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Blue light effects on rose photosynthesis and photomorphogenesis

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Through its impact on photosynthesis and morphogenesis, light is the environmental factor that most affects plant architecture. Using light rather than chemicals to manage plant architecture could reduce the impact on the environment. However, the understanding of how light modulates plant architecture is still poor and further research is needed. To address this question, we examined the development of two rose cultivars, *Rosa hybrida* 'Radrazz' and *Rosa chinensis* 'Old Blush', cultivated under two light qualities. Plants were grown from one-node cuttings for 6 weeks under white or blue light at equal photosynthetic efficiencies. While plant development was totally inhibited in darkness, blue light could sustain full development from bud burst until flowering. Blue light reduced the net CO₂ assimilation rate of fully expanded leaves in both cultivars, despite increasing stomatal conductance and intercellular CO₂ concentrations. In 'Radrazz', the reduction in CO₂ assimilation under blue light was related to a decrease in photosynthetic pigment content, while in both cultivars, the chl *a/b* ratio increased. Surprisingly, blue light could induce the same organogenetic activity of the shoot apical meristem, growth of the meta-mers and flower development as white light. The normal development of rose plants under blue light reveals the strong adaptive properties of rose plants to their light environment. It also indicates that photomorphogenetic processes can all be triggered by blue wavelengths and that despite a lower assimilation rate, blue light can provide sufficient energy *via* photosynthesis to sustain normal growth and development in roses.

INTRODUCTION

Light is one of the key environmental factors that have a major impact on plant architecture. In terms of light quality, both red and blue light have been shown to alter plant architectural development. Plant response to blue light is less constant than that to red light (Rajapakse & Kelly 1995; Khattak *et al.* 2004) and depends on the species. For example, under blue light, bud burst is stimulated in *Triticum aestivum* (Barnes & Bugbee 1992) and *Prunus cerasifera* (Muleo *et al.* 2001), whereas it is reduced in *Solanum tuberosum* (Wilson *et al.* 1993). Similarly, shoot elongation is increased under blue light in pepper (Brown *et al.* 1995) and cucumber (Piszczek & Glowacka 2008), whereas it is repressed in *Pinus* (Sarala *et al.* 2007) and in *S. tuberosum* (Wilson *et al.* 1993). Even within a single species, plant response to blue light can differ among varieties, as shown in tomato (Glowacka 2006). As an ornamental plant, the rose could benefit from light treatments that could modify its architecture. This could con-

tribute to the production of new plant shapes and improved aesthetic quality (Boumaza *et al.* 2009) or to better control of plant diseases (Gontijo *et al.* 2010). This reasoning has already been applied to other ornamental species such as *Antirrhinum*, *Zinnia* and *Dendranthema* (Rajapakse *et al.* 1992; Cremer *et al.* 1998; McMahon *et al.* 1991; Cerny *et al.* 2003). So far, very few attempts have been made to modulate rose architecture through qualitative light treatments. In the miniature rose (*Rosa hybrida*), assays to reduce plant height using far-red light-absorbing filters failed (Cerny *et al.* 2003), while some success was achieved in increasing stem length and dry weight of *Rosa hybrida* 'Mercedes' shoots by reducing the amount of blue light in the white fluorescent light (Maas & Bakx 1995).

The effects of light on plant architecture can be mediated either through photomorphogenic responses or through the direct impact of light on plant photosynthesis. However, the respective contribution of each process to the elaboration of plant architecture is poorly understood. In photomorphogenic

responses, light can affect meristem activity, organ differentiation and growth through control of genetic activities other than those involved in photosynthesis (McIntyre 1987; Benson & Kelly 1990; Brown *et al.* 1995; Li *et al.* 2000; Parks *et al.* 2001; Fukuda *et al.* 2008). In rose, where we showed that bud burst and shoot meristem organogenic activity are totally inhibited in the absence of light, we demonstrated that blue light was able to induce both of these processes (Girault *et al.* 2008) and stimulated the transcription of an acid vacuolar invertase gene, required for hexose supply during bud burst (Girault *et al.* 2010). To date, apart from the above-mentioned studies, no other close examination of the effect of blue light on the components of vegetative and floral developments of rose has been reported.

Concerning photosynthesis, blue light is known to have both positive and negative effects, depending on the dose and duration of the treatment. For example, blue light stimulates photosynthesis by inducing stomatal opening (Sharkey & Raschke 1981; Zeiger & Zhu 1998; Kinoshita *et al.* 2001), increasing stomatal conductance and intercellular CO₂ concentrations (Karlsson & Assmann 1990), or increases leaf mass area (LMA), nitrogen and chlorophyll content (Hogewoning *et al.* 2010). Under very high blue irradiance, photosynthetic efficiency can however be reduced through a decrease in mesophyll conductance (Loreto *et al.* 2009) or by a chloroplast avoidance response that preserves the photosynthetic apparatus from photodamage (Brugnoli & Bjorkman 1992; Wada *et al.* 2003). Little is known of the mechanisms that allow the adjustment of rose photosynthetic activity to qualitative light conditions. Most research have so far focused on the impact of white light irradiance on rose assimilation rate and plant production (Zieslin & Mor 1990; Maas *et al.* 1995b; Bredmose 1997). In roses, the photosynthetic rate has been reported as being mainly influenced by PAR (Pasian & Lieth 1994) and modulated by temperature (Ueda *et al.* 2000; Ushio *et al.* 2008) and atmospheric CO₂ level (Urban *et al.* 2002).

In order to understand the respective contribution of photosynthesis and photomorphogenesis on the elaboration of rose architecture, we monitored the effect of blue light throughout the development of plants derived from single node cuttings until the flowering stage in two rose cultivars, *Rosa hybrida* 'Radrazz' and *R. chinensis* 'Old Blush'. Photomorphogenic responses to blue light were studied by measuring the main components of vegetative and floral developments of the first- and second-order axes. Photosynthesis during light treatment was assessed through measurement of CO₂ assimilation rate, stomatal conductance, intercellular CO₂ concentration and pigment content.

MATERIAL AND METHODS

Plant material

Metamers (comprising a node bearing a leaf with five or seven leaflets, its axillary bud and the underlying internode) from *Rosa hybrida* 'Radrazz' (Knock out®) and *R. chinensis* 'Old Blush' were harvested from the medial part of mother plant stems and used as single-node cuttings. Cuttings were inserted into FERTISS peat plugs (FERTIL, Le Syndicat, France) and rooting was achieved after 4–5 weeks of culture under high humidity. Well-rooted cuttings were transferred

into 500-ml pots containing a 70/20/10 mixture (v/v/v) of neutral peat, coco fibre and perlite, and grown in a greenhouse at 25 ± 5 °C. Extra lighting was supplied with high-pressure sodium-vapour lamps below 200 W·m⁻². After 4 days of acclimation in the greenhouse, well-rooted cuttings were transferred to growth chambers for the light treatments. Plants were grown until all secondary axes, derived from the first wave of bud burst (Huché-Théliér *et al.* 2011), had reached the flowering stage 'petal colour visible' (PCV) or stopped their growth without flowering. On primary axes, three flowering stages were considered: (i) the 'flower bud visible' stage (FBV) corresponding to the time at which the floral bud can be seen but the peduncle is not yet fully elongated; (ii) the PCV corresponding to the moment at which the sepals begin to open, revealing the colour of the petals (red for 'Radrazz', pink for 'Old Blush'); and (iii) the 'open flower' (OF) stage corresponding to the time at which stamens are visible.

Climate conditions in growth chambers

Plants were grown in growth chambers under constant conditions (temperature: 25 ± 3 °C; relative humidity: 80 ± 5%; photoperiod: 16-h light/8-h dark) and irrigated with a nutrient solution prepared from fertilizer Peter Exel (1 g·l⁻¹; pH 5.6; EC: 1.77 ms·cm⁻¹). Plants were subjected to white or blue light treatments. White light was produced from white neon tubes (Mastec 36 W, white/33 cool), while blue light was produced with blue neon tubes (Philips TL-D 36 W/18 blue) (Fig. 1). The photosynthetic photon flux density (PPFD) and yield photon flux (YPF) were calculated using the formula of Sager *et al.* (1988) from the light spectrum measured with a calibrated spectrometer (AvaSpec-2048-6-RM). The photosynthetic efficiency was adjusted to 110 μmol·m⁻²·s⁻¹, by changing the distance between the plant apex and the light source, and was similar in the two light treatments. The height of the neon tubes was adjusted once every 2 weeks to maintain a constant PPFD at the plant apex level. The characteristics of light treatments are presented in the inset of Fig. 1.

Photosynthetic parameters

Gas exchange measurements

Gas exchange measurements were performed using a portable infrared gas analyser (IRGA; LI-6400; Li-Cor Inc., Lincoln, NE, USA) within a narrow leaf chamber (236 cm²; LI-6400-11). Stomatal conductance (gs), net CO₂ assimilation (A) and intercellular concentration of CO₂ (Ci) were then monitored under the two light conditions: on plants at the end of the flowering period of the primary axis (OF stage) and in the fully expanded last five-leaflet leaf of this axis.

Pigment analysis

Chlorophyll (*a* and *b*) and carotenoid contents were determined spectrophotometrically. Fresh leaf tissue (0.2 g) was extracted in 5 ml 80% acetone at 4 °C for 72 h, as described in Torrecillas *et al.* (1984). The absorbance of the extract was measured using a UV-visible spectrophotometer (Cary 100 scan) at 470.0, 646.8 and 663.2 nm. Pigment content was calculated according to the equations of Torrecillas *et al.* (1984):

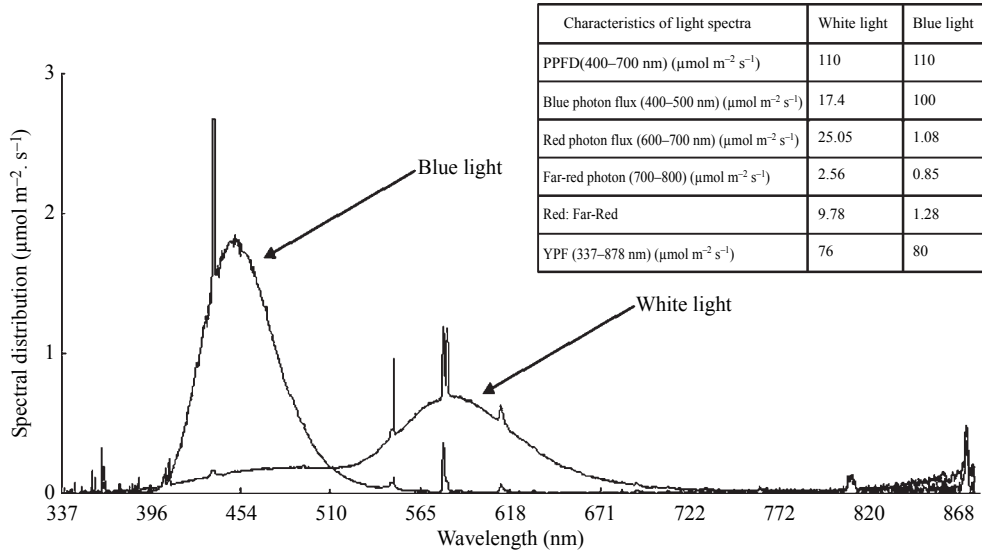


Fig. 1. Distribution of spectral photon fluence rate of the white and blue light treatments.

$$\text{Chl } a \text{ (mg g}^{-1}\text{FW)} = (12.25 * \text{OD}_{663.2}) - (2.79 * \text{OD}_{646.8})$$

$$\text{Chl } b \text{ (mg g}^{-1}\text{FW)} = (21.5 * \text{OD}_{646.8}) - (5.1 * \text{OD}_{663.2})$$

$$\begin{aligned} \text{Carotenoids (mg g}^{-1}\text{FW)} &= 1000 * \text{OD}_{470.0} - (1.82 * \text{Chl } a) \\ &\quad - (85.02 * \text{Chl } b) / 198 \end{aligned}$$

Organogenic activity and bursting of axillary buds

Evaluation of shoot apical meristem (SAM) organogenesis

The number of leaf-like organs (scales, young preformed leaves and leaf primordia) in the buds of the single-node cuttings was evaluated in the two genotypes: on the day of harvest from the mother shoots (T0), upon rooting (T1), just before transfer to light treatment (T2), and at the FBV stage, when the first axes produced after the burst of the single node cutting buds had reached their final length and entered flowering (T3). Buds were dissected under a stereomicroscope and leaf-like organs were removed and counted until only the SAM remained, as described previously (Girault *et al.* 2008).

Evaluation and cartography of bud burst

An axillary bud was considered as burst when its length was at least 1 cm and when at least the tip of the first leaf was visible outside the scales (Girault *et al.* 2008). For each cultivar, bud burst on the primary axis was recorded three times a week from the stage where the FBV at the apex of the primary axis until the first wave of secondary axes had flowered.

For cartography, since the two genotypes of rose showed very pronounced leaf polymorphism along the stem, the primary axis could be easily divided into three distinct zones: (i) the basal zone extending from the base of the stem to the first node bearing the first five-leaflet leaf, (ii) the apical zone extending from the node bearing the last apical five-leaflet leaf to the floral bud (not included), (iii) the medial zone including all the metamers located between the basal and the apical zone. In this medial zone, the leaves had between five

and seven leaflets. The percentage bud burst was determined for each zone.

Morphological characterisation of primary and secondary axes

Length and diameter

At the end of the experiments, the number of secondary axes with at least three internodes was determined. The length of primary and secondary axes and their stem diameter at 1 cm from the basis of the axis were measured. The leaf sequences (succession of nodes and number of leaflets per leaf) were also recorded.

Mass production and water content (WC)

Fresh (FW) and dry (DW) weight of stems was determined at the end of the experiments. Dry mass was determined after drying for 72 h in a drying oven (60 °C). Linear mass (LM) was calculated using the formula: LM = DW/length of axis. Water content (WC) was calculated using the formula: WC = (FW – DW/FW) * 100.

Leaf area (LA) and leaf mass area (LMA)

Total leaf area and leaf dry mass were measured on each plant at the end of the experiments. Leaf area was determined using ImageJ software (National Institutes of Health, Bethesda, MD, USA) and leaf dry mass was determined after drying for 72 h in an oven (60 °C). Leaf mass area (LMA) was determined using the formula: LMA = leaf dry mass/leaf area.

Statistical analysis

Experiments were replicated at least three times. The number of treated plants in each experiment is stated in the figures. Statistical analyses were carried out using StatBox 6.6 software (Grimmersoft, France). Analyses focused on a comparison using Student's *t*-test between means measured under blue light and white light. Asterisks (*), (**), and (***) indicate significant differences between light treatments at the 0.05, 0.01 and 0.001 levels, respectively.

Table 1. Effect of light quality on photosynthetic parameters and pigment content in leaves of *Rosa hybrida* 'Radrazz' and *R. chinensis* 'Old Blush' after 6 weeks of culture under white light (WL: 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or blue light (BL: 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

genotype	'Radrazz'		'Old Blush'	
	WL	BL	WL	BL
photosynthetic parameters				
CO ₂ assimilation rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	1.71 (± 0.45)	1.27 (± 0.35)*	2.87 (± 0.89)	1.20 (± 0.59)***
stomatal conductance ($\text{mmol}\cdot\text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	115 (± 25)	166 (31)***	105 (± 37)	178 (± 20)**
intercellular CO ₂ concentration ($\mu\text{mol}\cdot\text{CO}_2\cdot\text{mol}^{-1}$)	383 (± 30)	398 (± 10)	342 (± 25)	392 (± 10)***
pigment content (mg g^{-1})				
chlorophyll a	229 (± 32)	194 (± 25)*	199 (± 53)	210 (± 51)
chlorophyll b	99 (± 15)	67 (± 10)**	89 (± 18)	80 (± 31)
chlorophyll a/b	2.6 (± 0.1)	2.9 (± 0.2)***	2.2 (± 0.5)	2.7 (± 0.3)*
carotenoids	32 (± 7)	19 (± 4)***	43 (± 8)	41 (± 8)

Values in brackets represent SE with 20 plants. *, ** and *** significant differences between white and blue light treatments at 0.05, 0.01 and 0.001 levels, respectively.

RESULTS

Effect of blue light on photosynthesis in *Rosa*

Under white light, CO₂ assimilation (A) of mature leaves from 6-week-old plants of cv. 'Radrazz' and cv. 'Old Blush' was, respectively, 1.71 and 2.87 $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. When plants were grown under blue light, A dropped significantly to, respectively, 1.27 and 1.20 $\mu\text{mol}\cdot\text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Table 1). This was concomitant with a reduction in photosynthetic pigment (chl *a* and *b* and carotenoids) content in 'Radrazz' and with an increase of the chl *a/b* ratio in both cultivars (Table 1). Blue light also increased the stomatal conductance (gs) of leaves of both cultivars (Table 1), as well as the intercellular CO₂ content of leaves of 'Old Blush' (Table 1).

Effect of blue light on rose development

Morphological characteristics of the primary axes

While the organogenic activity of SAM in cutting buds was totally inhibited in darkness (data not shown) and as previously demonstrated in beheaded rose plants (Girault *et al.* 2008), white light induced organogenesis in cuttings buds (Table 2). Interestingly, when cuttings were grown under blue light, the same amount of organogenic activity was produced in both cultivars, as shown by the number of foliar organs and internodes on first axes upon growth arrest and flowering (Tables 2 and 3). Growth of these axes was as efficiently stimulated by blue as by white light, since no significant difference was observed in any of the six studied morphological characteristics (diameter and length, number and average length of internodes, linear mass and water content). Blue light also induced the same morphogenetic pattern of development in leaf primordia as similar compound leaves were obtained under both this light quality and under white light, and there was no difference in total leaf area (Table 3) or pattern of leaflet distribution (Fig. 2) compared to white light. The single significant difference was an increase in LMA under blue light in 'Radrazz' (Table 3).

Table 2. Mean number of leaf-like organs (primordia, young leaves and scales) within cutting buds on the day of stem severing (T0), in rooted cuttings (T1), at the beginning of the light treatment (T2) and average number of leaves and scales on the primary axis at the 'floral bud visible' stage (T3) under white light (WL: 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or blue light (BL: 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in *Rosa hybrida* 'Radrazz' and *R. chinensis* 'Old Blush'.

stage	T0	T1	T2	T3	
	WL	WL	WL	WL	BL
Cv. 'Radrazz'	8.2 (± 0.8)	9.4 (± 0.7)	10.5 (± 0.8)	11.4 (± 0.8)	11.8 (± 0.9)
Cv. 'Old Blush'	8.1 (± 0.8)	8.2 (± 0.8)	9.3 (± 0.9)	10.1 (± 0.7)	10.2 (± 0.8)

Values in brackets represent SE with $n = 40$ plants.

Table 3. Effect of light quality on morphological characteristics of the primary axes of *Rosa hybrida* 'Radrazz' and *Rosa chinensis* 'Old Blush' after 6 weeks of culture under white light (WL: 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or blue light (BL: 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

genotype	'Radrazz'		'Old Blush'	
	WL	BL	WL	BL
axis diameter (mm)	3.2 (± 0.4)	3.2 (± 0.2)	2.8 (± 0.2)	2.5 (± 0.4)
axis length (mm)	186 (± 53)	179 (± 75)	176 (± 87)	168 (± 71)
average number of internodes	11.4 (± 0.8)	11.9 (± 1.8)	10.0 (± 1.6)	10.2 (± 1.4)
average length of internodes (mm)	16.0 (± 3.4)	14.7 (± 4.2)	17.0 (± 6.0)	15.8 (± 4.7)
linear mass of primary stem ($\text{mg}\cdot\text{cm}^{-1}$)	17.6 (± 4.0)	18.0 (± 4.8)	12.5 (± 2.4)	11.6 (± 2.9)
water content (%)	70 (± 3)	68 (± 2)	71 (± 3)	70 (± 1)
leaf area (cm^2)	251 (± 52)	215 (± 45)	118 (± 37)	122 (± 35)
leaf mass area ($\text{mg}\cdot\text{cm}^{-2}$)	3.6 (± 0.6)***	4.5 (± 0.5)	3.6 (± 0.5)	3.5 (± 0.6)

Values in brackets represent SE with 40 plants. ***Significant difference between white and blue light treatments at 0.001 level.

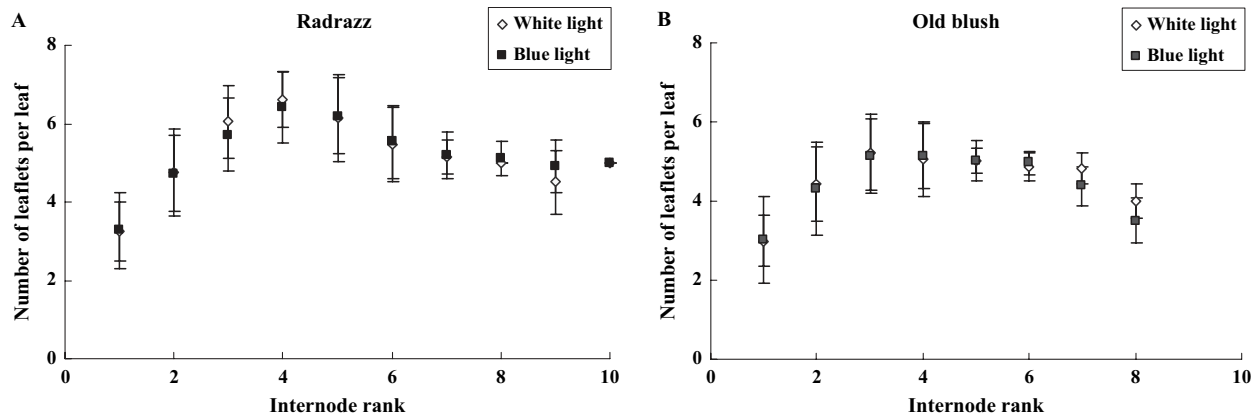


Fig. 2. Effect of light quality on the number of leaflets per leaf along the primary axis of *Rosa hybrida* 'Radrazz' (A) and *R. chinensis* 'Old Blush' (B) after 6 weeks of culture under white light ($110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or blue light ($110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Only nodes bearing at least one leaflet leaf were considered for the identification of internode rank. Error bars represent SE with $n = 40$ plants. No significant difference was noted between white and blue light treatments.

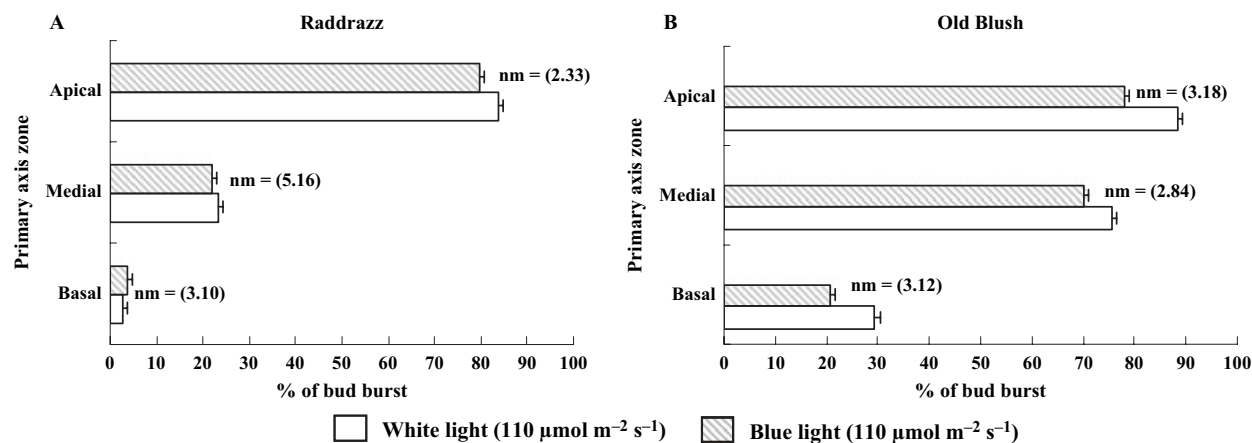


Fig. 3. Bud burst per zone along the primary axis of cultivars *Rosa hybrida* 'Radrazz' (A) and *R. chinensis* 'Old Blush' (B) after 6 weeks of culture under white or blue light. nm = number of buds per zone. Error bars represent SE with $n = 40$ plants. No significant difference was noted between white and blue light treatments.

Growth and development of secondary axes

Blue light induced the same amount of bud burst on primary axes of 'Radrazz' and 'Old Blush' ($24 \pm 13\%$, $46 \pm 18\%$, respectively) as white light ($27 \pm 9\%$, $59 \pm 18\%$, respectively), with no change in the cartography of bud burst along the primary axes (Fig. 3). The strong acrotonic bud burst pattern characterising 'Radrazz' under white light was similarly expressed under blue light (Fig. 3). Under blue light, the secondary axes derived from the burst buds were as long and composed of as many internodes as those produced under white light (Table 4).

Flower development

As well as vegetative development, blue light could sustain full reproductive development in both rose cultivars and as efficiently as white light. Hence, there was a similar percentage of flowering axes under both light conditions (Table 5) and normal development of floral organs was observed under blue light in both cultivars (Fig. 4). Only flower peduncles

Table 4. Effect of light quality on morphological characteristics of the secondary axes of *Rosa hybrida* 'Radrazz' and *Rosa chinensis* 'Old Blush' after 6 weeks of culture under white light (WL: $110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or blue light (BL: $110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

genotype	'Radrazz'		'Old Blush'	
	WL	BL	WL	BL
average number of axes	3.0 (± 0.5)	2.9 (± 0.5)	5.0 (± 0.4)	4.6 (± 0.9)
axis length (mm)	107 (± 10)	104 (± 11)	107 (± 24)	122 (± 5)
average number of internodes	8.3 (± 0.3)	8.0 (± 0.6)	7.4 (± 0.8)	8.5 (± 0.5)
average length of internodes (mm)	13.0 (± 0.8)	13.0 (± 0.2)	14.1 (± 1.6)	14.2 (± 1.3)

Values in brackets represent SE with 40 plants. No significant difference was noted between white and blue light treatments.

Table 5. Effect of light quality on percentage flowering of primary axes and on flower characteristics in *Rosa hybrida* ‘Radrazz’ and *R. chinensis* ‘Old Blush’.

genotype	‘Radrazz’		‘Old Blush’	
	WL	BL	WL	BL
percentage flowering of primary axes	90.8 (±2.3)	90.7 (±6.4)	80.8 (±6.3)	78.6 (±4.6)
flower diameter (mm)	83 (±10)	80 (±8)	57 (±8)	61 (±8)
petal number	9.1 (±1.3)	9.9 (±2.3)	24.3 (±5.7)	27.3 (±8.8)
peduncle length (mm)	49 (±5)***	35 (±5)	70 (±8)***	58 (±7)

Values in brackets represent SE with n = 20 plants. ***Significant difference between white light (WL: $110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and blue light (BL: $110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) treatments at 0.001 level.

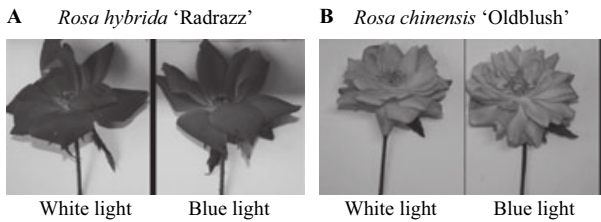


Fig. 4. Open flowers produced by *Rosa hybrida* ‘Radrazz’ (A) and *R. chinensis* ‘Old Blush’ (B) plants after 6 weeks of culture under white light ($110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) or blue light ($110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

appeared shorter under blue light (Table 5). Under blue light, and in both cultivars, the rate of floral development was slower by 3 days (Fig. 5).

DISCUSSION

The objective of this study was to measure the effects of blue light on both the photosynthetic activity and morphogenesis of two rose cultivars, *R. hybrida* ‘Radrazz’ and *R. chinensis* ‘Old

Blush’, and to evaluate whether such light treatment could modify plant architecture. Unlike most studies published to date on the impact of blue light on plants (Wilson *et al.* 1993; Maas *et al.* 1995a; Sarala *et al.* 2007), we examined the effects of blue light throughout the full development of the plants, starting from one single bud through to the entire vegetative development of second order axes and their flowering. This allowed precise evaluation of the impact of blue light on the most important morphogenetic events (SAM organogenesis, metamer and leaf growth and development, flower induction and organogenesis). We demonstrated that under blue light, the two rose genotypes had normal and similar vegetative and floral development to those observed under white light. In fact, blue light did not affect organogenetic activity of the SAM or growth capacity of the metamers. Nevertheless, photosynthesis was affected by blue light treatment.

Our measurements indeed revealed a strong reduction (–25% in ‘Radrazz’ and –58% in ‘Old Blush’) in leaf CO_2 assimilation in both cultivars under blue light. Since plants were grown under same photosynthetic efficiency ($110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in both light treatments, the observed reduction in CO_2 assimilation rate under blue light could not be explained by the reduced photosynthetic quantum yield of blue photons (McCree 1972), nor by a decrease in LMA, stomatal conductance or intercellular CO_2 concentrations under blue light. LMA, which is known to correlate positively with the photosynthetic capacity of leaves (Oguchi *et al.* 2003), was at least similar (‘Old Blush’) or higher (‘Radrazz’) under blue light as under white light. Similarly, blue light stimulated stomatal conductance in both cultivars, as well as intercellular CO_2 concentrations in ‘Old Blush’, thus reducing stomatal limitation to photosynthesis (Lawson *et al.* 2008). The increased values of these two parameters (stomatal conductance and intracellular CO_2 concentration) in roses are in accordance with the reported effect of blue light on stomatal opening in other plants (Karlsson & Assmann 1990; Hogewoning *et al.* 2010). In contrast, the reduction in photosynthetic pigment content (chl *a* and *b*, as well as carotenoids) in leaves of ‘Radrazz’ under blue light could contribute to a decrease in CO_2 assimilation, as found in bean (Barreiro *et al.* 1992). However, since no such reduction was observed in

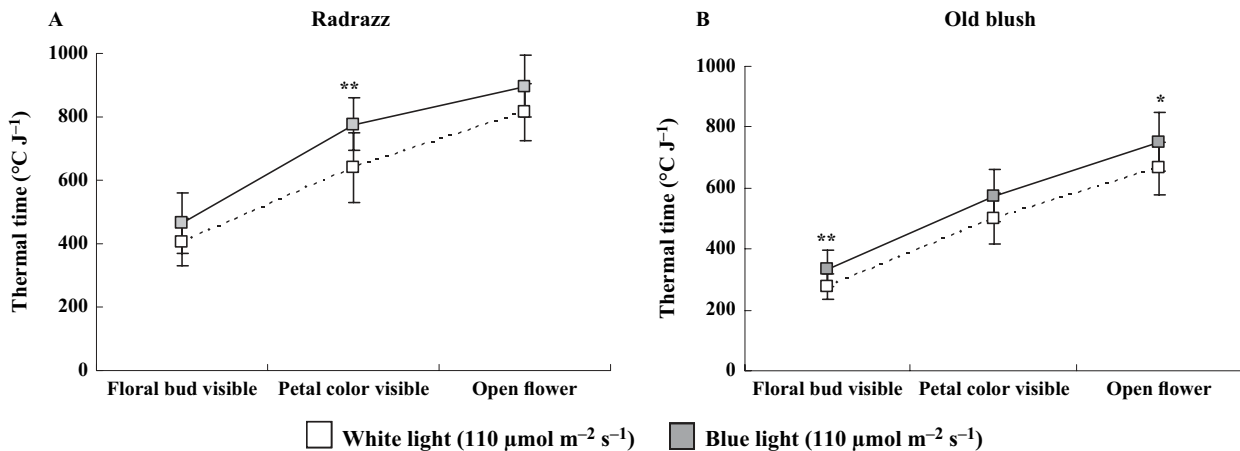


Fig. 5. Thermal time required for the primary axis of *Rosa hybrida* ‘Radrazz’ and *R. chinensis* ‘Old Blush’ cultivated under white or blue light to reach different flower stages. Error bars represent SE with n = 20 plants. *P = 0.05 and **P = 0.01 indicate significant differences between white and blue light treatments.

'Old Blush', other mechanisms, such as a reduction in mesophyll conductance (Brugnoli & Bjorkman 1992; Flexas *et al.* 2008; Loreto *et al.* 2009) or a change in chloroplast distribution (Wada *et al.* 2003) probably regulated carbon assimilation under blue light in rose.

The reduced CO₂ assimilation rates under blue light had surprisingly little impact on the growth of the two rose cultivars. Features such as shoot or internode length, diameter, dry weights of primary and secondary axes and leaf area were identical under both light treatments. The rate of development was only slowed by 3 days under blue light. Such a lack of effect of reduced assimilation rate on plant growth and biomass has also been reported in *Lindera melissifolia* under increasing irradiance (Aleric & Kirkman 2005). This may reflect modified carbon partitioning between roots and aerial organs (Aleric & Kirkman 2005), although no obvious difference in root system development was observed under either light regime in our rose genotypes (data not shown). Alternatively, it may reflect the impact of other environmental factors affecting our culture system.

The only effect of blue light on growth was observed in 'Radrazz', with an increase in LMA. Such an increase, together with a higher chl *a/b* ratio observed under blue light, may contribute to plant acclimation, as reported for other species under various blue light treatments (Rajapakse & Kelly 1993; Hogewoning *et al.* 2010; Macedo *et al.* 2011). The absence of a change in LMA in 'Old Blush' may reflect different strategies of adaptation to this particular light environment and could partly explain the difference in intensity of the impact of blue light on CO₂ assimilation between the two cultivars.

Concerning rose photomorphogenesis, while the absence of light completely abolished morphogenesis and bud burst in rose (Girault *et al.* 2008), our experiments demonstrate that blue light is able to induce full, normal vegetative and floral development in these same buds. More precisely, our morphometric data show that neither organogenetic activity of the apical shoot and axillary meristems nor the growth capacity of the metamers is affected by blue light. As such, there was a non-significant difference in number of internodes produced by the SAM on the first- and second-order shoots when grown under white or blue light. While most of the first-order shoot internodes were already formed within the cutting bud upon initiation of the light treatments (Table 2), it is striking that a reduced light spectrum, lacking important morphogenetically active wavelengths (MAR; Varlet-Grancher *et al.* 1993) such as red and far-red light, had no impact on differentiation of the axillary buds on the primary axis, nor on their capacity to produce normal metamers in similar numbers to those under white light. Moreover, the branching

pattern along the first-order shoots was not modified by blue light treatment. Observation of the leaves that developed on the axes of both ranks revealed no difference in leaf shape between the two light conditions, and no change in the distribution of the three-, five- and seven-foliolate leaves along the axis. Similarly, the SAMs were as efficiently induced to flower and were able to differentiate normal and as many floral organs under blue light as under white light. Even though flower initiation is an autonomous process in *Rosa* (Bredmose & Hansen 1996), which does not require a specific light regime, it is well known that in this plant, unfavourable light conditions such as too low irradiance (Nell & Rasmussen 1979; Maas *et al.* 1995b) can cause the arrest or abortion of flower buds, leading to blind shoots (Dambre *et al.* 2000).

Overall, the results indicate that unlike numerous other plants, the development of which is affected by blue light (Mortensen & Stromme 1987; Rajapakse & Kelly 1993; Brown *et al.* 1995; Li *et al.* 2000), *Rosa* is capable of quantitatively and qualitatively adjusting the mechanisms that sustain its growth under a modified light spectrum. This reflects the strong adaptive properties of this plant to its light environment. At the molecular level, this suggests that in rose, blue light can trigger all of the photomorphogenic processes induced by white light. For example, sink activity of rose shoot apices, which was shown to be modulated by red light (Mor *et al.* 1980), was likely induced by blue light in our experiments, since plant development, which requires strong control of sink/source allocations, was identical under both white and blue light conditions. This highlights the redundancy of the light signalling pathways involved in photomorphogenic responses in rose, as previously suggested for bud burst (Girault *et al.* 2008, 2010), and our results converge well with recent observations on the quintuple phytochrome mutant of *Arabidopsis thaliana*, where exposure to blue light could bypass several developmental arrests related to the lack of red light photomorphogenic signals (Strasser *et al.* 2010).

Our work thus confirms that blue light photoreceptors, mainly cryptochromes, phytochromes and phototropins (Whitelam & Halliday 2007) play important roles in the regulation of morphogenetic responses to light quality in rose. Their respective roles should be studied further.

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