoning et al., 2012). In another trial on cucumber, yield was not increased by HPS lighting supplemented by R LED lighting focused nearby the fructification zone, compared to an HPS control alone. Under this R LED lighting condition, the chlorophyll concentration increased, so that fruit color was improved, and in turn visual quality (Hao et al., 2012).

In culture chamber, lettuce (*Lactuca sativa*) cultivated under white fluorescent lamps supplemented by R LED lighting did not exhibit a significant difference in dry matter weight compared to control plants under white light. On the opposite, a significant 14.5% increase in dry matter weight was observed with supplemental FR LED lighting, due to an increase in leaf area, and therefore an increase in light interception (Li and Kubota, 2009). In that study, quality was assessed by antioxidant dosage. After R treatment, the phenol concentration increased by 6%. Similar observations were obtained in microgreens with HPS lighting supplemented by R LED lighting: phenol concentrations increased from 9.1% in mustard (*Brassica juncea*) to 40.8% in tatsoi (*Brassica rapa*); as for other antioxidants, results varied and were species-dependent (Samuolienė et al., 2012).

It thus appears that R light has no marked effect on biomass when it is used alone or as a supplement to natural or artificial light (HPS or fluorescence), unlike when it is used in combination with FR. However, R light alone can activate antioxidant production in numerous species and improve the nutritional value of products (Olle and Viršile, 2013).

Artificial lighting, as a supplement to natural light or not, has long been used in horticulture to modify the photoperiod and increase light intensity, whether in greenhouse or culture chamber. Taking into account light quality is more recent, especially the relationship between the wavelengths involved in photosynthesis and photo-morphogenesis. The lauch of photo-selective and spectrum conversion films, and especially of effective and cheap monochromatic LEDs, will certainly promote a fast development of these techniques. They will then allow for a more precise control of plant development by optimizing production conditions. These techniques are the subject of many experimental works for application in the horticultural field, in particular in the Netherlands. They could be applied in three different fields, with a view to (i) increasing biomass by applying high R:FR lighting near the photosynthetically active zones (for example for tomato production); (ii) applying effective wavelengths to influence on stem elongation, branching and flowering, in an appropriate sequence to obtain a high-value commercial product (for example for potted flower plants such as poinsettia); (iii) improving plant resistance to pathogens and pests by applying high R:FR lighting, as in cucumber against powdery mildew.

These different fields of light use should contribute to grow glasshouse ornamental and vegetable plants in a more environment-friendly way and thus help growers comply with increasingly tighter European regulations. Limiting stem elongation and improving plant resistance to pathogens through changes in light quality should contribute to reduce the use of growth regulators and pesticides.

Other fields of investigation are possible, notably genetic improvement, with the selection of plants more sensitive to specific wavelengths, for example to a high R:FR ratio, to obtain more compact and branched plants and/or plants more resistant to certain pathogens.

In an even more prospective vision, total control of climatic conditions, especially light quality and intensity, could be applied within entirely closed production sites. This system may respond to new emerging needs, such as vegetable production in towns or in very restrictive climatic environments (hot or cold deserts). It may allow producers to (i) intensify production, by optimizing inputs, such as water; (ii) meet the market needs throughout the year, independently of the season; (iii) produce plants closer to the consumption centers.

The ability to manipulate light quality thanks to recent technological evolutions opens onto many fields of investigation and requires new knowledge in plant physiology. Scientific questions arise (i) from identified knowledge gaps (for example what are the interactions between the different wavelengths? and between specific wavelengths and other growing conditions?); (ii) from the distinctive features of lighting systems (for example the ability to apply specific wavelengths on specific plant organs using LEDs makes it necessary to understand how plants respond to localized contrasted light qualities); (iii) from the need for growers to control certain processes (for example, to what extent can the floral initiation of photoperiodic plants be triggered by a particular combination of wavelengths rather than by light duration?).

10. Conclusion

Red far-red and the R:FR ratio regulate a large range of processes throughout plant life. The roles of PHYB and more recently of PHYA have been intensively investigated, but the roles of other phytochromes are less well-known. The phenotypic responses to R and FR are well described, but apart from a few processes such as germination or flowering, knowledge about the molecular events involved in light signal transduction still remains partial, so additional studies are needed to bridge this gap. One main future task will be to further investigate how plants respond to incoming light when they are grown under constraining conditions (drought, pest attacks, elevated temperatures . . .). This situation reflects what plants really experience during their life cycle and offers original opportunities to understand the importance of light cues in plant performance. For a more efficient use of light quality in horticulture, at least two points could be of great interest to study. Firstly, studying the effects of localized changes in light quality could improve knowledge about perception sites and inter-organ relationships, and be useful for applications in horticulture. For example, applying supplemental light at precise times and locations will help to optimize energy use. Secondly, a better understanding of the interactions between wavelengths of the light spectrum as well as between specific wavelengths and other growing conditions (temperature, mineral nutrition . . .) is also needed to better play with light quality in horticulture.

Acknowledgments

We wish to thank our colleagues from the ARCH-E (Architecture and Environment) team from the IRHS for fruitful discussions and collaboration in research work on plant response to environment, and light in particular, over the last years. We also thank Annie Buchwalter (a scientific translator) for reviewing the paper for English usage.

References

Abe, M., Kobayashi, Y., Yamamoto, S., Daimon, Y., Yamaguchi, A., Ikeda, Y., Ichinoki, H., Notaguchi, M., Goto, K., Araki, T., 2005. FD, a bZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. Science 309, 1052–1056.

Aguilar-Martinez, J.A., Poza-Carrion, C., Cubas, P., 2007. *Arabidopsis* BRANCHED1 acts as an integrator of branching signals within axillary buds. Plant Cell 19, 458–472.

Ahmad, M., Jarillo, J., Smirnova, O., Cashmore, A.R., 1998. The CRY1 blue light photoreceptor of *Arabidopsis* interacts with phytochrome A in vitro. Mol. Cell 1, 939–948.

An, H., Roussot, C., Suárez-López, P., Corbesier, L., Vincent, C., Piñeiro, M., Hepworth, S., Mouradov, A., Justin, S., Turnbull, C., et al., 2004. CONSTANS acts in the phloem to regulate a systemic signal that induces photoperiodic flowering of *Arabidopsis*. Dev. Camb. Engl. 131, 3615–3626.

Andrés, F., Coupland, G., 2012. The genetic basis of flowering responses to seasonal cues. Nat. Rev Genet. 13, 627–639.

Arana, M.V., Sánchez-Lamas, M., Strasser, B., Ibarra, S.E., Cerdán, P.D., Botto, J.F., Sánchez, R.A., 2014. Functional diversity of phytochrome family in the control of light and gibberellin-mediated germination in *Arabidopsis*. Plant Cell Environ. 37, 2014–2023.

Azari, R., Tadmor, Y., Meir, A., Reuveni, M., Evenor, D., Nahon, S., Shlomo, H., Chen, L., Levin, I., 2010. Light signaling genes and their manipulation toward modulation of phytonutrient content in tomato fruits. Biotechnol. Adv. 28, 108–118.

Bäckström, S., Elfving, N., Nilsson, R., Wingsle, G., Björklund, S., 2007. Purification of a plant mediator from *Arabidopsis thaliana* identifies PFT1 as the Med25 subunit. Mol. Cell 26, 717–729.
Ballaré, C.L., 2014. Light regulation of plant defense. Annu. Rev. Plant Biol. 65, 335–363.
Ballaré, C.L., Sanchez, Scopel, R.A., Casal, J.J., CM, 1987. Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. Plant Cell Environ. 10, 551–557.
Ballaré, C.L., Scopel, A.L., Sanchez, R.A., 1991. Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. Plant Cell Environ. 14, 57–65.
Ballaré, C.L., Scopel, Roush, M.L., SR, 1995. How plants find light in patchy canopies. A comparison between wild-type and phytochrome-B-deficient mutant plants of cucumber. Funct. Ecol. 9, 859–868.
Ballaré, C.L., Mazza, C.A., Austin, A.T., Pierik, R., 2012. Canopy light and plant health. Plant Physiol. 160, 145–155.
Barreiro, R., Guiamét, J.J., Beltrano, J., Montaldi, E.R., 1992. Regulation of the photosynthetic capacity of primary bean leaves by the red:far-red ratio and photosynthetic photon flux density of incident light. Physiol. Plant 85, 97–101.
Basu, D., Dehesh, K., Schneider-Poetsch, H.-J., Harrington, S.E., McCouch, S.R., Quail, P.H., 2000. Rice PHYC gene: structure expression, map position and evolution. Plant Mol. Biol. 44, 27–42.
Bäurle, I., Dean, C., 2006. The timing of developmental transitions in plants. Cell 125, 655–664.
Boccalandro, H.E., Ploschuk, E.L., Yanovsky, M.J., Sanchez, R.A., Gatz, C., Casal, J.J., 2003. Increased phytochrome B alleviates density effects on tuber yield of field potato crops. Plant Physiol. 133, 1539–1546.
Boccalandro, H.E., Rugnone, M.L., Moreno, J.E., Ploschuk, E.L., Serna, L., Yanovsky, M. J., Casal, J.J., 2009. Phytochrome B enhances photosynthesis at the expense of water-use efficiency in *Arabidopsis*. Plant Physiol. 150, 1083–1092.
Boumaza, R., Huché-Thélier, L., Demotes-Mainard, S., Coz, E.L., Leduc, N., Pelleschi-Travier, S., Qannari, E.M., Sakr, S., Santagostini, P., Symoneaux, R., et al., 2010. Sensory profiles and preference analysis in ornamental horticulture: the case of the rosebush. Food Qual. Preference 21, 987–997.
Bradbeer, J.W., 1971. Plastid development in primary leaves of *Phaseolus vulgaris*. The effects of short blue, red, far-red, and white light treatments on dark-grown plants. J. Exp. Bot. 22, 382–390.
Burdon, J.J., Chilvers, G.A., 1982. Host density as a factor in plant disease ecology. Annu. Rev. Phytopathol. 20, 143–166.
Cao, D., Hussain, A., Cheng, H., Peng, J., 2005. Loss of function of four DELLA genes leads to light- and gibberellin-independent seed germination in *Arabidopsis*. Planta 223, 105–113.
Carabelli, M., Possenti, M., Sessa, G., Ciolfi, A., Sassi, M., Morelli, G., Ruberti, I., 2007. Canopy shade causes a rapid and transient arrest in leaf development through auxin-induced cytokinin oxidase activity. Genes Dev. 21, 1863–1868.
Casal, J.J., 2012. Shade avoidance. Arab. Book Am. Soc. Plant Biol. 10, e0157.
Casal, J.J., 2013. Photoreceptor signaling networks in plant responses to shade. Annu. Rev. Plant Biol. 64, 403–427.
Casal, J.J., Sadras, V.O., 1987. Effects of end-of-day red/far-red ratio on growth and orientation of sunflower leaves. Bot. Gaz. 148, 463–467.
Casal, J.J., 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.
Casal, J.J., Smith, H., 1989. The function, action and adaptive significance of phytochrome in light-grown plants. Plant Cell Environ. 12, 855–862.
Casal, J.J., Deregibus, V.A., Sánchez, R.A., 1985. Variations in tiller dynamics and morphology in *Lolium multiflorum Lam*. vegetative and reproductive plants as affected by differences in red/far-red irradiation. Ann. Bot. 56, 553–559.
Casal, J.J., Sanchez, R.A., Deregibus, V.A., 1987a. The effect of light quality on shoot extension growth in three species of grasses. Ann. Bot. 59, 1–7.
Casal, J.J., Aphalo, P.J., Sanchez, R.A., 1987b. Phytochrome effects on leaf growth and chlorophyll content in *Petunia axilaris*. Plant Cell Environ. 10, 509–514.
Casal, J.J., Sáchez, R.A., Deregibus c), V.A., 1987c. Tillering responses of *Lolium multiflorum* plants to changes of red/far-red ratio typical of sparse canopies. J. Exp. Bot. 38, 1432–1439.
Casal, J.J., Sanchez, R.A., Gibson, D., 1990. The significance of changes in the red/far-red ratio, associated with either neighbour plants or twilight, for tillering in *Lolium multiflorum Lam*. New Phytol. 116, 565–572.
Casal, J.J., Sanchez, R.A., Yanovsky, M.J., 1997. The function of phytochrome A. Plant Cell Environ. 20, 813–819.
Casal, J.J., Candia, A.N., Sellaro, R., 2014. Light perception and signalling by phytochrome A. J. Exp. Bot. 65, 2835–2845.
Casson, S.A., Hetherington, A.M., 2014. Phytochrome B is required for light-mediated systemic control of stomatal development. Curr. Biol. 24, 1216–1221.
Cerdán, P.D., Chory, J., 2003. Regulation of flowering time by light quality. Nature 423, 881–885.
Cerny, T.A., Faust, J.E., Layne, D.R., Rajapakse, N.C., 2003. Influence of photoselective films and growing season on stem growth and flowering of six plant species. J. Am. Soc. Hortic. Sci. 128, 486–491.
Cerrudo, I., Keller, M.M., Cargnel, M.D., Demkura, P.V., Wit, M., de, Patitucci, M.S., Pierik, R., Pieterse, C.M.J., Ballaré, CL, 2012. Low red/far-red ratios reduce *Arabidopsis* resistance to *Botrytis cinerea* and jasmonate responses via a COI1-JAZ10-dependent, salicylic acid-independent mechanism. Plant Physiol. 158, 2042–2052.
Chelle, M., Evers, J.B., Combes, D., Varlet-Grancher, C., Vos, J., Andrieu, B., 2007. Simulation of the three-dimensional distribution of the red:far-red ratio within crop canopies. New Physiol. 176, 223–234.
Child, R., Smith, H., 1987. Phytochrome action in light-grown mustard: kinetics, fluence-rate compensation and ecological significance. Planta 172, 219–229.
Childs, K.L., Miller, F.R., Cordonnier-Pratt, M.-M., Pratt, L.H., Morgan, P.W., Mullet, J. E., 1997. The sorghum photoperiod sensitivity gene, Ma3, encodes a phytochrome B. Plant Physiol. 113, 611–619.
Cho, J.-N., Ryu, J.-Y., Jeong, Y.-M., Park, J., Song, J.-J., Amasino, R.M., Noh, B., Noh, Y.-S., 2012. Control of seed germination by light-induced histone arginine demethylation activity. Dev. Cell 22, 736–748.
Clack, T., Mathews, S., Sharrock, R.A., 1994. The phytochrome apoprotein family in *Arabidopsis* is encoded by five genes: the sequences and expression of PHYD and PHYE. Plant Mol. Biol. 25, 413–427.
Clack, T., Shokry, A., Moffet, M., Liu, P., Faul, M., Sharrock, R.A., 2009. Obligate heterodimerization of *Arabidopsis* phytochromes C and E and interaction with the PIF3 basic Helix-Loop-Helix transcription factor. Plant Cell Online 21, 786–799.
Clifford, S.C., Runkle, E.S., Langton, F.A., Mead, A., Foster, S.A., Pearson, S., Heins, R.D., 2004. Height control of poinsettia using photoselective filters. HortScience 39, 383–387.
Corbesier, L., Vincent, C., Jang, S., Fornara, F., Fan, Q., Searle, I., Giakountis, A., Farrona, S., Gissot, L., Turnbull, C., et al., 2007. FT protein movement contributes to long-distance signaling in floral induction of *Arabidopsis*. Science 316, 1030–1033.
Costigan, S.E., Warnasooriya, S.N., Humphries, B.A., Montgomery, B.L., 2011. Root-localized phytochrome chromophore synthesis is required for photoregulation of root elongation and impacts root sensitivity to jasmonic acid in *Arabidopsis*. Plant Physiol. 157, 1138–1150.
Craig, D., Runkle, E., 2012. Using leds to quantify the effect of the red to far-red ratio of night-interruption lighting on flowering of photoperiodic crops. Acta Hortic. 956, 179–185.
Dechaine, J.M., Gardner, G., Weinig, C., 2009. Phytochromes differentially regulate seed germination responses to light quality and temperature cues during seed maturation. Plant Cell Environ. 32, 1297–1309.
Dedonder, A., Rethy, R., Fredericq, H., De Greef, J.A., 1992. Phytochrome-mediated changes in the ATP content of *Kalanchoë blossfeldiana* seeds. Plant Cell Environ. 15, 479–484.
Dehesh, K., Tepperman, J., Christensen, A.H., Quail, P.H., 1991. phyB is evolutionarily conserved and constitutively expressed in rice seedling shoots. Mol. Gen. Genet. MGG 225, 305–313.
Deitzer, G.F., Hayes, R., Jabben, M., 1979. Kinetics and time dependence of the effect of far red light on the photoperiodic induction of flowering in wintex barley. Plant Physiol. 64, 1015–1021.
Deregibus, V.A., Sanchez, R.A., Casal, J.J., Trlica, M.J., 1985. Tillering responses to enrichment of red light beneath the canopy in a humid natural grassland. J. Appl. Ecol. 22, 199–206.
Devitt, M.L., Stafstrom, J.P., 1995. Cell-cycle regulation during growth-dormancy cycles in pea axillary buds. Plant Mol. Biol. 29, 255–265.
Devlin, P.F., Patel, S.R., Whitelam, G.C., 1998. Phytochrome E influences internode elongation and flowering time in *Arabidopsis*. Plant Cell 10, 1479–1487.
Distefano, G., Cirilli, M., Las Casas, G., La Malfa, S., Continella, A., Rugini, E., Thomas, B., Long, G., Gentile, A., Muleo, R., 2013. Ectopic expression of *Arabidopsis* phytochrome B in Troyer cirange affects photosynthesis and plant morphology. Sci. Hortic. 159, 1–7.
Djakovic-Petrovic, T., de Wit, M., Voesenek, L., Pierik, R., 2007. DELLA protein function in growth responses to canopy signals. Plant J. 51, 117–126.
Domagalska, M.A., Leyser, O., 2011. Signal integration in the control of shoot branching. Nat. Rev. Mol. Cell Biol. 12, 211–221.
Duanmu, D., Bachy, C., Sudek, S., Wong, C.-H., Jiménez, V., Rockwell, N.C., Martin, S.S., Ngan, C.Y., Reistetter, E.N., van Baren, M.J., et al., 2014. Marine algae and land plants share conserved phytochrome signaling systems. Proc. Natl. Acad. Sci. 111, 15827–15832.
Endo, M., Tanigawa, Y., Murakami, T., Araki, T., Nagatani, A., 2013. PHYTOCHROME-DEPENDENT LATE-FLOWERING accelerates flowering through physical interactions with phytochrome B and CONSTANS. Proc. Natl. Acad. Sci. U. S. A 110, 18017–18022.
Eskins, K., Duysen, M., 1984. Chloroplast structure in normal and pigment-deficient soybeans grown in continuous red or far-red light. Physiol. Plant 61, 351–356.
Evers, J.B., Vos, J., Andrieu, B., Struik, P.C., 2006. Cessation of tillering in spring wheat in relation to light interception and red: far-red ratio. Ann. Bot. 97, 649–658.
Fairchild, C.D., Schumaker, M.A., Quail, P.H., 2000. HFR1 encodes an atypical bHLH protein that acts in phytochrome A signal transduction. Genes Dev. 14, 2377–2391.
Fankhauser, C., Chen, M., 2008. Transposing phytochrome into the nucleus. Trends Plant Sci. 13, 596–601.
Finlayson, S.A., Krishnareddy, S.R., Kebrom, T.H., Casal, J.J., 2010. Phytochrome regulation of branching in *Arabidopsis*. Plant Physiol. 152, 1914–1927.
Fletcher, J.M., Tatsiopoulou, A., Mpezamihigo, M., Carew, J.G., Henbest, R.G.C., Hadley, P., 2005. Far-red light filtering by plastic film, greenhouse-cladding materials: effects on growth and flowering in *Petunia* and Impatiens. J. Hortic. Sci. Biotechnol. 80, 303–306.
Frado, T.M., Stern, A.I., 1982. Photosynthesis and chloroplast development in primary leaves of *Phaseolus vulgaris* illuminated with continuous far-red light. Z Pflanzenphysiol 105, 255–265.
Franklin, K.A., 2008. Shade avoidance. New Phytol. 179, 930–944.

Franklin, K.A., Quail, P.H., 2010. Phytochrome functions in *Arabidopsis* development. J. Exp. Bot. 61, 11–24.
Franklin, K.A., Praekelt, U., Stoddart, W.M., Billingham, O.E., Halliday, K.J., Whitelam, G.C., 2003. Phytochromes B, D, and E act redundantly to control multiple physiological responses in *Arabidopsis*. Plant Physiol. 131, 1340–1346.
Galvão, V.C., Fankhauser, C., 2015. Sensing the light environment in plants: photoreceptors and early signaling steps. Curr. Opin. Neurobiol. 34, 46–53.
Girault, T., Bergougnoux, V., Combes, D., Viemont, J.-D., Leduc, N., 2008. Light controls shoot meristem organogenic activity and leaf primordia growth during bud burst in *Rosa sp*. Plant Cell Environ. 31, 1534–1544.
Glazebrook, J., 2005. Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. Annu. Rev. Phytopathol. 43, 205–227.
González, C.V., Ibarra, Piccoli, S.E., Botto, J.F., HE, 2012. Phytochrome B increases drought tolerance by enhancing ABA sensitivity in *Arabidopsis thaliana*. Plant Cell Environ. 35, 1958–1968.
González, C.V., Fanzone, Cortés, M.L., Bottini, L.E., Lijavetzky, R., Ballaré, C.L., HE, 2015. Fruit-localized photoreceptors increase phenolic compounds in berry skins of field-grown *Vitis vinifera* L. cv. Malbec. Phytochemistry 110, 46–57.
Gonzalez-Grandio, E., Cubas, P., 2014. Identification of gene functions associated to active and dormant buds in *Arabidopsis*. Plant Signal. Behav. ee27994–927994.
Gonzalez-Grandio, E., Poza-Carrion, C., Sorzano, C.O.S., Cubas, P., 2013. BRANCHED1 promotes axillary bud dormancy in response to shade in *Arabidopsis*. Plant Cell 25, 834–850.
Halliday, K.J., Koornneef, M., Whitelam, G.C., 1994. Phytochrome B and at least one other phytochrome mediate the accelerated flowering response of *Arabidopsis thaliana* L. to low red/far-red ratio. Plant Physiol. 104, 1311–1315.
Hao, X., Zheng, J., Little, C., Khosla, S., 2012. Led inter-lighting in year-round greenhouse mini-cucumber production. Acta Hortic. 956, 335–340.
Hauser, B.A., Pratt, L.H., Cordonnier-Pratt, M.-M., 1997. Absolute quantification of five phytochrome transcripts in seedlings and mature plants of tomato (*Solanum lycopersicum L.*). Planta 201, 379–387.
Heo, J., Lee, C., Chakrabarty, D., Paek, K., 2002. Growth responses of marigold and salvia bedding plants as affected by monochromic or mixture radiation provided by a light-emitting diode (LED). Plant Growth Regul. 38, 225–230.
Heraut-Bron, V., Robin, C., Varlet-Grancher, C., Afif, D., Guckert, A., 1999. Light quality (red:far-red ratio): does it affect photosynthetic activity, net CO2 assimilation, and morphology of young white clover leaves? Can. J. Bot. 77, 1425–1431.
Hertel, C., Leuchner, M., Menzel, A., 2011. Vertical variability of spectral ratios in a mature mixed forest stand. Agric. For. Meteorol. 151, 1096–1105.
Hirose, F., Inagaki, N., Hanada, A., Yamagushi, S., Kamiya, Y., Miyao, A., Hirochika, H., Takano, M., 2012. Cryptochrome and phytochrome cooperatively but independently reduce active gibberellin content in rice seedlings under light irradiation. Plant Cell Physiol. 53, 1570–1582.
Hogewoning, S.W., Trouwborst, G., Meinen, E., van Ieperen, W., 2012. Finding the optimal growth-light spectrum for greenhouse crops. Acta Hortic. 956, 357–363.
Holmes, M.G., Smith, H., 1975. Function of phytochrome in plants growing in natural environment. Nature 254, 512–514.
Holmes, M.G., Smith, H., 1977a. Function of phytochrome in natural environment 1. Characterization of daylight for studies in photomorphogenesis and photoperiodism. Photochem. Photobiol. 25, 533–538.
Holmes, M.G., Smith, H., 1977b. The function of phytochrome in natural environment 4. Ligth quality and plant development. Photochem. Photobiol. 25, 551–557.
Hornitschek, P., Kohnen, M.V., Lorrain, S., Rougemont, J., Ljung, K., Lopez-Vidriero, I., Franco-Zorrilla, J.M., Solano, R., Trevisan, M., Pradervand, S., et al., 2012. Phytochrome interacting factors 4 and 5 control seedling growth in changing light conditions by directly controlling auxin signaling. Plant J. 71, 699–711.
Hou, X., Lee, L.Y.C., Xia, K., Yan, Y., Yu, H., 2010. DELLAs modulate jasmonate signaling via competitive binding to JAZs. Dev. Cell 19, 884–894.
Howe, G.T., Bucciaglia, P.A., Hackett, W.P., Furnier, G.R., Cordonnier-Pratt, M.-M., Gardner, G., 1998. Evidence that the phytochrome gene family in black cottonwood has one PHYA locus and two PHYB loci but lacks members of the PHYC/F and PHYE subfamilies. Mol. Biol. Evol. 15, 160–175.
Huché-Thélier, L., Crespel, L., Le Gourrierec, J., Morel, P., Sakr, S., Leduc, N., 2016. Light signaling and plant responses to blue light and UV radiation – perspectives for applications in horticulture. Environ. Exp. Bot. 121, 22–38.
Ilias, I.F., Rajapakse, N., 2012. Growth and flowering responses of *petunia x hybrida* to different photoperiods, light qualities and temperatures does light quality affect photosynthetic apparatus of petunia. Phyton. Horn. Austria. 52, 163–175.
Islam, M.A., Kuwar, G., Clarke, J.L., Blystad, D.-R., Gislerød, H.R., Olsen, J.E., Torre, S., 2012. Artificial light from light emitting diodes (LEDs) with a high portion of blue light results in shorter poinsettias compared to high pressure sodium (HPS) lamps. Sci. Hortic. 147, 136–143.
Islam, S.Z., Honda, Y., Arase, S., 1998. Light-induced resistance of broad bean against *Botrytis cinerea*. J. Phytopathol. 146, 479–485.
Iwamoto, M., Kiyota, S., Hanada, A., Yamaguchi, S., Takano, M., 2011. The multiple contributions of phytochromes to the control of internode elongation in rice. Plant Physiol 157, 1187–1195.
Johnson, C.B., 1976. Rapid activation by phytochrome of nitrate reductase in the cotyledons of *Sinapis alba*. Planta 128, 127–131.
Johnson, C.B., Smith, H., 1978. Phytochrome control of amino acid synthesis in cotyledons of *Sinapis alba*. Phytochemistry 17, 667–670.
Kami, C., Lorrain, S., Hornitschek, P., Fankhauser, C., 2010. Chapter two –light-regulated plant growth and development. In: Marja Timmermans, C.P. (Ed.), Current Topics in Developmental Biology. Academic Press, pp. 29–66.
Kang, C., Lian, H., Wang, F., Huang, J., Yang, H., 2009. Cryptochromes, phytochromes, and COP1 regulate light-controlled stomatal development in *Arabidopsis*. Plant Cell 21, 2624–2641.
Kasperbauer, M.J., 1971. Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. Plant Physiol. 47, 775–778.
Kasperbauer, M.J., 1987. Far-red light reflection from green leaves and effects on phytochrome-mediated assimilate partitioning under field conditions. Plant Physiol. 85, 350–354.
Kazan, K., Manners, J.M., 2011. The interplay between light and jasmonate signalling during defence and development. J. Exp. Bot. 62, 4087–4100.
Kebrom, T.H., Burson, B.L., Finlayson, S.A., 2006. Phytochrome B represses Teosinte Branched1 expression and induces sorghum axillary bud outgrowth in response to light signals. Plant Physiol. 140, 1109–1117.
Kebrom, T.H., Brutnell, T.P., Finlayson, S.A., 2010. Suppression of sorghum axillary bud outgrowth by shade, phyB and defoliation signalling pathways. Plant Cell Environ. 33, 48–58.
Keller, M.M., Jaillais, Y., Pedmale, U.V., Moreno, J.E., Chory, J., Ballaré, C.L., 2011. Cryptochrome 1 and phytochrome B control shade-avoidance responses in *Arabidopsis* via partially independent hormonal cascades. Plant J. 67, 195–207.
Keuskamp, D.H., Pollmann, S., Voesenek, L.A.C.J., Peeters, A.J.M., Pierik, R., 2010. Auxin transport through pin-formed 3 (PIN3) controls shade avoidance and fitness during competition. Proc. Natl. Acad. Sci. U. S. A 107, 22740–22744.
Kim, S.Y., Yu, X., Michaels, S.D., 2008. Regulation of CONSTANS and FLOWERING LOCUS T expression in response to changing light quality. Plant Physiol. 148, 269–279.
Kozuka, T., Horiguchi, G., Kim, G.T., Ohgishi, M., Sakai, T., Tsukaya, H., 2005. The different growth responses of the *Arabidopsis thaliana* leaf blade and the petiole during shade avoidance are regulated by Photoreceptors and sugar. Plant Cell Physiol. 46, 213–223.
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 Physiol. 153, 1608–1618.
Kristiansen, K., 1988. Light quality regulates flower initiation, differentiation and development of *Campanula carpatica* Jacq. Karl Forster. Sci. Hortic. 35, 275–283.
Kurepin, L.V., Emery, R.J.N., Pharis, R.P., Reid, D.M., 2007. Uncoupling light quality from light irradiance effects in *Helianthus annuus* shoots: putative roles for plant hormones in leaf and internode growth. J. Exp. Bot. 58, 2145–2157.
Leduc, N., Roman, H., Barbier, F., Péron, T., Huché-Thélier, L., Lothier, J., Demotes-Mainard, S., Sakr, S., 2014. Light signaling in bud outgrowth and branching in plants. Plants 3, 223–250.
Lee, K.P., Lopez-Molina, L., 2012. Control of seed germination in the shade. Cell Cycle 11, 4489–4490.
Lee, K.P., Piskurewicz, U., Turečková, V., Carat, S., Chappuis, R., Strnad, M., Fankhauser, C., Lopez-Molina, L., 2012. Spatially and genetically distinct control of seed germination by phytochromes A and B. Genes Dev. 26, 1984–1996.
Leivar, P., Quail, P.H., 2011. PIFs: pivotal components in a cellular signaling hub. Trends Plant Sci. 16, 19–28.
Leone, M., Keller, M.M., Cerrudo, I., Ballaré, C.L., 2014. To grow or defend? Low red: far-red ratios reduce jasmonate sensitivity in *Arabidopsis* seedlings by promoting DELLA degradation and increasing JAZ10 stability. New Phytol. 204, 355–367.
Li, Q., Kubota, C., 2009. Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. Environ. Exp. Bot. 67, 59–64.
Libenson, S., Rodriguez, V., Pereira, M.L., Sanchez, R.A., Casal, J.J., 2002. Low red to far-red ratios reaching the stem reduce grain yield in sunflower. Crop Sci. 42, 1180–1185.
Linkosalo, T., Lechowicz, M.J., 2006. Twilight far-red treatment advances leaf bud burst of silver birch (*Betula pendula*). Tree Physiol. 26, 1249–1256.
Liu, J., Zhang, F., Zhou, J., Chen, F., Wang, B., Xie, X., 2012. Phytochrome B control of total leaf area and stomatal density affects drought tolerance in rice. Plant Mol. Biol. 78, 289–300.
Lötscher, M., Nösberger, J., 1997. Branch and root formation in *Trifolium repens* is influenced by the light environment of unfolded leaves. Oecologia 111, 499–504.
Maddonni, G.A., Otegui, M.E., Andrieu, B., Chelle, M., Casal, J.J., 2002. Maize leaves turn away from neighbors. Plant Physiol. 130, 1181–1189.
Más, P., Devlin, Panda, S., SA, 2000. Functional interaction of phytochrome B and cryptochrome 2. Nature 408, 207–211.
Mata, D.A., Botto, J.F., 2009. Manipulation of light environment to produce high-quality poinsettia plants. HortScience 44, 702–706.
Mazza, C.A., Ballaré, C.L., 2015. Photoreceptors UVR8 and phytochrome B cooperate to optimize plant growth and defense in patchy canopies. New Phytol. doi: http://dx.doi.org/10.1111/nph.13332.
Minakuchi, K., Kameoka, H., Yasuno, N., Umehara, M., Luo, L., Kobayashi, K., Hanada, A., Ueno, K., Asami, T., Yamaguchi, S., et al., 2010. FINE CULM1 (FC1) works downstream of strigolactones to inhibit the outgrowth of axillary buds in rice. Plant Cell Physiol. 51, 1127–1135.
Mockler, T., Yang, H., Yu, X., Parikh, D., Cheng, Y., Dolan, S., Lin, C., 2003. Regulation of photoperiodic flowering by *Arabidopsis* photoreceptors. Proc. Natl. Acad. Sci. U. S. A 100, 2140–2145.
Montgomery, B.L., Lagarias, J.C., 2002. Phytochrome ancestry: sensors of bilins and light. Trends Plant Sci. 7, 357–366.

Mor, Y., Halevy, A.H., 1984. Dual effect of light on flowering and sprouting of rose shoots. Physiol. Plant 61, 119–124.
Moreno, J.E., Tao, Y., Chory, J., Ballaré, C.L., 2009. Ecological modulation of plant defense via phytochrome control of jasmonate sensitivity. Proc. Natl. Acad. Sci. 106, 4935–4940.
Moreno, J.E., Shyu, C., Campos, M.L., Patel, L.C., Chung, H.S., Yao, J., He, S.Y., Howe, G. A., 2013. Negative feedback control of jasmonate signaling by an alternative splice variant of JAZ10. Plant Physiol. 162, 1006–1017.
Morgan, D.C., Smith, H., 1978. The relationship between phytochrome-photoequilibrium and Development in light grown *Chenopodium album L.* Planta 142, 187–193.
Morgan, D.C., Smith, H., 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. Planta 145, 253–258.
Morgan, D.C., O'Brien, T., Smith, H., 1980. Rapid photomodulation of stem extension in light-grown *Sinapis alba L.* Planta 150, 95–101.
Nagatani, A., 2010. Phytochrome: structural basis for its functions. Curr. Opin. Plant Biol. 13, 565–570.
Nagatani, A., Chory, J., Furuya, M., 1991. Phytochrome B Is not detectable in the hy3 mutant of *Arabidopsis*, which is deficient in responding to end-of-day far-red light treatments. Plant Cell Physiol. 32, 1119–1122.
Nigg, E.A., 1995. Cyclin-dependent protein kinases: key regulators of the eukaryotic cell cycle. Bioessays 17, 471–480.
Nishidate, K., Kanayama, Y., Nishiyama, M., Yamamoto, T., Hamaguchi, Y., Kanahama, K., 2012. Far-red light supplemented with weak red light promotes flowering of *Gypsophila paniculata*. J. Jpn. Soc. Hortic. Sci. 81, 198–203.
Nishimura, Y., Wada, E., Fukumoto, Y., Aruga, H., Shimoi, Y., 2012. The effect of spectrum conversion covering film on cucumber in soilless culture. Acta Hortic. 956, 481–487.
Niwa, M., Daimon, Y., Kurotani, K., Higo, A., Pruneda-Paz, J.L., Breton, G., Mitsuda, N., Kay, S.A., Ohme-Takagi, M., Endo, M., et al., 2013. BRANCHED1 interacts with flowering locus t to repress the floral transition of the axillary meristems in *Arabidopsis*. Plant Cell 25, 1228–1242.
O'Carrigan, A., Babla, M., Wang, F., Liu, X., Mak, M., Thomas, R., Bellotti, B., Chen, Z.-H., 2014. Analysis of gas exchange, stomatal behaviour and micronutrients uncovers dynamic response and adaptation of tomato plants to monochromatic light treatments. Plant Physiol. Biochem. 82, 105–115.
Oh, E., Kim, J., Park, E., Kim, J.-I., Kang, C., Choi, G., 2004. PIL5, a Phytochrome-interacting basic helix-loop-helix protein, is a key negative regulator of seed germination in *Arabidopsis thaliana*. Plant Cell Online 16, 3045–3058.
Olle, M., Viršile, A., 2013. The effects of light-emitting diode lighting on greenhouse plant growth and quality. Agric. Food Sci. 22, 223–234.
Orr, G.L., Haidar, M.A., Orr, D.A., 1996. Smallseed dodder (*Cuscuta planiflora*) phototropism toward far-red when in white light. Weed Sci. 44, 233–240.
Ouedraogo, M., Hubac, C., 1982. Effect of far red light on drought resistance of cotton. Plant Cell Physiol. 23, 1297–1303.
Ouedraogo, M., Tremolières, A., Hubac, C., 1984. Change in fatty acids composition during water stress in cotton plants. Relation with drought resistance induced by far-red light. Z Pflanzenphysiol 114, 239–245.
Penfield, S., Josse, E.-M., Halliday, K.J., 2010. A role for an alternative splice variant of PIF6 in the control of Arabidopsis primary seed dormancy. Plant Mol. Biol. 73, 89–95.
Pierik, R., Djakovic-Petrovic, T., Keuskamp, D.H., de Wit, M., Voesenek, L., 2009. Auxin and ethylene regulate elongation responses to neighbor proximity signals independent of gibberellin and della proteins in Arabidopsis. Plant Physiol. 149, 1701–1712.
Possart, A., Fleck, C., Hiltbrunner, A., 2014. Shedding (far-red) light on phytochrome mechanisms and responses in land plants. Plant Sci. 217, 36–46.
Putterill, J., Laurie, R., Macknight, R., 2004. It's time to flower: the genetic control of flowering time. BioEssays News Rev. Mol. Cell. Dev. Biol 26, 363–373.
Quail, P.H., 2010. Phytochromes. Curr. Biol. 20, R503–R504.
Rajapakse, N.C., Kelly, J.W., 1994. Influence of spectral filters on growth and postharvest quality of potted miniature roses. Sci. Hortic. 56, 245–255.
Rajasekhar, V.K., Gowri, G., Campbell, W.H., 1988. Phytochrome-mediated light regulation of nitrate reductase expression in squash cotyledons. Plant Physiol. 88, 242–244.
Rausenberger, J., Tscheuschler, A., Nordmeier, W., Wüst, F., Timmer, J., Schäfer, E., Fleck, C., Hiltbrunner, A., 2011. Photoconversion and nuclear trafficking cycles determine phytochrome a's response profile to far-red light. Cell 146, 813–825.
Reddy, S.K., Finlayson, S.A., 2014. Phytochrome B promotes branching in *Arabidopsis* by suppressing auxin signaling. Plant Physiol. 164, 1542–1550.
Reddy, S.K., Holalu, S.V., Casal, J.J., Finlayson, S.A., 2013. Abscisic acid regulates axillary bud outgrowth responses to the ratio of red to far-red light. Plant Physiol. 163, 1047–1058.
Reed, J.W., Nagpal, P., Poole, D.S., Furuya, M., Chory, J., 1993. Mutations in the gene for the red/far-red light receptor phytochrome B alter cell elongation and physiological responses throughout *Arabidopsis* development. Plant Cell Online 5, 147–157.
Reymond, P., Weber, H., Damond, M., Farmer, E.E., 2000. Differential gene expression in response to mechanical wounding and insect feeding in *Arabidopsis*. Plant Cell 12, 707–720.
Roberts, M.R., Paul, N.D., 2006. Seduced by the dark side: integrating molecular and ecological perspectives on the influence of light on plant defence against pests and pathogens. New Phytol. 170, 677–699.
Robin, C., Hay, M.J.M., Newton, P.C.D., Greer, D.H., 1994a. Effect of light quality (red: far-red ratio) at the apical bud of the main stolon on morphogenesis of *Trifolium repens* L. Ann. Bot. 74, 119–123.
Robin, C., Hay, M.J.M., Newton, P.C.D., 1994b. Effect of light quality (red: far-red ratio) and defoliation treatments applied at a single phytomer on axillary bud outgrowth in *Trifolium repens L.* Oecologia 100, 236–242.
De la Rosa, T.M., Aphalo, P.J., Lehto, T., 1998. Effects of far-red light on the growth, mycorrhizas and mineral nutrition of Scots pine seedlings. Plant Soil 201, 17–25.
Rousseaux, M.C., Hall, A.J., Sánchez, R.A., 2000. Basal leaf senescence in a sunflower *(Helianthus annuus)* canopy: responses to increased R/FR ratio. Physiol. Plant 110, 477–482.
Ruberti, I., Sessa, G., Ciolfi, A., Possenti, M., Carabelli, M., Morelli, G., 2012. Plant adaptation to dynamically changing environment: the shade avoidance response. Biotechnol. Adv. 30, 1047–1058.
Sager, J., Smith, W., Edwards, J., 1988. Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. Trans. ASAE 31, 1882–1888.
Sakamoto, A., Takeba, G., Shibata, D., Tanaka, K., 1990. Phytochrome-mediated activation of the gene for cytosolic glutamine-synthetase (GS1) during imbibition of photosensitive lettuce seeds. Plant Mol. Biol. 15, 317–323.
Salisbury, F.J., Hall, A., Grierson, C.S., Halliday, K.J., 2007. Phytochrome coordinates *Arabidopsis* shoot and root development. Plant J. 50, 429–438.
Samach, A., Smith, H.M., 2013. Constraints to obtaining consistent annual yields in perennials. II: environment and fruit load affect induction of flowering. Plant Sci. Int. J. Exp. Plant Biol. 207, 168–176.
Samuolienė, G., Brazaitytė, A., Sirtautas, R., Sakalauskienė, S., Jankauskienė, J., Duchovskis, P., Novičkovas, A., 2012. The impact of supplementary short-term red led lighting on the antioxidant properties of microgreens. Acta Hortic. 956, 649–655.
Sasidharan, R., Chinnappa, C.C., Staal, M., Elzenga, J.T.M., Yokoyama, R., Nishitani, K., Voesenek, L., Pierik, R., 2010. Light quality-mediated petiole elongation in *Arabidopsis* during shade avoidance involves cell wall modification by Xyloglucan endotransglucosylase/hydrolases. Plant Physiol. 154, 978–990.
Schäfer, E., Bowler, C., 2002. Phytochrome-mediated photoperception and signal transduction in higher plants. EMBO Rep. 3, 1042–1048.
Schittenhelm, S., Menge-Hartmann, U., Oldbenburg, E., 2004. Photosynthesis, carbohydrate metabolism, and yield of phytochrome-B-overexpressing potatoes under different light regimes. Crop Sci. 44, 131–143.
Schuerger, A.C., Brown, C.S., 1997. Spectral quality affects disease development of three pathogens on hydroponically grown plants. HortScience 32, 96–100.
Seith, B., Sherman, A., Wray, J.L., Mohr, H., 1994. Photocontrol of nitrite reductase gene expression in the barley seedling (*Hordeum vulgare L.*). Planta 192, 110–117.
Sharrock, R.A., 2008. The phytochrome red/far-red photoreceptor superfamily. Genome Biol. 9, 230.
Sharrock, R.A., Quail, P.H., 1989. Novel phytochrome sequences in *Arabidopsis thaliana*: structure, evolution, and differential expression of a plant regulatory photoreceptor family. Genes Dev. 3, 1745–1757.
Sheerin, D.J., Menon, C., zur Oven-Krockhaus, S., Enderle, B., Zhu, L., Johnen, P., Schleifenbaum, F., Stierhof, Y.-D., Huq, E., Hiltbrunner, A., 2015. Light-activated phytochrome A and B interact with members of the SPA family to promote photomorphogenesis in *Arabidopsis* by reorganizing the COP1/SPA complex. Plant Cell 27, 189–201.
Shen, H., Zhu, L., Castillon, A., Majee, M., Downie, B., Huq, E., 2008. Light-Induced Phosphorylation and degradation of the negative regulator PHYTOCHROME-INTERACTING FACTOR1 from *Arabidopsis* depend upon its direct physical interactions with photoactivated phytochromes. Plant Cell Online 20, 1586–1602.
Shi, H., Zhong, S., Mo, X., Liu, N., Nezames, C.D., Deng, X.W., 2013. HFR1 Sequesters PIF1 to Govern the transcriptional network underlying light-initiated seed germination in *Arabidopsis*. Plant Cell Online 25, 3770–3784.
Shibuya, T., Komuro, J., Hirai, N., Sakamoto, Y., Endo, R., Kitaya, Y., 2010. Preference of sweetpotato whitefly adults to cucumber seedlings grown under two different light sources. HortTechnology 20, 873–876.
Shibuya, T., Itagaki, K., Tojo, M., Endo, R., Kitaya, Y., 2011. Fluorescent illumination with high red-to-far-red ratio improves resistance of cucumber seedlings to powdery mildew. HortScience 46, 429–431.
De Simone, S., Oka, Y., Inoue, Y., 2000a. Effect of light on root hair formation in *Arabidopsis thaliana* phytochrome-deficient mutants. J. Plant Res. 113, 63–69.
De Simone, S., Oka, Y., Nishioka, N., Tadano, S., Inoue, Y., 2000b. Evidence of phytochrome mediation in the low-ph-induced root hair formation process in lettuce (*Lactuca sativa* L. cv. grand rapids) Seedlings. J. Plant Res. 113, 45–53.
Skinner, R.H., Simmons, S.R., 1993. Modulation of leaf elongation, tiller appearance and tiller senescence in spring barley by far-red light. Plant Cell Environ. 16, 555–562.
Smith, H., Holmes, M.G., 1977. Function of phytochrome in natural environment 3. Measurement and calculation of phytochrome photo-equilibria. Photochem. Photobiol. 25, 547–550.
Song, Y.H., Shim, J.S., Kinmonth-Schultz, H.A., Imaizumi, T., 2015. Photoperiodic flowering: time measurement mechanisms in leaves. Annu. Rev. Plant Biol. 66, 441–464.
Spoel, S.H., Mou, Z., Tada, Y., Spivey, N.W., Genschik, P., Dong, X., 2009. Proteasome-mediated turnover of the transcription co-activator NPR1 plays dual roles in regulating plant immunity. Cell 137, 860–872.
Srikanth, A., Schmid, M., 2011. Regulation of flowering time: all roads lead to Rome. Cell. Mol. Life Sci. CMLS 68, 2013–2037.

Stagnari, F., Galieni, A., Cafiero, G., Pisante, M., 2014. Application of photo-selective films to manipulate wavelength of transmitted radiation and photosynthate composition in red beet (*Beta vulgaris* var. *conditiva* Alef.). J. Sci. Food Agric. 94, 713–720.

Strasser, B., Sanchez-Lamas, M., Yanovsky, M.J., Casal, J.J., Cerdan, P.D., 2010. *Arabidopsis thaliana* life without phytochromes. Proc. Natl. Acad. Sci. 107, 4776–4781.

Su, H., Abernathy, S.D., White, R.H., Finlayson, S.A., 2011. Photosynthetic photon flux density and phytochrome B interact to regulate branching in *Arabidopsis*. Plant Cell Environ. 34, 1986–1998.

Suárez-López, P., Wheatley, K., Robson, F., Onouchi, H., Valverde, F., Coupland, G., 2001. CONSTANS mediates between the circadian clock and the control of flowering in *Arabidopsis*. Nature 410, 1116–1120.

Suzuki, A., Suriyagoda, L., Shigeyama, T., Tominaga, A., Sasaki, M., Hiratsuka, Y., Yoshinaga, A., Arima, S., Agarie, S., Sakai, T., et al., 2011. Lotus japonicus nodulation is photomorphogenetically controlled by sensing the red/far red (R/FR) ratio through jasmonic acid (JA) signaling. Proc. Natl. Acad. Sci. 108, 16837–16842.

Sweere, U., 2001. Interaction of the response regulator ARR4 with phytochrome B in modulating red light signaling. Science 294, 1108–1111.

Takaki, M., 2001. New proposal of classification of seeds based on forms of phytochrome instead of photoblastism. Rev. Bras. Fisiol. Veg. 13, 104–108.

Takano, M., Inagaki, N., Xie, X., Kiyota, S., Baba-Kasai, A., Tanabata, T., Shinomura, T., 2009. Phytochromes are the sole photoreceptors for perceiving red/far-red light in rice. Proc. Natl. Acad. Sci. 106, 14705–14710.

Tao, Y., Ferrer, J.L., Ljung, K., Pojer, F., Hong, F.X., Long, J.A., Li, L., Moreno, J.E., Bowman, M.E., Ivans, L.J., et al., 2008. Rapid synthesis of auxin via a new tryptophan-dependent pathway is required for shade avoidance in plants. Cell 133, 164–176.

Teller, S., Appenroth, K.-J., 1994. The appearance of glutamine synthetase in turions of *Spirodela polyrhiza* (*L.*) Schleiden as regulated by blueand red light, nitrate and ammonium. J. Exp. Bot. 45, 1219–1226.

Tezuka, T., Yamamoto, Y., 1975. Control of ion absorption by phytochrome. Planta 122, 239–244.

Thiele, A., Herold, M., Lenk, I., Quail, P.H., Gatz, C., 1999. Heterologous expression of *Arabidopsis* phytochrome B in transgenic potato influences photosynthetic performance and tuber development. Plant Physiol. 120, 73–82.

Trupkin, S.A., Legris, M., Buchovsky, A.S., Tolava Rivero, M.B., Casal, J.J., 2014. Phytochrome b nuclear bodies respond to the low red to far-red ratio and to the reduced irradiance of canopy shade in *Arabidopsis*. Plant Physiol. 165, 1698–1708.

Tucker, D.J., 1981. Phytochrome regulation of leaf senescence in cucumber and tomato. Plant Sci. Lett 23, 103–108.

Turnbull, M.H., Yates, D.J., 1993. Seasonal variation in the red/far-red ratio and photon flux density in an Australian subtropical rain-forest. Agric. For. Meteorol. 64, 111–127.

Ugarte, C.C., Trupkin, S.A., Ghiglione, H., Slafer, G., Casal, J.J., 2010. Low red/far-red ratios delay spike and stem growth in wheat. J. Exp. Bot. 61, 3151–3162.

Valverde, F., Mouradov, A., Soppe, W., Ravenscroft, D., Samach, A., Coupland, G., 2004. Photoreceptor regulation of CONSTANS protein in photoperiodic flowering. Science 303, 1003–1006.

Wan, C.G., Sosebee, R.E., 1998. Tillering responses to red: far-red light ratio during different phenological stages in *Eragrostis curvula*. Environ. Exp. Bot. 40, 247–254.

Wang, H., Jiang, Y.P., Yu, H.J., Xia, X.J., Shi, K., Zhou, Y.H., Yu, J.Q., 2010. Light quality affects incidence of powdery mildew, expression of defence-related genes and associated metabolism in cucumber plants. Eur. J. Plant Pathol. 127, 125–135.

Weinig, C., 2002. Phytochrome photoreceptors mediate plasticity to light quality in flowers of the Brassicaceae. Am. J. Bot. 89, 230–235.

Weller, J.L., Murfet, I.C., Reid, J.B., 1997. Pea mutants with reduced sensitivity to far-red light define an important role for phytochrome A in day-length detection. Plant Physiol. 114, 1225–1236.

Von Wettberg, E.J., Schmitt, J., 2005. Physiological mechanism of population differentiation in shade-avoidance responses between woodland and clearing genotypes of *Impatiens capensis*. Am. J. Bot. 92, 868–874.

Whitelam, G.C., Johnson, C.B., 1982. Photomorphogenesis in *Impatiens-Parviflora* and other plant-species under simulated natural canopy radiations. New Phytol. 90, 611–618.

Williamson, M.M., Wilson, G.W.T., Hartnett, D.C., 2012. Controls on bud activation and tiller initiation in C-3 and C-4 tallgrass prairie grasses: the role of light and nitrogen. Bot. -Bot 90, 1221–1228.

De Wit, M., Kegge, W., Evers, J.B., Eijk, M.H.V., Gankema, P., Voesenek, L.A.C.J., Pierik, R., 2012. Plant neighbor detection through touching leaf tips precedes phytochrome signals. Proc. Natl. Acad. Sci. 109, 14705–14710.

De Wit, M., Spoel, S.H., Sanchez-Perez, G.F., Gommers, C.M.M., Pieterse, C.M.J., Voesenek, L.A.C.J., Pierik, R., 2013. Perception of low red:far-red ratio compromises both salicylic acid- and jasmonic acid-dependent pathogen defences in *Arabidopsis*. Plant J. 75, 90–103.

Zhao, D., Hao, Z., Tao, J., 2012. Effects of shade on plant growth and flower quality in the herbaceous peony (*Paeonia lactiflora Pall.*). Plant Physiol. Biochem. 61, 187–196.

Zhu, B., Coleman, G.D., 2001. Phytochrome-mediated photoperiod perception, shoot growth, glutamine, calcium, and protein phosphorylation influence the activity of the poplar bark storage protein gene promoter (bspA). Plant Physiol. 126, 342–351.