

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

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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.

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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

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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 (bilin) 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 bilin 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 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

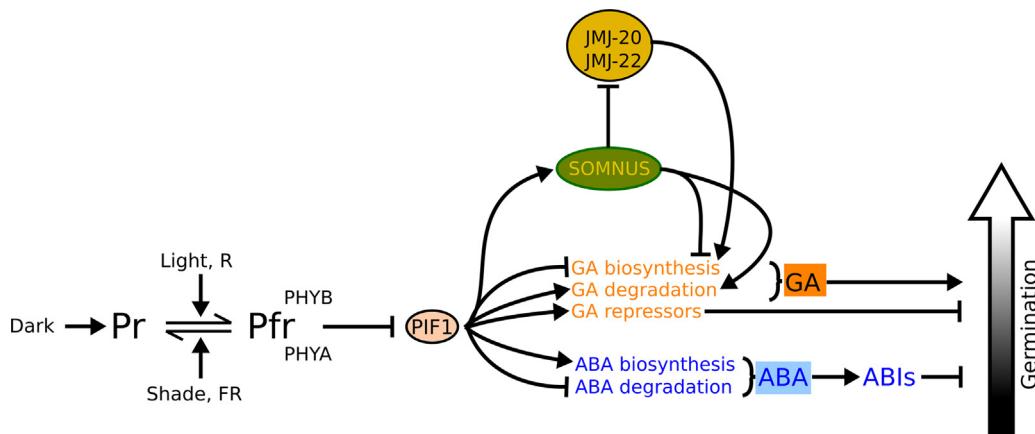


Fig. 1. Schematic representation of the network involved in the regulation of germination by phytochromes.

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

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

			phytomer(no effect on phytomers formed on parent axis before light treatment)						
			ca -15%	<i>Lolium multiflorum</i>		0.8 vs 1.6	107		Casal et al., 1985
	=			<i>Dichanthelium oligosanthes</i>		0.2 vs 1.4	NA	similar PPFD for the two R:FR treatments	Williamson et al., 2012
				<i>Andropogon gerardii</i>				R:FR=2.98 until day7 then application of lower R:FR treatment	Finlayson et al., 2010
Standardized primary rosette branches	↓		ca -35%	<i>Arabidopsis thaliana</i>		0.05 vs 2.98	175		
			ca -30%			phyB vs WT	2.08	180	
Bud length	↓		ca -54% 9 days after planting	<i>Sorghum bicolor</i>	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	<i>Betula pendula</i>	WT	0.58 vs 1.3 during twilight	From 72 to 85 during twilight	Rest of the day: R:FR=1.3, PPFD =180 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Linkosalo and Lechowicz, 2006
			-1.03 day top rosette bud (=n)	<i>Arabidopsis thaliana</i>		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	<i>Trifolium repens</i>		0.32 vs 1.12	175		Lötscher and Nösberger, 1997
			NQ	<i>Eragrostis curvula</i>		0.59 vs 1.1	69		Wan and Sosebee, 1998
			NQ	<i>Triticum aestivum</i>		0.6 vs 1.2 (two hours before sunset)	NA	Natural light supplemented with FR vs R ($10 \mu\text{mol m}^{-2}\text{s}^{-1}$) during 4h in the afternoon to beginning of full darkness.	Ugarte et al., 2010
			+2.91 days bud n-2	<i>Arabidopsis thaliana</i>	phyB vs WT	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	<i>Arabidopsis thaliana</i>		2.08	180		
	=		bud n-1	<i>Arabidopsis thaliana</i>	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.	<i>Arabidopsis thaliana</i>	WT	0.13 vs 6.81	100		Halliday et al., 1994
			-13 d.	<i>Hordeum vulgare</i>		0.45 vs 5.6	428	Photoperiod: 12h	Deitzer et al., 1979
			-3.1 d.	<i>Petunia hybrida</i>			450	FR light vs R light,12h photoperiod	Ilias and Rajapakse, 2012
			-1 d.	<i>Zinnia elegans</i>		0.77 vs 1.51		Daily light integral=9 to 10 $\text{mol m}^{-2} \text{d}^{-1}$	Cerny et al., 2003
			-2 d.	<i>Dendranthema × grandiflorum</i>				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 $\text{mol m}^{-2} \text{d}^{-1}$	
			-9 d.	<i>Antirrhinum majus</i>		0.77 vs 1.51			
			From -1 to -12 d. Depending on photoperiod	<i>Petunia xhybrida</i>		0.77 vs 1.51		daily light integral=9 to 10 $\text{mol m}^{-2} \text{d}^{-1}$	
	=			<i>Cosmos bipinnatus</i> <i>Rosa hybrida</i>		0.77 vs 1.51			
Photosynthesis	CO ₂ stomatal conductance	↓	ca -35%	<i>Solanum tuberosum</i>	WT vs phyB-OEM ^a			Natural light conditions in field	Boccalandro et al., 2003
			ca -20%	<i>Arabidopsis thaliana</i>	phyB vs WT	3.8	185		Gonzalez et al., 2012
		↑	+19%	<i>Citrus × insitorum</i>	WT vs phyB-OEM ^a	NA	NA	Natural light conditions in greenhouse	Distefano et al., 2013
	Enzyme activity of Calvin cycle	↓	RBC ^b : -71% PK ^c : -60%	<i>Phaseolus vulgaris</i>	WT	FR vs WL	150 (FR) vs 400 (WL)	Dark conditions, with brief exposure to FR (20 min) vs	Bradbeer, 1971

			GDD ^b : -63% T ^b : -76%			($\mu\text{W cm}^{-2}$)	white light (5 min)	
Chlorophyll content	↓		-20% chl a -23% chl b	<i>Citrus × insitorum</i>	WT vs phyB-OEM ^a	NA	NA	Natural light conditions in greenhouse
			ca -32%	<i>Solanum tuberosum</i>			From 150 to 500	Natural light conditions in greenhouse
			ca -40%			Value NA, stable	300, 600 or 900	
			-15,9% -10,3% -24% -40%	<i>Trifolium repens</i> <i>Solanum lycopersicum</i> <i>Cucumis sativus</i>		0.4 vs 2.4	320 110	
			-10 to -21%	<i>Phaseolus vulgaris</i>	WT	EOD FR (5min, 0.99 Wm ⁻²) vs no FR	5W m ⁻² white light	
			-42 to -88%			300		Heraut-Bron et al., 1999
			ca -40%	<i>Oryza sativa</i>		0.7 vs 1.3	800	Tucker, 1981
			ca -40%	<i>Arabidopsis thaliana</i>		phyB vs WT (Ler accession)	4.1	
			-19% -30 to -55% depending on foliar stratum -13 to -19% depending on PPFD, average on plant cycle	<i>Solanum tuberosum</i>			From 150 to 500	Measurements performed under a range of PPFD from 100 to 850 $\mu\text{mol m}^{-2} \text{s}^{-1}$
			+13%	<i>Citrus × insitorum</i>	WT vs phyB-OEM ^a			Barreiro et al., 1992
Net assimilation rate	↓			<i>Trifolium repens</i>		0.4 vs 2.4	110 or 320	
			=	<i>Arabidopsis thaliana</i>		phyB vs WT (Col accession)	11.7	
							160 or 280	
						NA	NA	
Mineral nutrition	Mycorhize formation	↓	-27%	<i>Pinus sylvestris</i>	WT	0.39 vs 1.3	200	
	Nodule formation (nb.plant ⁻¹)	↓	-80%	<i>Lotus japonicus</i>		low (0.1) vs high (∞)	100	
			-60%					Suzuki et al., 2011
	Ion content	↑	N content in stems : +16 %	<i>Pinus sylvestris</i>		0.39 vs 1.3	200	
			Concentrations in tuberous roots K :+125% P : +44% Mg: +217% Fe: +87% Zn: +77% Mn:+21% Ca: +10%	<i>Beta vulgaris</i>	WT	Green film (R:FR=0.43) vs natural light	NA	
			Stem contents : ca +255% K ca +111% P	<i>Phaseolus aureus</i>		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	<i>Pinus sylvestris</i>		0.39 vs 1.3	200	
			Contents in roots N : -27% P: -31%					
			Concentrations in leaves Fe : -28% B : -23% Mn: -35% Cu: -42%	<i>Solanum lycopersicum</i>		NA	300 (WL) vs 100 (R)	

		Zn : -72% Ni : -27%							
Protein content	↓	-41% -32%	<i>Cucumis sativus</i>		NA	WL: 5W m ⁻²	white light + EOD FR (5min, 0.99 W m ⁻²)	Tucker, 1981	
NR gene expression	↓	ca -73%	<i>Cucurbita maxima</i>				FR light pulses (5min, 0.003W m ⁻²) vs R light pulses (5 min, 0.45W m ⁻²)	Rajasekhar et al., 1988	
NR activity	↓	-50% -60%	<i>Sinapis alba</i> <i>Cucurbita maxima</i>		NA		FR light (12h, value not available) vs white light (12h) after darkness	Johnson, 1976	
NiRactivity	↓	-37%	<i>Hordeum vulgare</i>				FR light pulses (5min, 0.003W m ⁻²) vs R light pulses (5 min, 0.45W m ⁻²)	Rajasekhar et al., 1988	
GS gene expression	↓	High inhibition, NQ	<i>Lactuca sativa</i>				FR light pulses (3x5min, 3.5W m ⁻²) vs R light pulses (3x5 min, 6.8W m ⁻²)	Seith et al., 1994	
GS activity	↓	-16%	<i>Spirodella polyrhiza</i>				FR pulse (2min) vs R pulse (2min)	Sakamoto et al 1990	
N Allocation	↑	+18.5% in aerial organs in 5 days	<i>Pinus sylvestris</i>		0.39 vs 1.3	200	FR light (3.5W m ⁻²) vs R light (6.8W m ⁻²)	Teller and Appenroth 1994	
								De la Rosa et al., 1998	
Drought	Tolerance	days of plant survival under water stress: ca +108%	<i>Gossypium hirsutum</i>	<i>phyB</i> vs WT					
					NA	270 (at noon on sunny days)	Natural light conditions in greenhouse	Liu et al., 2012	
		+80% of plants recovered after being re-watered	<i>Oryza sativa</i>		3.8	185		Gonzalez et al., 2012	
	ABA sensitivity	↓ NQ	<i>Arabidopsis thaliana</i>						
		ABA signaling genes: ABCG22: ca-71% PYL5: ca -72% HAB1:ca -95%							
	Stomatal resistance	↑ +273%	<i>Gossypium hirsutum</i>		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%							
	Gene expression	↑ ERECTA family: x 1.8 EXPANSIN family: x 2.0	<i>Oryza sativa</i>				Natural light conditions in greenhouse, after 2 days of water shortage	Liu et al., 2012	
	Osmotic potential	↑ +32%	<i>Gossypium hirsutum</i>		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%	<i>Oryza sativa</i>		<i>phyB</i> 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%	<i>Arabidopsis thaliana</i>			3.8	185	After 7 days of water shortage	Gonzalez et al., 2012
Pathogens and herbivore resistance	Number of pathogen colonies	+25% (cotyledon) +61% (first leaf)	<i>Cucumis sativus/Powdery mildew</i>	WT	1.1 vs 7.0	300	Fluorescent lamps	Shibuya et al., 2011	
					5.1 vs 99	330	LED (660/735)	Schuerger and Brown, 1997	
		+115% (leaf)	<i>Cucumissativus</i> /Sweetpotato Whitefly		1.2 vs 7.0	350	Metal-halidelamps vs. fluorescent lamps	Shibuya et al., 2010	
		+78% (seedling)			NA	328 vs 287 (μ W m ⁻²)	Pre-treatment of detached leaf under fluorescent lamps during 24h before inoculation. Max. wavelength 740 vs 650 nm	Islam et al., 1998	
	Area of necrosis /inoculum droplet	↑ Around +600%	Broad bean/ <i>Botrytis cinerea</i>						

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

^aphyB-OEM: phyB-overexpressing mutant.^bRibulose biphosphate carboxylase, Phosphoglycerate kinase, Glyceraldehyde phosphate deshydrogenase, Transketolase.

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 phototropic 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

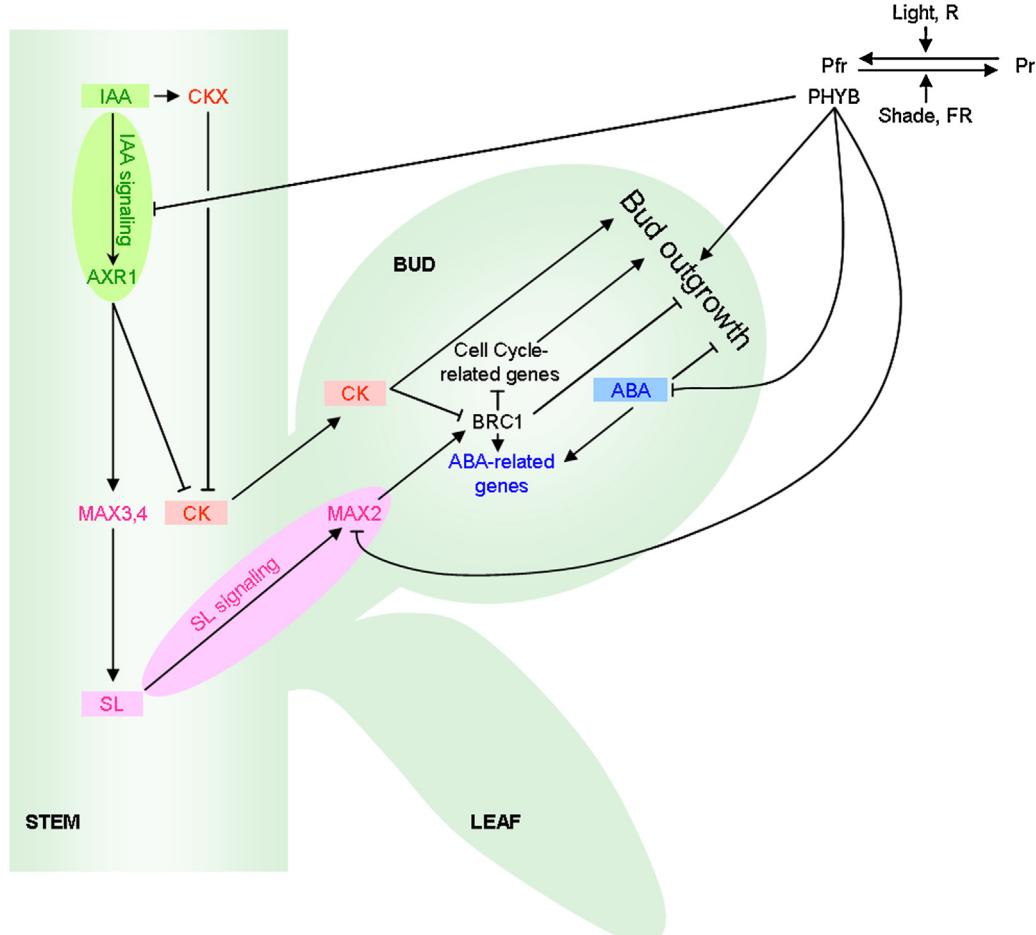


Fig. 2. Schematic representation of the network involved in bud outgrowth regulation by PHYB.

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 cytokinin (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).

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 an 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

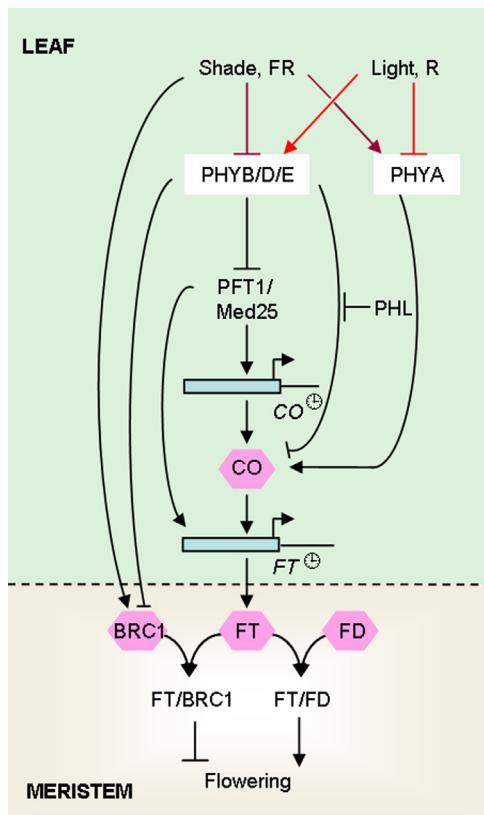


Fig. 3. Schematic representation of the network involved in the regulation of flowering by phytochromes.

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.

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 lycopersicum*, 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 N₂ 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 represses 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 launch 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.

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