ELSEVIER

Scientia Horticulturae 61 (1995) 251–262

SCIENTIA HORTICULTURÆ

Effects of different light treatments on the nocturnal transpiration and dynamics of stomatal closure of two Rose cultivars

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Accepted 10 November 1994

Abstract

In the cultivation of roses, supplementary lighting is thought to cause an increase in nocturnal transpiration and consequent low turgidity of the cut flowers, leading to problems in quality. Two cultivars with diverging tolerances to this phenomenon were subjected to high and low light intensities, followed by periods of supplementary lighting of different duration and with different spectral composition. Daily water consumption showed genetic variation. Supplementary lighting, both with respect to its duration and its spectral composition, had hardly any influence on water usage or nocturnal stomatal conductance, but increased stomatal opening during the day. The diurnal rhythm of stomatal movement, measured with a computer-modulated high-intensity light source, appeared to be determined by the integrated irradiance in the previous light period. High irradiance caused a faster stomatal opening during the next light period. Similar to this response, stomatal closing rates were also stimulated by high light intensity during the previous day. The observed effects were most pronounced for the cultivar reported to be the least sensitive to post-harvest damage by excessive transpiration. It is concluded that supplementary lighting does not have a negative impact on the water use efficiency of cut roses. In addition, the stomatal dynamics suggest that flower quality would benefit from being transferred to darkness following a period of several hours of high light intensity.

Keywords: Light; Stomatal movement; Rose

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Abbreviations: G_s = Stomatal conductance; SL = Supplementary lighting; PAR = Photosynthetically active radiation.

SSDI 0304-4238(94)00751-9

1. Introduction

Opening and closing of stomata are regulated by light-induced physiological processes (Holmes and Klein, 1986; MacRobbie, 1987; Outlaw, 1987). Dark-induced closing of stomata is not simply a reversal of light-induced opening, but is achieved by a stimulation of ion effluxes in response to a closing signal (MacRobbie, 1987). The kinetics of stomatal closing and opening may differ significantly as described for *Vicia faba* (Kassam, 1973). The nature of control of stomatal closure has not yet been solved.

Stomata do not always close completely during darkness as shown with micropropagated flowers (Santamaria et al., 1993) and roses, grown in greenhouses under low-light conditions and supplementary lighting (Slootweg and Van Meeteren, 1991). Owing to the resulting nocturnal transpiration, the post-harvest quality of roses may be negatively affected (Armitage and Tsujita, 1979). This is the result of greater water loss than that shown by roses with a complete dark-induced stomatal closure (Durkin, 1985). This water loss may result in enhanced wilting of the cut flowers or, even worse, in a phenomenon known as bent-neck during their vase life (Slootweg and Van Meeteren, 1991).

During low light conditions, supplementary lighting as an extension of natural daylight is common practice for roses grown in greenhouses. Extension of the daylength by a subsequent low-light treatment of approximately 30 μmol $m^{-2} s^{-1}$ photosynthetically active radiation (PAR) increases the number of flowers (references in Zieslin and Mor, 1990), especially in winter when natural light intensity is low. The sensitivity of roses to extension of the daylength differs between cultivars (Moe, 1972; Carpenter and Anderson, 1972; Carpenter et al., 1972; Byrne et al., 1978). It is not yet clear why dark-induced stomatal closure is not complete under certain circumstances or how big genetic variance for this trait may be. It has been suggested that supplementary lighting causes a disturbance in the control mechanism (Slootweg and Van Meeteren, 1991). The fact that the negative effect of supplementary lighting seems most pronounced in winter suggests that the amount of supplementary lighting with regard to the total light sum during the day seems important. The supposed disturbance of stomatal closure upon supplementary lighting may also be due to a light quality effect. Light quality is important in signalling stomatal movement. Opening of stomata is induced by blue light (Assman and Zeiger, 1987). It is, however, not known whether closing is also induced by light of a specific wavelength such as the spectral distribution of sunlight during sunset (Hughes et al., 1984).

In this paper, we evaluate water consumption and stomatal function of two rose cultivars: 'Madelon', known for its high nocturnal transpiration during the winter (Slootweg and Van Meeteren, 1991) and 'Sonia', with a low nocturnal transpiration. We studied the effect of light intensity during the day and the effects of duration and light quality of supplementary lighting on the water usage of intact plants. In addition, we studied the dynamics of stomatal movement under those conditions.

2. Materials and methods

2.1. Plant growth conditions

Flowering stalks of two rose cultivars, 'Madelon' and 'Sonia', were obtained from a commercial grower. Single-node stem segments with a mature leaf (five leaflets) were cut at approximately 1 cm above and 4 cm below the leaf joint. The leaves and stem of the cuttings were treated with 0.1% (w/v) Benlate and 10% (w/v) Captan to prevent bacterial and fungal growth, respectively. Rooting of the cuttings was promoted by placing the basal stem parts into a 10 μM solution of α-naphthaleneacetic acid (NAA) for 24 h. After 3 weeks incubation at 25°C in a 10% Steiner's nutrient solution (for composition, see Blom-Zandstra et al., 1991) at 60 μmol m^{-2} s^{-1} PAR (Philips 58W/84 white fluorescent tubes, 14 h day^{-1}), 95–100% of the cuttings had rooted. The rooted cuttings were transferred to aerated 1 l pots containing a full-strength Steiner's nutrient solution. Using the same light source, PAR was increased to 270 μmol m^{-2} s^{-1} (12 h day^{-1}), and the day and night temperatures were changed to 20°C and 18°C, respectively. Relative humidity was 70%. After 5–6 weeks, when the flower buds on the single shoot started to open, the shoots were decapitated above the most basal mature leaves with five leaflets. The original leaf from the cutting and any other leaves with less than five leaflets below this leaf were removed. At this stage the light treatments were started. Only the axillary buds of the remaining leaf were allowed to develop into new shoots. After 3 weeks the first developed five-handed leaf of the new shoot was labelled and used for measurements.

2.2. Light treatments

Experiments were performed to measure transpiration, stomatal conductance or stomatal movement. Variables examined were: light intensity (150, 100 or 50 μmol m^{-2} s^{-1}) during a 12 h day; quality of the supplementary lighting (25 μmol m^{-2} s^{-1} orange, blue or white); duration of the supplementary lighting (0 (control), 4 or 8 h). Lamps used for supplementary lighting were as follows: White, fluorescent tubes (Philips 58W/84); blue, fluorescent tubes (Thorn Lighting, London, UK; 58W/blue); orange, either (1) cool white fluorescent tubes (Philips, Eindhoven), filtered by one layer of orange Strand cinelux filter (no. 405; Rank Strand Electric, Brentford, UK) or (2) high pressure sodium lamps (Philips SON-T 70 W). The orange lamps did not differ from each other in spectral distribution as measured by a Licor-1800 spectroradiometer.

2.3. Growth, transpiration and stomatal characteristics

Growth was measured at regular time intervals as fresh weight increase. Transpiration was measured by weighing the pots before and after the light period and after the dark period including a period of supplementary lighting if applied. Water consumption (g H_2O g^{-1} fresh weight h^{-1}) represented transpiration by the leaves

as it was corrected for fresh weight increase during the period between the measurements. Water loss from aerated pots without plants was measured as a control for evaporation.

Leaves which were fully expanded 3 weeks after the start of the light treatments were marked. Measurements on marked leaves were made using a steady state porometer LI-1600 (LI-COR, Lincoln, NB). Stomatal conductances were determined three times during a day cycle, every 2.5 h after a change in the light conditions: (1) during the light period; (2) during the daylength extension period with supplementary lighting; (3) during the dark.

2.4. Diurnal dynamics of stomatal movement

Dynamics of stomatal opening were determined on both cultivars at the end of the dark period. Single leaves were subjected to high light intensities (much higher than they received during growth) in order to measure the effect of a sudden change in light intensity. Prior to this treatment, plants received two different light periods (2.5 and 3.5 h at 50 or 150 μmol m^{-2} s^{-1}). Responses to light modulations were measured with only 'Madelon' grown at two light intensities (50 and 150 μmol m^{-2} s^{-1} and supplementary lighting (SL)). Changes in stomatal conductance were induced by a computer-modulated high-intensity light source, with the capability of changing light intensity rapidly (seconds) in a programmable manner. The measuring device (Fig. 1) can be described as a set of high

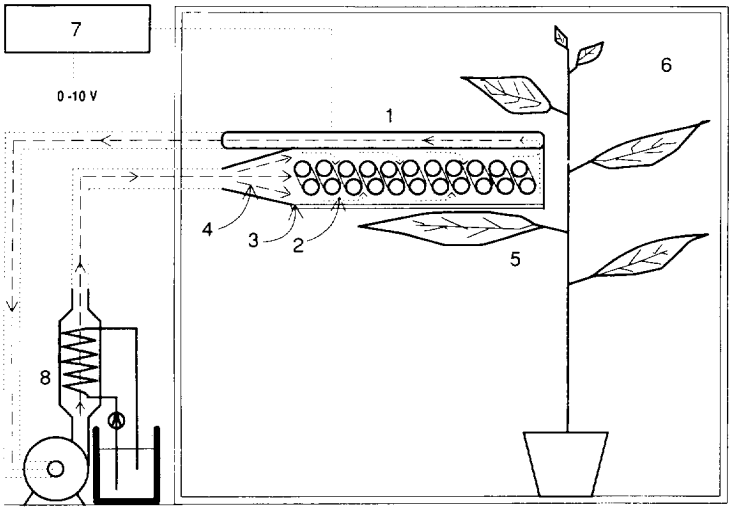

Fig. 1. Schematic cross section of the computer-controlled light source in a gas exchange system. 1, light source (length 65 cm, depth 46 cm, height 8 cm); 2, U-shaped fluorescence tube (length, 41.5 cm, diameter, 1.75 cm); 3, infra-red filter; 4, plates for dividing the air over the tubes; 5, single leaf to be measured; 6, controlled environment chamber; 7, quicktronics (either manual or computer-controlled by a 0–10 voltage signal); 8, heat exchanger with ventilator and water-bath.

frequency fluorescence tubes (Osram, Dulux-l, 36W/76; Osram, Munchen) which can vary rapidly in light output from ±4% to full capacity (90–2160 μmol m^{-2} s^{-1}), composed by a computer controlled signal (0–10 V). Light intensity could be changed over the full range in 40 s to within 5% of the new setpoint. The stability of the light output was better than 1%. The spectral distribution was not influenced by the light intensity. The variation in the horizontal distribution of the light over the leaf surface was less than 5% over an area of 200 cm^2. To realise an optimal operating temperature the tubes were cooled by forcing an airstream through the tube-housing. An external ventilator and flexible pipes were used to recirculate the air over a heat exchanger.

The light source was used in combination with an open gas exchange system (Sestak et al., 1971) operating fully automatically, using data acquisition (HP 75000, Hewlett Packard, CO) and control software (LT/control version 3.0.2, Laboratory Technologies, Wilmington, USA) run on a 386 25 MHz personal computer. Light intensity in the leaf chamber was measured with an energy response PPFD-sensor (Technical and Physical Engineering Research Service (TFDL-DLO), Wageningen). A main flow of compressed air was divided into an analysis flow which passes through the leaf chamber, and a reference flow which bypasses the chamber. The partial pressure of H_2O in the analysis flow was measured with an absolute infra-red gas analyser (ADC, model 225 MK3). A dewpoint meter (Michell Instruments, Cambridge; series 3000) was included to measure the dewpoint of the ingoing airstream. The difference in the partial pressure of CO_2 and H_2O of the analysis and reference flow were measured with two differential infra-red analysers (ADC, model 225 MK3). The wind velocity over the leaf was 1.5 m s^{-1} resulting in a boundary layer conductance to H_2O of 0.7 mol m^{-2} s^{-1}. Leaf temperature was measured with a small thermocouple (0.05 mm) fixed to the lowerside of the leaf. Transpiration and stomatal conductance were calculated using the equations of Von Caemmerer and Farquhar (1981).

3. Results

3.1. Effects of supplementary lighting

3.1.1. Growth

An increase in light intensity during the day from 50 to 150 μmol m^{-2} s^{-1} increased daily fresh weight production of 'Madelon' and 'Sonia' plants almost three times. Increase of fresh weight production was not significantly affected by SL for 4 or 8 h ($P=0.05$; data not presented).

3.1.2. Water consumption

Although plants without SL (control) were not expected to transpire during the night period, roses grown both without and with 4 h SL showed loss of water during the night: 'Sonia' used approximately 35% water during the night compared with the light, while this was significantly higher (approximately 55%) for

'Madelon'. The ratio between dark and light consumption did not depend on the light intensity during the day (within the range of 50–150 μmol cm^{-2} s^{-1}) and it did not vary with the duration of the SL light treatment nor with the light quality of the SL source. The cuticular conductance appeared to be low (0.01 mol m^{-2} s^{-1}). So, the water loss was primarily caused by stomatal transpiration.

3.1.3. Stomatal conductance

The data on water usage suggest that stomata did not fully close during periods of SL and darkness. To evaluate their closing ability we measured stomatal conductances 2.5 h after transition from one to another light/dark condition.

3.1.3.1. Duration of SL supply. The stomatal conductances decreased after the end of the light period (Fig. 2), irrespective of an SL treatment and its duration. For 'Sonia' the decrease in stomatal conductances did not depend on the duration of the SL treatment (Fig. 2). For 'Madelon', however, stomatal conductance was only reduced by 60% in the 4 h SL treatment and by 20% in the dark, while in the 8 h SL treatment the stomatal conductance immediately reduced to 20%. Remarkably, stomatal conductances in the light period (white bars) were enhanced by an SL treatment.

3.1.3.2. Light intensity during the day. Because the effect of SL on the water usage profile seems to be most pronounced in the winter, we varied the light intensity during the day (50–150 μmol m^{-2} s^{-1}). Stomatal conductances were measured 3 and 6 weeks after the start of SL supply (Fig. 3). Light intensity had a clear positive effect on daily transpiration, especially for 'Sonia'. It did not affect stomatal conductances in the SL and dark period, except for 'Madelon' after 3 weeks low light treatment. Average levels of stomatal conductances were higher for 'Madelon'. Moreover, 'Madelon' showed a clear developmental effect: after an SL treatment of 3 weeks the stomatal conductance of a fully expanded leaf decreased

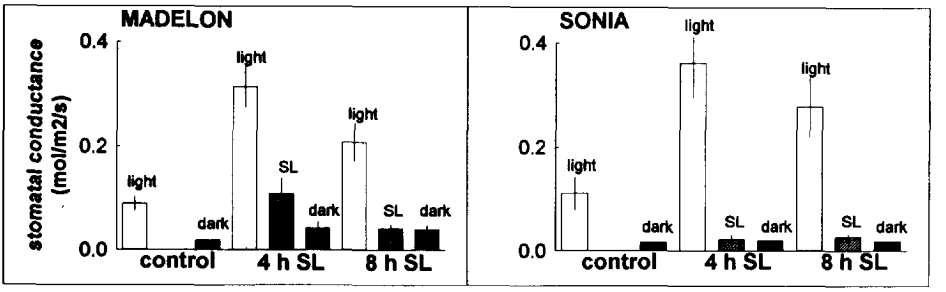

Fig. 2. Stomatal conductances (mol m^{-2} s^{-1}) of fully developed five-handed leaves from plants of two rose cultivars 'Madelon' and 'Sonia', treated for 6 weeks, grown with or without supplementary lighting for 4 or 8 h. Light intensity during the day was 150 μmol m^{-2} s^{-1}. Measurements were performed at three different times during the day: 2.5 h after the onset of light, 2.5 h after the onset of supplementary lighting and 2.5 h after the onset of the dark period. Each value is the mean of four replicates. Vertical small bars represent standard errors of the mean.

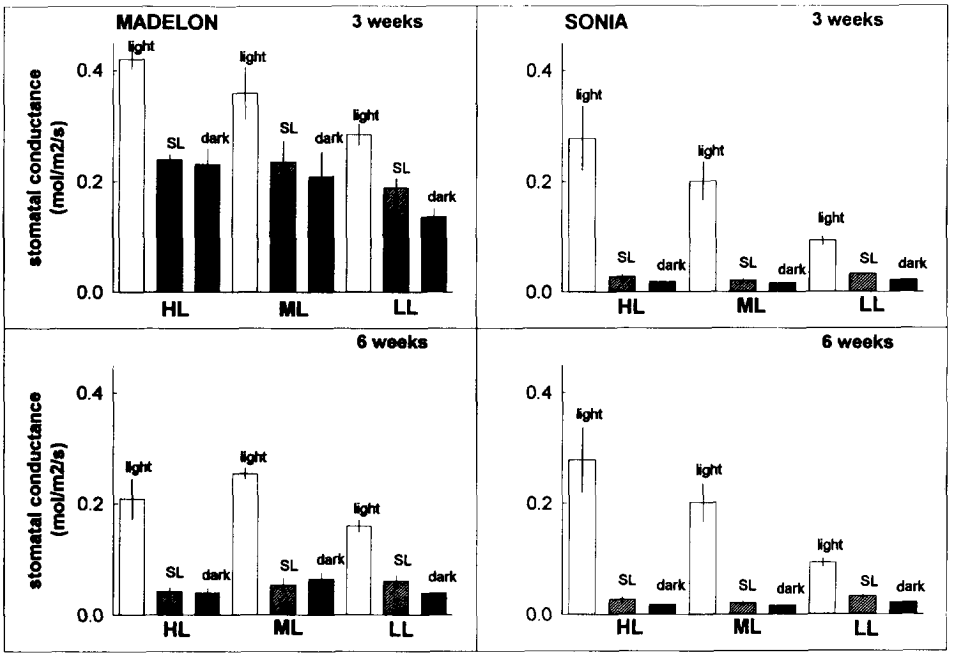

Fig. 3. Stomatal conductances (mol m^{-2} s^{-1}) of the first developed five-handed leaf from plants of two rose cultivars 'Madelon' and 'Sonia', treated for 3 or 6 weeks, grown at different light intensities during the day: HL (150 μmol m^{-2} s^{-1}); ML (100 μmol m^{-2} s^{-1}) and LL (50 μmol m^{-2} s^{-1}). The light period was followed in all cases by an 8 h period with supplementary lighting (25 μmol m^{-2} s^{-1}). Measurements were performed at three different times during the day: 2.5 h after the onset of light, 2.5 h after the onset of supplementary lighting and 2.5 h after the onset of the dark period. Each value is the mean of four replicates. Vertical bars represent standard errors of the mean.

by at most 50% during the SL period and darkness, while it decreased by about 80% in the same leaf after a treatment of 6 weeks. Every leaf newly developed between weeks 3 and 6 showed the same developmental effect. The change in stomatal conductances from 50 to 80% took less than 1 week.

3.1.3.3. Light quality of the SL treatment. Light quality affected stomatal conductances (Fig. 4) with consequential changes in water consumption. Daily transpiration was affected similarly in both cultivars. Orange light stimulated stomatal conductance in the light by about 100% compared with the control.

Light quality affected dark-induced decrease of stomatal conductances for 'Madelon' only. Orange light gave less reduction in stomatal conductance during SL supply than blue or white. During the period of full darkness, the stomatal conductances reduced to a value comparable with cuticular conductance (0.01 mol m^{-2} s^{-1}) in control and white SL light, while they did not reach these value when orange and blue SL were given.

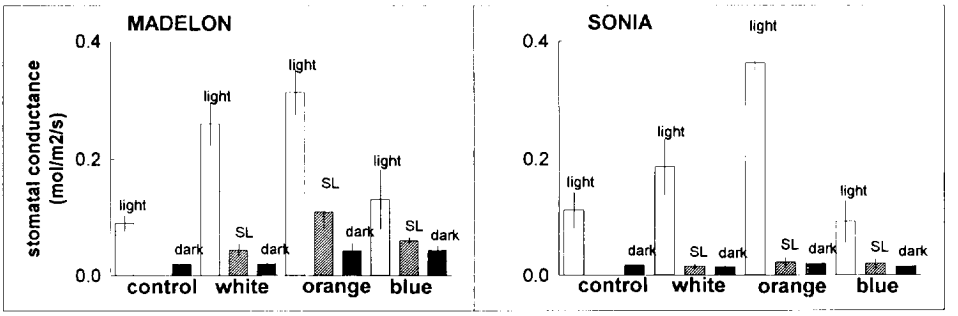

Fig. 4. Stomatal conductances (mol m^{-2} s^{-1}) of leaves from plants of two rose cultivars 'Madelon' and 'Sonia', treated for 6 weeks, grown at a light intensity of 150 μmol m^{-2} s^{-1} during the day. The light period was followed by a period without or with supplementary lighting of different qualities: white, orange or blue. Measurements were performed at three different times during the day: 2.5 h after the onset of light, 2.5 h after the onset of supplementary lighting and 2.5 h after the onset of the dark period. Each value is the mean of four replicates. Vertical bars represent standard errors of the mean.

Table 1
Stomatal conductances (mol m^{-2} s^{-1}) ± standard errors of leaves of two rose cultivars grown at two light intensities (50 and 150 μmol m^{-2} s^{-1}) with SL, measured at the end of the dark period and at two different instances during the day. Each value is the mean of three determinations

Light regime	'Madelon'		'Sonia'	
	50	150	50	150
End of the night	0.10 ± 0.008	0.14 ± 0.009	0.02 ± 0.005	0.02 ± 0.010
2.5 h light	0.11 ± 0.010	0.22 ± 0.035	0.10 ± 0.009	0.26 ± 0.007
3.5 h light	0.15 ± 0.002	0.20 ± 0.018	0.13 ± 0.017	0.29 ± 0.017

3.2. Dynamics of stomatal movement

Data obtained from porometer measurements show a clear decrease of stomatal conductances in the dark. These data are snapshots only. Our data on water consumption (see above) suggest that there is still considerable cultivar-dependent water loss after the light period. This suggests that stomata respond slowly to changes in light conditions, and that the response time may differ between the cultivars. To study this phenomenon we evaluated the dynamics of stomatal movement with a computer-controlled gas exchange system. Values for stomatal conductances at the end of the night period and at two times during the day are summarised in Table 1. In contrast to 'Madelon', stomata of leaves from 'Sonia' closed almost completely.

3.2.1. Stomatal opening

Rates of light-induced change in stomatal conductances differed considerably between 'Madelon' and 'Sonia' (Fig. 5(A)). Besides that, the kinetics of opening differed clearly between both cultivars.

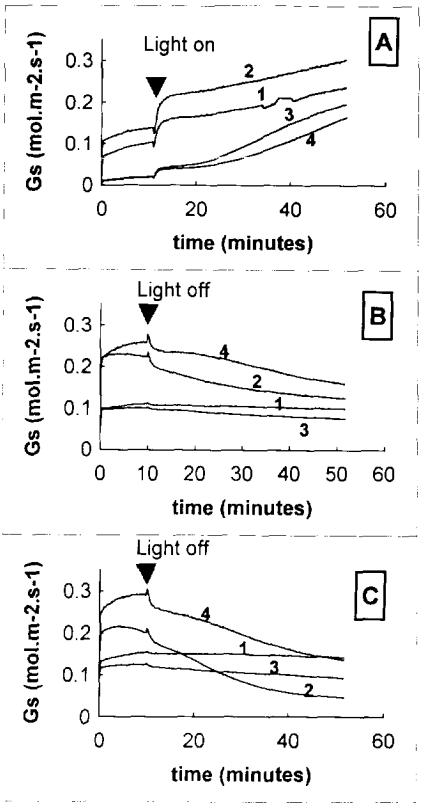

Fig. 5. Typical responses of stomatal conductances (G_s) to switching the light on (A) or off after light treatment of 2.5 h (B) or 3.5 h (C). Responses are measured with two rose cultivars 'Madelon' (curves 1 and 2) and 'Sonia' (curves 3 and 4) grown at a light intensity of 150 μmol m^{-2} s^{-1} (curves 2 and 4) or 50 μmol m^{-2} s^{-1} (curves 1 and 3). Measurements are the means of three replicates.

3.2.2. Stomatal closure

Rates of dark-induced stomatal closure depended on the light intensity during the day (Figs. 5(B) and 5(C) after a light period of 2.5 h or 3.5 h, respectively). Plants grown at high light intensity (curves 2 and 4) responded much faster to the light-off signal than those grown at low light intensity (curves 1 and 3). Surprisingly, for 'Madelon' the duration of the light period appeared to be important. After a light period of 2.5 h (Fig. 5(B)) the stomata closed more slowly and less completely than after a period of 3.5 h (Fig. 5(C)).

3.2.3. Responses to light modulations

The reaction of the stomates (G_s) as a result of a light modulation slightly depends on the light treatment during plant cultivation, as shown for a leaf of 'Madelon' (Fig. 6). The opening of the stomates with increasing light intensity is most rapid for the plants grown at 150 μmol m^{-2} s^{-1} (curve B). Closing the

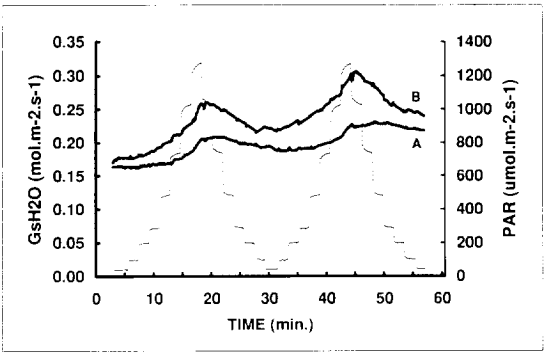

Fig. 6. The reaction of stomata of roses treated at PPFD is 50 μmol m^{-2} s^{-1} (A) and 150 μmol m^{-2} s^{-1} (B) as a result of the light modulation (dotted line). Measurements started at the end of the dark period. PPFD was changed in seven time steps, each of 2 min, from a minimum of 50 to a maximum of 1300 μmol m^{-2} s^{-1}.

stomates with decreasing light intensity is a slower process than opening them, especially for the plants grown at 50 μmol m^{-2} s^{-1} (curve A).

4. Discussion

The purpose of this study was to evaluate transpiration and stomatal characteristics of two rose cultivars after cultivation under different light conditions. Transpiration was measured as daily and nocturnal net water loss to the atmosphere. The data represented cumulative water loss by the plants, but did not give any information about stomatal opening or closing. The state of stomatal opening was evaluated by measuring stomatal conductances using a porometer, providing a snapshot of the stomatal situation. For a study of the dynamics of stomatal movement we evaluated the rate of stomatal opening and closing using a computer-controlled gas exchange system.

Supplementary lighting did not stimulate fresh weight production as in other plant species (reviewed by Zieslin and Mor, 1990). As the light intensity of SL was low (25 μmol m^{-2} s^{-1}) its effect on growth might have been so small that it did not exceed the variation between the plants. Stimulation of flower production by SL (Zieslin and Mor, 1990) may possibly be caused by an effect of SL on assimilate translocation within the plant. Indeed, a promotion of sink activity by light has been described for roses (Mor and Halevy, 1980).

The plants showed abundant water loss during the dark period with and without SL, which could not be ascribed to cuticular conductance. Contrary to previously presented data (Durkin, 1985), water loss during the dark measured in our experiments was not related to the light intensities during the light period (in the range 50–150 μmol m^{-2} s^{-1}), nor to the supply of SL, irrespective of its duration or spectral composition. The absence of an effect of blue light on stomatal con-

ductances (Fig. 4) was unexpected, as blue light is known to result in a transient increase in stomatal conductance in attached leaves (Sharkey and Ogawa, 1987; Assman, 1988; Karlsson, 1988). Apparently, these transient changes did not extrapolate to a long-term effect. Our results agree with data presented by Mansfield and Heath (1964), who found no effect of daylight extension by low light on stomatal conductances.

For 'Madelon', both water loss and stomatal conductance depended on the developmental stage of the leaves. Stomatal conductances of leaves studied after a 6 week SL treatment (Fig. 3) decreased to the level of cuticular conductance during the night, while they did not after a 3 week SL treatment. This is undoubtedly caused by changing responses during growth. As shown for micropropagated plants (Santamaria et al., 1993), the development of cell walls during aging may play a role in the behaviour of stomata. Water loss of whole plants results from a mixture of old and young leaves per plant. Yet, young leaves change their stomatal behaviour very quickly: within 1 week stomatal conductances during the SL and dark period changed from 50 to 80%. So, the contribution of young leaves to the transpiration of the whole plant is small.

Because the stomatal conductances reduced in SL or dark periods (Figs. 2–4), stomatal movement clearly responded to changes in light conditions. The nocturnal transpiration must be explained by a delay in the rate of closure. Indeed, the stomata closed rather slowly (Fig. 5), while not completely for 'Madelon' (Table 1). The dynamics of opening also differed between the cultivars (Fig. 5(A)). Apart from genetic differences, the rate of stomatal closure depended on the duration of the light period prior to the measurements (Figs. 5(B) and 5(C)), indicating that the dynamics of stomatal closure were controlled by endogenous factors. Unfortunately, little is known about the mechanism of this phenomenon. As knowledge about this control mechanism may have important implications for growth and harvest planning of consumption and ornamental crops, further research is worthwhile.

The response rates of stomata to rapid changes in light conditions depended on growth conditions. Low light conditions during growth (Fig. 6, curve A) caused slow stomatal reactions upon changing light intensity. The rate of closure was more affected than the rate of opening.

To understand how transpiration quantitatively relates to stomatal dynamics, the pattern should be measured in more detail. In a pilot experiment (not presented), we found that stomata open before the light-on signal, while they start closing six hours before the light is switched off. Taking this effect into account calculated values for daily and nocturnal water usage agree with the measured transpiration.

We conclude that supplementary lighting affects stomatal opening during the day, but does not affect the mechanism of stomatal closure. However, the rate of closure depends on the duration of the light period (Figs. 5(B) and 5(C), respectively) and might be affected by endogenous factors. Although the behaviour of plants grown in greenhouses is hard to predict, growers may be recommended

to cut flowers and transfer them to darkness several hours after a period of high light intensity.

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