Spectral dependence of photosynthesis and light absorptance in single leaves and canopy in rose

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ABSTRACT

Little is known about the effects of leaf pigmentation (related to leaf ontogeny), on the spectral dependence of photosynthesis and most observations have been limited so far to single leaves. This study aimed to investigate photosynthesis and the related optical properties of two types of rose leaves, young reddish leaves and middle age green leaves, and to quantify the spectral dependence of photosynthesis at the canopy level.

Photosynthesis was measured with CO_2/H_2O gas analyzer on intact leaves of rose 'Akito' at narrow band light of 18 wavelengths. Subsequently, the optical properties (transmittance, absorptance and reflectance) were measured with spectrophotometer. A mechanistic crop model was used for up scaling measurements at the single leaf level to the crop level (crop with LAI = 3).

The green and the reddish leaves had similar total PAR absorptance, even though absorptance around 550 nm was slightly lower in the green leaves. The maxima of photosynthesis efficiency were at 640–680 nm for quantum yield (per absorbed light unit) and at 660–680 nm for action spectrum (per incident light unit), regardless the colour of the leaf blade. In the range 500–580 nm, both the quantum yield and the action spectrum were lower in reddish than in green leaves. Differences in optical properties and photosynthetic behaviour were related to the higher content of anthocyanins in red leaves.

The spectral dependence of light absorption and photosynthesis at the canopy level differed distinctly from that at leaf level. The spectral differences in absorption at the leaf level almost disappeared at the canopy level. Consequently, while the action spectrum of green light (520–570 nm) was only 67% of that of red light (680 nm) at the leaf level, it increased to 79% at the crop level.

Young reddish leaves had higher absorptance but lower action spectrum and quantum yield at green light. Spectral differences in photosynthesis at the canopy level are much smaller than at the leaf level. Our short term measurements suggest that optimizing spectral output of LED lamps may increase photosynthesis up to 12% for a canopy with green leaves and up to 17% for a canopy with reddish leaves when compared to the spectrum of HPS lamps.

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1. Introduction

At the same light intensity, photosynthesis efficiency changes with the wavelength: it is known that most plant crops reach a major peak in the red region and a relatively lower peak in the blue, with a typical pattern closely related with the absorption spectra of photosynthetic pigments (Atwell et al., 1999). However, current knowledge about spectral dependence of photosynthesis in higher plants is mainly based on early observations on arable or vegetable crops (Balegh and Biddulph, 1970; McCree, 1972; Inada,

1976, 1977; Evans, 1987). Particularly, the action spectrum of photosynthesis (efficiency of photosynthesis at different wavelengths, expressed as μmol of CO_2 per μmol of incident light), the spectral quantum yield (per μmol of absorbed light) and the spectral properties of the leaf (absorptance, transmittance, reflectance) have hardly been investigated in greenhouse ornamental crops. Furthermore, a few data are available on species with different pigment composition of the leaves in the young and mature developmental stages (Burger and Edwards, 1996; Dodd et al., 1998) and a part of the experiments have been carried out on cut leaves (or portions of them), rather than intact leaves.

In many greenhouse crops, supplemental lighting is often used in Northern countries from fall to spring, to enhance plant growth and to obtain all year round high production and good quality.

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In commercial practice of Dutch greenhouses, roses are often lighted till 20 h a day and the light intensity obtained at the canopy level is usually between 100 and 200 μmol m^{-2} s^{-1}. However, under the common lighting systems (lamps at the top of the canopy), light is not uniformly distributed along the leaf layers. Particularly, it has been calculated that, considering a crop with LAI = 3, even when the light intensity at the top of the plant is 400 μmol m^{-2} s^{-1}, roughly 33% of the leaves in the lower and inner zone of the canopy receive less than 100 μmol m^{-2} s^{-1} because of self shading (data not shown).

This practice is relatively expensive and the most common lighting systems (high pressure sodium – HPS lamps) seem to be neither spectrally nor energetically optimal (Heuvelink et al., 2006; Marcelis et al., 2006).

Potential benefits could be obtained by modifying the spectral energy distribution (light quality) of lamps (Moore et al., 2006; Brazaitytė et al., 2006). In this respect, recently, light emitting diodes (LEDs) have been introduced experimentally by commercial growers for supplemental lighting. LEDs have a variety of advantages over traditional lighting systems: small size, long lifetime, low heat emission and potentially a high energy conversion efficiency (Massa et al., 2008; van Ieperen and Trouwborst, 2008). These narrow-band lighting devices are available in several colours, giving the opportunity to select the most favourable light spectrum for photosynthesis. However, in order to combine both efficient LED operation and efficient plant photosynthesis, optimizing the lighting strategies and reducing the energy inputs, more information is needed about the spectral dependence of photosynthesis.

The aim of this research was to investigate, in terms of instantaneous effects at single leaf level, the photosynthesis and the related leaf optical properties at different wavelengths, in two types of rose leaves which differed in their pigment composition. For this objective, the spectral dependence of photosynthetic efficiency was studied under light-limited irradiance, on incident and absorbed light basis, on young leaves (reddish colour) and middle age leaves (green colour). Finally, it was studied what the consequences of these measurements at the leaf level are for the whole canopy photosynthesis. This up-scaling of leaf scale processes to the canopy level was achieved with a dynamic simulation model.

2. Materials and methods

2.1. Plant material and growth conditions

The experiment was carried out in Wageningen (The Netherlands, latitude 51.97 N, longitude 5.67 E) in July 2008, in a heated experimental greenhouse. Rose plants 'Akito' were grown on rockwool slabs (transplant 25 February 2008), in double rows, at the plant density of 6.5 plants m^{-2}. Water and fertilizers were supplied via a drip-system, automatically controlled by a fertigation computer.

During the growing cycle, the night temperature inside the greenhouse ranged from 17.2 to 21.5 °C (heating set point: 18 °C) while the day temperature was between 23.7 and 34.9 °C. Relative humidity was kept around 70% and the CO_2 concentration near 500 ppm. Supplemental lighting by High Pressure Sodium lamps (Philips SON-T Green Power 600 W; Koninklijke Philips Electronics N.V., the Netherlands) provided a minimum photon flux density of 150 W m^{-2} at the crop level, extending the natural day-length to 16 h (3:00 till 19:00). Lamps switched off when the outside global radiation exceeded a 250 W m^{-2} threshold.

In order to reduce the possible stress because of the moving, on the two days prior to the photosynthesis, transmittance and reflectance measurements, plants were placed in a climate chamber at the following conditions: day/night temperature 20/18 °C, pho-

ton flux density 100 μmol m^{-2} s^{-1} (Philips TLD 50 W 840 HF), 16 h long day, relative humidity 65% and ambient CO_2 concentration.

2.2. Photosynthesis, leaf optical properties and anthocyanin content

The following types of leaves were compared: (i) leaves with a red visual appearance (2nd to 5th leaf from the top of the stem), and (ii) leaves with a green visual appearance (5th to 8th leaf from the top of the stem). All leaves measured were tri- or penta-foliate and fully expanded, from stems with 13 to 16 leaves, when flower bud was not yet or barely visible.

Rockwool slabs of the plant samples were cut to make the plants transportable and plants were pruned in order to remove the bent shoots and reduce the upright shoots to 4 per plant.

Photosynthesis measurements were carried out on the top leaflet, with a LICOR 7000 CO_2/H_2O Gas analyzer (LI-COR, Lincoln, NE, USA) connected to a custom made leaf chamber (area: 4.52 cm^2). The conditions inside the leaf chamber were kept constant (temperature 26 °C, CO_2 concentration 380 ppm, O_2 concentration 2%, RH 72%, air flow rate 204 μmol s^{-1}).

Photosynthesis was measured with narrow band light at 18 wavelengths in the interval 406–720 nm. The bandwidth was 10 nm in the interval 460–720 nm and 20 nm at 406, 427 and 445 nm. The leaf was illuminated by two 250 W halogen lamps, via a 4-armed fibre optics light guide. Lamp 1 provided a continuous broad-band background light (40 μmol m^{-2} s^{-1}), of which the halogen spectrum was filtered with a heat filter and a filter to convert tungsten halogen light to day-light (Lee filters, Hampshire, UK). Narrow band light was obtained by placing a narrow band interference filter between lamp 2 and an arm of the fibre optics. The light from the two lamps was projected fully mixed on the leaf surface. At each wavelength, photosynthesis was measured at the background light plus 0, 30 or 60 μmol m^{-2} s^{-1} narrow band light, after a 3-min exposure to 100 μmol m^{-2} s^{-1} of broad-band light. This low light intensity is usually adopted in research on spectral dependence of photosynthesis in order to count on a reliable light response, since, at this level, the relationship between photosynthesis and light radiation is supposed to be linear.

Photosynthesis efficiency was calculated as μmol of CO_2 assimilated per μmol of incident light for the action spectrum and as μmol CO_2 per μmol of absorbed light for the spectral quantum yield. As quantum yield was very similar at both light intensities, the quantum yield was calculated as the average of yields at 30 and at 60 μmol m^{-2} s^{-1} narrow band light. All values are expressed as a fraction of the maximum value, recorded for both the treatment at 680 nm.

After the photosynthesis measurements, the top leaflet was removed from the plant and leaf transmittance (Tr) and reflectance (Ref) spectra were measured between 400 and 740 nm (bandwidth 1 nm), with a spectrophotometer (Perkin Elmer Lambda 950 UV/NIR; Perkin Elmer Inc. Waltham, MA, USA). For transmission measurements, the leaf was clamped to the input port of the integrating sphere with the bottom (abaxial side) facing the integrating sphere. For reflection measurements, the leaf was clamped to the exit port with the top (adaxial side) facing the sphere. In all measurements, the leaves were illuminated from the top side and the direction of the collimated light was perpendicular to the leaf plane. Leaf absorptance (Abs) at the used wavelengths was calculated as Abs = 100 − (Ref + Tr). All values were expressed as percentage of the incoming light.

Measurements were carried out on 4 leaves (from 4 plants) per developmental stage (green or red), according to a randomized block design with four blocks. Significance of the differences in optical properties was tested with ANOVA, followed by a Student's *t*-test ($P = 0.05$).

Anthocyanin content (A, $\mu mol\,m^{-2}$) of rose leaves was estimated from reflectance at 550 nm ($R550$, %), 700 nm ($R700$, %) and 774 nm ($R774$, %), as described by Gitelson et al. (2001):

$$A = a + b \left[R774 \left(\frac{1}{R550} - \frac{1}{R700} \right) \right] \tag{1}$$

where a and b are regression coefficients for the relation between anthocyanin content and reflectance. Reflectance measurements were performed with a spectrophotometer as described above. The regression coefficients for rose leaves *cultivar* 'Akito' were determined on 18 leaves of different ages (and colour) and they were 54.52 for coefficient a and 45.93 for coefficient b. In these 18 leaves reflectance was measured and the anthocyanin content was analytically determined according to Martin et al. (2002). Regression analysis on these data showed that Eq. (1) gave a reliable estimate of anthocyanin content ($R^2 = 0.74$).

In order to simulate the potential short-term light use efficiency (LUE per incident light) of photosynthesis under different light sources, the normalized spectral power of three types of commercial lamps (HPS: Philips Green Power 600 W–400 V; LED 645 nm: Roithner LED type 645-66-60; LED 680 nm: Roithner LED type 680-66-60) were multiplied with the photosynthetic rate at each wavelength, for the different lamp/leaf combinations (for spectral output of the lamps see Paradiso et al. (in press)). The LUE at a given light source wavelength was calculated from the LUE data by linear interpolation.

2.3. Modelling the action spectrum at crop level

Light attenuation within the canopy was modelled for a homogeneous crop on the basis of an exponential decay, giving a light intensity I at layer n, according to Monsi and Saeki (2005):

$$I_n = I_0 e^{-kLAI_n} \tag{2}$$

where I_0 is the light intensity above the crop, k the extinction coefficient, and LAI_n the leaf area (m^2) per ground floor (m^2). The model calculated light intensity, and the resulting absorption and photosynthesis, using a 5-point Gaussian distribution for the different leaf layers, which were then integrated at crop level. Calculations were performed for diffuse light.

The extinction coefficient for the crop (k_{crop}) was calculated as:

$$k_{crop} = k_{bl} \sqrt{(1 - \sigma)} \tag{3}$$

where k_{bl} (0.84) is the extinction coefficient for a crop with spherical leaf angle distribution, when the crop is composed of black leaves and σ is the scattering coefficient.

The wavelength dependent scattering coefficient σ equals the sum of reflection and transmission and was derived from the spectrometer measurements per wavelength at the leaf level. Consequently, Eq. (3) scales up this leaf property to crop level. Moreover, σ is used to simulate the canopy reflection coefficient ρ_c, using the expression:

$$\rho_c = \frac{1 - \sqrt{1 - \sigma}}{1 + \sqrt{1 - \sigma}} \tag{4}$$

In the model this reflection is subtracted from the incoming diffuse light. All the above methods were derived from and elaborated by Goudriaan and van Laar (1993).

The relative contribution of photosynthesis resulting from the 18 different wavelengths at crop level was estimated with a mechanistic photosynthesis model based on Farquhar et al. (1980), using a maximal rate of electron transport (J_{max}) of 110 μmol electrons $m^{-2}\,s^{-1}$ (at 25 °C), a carboxylation rate (VC_{max}) at a value of ½ J_{max} (in $\mu mol\,CO_2\,m^{-2}\,s^{-1}$), and a curvature parameter (θ) of 0.75. All parameters were calibrated to measured light-response curves

Table 1
Percentage mean values of leaf transmission (Tr), reflection (Ref) and absorption (Abs) in reddish and green leaves of rose cv. 'Akito' ($n = 4$) in all the visible portion (400–700 nm) and in the green region (520–570 nm) of the spectrum.

	Visible (400–700 nm)			Green region (520–570 nm)		
	Tr	Ref	Abs	Tr	Ref	Abs
Green	5.78	6.30	87.93	13.15	10.73	76.11
Red	5.63	6.86	87.51	10.85	10.74	78.41
SE_{mean}	0.08	0.25	0.26	0.62	0.59	1.07

of CO_2 assimilation (data not shown) by a reiteration procedure based on a genetic algorithm which looked for parameter values that realized the minimum sum of squares between observations and simulations.

The parameter value α (quantum efficiency in μmol electrons per μmol photons) was set at the value as derived for each wavelength from the LICOR 7000 measurements. The measurements used to calculate α were under non-photorespiratory conditions. Gross photosynthesis per wavelength was calculated for a rose crop having a leaf area index (LAI) of 3, receiving 30 $\mu mol\,m^{-2}\,s^{-1}$ of diffuse photosynthetically active radiation at the top of the canopy, at a CO_2 concentration of 350 ppm and an air temperature of 22 °C.

3. Results

Rose leaves showed low values of transmittance and reflectance of violet (400–455 nm) and blue (455–500 nm) light, higher levels in the green region (500–580 nm), followed by a decrease from the yellow (580–600 nm) to the red light (620–700 nm) and drastic increases in the far red (from 700 nm) (Fig. 1). Consequently, absorptance was higher from 400 to 500 nm and around 670–690 nm (with two shoulders under shorter red wavelengths) and showed a large depression from 500 to 580 nm and a drastic drop from 700 nm (Fig. 1).

In the visible region (from 400 to 700 nm), the green and the red leaves had similar mean values of reflectance and transmittance (6.58% and 5.70% respectively, on the average of the leaf types) (Table 1). As a consequence, they also showed similar total absorptance (87.7% on average) (Fig. 1). However, green leaves had a slightly higher transmittance than young red leaves between 520 and 560 nm ($P < 0.10$), with a consequently slightly lower absorptance in this region (Table 1).

The spectral quantum yield of photosynthesis (μmol of CO_2 per μmol of absorbed photon) reached the highest value in the 640–680 nm interval and a lower peak around 445 nm, for both the leaf types (Fig. 2A). In red leaves, the quantum yield at 680 nm was 2.2% lower compared to the green leaves (0.0663 ± 0.0010 vs. $0.0678 \pm 0.0003\,\mu mol$ of CO_2 per μmol of absorbed photon; average ± S.E. mean). In the green wavelengths (500–580 nm) spectral quantum yield was distinctly lower in red than in green leaves (Fig. 2A).

In both green and red leaves, the action spectrum (μmol of CO_2 per μmol of incident light) of rose leaves reached the highest values under red light, with one major peak at 660–680 nm; the action spectrum at 680 nm was $0.0609 \pm 0.0005\,\mu mol$ of CO_2 per μmol of incident photon in red leaves and 0.0631 ± 0.0001 in green leaves. Furthermore, there was a relatively high maximum in the blue region (445 nm) (Fig. 2B). A broad minimum was found in the green region (500–580 nm), while the photosynthetic rate declines rapidly above 680 nm, with a very low photosynthesis at 720 nm.

The action spectrum changed with the colour of the leaf blades: in green leaves it was higher than in red leaves under the violet light (filter 406 nm) and slightly higher throughout the green wavelength interval from 520 to 560 nm (Fig. 2B).
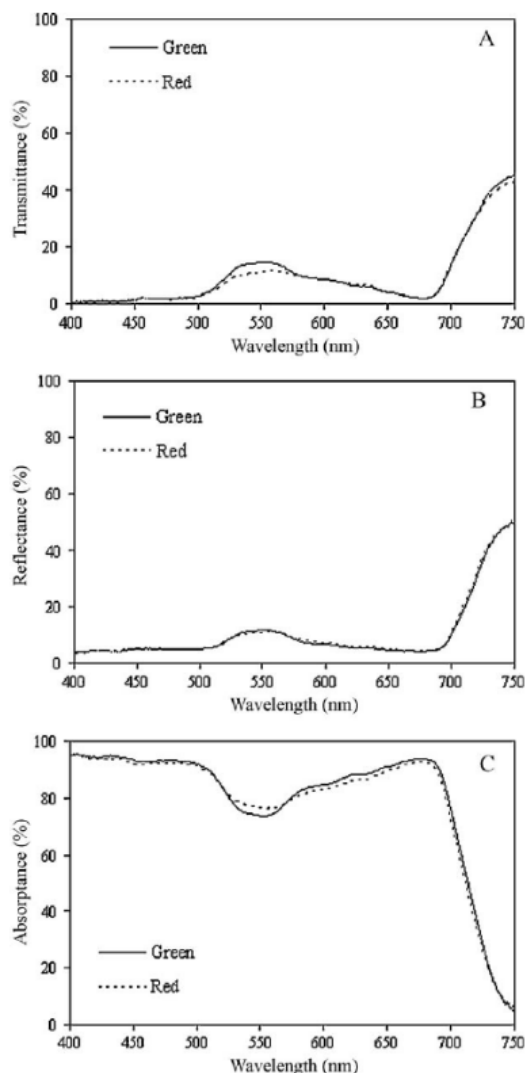
Fig. 1. Percentage of transmittance (A), reflectance (B) and absorptance (C) spectra in green and reddish leaves of rose cv. 'Akito' (*n* = 4).

Fig. 2. Spectral quantum yield (μmol CO_2/μmol absorbed photon) (A) and Action spectrum (μmol CO_2/μmol incident photon) (B) of photosynthesis in green and reddish leaves of rose cv. 'Akito'. Values presented are relative to the maximum value at 680 nm for each type of leaves (*n* = 4; Average ± S.E.).

In both leaf types, spectral quantum yield was relatively higher than action spectrum in the green region, because of the relatively low absorption of green wavelengths. The difference between relative spectral quantum yield and relative action spectrum was greater in green leaves (0.80 vs. 0.70, respectively) than in red leaves (0.69 vs. 0.64) (Fig. 2).

The concentration of anthocyanins in leaf tissues was higher in reddish leaves (52 ± 15 μmol m^{-2}) then in green leaves (23 ± 10 μmol m^{-2}) (*n* = 6; average ± S.E.).

At the leaf level, the low absorption of green light resulted in a strong reduction of the action spectrum of green light in both green and reddish leaves. However, at the crop level the model calculated that a large part of the scattered green light is absorbed by leaves situated lower in the canopy, such that the absorption of green light is not that much lower than that of red light (Fig. 3).

For reddish leaves the action spectrum of green light (520–570 nm) was 60% of that of red light (680 nm) at the leaf level, while this was 68% at the crop level. For green leaves the difference
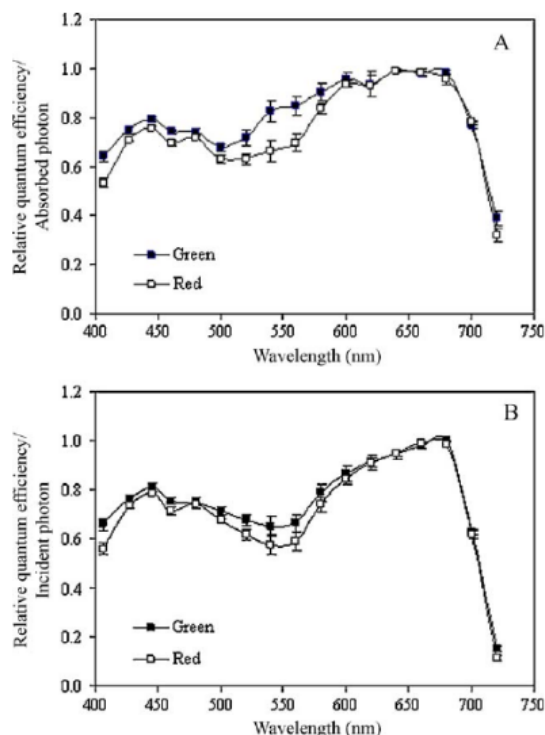
between action spectrum at crop level differed even more from that at the leaf level. The action spectrum of green light (520–570 nm) was 67% of that of red light (680 nm) at the leaf level, while this was 78% at the crop level (Fig. 4). So an absolute increase of crop vs. leaf of 11% at green light is calculated, while for the whole PAR spectrum an increase of 6% (i.e. the surface area between leaf and crop curve in Fig. 4) is calculated per incident photon.

A higher action spectrum in the red compared to the blue region was found because the quantum efficiency at red light (Fig. 2B) was highest, although absorptance at blue light was slightly lower than in the blue region (Fig. 1C). For getting an impression of the impact of quantum efficiency and scattering being different per wavelength, we did model calculations that showed that 1% change in quantum efficiency increased crop gross photosynthesis by 0.88%, while 1% change in scattering changed crop photosynthesis by only 0.03%. This is confirmed by the rather modest variation in quantum efficiency (α ranged from 0.31 to 0.47) which resulted in large variations in photosynthesis (±17.9% from the mean) yet the larger variation of scattering between wavelengths (reflection ranged from 5 to 16%) changed photosynthesis by only ±1.7%.

Calculations with the reported action spectra show that significant increase of photosynthesis can be obtained by using LEDs compared to HPS lamps (Table 2), when ignoring all physiological considerations beyond instantaneous effects of narrow-band light on photosynthetic efficiency. We compared 645 nm LED and HPS lamps at the same total radiant power. The 645 nm LED showed a higher calculated LUE than the 680 nm LED at both leaf and crop level (Table 2).
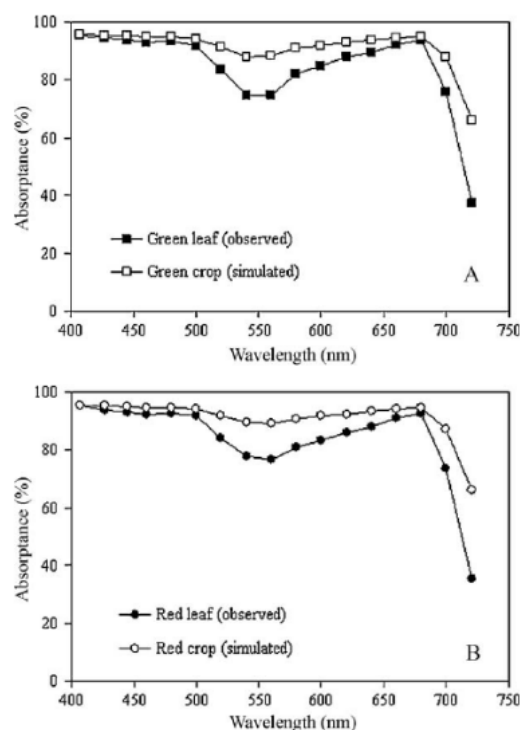
Fig. 3. Fraction absorptance simulated at crop level and observed at leaf level (see also Fig. 1) for green leaves (A) and reddish leaves (B).
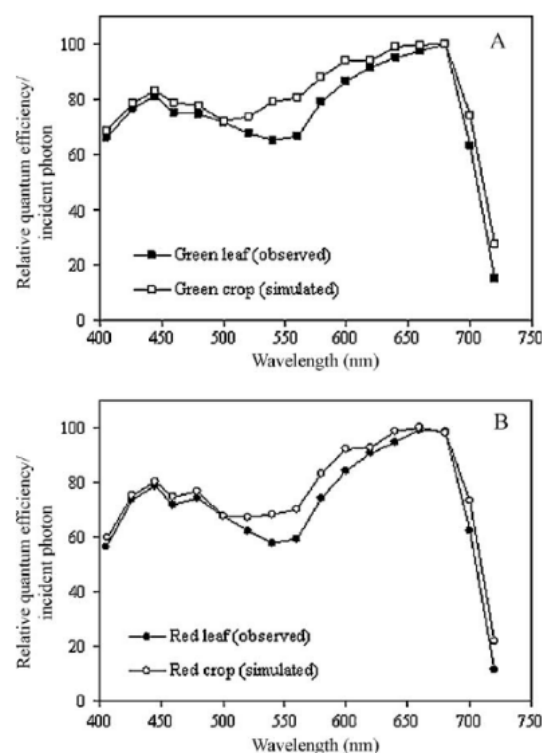

Fig. 4. Relative spectral quantum efficiency simulated at crop level and observed at leaf level (see also Fig. 2) for green leaves (A) and reddish leaves (B).

4. Discussion and conclusions

In this research we evaluated the spectral dependence of light absorptance and photosynthesis in intact leaves of rose, differing for developmental stage and concomitant colour of the leaf blade. Further up-scaling from leaf to crop was done by simulation, in order to evaluate the spectral dependence on crop level.

4.1. Light absorption

Absorptance spectra measured in leaves of rose cv 'Akito' are qualitatively similar to those reported by McCree (1972) for the "average plant" (from 22 plant species grown in growth chamber) and from other authors for different herbaceous crops. In particular, both red and green leaves of rose absorb more than 90% of the incident radiation in the violet and blue regions and in the 640–680 nm band of the red light, similarly to those reported for strawberry (Inada, 1976), rice and perilla (Inada, 1977) grown in greenhouse and for bean in growth chamber (Balegh and Biddulph, 1970).

Table 2
Simulated short term light use efficiency (LUE; photosynthesis per incident light in the 400–720 nm interval) of single red or green leaves and of a green or red leaves canopy (LAI = 3). Values presented are percentage increase in LUE under LED light compared to HPS light.

	645 nm LED	680 nm LED
Leaf level		
Single green leaf	17.9	4.5
Single red leaf	23.2	7.5
Crop level		
Crop with green leaves	11.5	0.7
Crop with red leaves	16.9	4.1

However some quantitative differences are apparent in comparison to other greenhouse grown species, such as maize and lettuce (Inada, 1976; Maas and Dunlap, 1989), that showed generally lower absorptance values throughout the visible spectrum.

The absorptance pattern and the consequent quantum yield spectrum of leaves in vivo are both affected by the pigment composition (Inada, 1980). Chlorophylls are the pigment-types known to contribute most to the harvesting of light-energy applied for photosynthesis (Gates et al., 1965) and are the most important absorbing leaf pigments in the green–red part of the spectrum. At lower wavelengths, light is also partially absorbed by carotenoids, which are less efficient in excitation energy transfer than chlorophylls (Merzlyak, 1996; Terashima et al., 2009). Additionally, pigments which do not contribute to photosynthesis absorb in the blue/violet/uv region (flavonoids; Havaux and Kloppstech, 2001) and in the green region (anthocyanins; Merzlyak et al., 2008).

Absorptance of rose leaves decreases to 70–80% at green wavelengths (520–560 nm), because of both higher transmittance and reflectance in this band. The red leaves contained a higher concentration of anthocyanins and showed a slightly higher absorptance of green light compared to the green leaves. Similar results have been observed in several species with leaves with different visual appearance (Burger and Edwards, 1996; Woodall et al., 1998; Neill and Gould, 1999), in which the differences in absorptance of green light were attributed to the contribution of anthocyanins (Gould et al., 1995; Smillie and Hetherington, 1999).

4.2. Leaf photosynthesis

In terms of photosynthesis, in the short term, red light is the most effective in rose cv 'Akito' in both leaf types. Previous papers

showed similar action spectra for a number of species and, similarly to our results, purple and red leaves had a higher absorptance but a lower photosynthesis efficiency than green leaves under green wavelengths (Inada, 1977; Burger and Edwards, 1996; Dodd et al., 1998; Gould et al., 2002). This inversion is in accordance to the higher content of anthocyanins. Particularly, it is known that these pigments, in the cell vacuole, can modify the photosynthetic performance of leaves by restricting the absorptance of green light by chloroplasts: according to the photoprotective hypothesis, they would function as "light filter", reducing the quantum fluence rate absorbed by chlorophyll (Gould et al., 2000).

4.3. Leaf vs. crop photosynthesis

As far as we know, no action spectra on crop level have been reported before. We achieved the action spectrum on crop level by using a model that explicitly simulates light extinction in a crop and integrates leaf photosynthesis into crop photosynthesis based on measured optical and photosynthetic properties of individual leaves. The model results showed an increased utilization of green light at canopy level relative to leaf level, as indicated by the presented absorptance and action spectra. More importantly, our results indicate that the action spectrum at crop level deviates from that at leaf level. Hence, findings at leaf level should not automatically be extrapolated to crop level without considering interactions within the crop.

4.4. Optimizing spectral output of lamps

Recently LED lamps have been introduced experimentally by commercial growers, raising questions to which extent production can be increased by choosing different spectrum than that of HPS lamps. Our results on the effect of different wavelengths on the instantaneous quantum yield suggest potential beneficial effects of optimizing the spectral output of assimilation light sources in roses. These effects are apparent at the leaf as well as the crop level, though they are smaller at crop than at leaf level. In particular, when leaves are reddish the advantage of optimising lamp spectrum is largest. For a rose crop with green leaves optimizing spectrum was estimated to increase instantaneous crop photosynthesis per incident photon up to 12% and for a crop with reddish leaves up to 17%, compared to HPS lamps. However, care is needed to draw conclusions from instantaneous effects. Indeed, whether this can result in comparable benefits in practise depends on the extent at which the short-term (instantaneous) spectral effects on leaf photosynthesis will sustain on the long term and how differences in the spectral emission applied by LEDs further influence crop physiology and morphology under a prolonged illumination (Hogewoning et al., 2007).

It is known that light quality affects morphogenesis and overall appearance of rose plants. For instance, an increased red/far red ratio on rose reduced plant height and increased leaf chlorophyll content (McMahon and Kelly, 1990) and the number of flowers (Roberts et al., 1993; Girault et al., 2008). These effects are probably phytochrome-mediated, as lateral branching is in other species (Mortensen and Stromme, 1987; Devlin et al., 2007). In this respect, further investigations are needed in order to evaluate potential spectral effects on physiology and morphology when the whole crop is illuminated for a prolonged period by a specific spectrum.

Acknowledgements

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