GROWTH AND FLOWER DEVELOPMENT IN ROSES AS AFFECTED BY LIGHT
Refereed

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Abstract

Growth and flowering of shoots of rose 'Mercedes' were investigated as a function of the level and spectral quality of the photosynthetically active radiation (PAR). Experiments were performed with single-shoot plants decapitated above the two most basal leaves with five leaflets. The development of the two lateral shoots emerging from the axillary buds of these leaves was studied over a period of 4 to 6 weeks. In order to discriminate between the effects of irradiance level and light quality, plants were grown in growth chambers in which both the amount of PAR and its spectral composition could be controlled. At a photoperiod of 12 h the length, weight, and flowering of the shoots strongly increased with irradiance. Weight and number of flowering shoots were always higher for the uppermost than for the second shoot. At the highest PAR level (270 μmol $m^{-2}s^{-1}$) flowering occurred in 89 and 33 % of the uppermost and second shoots, respectively. At an irradiance level of 90 μmol $m^{-2}s^{-1}$ these percentages were 6 and 0%. Although the length of both types of shoots was significantly increased by reducing the amount of blue light at constant PAR, flower development was not affected. In a second experiment plants grown in white light (12 h/day) received a short treatment with low intensity red or far-red light at the end of each photoperiod. An end-of-day treatment with red light resulted in significantly more flowering shoots than far-red. The red/far-red reversibility of this flowering response indicates the involvement of the photoreceptor phytochrome.

1. Introduction

The production of cut roses strongly depends on the levels of irradiance in the greenhouse (Mor & Halevy 1984, Zieslin & Mor 1985, Zieslin & Mor 1990). Light has a twofold effect on flower production in roses. First, light affects the number of buds sprouting from both the base of the plant and the remaining part of a branch after harvesting the flowers. Second, light influences the development of the flowers. Although the initiation of the flower primordium is independent from light intensity and photoperiod (Horridge & Cockshull 1974, Zieslin & Mor 1985), the subsequent development of the flower may be arrested under unfavourable light conditions and the flower bud may abort, resulting in a blind shoot. Both the quantity and quality of the light may affect sprouting as well as flower developmental processes. The availability of assimilates has been shown to be a major factor involved in the growth and flower development of rose shoots. Increased transport of assimilates to young shoots, either as a result of higher rates of photosynthesis (Cockshull 1975, Khosh-Khui & George 1977, Hand & Cockshull 1979, Mortensen *et al.* 1992) or by a shift in assimilate partitioning (Zieslin & Halevy 1976, Mor *et al.* 1981), stimulate growth and flower development of roses. Mor and Halevy (1980) and Mor *et al.* (1980) demonstrated the importance of light in the control of assimilate partitioning in roses. The amount of assimilates transported to a darkened shoot in a well illuminated plant was significantly reduced compared with that to a similar shoot exposed to low levels of light (≤11 μmol $m^{-2}s^{-1}$) by fibre optics (Mor & Halevy 1984). Red light proved to be more effective in stimulating the import of assimilates by a shoot than blue or

far-red light. Shoots treated with low intensities red light showed improved growth and flower development.
The aim of this study was to examine the effects of light quality on shoot growth and flower formation in Rosa hybrida 'Mercedes' at a level of irradiance insufficient for all shoots to fully develop a flower, a situation that normally occurs during the winter period in Dutch greenhouses. In addition, the effects of light on dry weight partitioning were also evaluated.

2. Material and methods

2.1. Cultivation of rose plants

Shoots of roses were provided by a commercial grower. Single-node stem segments with a mature leaf (five leaflets) and approx. 1 cm stem above and 4 cm stem below the leaf joint were used as cuttings. Leaf and stem of the cuttings were treated with 0.1% (w/v) benlate and 10% (w/v) captan, respectively, to prevent bacterial and fungal growth. Rooting was promoted by placing the base of the stem in a 10 μM solution of NAA (α-Naphtaleneacetic acid) for 24 hours. After 3 weeks incubation at 25°C in a 10% nutrient solution (Steiner 1984) at 60 μmol $m^{-2}s^{-1}$ PAR (Philips 58W/84 white fluorescent tubes, 14 hrs/day), 95 to 100% of the cuttings had rooted. Then, the cuttings were transferred to full-strength Steiner's nutrient solution, PAR was increased to 270 μmol $m^{-2}s^{-1}$ (12 hrs/day), and day and night temperatures were changed to 20 and 18°C, respectively. After 5 to 6 weeks, when the flower bud started to open, the shoot was decapitated above the two most basal mature leaves with less than five leaflets below the two upper leaves were removed. At this stage the light treatment was started. Only the axillary buds of the remaining leaves were allowed to develop into new shoots (Figure 1). According to their position on the main stem these shoots will be referred to as the upper shoot and lower shoot, respectively.

Figure 1. Rose 'Mercedes' approx. 10 days after pruning and the onset of the light treatment

2.2. Lighting conditions

Photosynthetically active radiation (PAR, 400-700nm) at plant level was measured with a horizontally placed Licor cosine corrected quantum sensor (LI-190SA). A spectroradiometer (Licor LI-1800) was used to determine the spectral distribution or quality of the light. Light quality was characterized by its blue (400-500 nm) content

(B/PAR) and by its red (655-665nm) to far-red (725-735) ratio (R/FR). Amber and orange light were obtained by filtering the light of the white fluorescent lamps through an amber or orange-coloured cinemoid filter (filters 434 and 405, respectively, Strand Lighting Ltd, Isleworth, U.K.). These filters filtered out 85% (amber) or 100% (orange) of the blue light (400 to 500 nm) of the white lamps. End-of-day far-red (FR)was provided by incandescent lamps filtered through one layer of a red filter and one layer of a blue filter (Strand filter 406 and 419, respectively) and red light (R) by red fluorescent tubes (Philips TL 40W/16). End-of-day light treatments were given directly at the end of each photoperiod period as 10 min R followed by 10 min FR, 10 min FR followed by 10 min R or as 20 min R (control). Photon fluxes at plant level, blue light contents, R/FR ratios, and the phytochrome equilibria calculated from the spectral data of the different light sources are presented in Table 1.

Table 1. Spectral data of light sources used during the entire photoperiod (White, Amber, Orange) or at the end of day only (e.o.d. R or e.o.d. FR). B = blue light, R = red light, FR = far-red light. Photon flux intervals were 400 to 700 nm (PAR; White, Amber, Orange), 600 to 700 m, (e.o.d. R), and 700 to 800 nm (e.o.d. FR). The numbers below the ratios of B/PAR and R/FR represent the wavelength intervals used to calculate these ratios. Extinction coefficients from rye phytochrome (Lagarias *et al.* 1987) were used to calculate phytochrome equilibria (φ_c)

Light quality	PAR (μmol $m^{-2}s^{-1}$)	B/PAR (400-500nm/400-700nm)	R/FR (655-665nm/725-735nm)	φ_c
White	130	0.18	9.4	0.81
Amber	130	0.04	9.0	0.83
Orange	130	0.02	9.0	0.83
e.o.d. R	4.5	<0.01	216	0.87
e.o.d. FR	14.4	0.13	< 0.01	0.04

2.3. Growth measurements

Four or six weeks after decapitation of the primary shoot and the start of light treatments, the length of the upper and lower shoots of the plants was measured. On the same day the plants were harvested (always 6 hours after the start of the light period) and divided into upper and lower shoot (either as a whole or divided into leaves and stem), stem tissue from the original cutting (referred to as primary wood), and roots. Dry weights were measured after lyophilization of the plant material at -50 °C and 0.07 mbar.

3. Results

3.1. Effects of PAR-level on plant growth and development

The growth of the lateral shoots was strongly affected by the level of irradiance. Compared with plants grown for six weeks at 90 μmol $m^{-2}s^{-1}$, the dry weights of the upper shoot, lower shoot, primary wood and roots of plants grown at 180 μmol $m^{-2}s^{-1}$ were 2.6, 2.2, 1.4, and 1.8 times higher, respectively (Table 2, Exp. I). For plants grown at 270 μmol $m^{-2}s^{-1}$ these values were respectively 3.2, 2.8, 1.5, and 2.2. These data indicate that in both cases the effect of increasing PAR on dry weight decreased in the following order: upper shoot, lower shoot, roots, primary wood.

After a growth period of 6 weeks, the length of the upper and lower shoots was only significantly enhanced by increasing PAR from 90 to 180 µmol $m^{-2}s^{-1}$ (Table 3, Exp. l). No further stimulation of shoot elongation was observed if the level of PAR was increased from 180 to 270 µmol $m^{-2}s^{-1}$. The ratio of leaf to stem dry weight of the shoots determined after a growth period of 4 weeks (Table 4) demonstrated that the partitioning of dry matter between leaf and stem tissue was not affected by the level of PAR.

The percentage of flowering shoots was increased approx. 75% for the upper shoot and 25% for the lower shoot when PAR increased from 90 to 180 µmol $m^{-2}s^{-1}$. Increasing PAR from 180 to 270 µmol/m2/s raised the flowering of both types of shoots by only an additional 10% (Table 3, Exp. l).

Table 2. Effects of light quantity (PAR) and quality (spectral distribution) on the dry weight (g) of different parts of rose 'Mercedes'. Weights were determined 6 weeks after the start of the light treatment and represent the means of 3 measurements with 3 plants in each (±s.d.). Values of the same plant part within an experiment followed by different letters are significantly different ($p<0.05$). PAR levels during the photoperiod in experiments II and III were 130 µmol $m^{-2}s^{-1}$. End-of-day light treatments were given as 20 min red light (R), or as 10 min red followed by 10 min far-red (R/FR) or *vice versa* (FR/R).

Plant part		Light treatment	
Experiment I	White 90	White 180	White 270
Upper shoot	2.26±0.15^a	5.89±0.66^b	7.20±1.08^b
Lower shoot	1.96±0.23^a	4.30±0.70b	5.55±0.63^b
Primary wood	1.22±0.07^a	1.70±0.38^b	1.79±0.14^b
Roots	1.01±0.12^a	1.86±0.20^b	2.27±0.36^b
Total plant	6.93±0.32^a	14.40±1.86^b	17.50±2.10^b
Experiment II	White	Amber	Orange
Upper shoot	3.98±0.55^a	4.57±0.59^a	4.69±0.21^a
Lower shoot	3.45±0.48^a	4.46±1.03^a	4.48±0.72^a
Primary wood	0.99±0.10^a	1.15±0.14^a	0.93±0.22^a
Roots	1.56±0.19^a	1.70±0.29^a	1.80±0.13^a
Total plant	11.19±1.46^a	11.95±1.69^a	12.27±0.73^a
Experiment III	e.o.d. R	e.o.d. R/FR	e.o.d. FR/R
Upper shoot	2.62±0.21^a	2.98±0.21 a	2.79±0.04^a
Lower shoot	1.97±0.24^a	2.15±0.34a	2.16±0.37^a
Primary wood	0.94 ±0.06^a	1.10±0.05^b	1.12±0.09^b
Roots	1.16±0.03^a	1.27±0.10^a	1.21±0.09^a
Total plant	6.83+0.07^a	7.53+0,59^a	7 36+0.49^a

3.2. Effects of light quality on plant growth and development

Changing the quality of the light during the entire photoperiod over a 6-week growth period while keeping the level of PAR did not affect the plant dry weights (Table 2, Exp. II). Elongation of both lateral shoots was significantly enhanced by decreasing the blue-light content of PAR. After 6 weeks of growth, both types of shoots in amber- and orange-light grown plants were respectively approx. 10 cm and 16 cm longer than the shoots of white-light grown plants (Table 3, exp. II). In amber as well as in orange light, plants partitioned relatively more dry weight into stem than into leaves than in white light as the ratio of leaf to stem dry weight was significantly lower (Table 4, Exp. II). Amber and orange light did not significantly affect the number of flowering shoots per plant, although in orange light there was a small shift in flowering between the upper and lower shoots (Table 3, Exp. II).

An end-of-day light treatment with R or FR did not affect the dry weights of shoots, primary wood or roots (Table 2, Exp. III). However, ending the photoperiod with FR resulted in significant decreases in the ratio of leaf dry weight to stem dry weight of the upper and lower shoots (Table 4, exp. III). The effect of FR was reversible by giving the plants a second brief irradiation with R directly after the FR treatment, suggesting the involvement of the photoreceptor phytochrome. Ending each photoperiod with a high R/FR (R or FR followed by R) resulted in 1.7 times more flowering upper shoots and 9 times more flowering lower shoots than with a low R/FR (Table 3, Exp. III). This negative effect of e.o.d. FR on flower development was also R reversible.

Table 3. Effects of light quantity (PAR) and quality (spectral distribution) on the length and flower development of the upper and lower shoot of rose 'Mercedes'. Length and flower development were determined 6 weeks after the start of the light treatment and represent the means of 9 (Exp. I), 18 (Exp. II) or 12 plants (Exp. III). Significant differences ($p<0.05$) in the lengths of shoots of similar stem position are indicated by different letters. PAR represents the irradiance during the daily photoperiod. Irradiance levels of the end of day red or far-red light are presented in Table 1. End-of-day treatments with red or far-red were as described in Table 2.

Light treatment		Shoot length (cm)		Shoots with flowers (%)	
Quality	PAR	Upper	Lower	Upper	Lower
Experiment I					
White	90	29.4 ± 3.4^{a}	27.9 ± 3.9^{a}	6	0
White	180	41.0 ± 3.5^{b}	39.0 ± 5.1^{b}	78	22
White	270	39.4 ± 2.6^{b}	41.1 ± 5.7^{b}	89	33
Experiment II					
White	130	38.3 ± 4.2^{a}	35.2 ± 6.2^{a}	56	33
Amber	130	48.7 ± 3.8^{b}	44.1 ± 8.5^{b}	58	32
Orange	130	55.0 ± 5.3^{c}	50.4 ± 6.0^{c}	65	18
Experiment III					
e.o.d. R	130	$35.8\pm4\ 0^{a}$	29.9 ± 6.5^{a}	42	18
e.o.d R/FR	130	43.1 ± 5.8^{b}	38.6 ± 3.9^{b}	15	2
e.o.d. FR/R	130	37.6 ± 4.2^{a}	33.1 ± 5.1^{ab}	40	23

Table 4. Ratio of leaf to stem dry weight and total dry weight of the upper and lower shoots of rose 'Mercedes'. Weights were determined 4 weeks after the start of the light treatment and represent the means of 3 measurements with 3 plants in each (± s.d.). Values of the same light treatment and plant part followed by different letters are significantly different ($p < 0.05$). Light conditions were as described in Table 2.

Light quality	Upper shoot Dry weight (g)	Leaf/Stem	Lower shoot Dry weight (g)	Leaf/Stem
Experiment I				
White 90	1.16 ± 0.15^{a}	3.4 ± 0.3^{a}	0.37 ± 0.29^{a}	3.8 ± 0.5^{a}
White 180	2.08 ± 0.13^{b}	3.4 ± 0.3^{a}	1.41 ± 0.30^{b}	3.9 ± 0.3^{a}
White 270	2.31 ± 0.35^{b}	3.5 ± 0.1^{a}	1.72 ± 36^{b}	4.0 ± 0.2^{a}
Experiment II				
White	1.36 ± 0.21^{a}	3.5 ± 0.3^{a}	0.70 ± 0.04^{a}	3.8 ± 0.2^{a}
Amber	1.43 ± 0.35^{ab}	2.4 ± 0.4^{b}	0.87 ± 0.50^{ab}	3.2 ± 0.3^{b}
Orange	1.81 ± 0.07^{b}	2.4 ± 0.2^{b}	0.86 ± 0.03^{b}	2.6 ± 0.2^{c}
Experiment III				
e.o.d. R	1.27 ± 0.07^{a}	3.8 ± 0.2^{a}	0.87 ± 0.10^{a}	3.9 ± 0.3^{a}
e.o.d. R/FR	1.29 ± 0.30^{a}	3.1 ± 0.1^{b}	0.87 ± 0.22^{a}	3.3 ± 0.3^{a}
e.o.d. FR/R	1.31 ± 0.23^{a}	3.8 ± 0.1^{a}	0.77 ± 0.19^{a}	3.8 ± 0.2^{a}

4. Discussion

Lack of assimilates is generally assumed to cause flower abortion in roses (Zieslin & Moe 1985). This assumption is based on experiments which have shown that enhancement of photosynthetic assimilate production, either by increased levels of PAR or by elevated levels of CO_2, promote the growth and flower development of the treated shoots. Besides a general increase in assimilates, a shift in the partitioning of assimilates within the plant without an increase in photosynthesis may also promote shoot growth and flower development, as was demonstrated by the promoting effects on assimilate import by shoots treated with plant growth regulators such as benzyladenine or gibberellic acid (Zieslin & Halevy 1976, Mor *et al.* 1981). Our experiments with PAR levels ranging from 90 to 270 $\mu mol.m^{-2}s^{-1}$ (12 h/day), representing average daily light sums in Dutch greenhouses from the middle of autumn to the beginning of spring, showed that PAR-levels below 180 $\mu mol.m^{-2}s^{-1}$ were insufficient for most shoots to flower (Table 3). Changing the quality of the light at a PAR level of 130 $\mu mol.m^{-2}s^{-1}$ at which in white light about 40 to 60 % of the upper and 20 to 30 % of the lower shoots flowered, resulted in significant changes in shoot morphogenesis without affecting total plant biomass. The main photomorphogenetic response to amber and orange light as well as to e.o.d. FR, was an increase in shoot length. The strongest effect, occurring in amber, orange and e.o.d. FR, was a shift in dry weight between the leaves and the stem. Shoots grown in these light qualities partitioned more dry weight into stems than into leaves (Table 4). Amber, orange, and e.o.d. FR light had a similar effect on shoot elongation and dry weight partitioning within upper and lower shoots. However, the effect on flower development differed completely. Amber and orange hardly affected the number of flowering shoots per plant. The small increase in the percentage of flowering upper shoots in orange light was compensated by a decrease in the number of flowering lower shoots.

However, e.o.d. FR strongly reduced flowering of both upper and lower shoots. As the general growth pattern of shoots as a response to amber and orange light or e.o.d. FR was similar, it seems unlikely that it is the amount of assimilates imported by the shoots that determines whether abortion or full development of a flower bud will take place. In order to clarify the role of assimilate availability on flower development during various stages of shoot growth, the transport of assimilates to the apex or flower bud itself should be studied instead of the overall import by the shoots.

Light-quality-controlled stem elongation may well be mediated by gibberellins, as this plant growth regulator has been shown to be involved in the control of stem elongation (Reid *et al.* 1990, 1992, Ross & Reid 1992). Besides enhancing stem elongation, gibberellic acid also stimulated flower development in roses (Zieslin & Halevy 1976, Mor & Zieslin 1987). Since it has been demonstrated in several plant species that red light influences gibberellin metabolism (Reid *et al.* 1968, Garcia-Martinez & Garcia-Martinez 1992), it would be interesting to study whether the morphogenetic responses of rose 'Mercedes' to changes in the blue-light content of PAR or e.o.d. R/FR are mediated by changes in the synthesis or metabolism of gibberellins.

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