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Light response of photosynthesis and stomatal conductance of rose leaves in the canopy profile: the effect of lighting on the adaxial and the abaxial sides

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Abstract. We investigated the light response of leaf photosynthesis, stomatal conductance and optical properties in rose plants grown in a glasshouse with bending technique. Leaves were lighted from the adaxial or the abaxial side during measurements, performed in four positions in the upright and bent shoots: top leaves, middle leaves, bottom leaves, and bent shoot leaves. Moreover, the effect of the irradiation on the adaxial or abaxial leaf side on whole canopy photosynthesis was estimated through model simulation. No significant differences were found in light transmission, reflection and absorption of leaves and in photosynthesis light response curves among the four positions. In all the leaf positions, light absorption, stomatal conductance and photosynthesis were higher when leaves were lighted from the adaxial compared with the abaxial side. The model showed that a substantial part of the light absorbed by the crop originated from light reflected from the greenhouse floor, and thus the abaxial leaf properties have impact on whole crop light absorbance and photosynthesis. Simulations were performed for crops with leaf area index (LAI) 1, 2 and 3. Simulation at LAI 1 showed the highest reduction of simulated crop photosynthesis considering abaxial properties; however, to a lesser extent photosynthesis was also reduced at LAI 2 and 3. The overall results showed that the model may be helpful in designing crop systems for improved light utilisation by changing lamp position or level of leaf bending and pruning.

Additional keywords: absorptance, bent shoot, hydroponics, mechanistic model, reflectance, *Rosa hybrida*, transmittance.

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Introduction

In most plant species with upright growth, the adaxial (upper) and the abaxial (lower) leaf surfaces develop and function in different environments, with respect to both the prevailing light intensity (photosynthetic photon flux density, PPFD) and the light quality (wavelength composition). Specifically, adaxial surfaces are exposed to more direct radiation with higher light intensity (from solar radiation or artificial lighting) and broader spectra, whereas abaxial surfaces are shaded by the leaf blade itself and usually receive only ~10% of the light incident on the adaxial ones, transmitted through the mesophyll (self-transmitted light) and reflected from the surroundings (mainly leaf-reflected light), which is relatively enriched in green and far red light (Pemadasa 1979; Pospíšilová and Solárová 1987). Generally, the self-transmitted light, rather than the light reflected from the environment, is the major light source for the abaxial side (Wang *et al.* 2008).

Most studies concerning the differential response of leaf sides to light *stimuli* have focussed only on stomatal behaviour (Turner and Singh 1984; Wong *et al.* 1985; Yera *et al.* 1986; Lu *et al.* 1993). Different photosynthetic responses to lighting of the adaxial and abaxial sides were reported for a wide number of C₃ plant species usually grown in open field such as *Helianthus annuus* L. (Syvertsen and Cunningham 1979; Mott and O’Leary 1984; Wang *et al.* 2008), *Glycine max* L. (Terashima 1986), *Ricinus communis* L. (Postl and Bolhar-Nordenkamp 1992) and *Spinacia oleracea* L. (Sun and Nishio 2001).

The photosynthetic behaviour of adaxial and abaxial surfaces may differ because of several reasons, including distribution of stomata (amphistomatic and hypostomatic distribution) and anatomical and functional differences in palisade and mesophyll cells (Terashima and Takenaka 1990; Richardson *et al.* 2017). In some hypostomatic species (e.g. rose) under equal light intensity,

photosynthesis is higher under lighting on the adaxial than on the abaxial side (Mott and O'Leary 1984), and the relative difference increases as the irradiance increases (Syvertsen and Cunningham 1979; Proietti and Palliotti 1997).

In plants grown under natural light the outer leaves of a hedge row of the plant are differently irradiated than those inside and in lower positions of the canopy. In general, at equal light intensity, the photosynthesis in unshaded and younger leaves is higher than in the shaded and older ones, with higher saturating PPFD (Jones 1998; Lambers *et al.* 2008). Conversely, due to their developing at lower light intensity, shade-adapted leaves show a higher light use efficiency for CO₂ fixation at low light intensity compared with sun-adapted leaves (Palliotti and Cartechini 2001). Furthermore, in plants lighted from the top, difference between the adaxial and abaxial side may change depending on the depth in the canopy.

In open field cultivation, alternating exposure of adaxial (Ad) and abaxial (Ab) surfaces to sunlight naturally occurs as leaves sway because of wind. Alternating Ad-Ab-Ad irradiation to simulate this condition demonstrated that the alternating exposure of the leaf sides reduced both the net photosynthesis (P_n) and the P_n integral at leaf level compared with constant Ad-irradiation in of two trees (*Platanus orientalis* L. and *Melia azedarach* L.) and a herb (*Solanum lycopersicum* L.) (Zhang *et al.* 2016).

In soilless culture in greenhouses the floor is often covered by white plastic, reflecting light at the abaxial leaf sides from below. In addition, if intracanopy lighting (e.g. with LEDs) would be applied, an even greater proportion of light might be directed at abaxial leaf surfaces. Both these conditions make the study of light on the abaxial side of leaves highly relevant.

In many greenhouse crops, manipulations of the plant architecture are applied to increase the light interception and to optimise the photosynthesis efficiency of the different leaf layers (Buck-Sorlin *et al.* 2011). For instance, in cut rose crops, shoot bending results in an increased photosynthetically active surface per plant, by forming an extended horizontal canopy (Kim *et al.* 2004). This technique can provide several advantages, such as an enhancement in plant growth rate and in number and length of the flower stems (Kool and Lenssen 1997), because bent canopy acts as a reserve pool of assimilates for the growth of upright flower shoots, particularly in low light intensity conditions and after harvest of the upright flower shoots (Baille *et al.* 2006; Gutierrez Colomer *et al.* 2006; González-Real *et al.* 2007).

Information about the response of photosynthesis to artificial lighting (Baille *et al.* 1996; Gonzalez-Real and Baille 2000) and gas exchange-based crop simulation models (Pasian and Lieth 1989; Kim and Lieth 2003; Buck-Sorlin *et al.* 2011) is available for rose plants managed by classical techniques without bent shoots. Some studies also investigated photosynthesis in plants grown hydroponically with the bending technique, with respect to the different position in the plant profile (Pien *et al.* 2001; Kim *et al.* 2004; González-Real *et al.* 2007). The rate of leaf gas exchange (net photosynthesis, stomatal conductance and transpiration rate) of the bent canopy is lower than that of

upright shoot (Kim *et al.* 2004; González-Real *et al.* 2007), such that the lowest leaves might not always contribute to the carbon gain and, ultimately might become parasitic under low light conditions (Pien *et al.* 2001).

In greenhouse production under artificial lighting, lamps are usually mounted above the crop, providing imbalanced light distribution along the canopy profile. Greater benefits could be achieved by lighting plants more uniformly along the vertical profile and by increasing the light penetration into the inner part, preventing the lower and inner leaves being below the compensation point (Aikman 1989). Accordingly, inter-lighting, performed by placing lamps in between of the plant rows, has been applied in several vegetable crops, such as cucumber (Hovi-Pekkanen and Tahvonen 2008; Trouwborst *et al.* 2010) and tomato (Dueck *et al.* 2012; Tewolde *et al.* 2016). This lighting strategy aims to improve the energy budget and the photosynthetic efficiency of whole plants, by enhancing the contribution of lower and inner leaves to carbon gain. However, in inter-lighting systems a reasonable fraction of light may irradiate the abaxial side of the leaves, raising the question about the effects of lighting on abaxial instead than on adaxial leaf surface.

At present, information about the light response of the abaxial leaf side in terms of photosynthesis and stomatal conductance regarding the effects of leaf age and position and the related light adaptation in the canopy is limited. Further, to the best of our knowledge, no data is currently available for ornamental crops such as roses. Consistent with the above-mentioned results, leaves in different positions along the plant profile might show differences in the response to the light intensity and to the direction of lighting, on the adaxial or the abaxial leaf side.

The aim of the present experiment was to investigate the response of photosynthesis and stomatal conductance to light intensity and the leaf optical properties in intact leaves of rose for cut flowers, grown with the bending technique, in relation to the following variables: leaf side lighted (adaxial vs abaxial), leaf position in the canopy (leaves of bent shoot and bottom, middle and top part of upright shoot). We reported preliminary results of this experiment, for only net photosynthesis in only middle leaves, in Paradiso and Marcelis (2012). In the present paper, we show detailed results of net photosynthesis and stomatal conductance in all the leaf layers mentioned, as a function of the direction of lighting. In addition, the consequence of irradiating the adaxial or the abaxial leaf side on the whole canopy photosynthesis was estimated through modelling the light gradient through the canopy (i.e. crop) and the photosynthesis of the different leaf layers. The role of the abaxial properties has to our knowledge not been considered before in canopy photosynthesis modelling. Consequently, the model has been adapted to compute the impact of the abaxial leaf side.

Materials and methods

Plant material and growth conditions

The experiment was conducted in Wageningen (the Netherlands, latitude 51°58'N, longitude 5°40'E), in a

heated experimental glasshouse. Plants of rose (*Rosa hybrida* L.) cultivar 'Akito' were grown with bent shoot technique on rockwool slabs, in a 144-m² compartment. Cuttings were transplanted on 25 February 2008, in double rows, 25 cm apart, with an in-row spacing of 0.20 m (plant density 6.5 plants m⁻²). During the experiment, from the beginning of October to the end of November, the temperature inside the greenhouse was 18.2°C on average during the night (heating set point of 17.5°C) and 21.1°C during the day (heating set point of 21°C).

Supplemental lighting was performed by High Pressure Sodium lamps (Philips SON-T Green Power 600 W; Koninklijke Philips Electronics N.V.). Lamps switched on when global radiation dropped below 200 W m⁻² and switched off when it exceeded 250 W m⁻², extending the natural day length to 16 h (0300 to 1900 hours). During the daytime, a mist system was used to maintain the relative humidity around 70% and CO₂ concentration in the air was kept around 500 micromol mol⁻¹.

Plants were managed with the bending technique, bending the weaker shoots and the blind stems down into the paths and leaving the harvestable flower stems to form the upright canopy (Kool 1997). Water and fertilisers were supplied via a drip-system, which was automatically controlled by a fertigation computer. Details on crop management are reported by Paradiso *et al.* (2011).

Measurements of gas exchanges, leaf optical properties and specific leaf weight

Measurements were conducted considering the following variables: (i) the 4-leaf position in the upright and bent canopy. From the bent shoot (BS), old, penta-foliolate leaves were used. From the upright shoots (US), bottom leaves (old, epta-foliolate leaves; US-BL), middle leaves (middle age, penta-foliolate leaves; US-ML), top leaves (young, tri-foliolate leaves; US-TL) were taken; and (ii) two directions of lighting during gas-exchange measurements: on the adaxial leaf side (Ad), on the abaxial leaf side (Ab).

Measurements were performed during the fourth week of the growing cycle (starting from the day that all upright shoots were pruned, October 6), on bent shoots and on upright shoots with 13–16 leaves, with small flower bud just visible (Fig. 1). All sampled leaves were fully expanded and presented the following characteristics: BS) randomly chosen in the bent canopy (28 days from the unfolding); BL) from the 10th and the 12th leaf from the top of the stem (16 days from the unfolding); ML) from the 6th and the 8th (11 days from the unfolding); TL) within the 2nd and the 3th (6 days from the unfolding).

Net photosynthesis and stomatal conductance were measured on the top leaflet, with a portable photosynthesis open system (LCpro), connected to a 6.25 cm² leaf chamber. Measurements in leaves lighted abaxially were performed by rotating the leaf chamber upside down. Light saturation curves were performed at decreasing levels of light intensity (PPFD of 1500, 1000, 500, 250, 100, 50 and 0 μmol m⁻² s⁻¹, by using a red-blue LED array (85% red, emission peak at 655nm + 15% blue, emission peak at 465 nm). Measurements lasted 10 min at

1500 μmol m⁻² s⁻¹ PPFD, 5 min in all the intermediate light levels and 15 min in the darkness. At each light intensity one measurement per minute was logged, with a total number of 10, 5 and 15 measurements respectively. From these data, only the last three values were selected (after 7, 2 and 12 min of adaptation respectively), in order to obtain a reliable average value. The conditions inside the leaf chamber were kept constant (temperature 25°C, CO₂ concentration 400 ppm, RH 70%, air flow rate 250 mL min⁻¹). Photosynthesis was calculated by the software operating in LCpro according to von Caemmerer and Farquhar (1981).

After the photosynthesis measurements, the top leaflet of sampled leaves was removed and leaf transmission (Tr) and reflection (Ref) spectra were measured between 400 and 750 nm (bandwidth 1 nm), with a spectrophotometer (Perkin Elmer Lambda 950 UV/NIR; Perkin Elmer Inc.). 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 the measurements, the leaves were illuminated from the top side for the adaxial leaf properties and from the bottom side for the abaxial leaf properties, and the direction of the collimated light was perpendicular to the leaf plane. Leaf absorbance (Abs) at the used wavelengths was calculated as Abs = 100 – (Ref + Tr). All values were expressed as percentage of the incoming light.

Measurements of gas exchanges and leaf optical properties on adaxial- and abaxial-lighted leaves were performed on the same leaf sample, in four plants randomly chosen in the compartment (one type of leaf per plant), and the sequence of the measurements (leaf position, leaf side) was completely randomised. At the end of the physiological measurements, specific leaf weight (SLW, in mg fresh weight per cm² of leaf) was measured on the top leaflet of 10 leaves per leaf type.

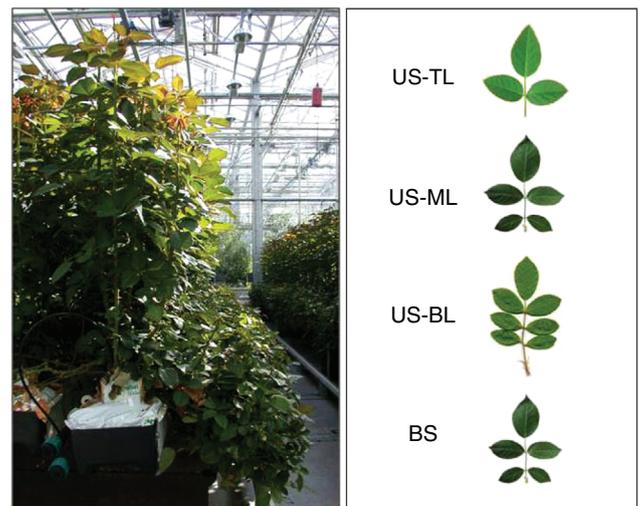


Fig. 1. Plant canopy profile of rose cultivar 'Akito' grown with bent shoot technique on rockwool slabs and (to the right) particular of the different type of leaves in the different positions in the upright and bent canopy.

Modelling of photosynthetic parameters at canopy level

Model calculations were carried out with a mechanistic photosynthesis model based on Farquhar *et al.* (1980). According to this model, there is a cubic relationship between the rate of photosynthesis and light level, which also depends on CO₂-concentration. CO₂-assimilation is modelled for C₃ plants and shows temperature-dependent kinetics describing the CO₂-binding effects of the enzyme Rubisco. The model subsequently calculates photosynthesis based on the most rate-limiting factor, either light or CO₂. On basis of the measured light-response (LR) curves, for leaves at four different canopy levels (bent canopy leaves, and low, medium and high positioned leaves on the upright shoot) photosynthetic parameters were fitted using a genetic algorithm based on Goldberg (1989). The genetic algorithm used 20 populations that converged to a solution in 20 generations and a mutation factor of 0.1 per generation. For reaching the fit, the three following parameters were varied in a specific range: maximal rate of electron transport (J_{\max} , between 50 and 625 $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$), the curvature of the LR curve (θ , between 0.2 and 0.56 unitless), quantum efficiency (α , between 0.15 and 0.42 in $\mu\text{mol electrons } \mu\text{mol}^{-1}$ photons). According to Wullschlegel (1993) the maximum carboxylation rate ($V_{C_{\max}}$) was assumed at a value of $1/2 J_{\max}$ (in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The values were fitted for adaxial and abaxial leaf sides separately, and likewise incorporated in the model. Light reflection and absorption were simulated for each of five canopy levels (the bent canopy is split in two levels) using the five-point Gaussian integral of the Lambert-Beer's law for exponential decay of the light level (see, for example, Ross 1981; Marcelis *et al.* 1998), for both the downward light gradient and the upward gradient of light reflected from the greenhouse floor. The reflectance and transmittance by leaves were different for these two light directions and were based on the measurements of adaxial and abaxial leaf surface per canopy layer.

The contribution of floor reflected light to crop absorption and photosynthesis was estimated by comparing model calculations that included or excluded light absorption of the abaxial side of leaves. Light incident on abaxial side originated from greenhouse floor reflection (the assumed PAR reflectance from the floor was 40%; this included reflection from a concrete, white-painted floor, as well as heating pipes and slabs covered with white plastic). The backscatter and subsequent absorption of downward light reflecting from adaxial surface of lower leaves could not be distinguished separately, being implicitly accounted for in the Lambert-Beer extinction of downward light. The same holds for backscatter from abaxial leaf side of soil reflected light. The effect of incorporating observed abaxial photosynthetic properties instead of using adaxial properties for both leaf sides was tested for gross crop photosynthesis by combining three separate model runs as follows: (A) floor reflected light NOT used by the plant, photosynthetic parameters according to adaxial measurements and optical properties according to values of adaxial measurements; (B) floor reflected light NOT used by the plant, photosynthetic parameters according to abaxial measurements and optical properties according to values of adaxial measurements; and (C) floor reflected

light is used, photosynthetic parameters according to abaxial measurements; optical properties different for both leaf sides.

Photosynthesis at the leaf level was calculated based on sum of light absorbed from adaxial and abaxial side. The difference in gross crop photosynthesis between B and C is an estimate of the additional crop photosynthesis due to reflected light. Adding this difference to the crop photosynthesis of A (hence $A + (C - B)$), results in an estimate of photosynthesis of a canopy, that considers reflected light and different optical and photosynthetic properties of the two sides of a leaf. This estimate by the modified model is compared with the default model (A) that uses adaxial optical and photosynthetic properties for both leaf sides and includes reflected light as well. The comparisons are carried out for two light levels (100 and 500 $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ diffuse light above the crop) and three crop sizes (leaf area index, LAI 1, 2 and 3).

Statistical analysis

All experimental data were analysed by two-way analysis of variance (ANOVA). To compare the means of the treatments for each parameter measured, Tukey's *post hoc* tests were performed at significance levels of $P \leq 0.05$ and $P \leq 0.01$. The correspondence between simulated and observed gross photosynthesis per shoot type was realised by optimising the most influential parameters of the photosynthesis model using a genetic algorithm (GA) based on Goldberg (1989), see above. Since the fit per canopy level and leaf side was done for their average light-response curve and could thus not be replicated, parameter values among the different fits could not be statistically tested by non-existence of repetition, except for values of A_{\max} . A proxy for the variation of J_{\max} values was derived from a fit on the replicate datasets and statistically tested between replicates, while keeping the values of α and θ constant.

Results

Leaf optical properties

Rose leaves from different positions in the canopy profile showed similar optical properties in the visible spectrum. As example, Fig. 2 shows typical spectra of light transmission, reflection and absorption obtained in the middle leaves of the upright shoot (US-ML). Rose leaves lighted from the adaxial side showed low values of transmission and reflection of violet (400–455 nm) and blue (455–500 nm) light, slightly higher levels in the green region (500–580 nm), followed by a decrease in the red light (620–700 nm) and a drastic increase in the far red (from 700 nm). As a consequence, absorption was high from 400 to 500 nm and around 670–690 nm, but showed a depression from 500 to 650 nm and a large drop from 700 nm (Fig. 2). Optical properties of abaxial side of leaves followed similar pattern as those of adaxial leaf side. However, light reflection and to a small extent also light transmission were higher for abaxial leaf side compared with adaxial, with consequent lower values in light absorption (Fig. 2).

Averaged over the whole visible spectrum (400–700 nm) and leaf layers, rose leaves lighted from the adaxial side transmitted 4.5%, reflected 5.8% and absorbed 89.7% of the

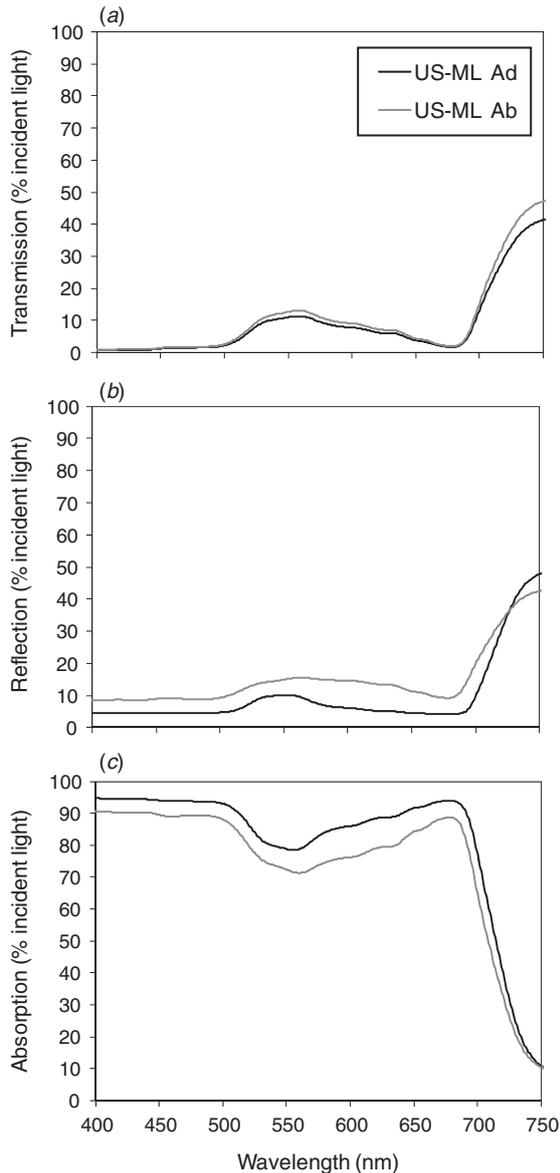


Fig. 2. Transmission (a), reflection (b) and absorption (c) spectra in middle leaves of upright shoot (US-ML) of rose cultivar 'Akito' as a function of lighting from the adaxial (Ad) and the abaxial (Ab) leaf sides ($n = 4$).

incident light (Table 1). Lighting from the abaxial side increased the average value of transmission to 5.60% and of reflection to 11.34%, with a consequent decrease of absorption to 83.06% (Table 1). Within the PAR range, green light had lowest absorption in both adaxial- and abaxial-lighted leaves, in all the leaf positions, because of increase in both light reflection and transmission (Table 1). Differences between the leaf sides were stronger in reflection than in transmission (Table 1).

The average absorption of the blue-red light of the LC Pro LED array of the photosynthesis system was slightly higher compared with the white light used in spectrophotometer, in both adaxial- and abaxial-lighted leaves (Table 1).

Photosynthesis and stomatal conductance and Specific leaf weight

When light was provided on the adaxial leaf side, at each light intensity, net photosynthesis was not different ($P \leq 0.05$) among the different leaf positions within the canopy, even though a tendency to increasing values from the basal to the top positions was observed at the higher light intensities ($>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 3). Particularly, no significant difference was found among the leaf layers in the saturation rate of photosynthesis ($11.5 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ on average around $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD) (Fig. 3).

At all the light intensities, net photosynthesis was lower when the leaf was lighted on the abaxial side compared with adaxial side, with no substantial differences among the leaf layers (Fig. 3). The decrease in maximum net photosynthesis in abaxially-lighted leaves compared with adaxially-lighted leaves was smaller in the lower positions in the canopy (-16% in BS and -18% in US-BL), whereas it increased moving to the upper leaves of the upright shoot (-22% in US-ML and -33% in US-TL) (Table 2).

In leaves lighted from the adaxial side, the maximum capacity of net CO_2 assimilation (A_{max}) and the electron transport rate (J_{max}) seemed to decrease as the distance from the top of the canopy increased, however differences among the leaf positions were found to be not significantly different (Fig. 4; Table 2). These more shade-adapted properties seemed to show up less in the bent shoot leaves (BS) that had a tendency for a higher A_{max} , both ad- and abaxially, then the US-BL and US-ML leaves (Table 2).

The lighting provided on the different leaf sides influenced significantly the photosynthesis parameters (Table 2). Specifically, lighting on the abaxial side reduced the maximum rate of electron transport (J_{max}) and the linear electron transport efficiency (α), according to the mean of all the leaf positions along the plant profile (Table 2).

Light response curves of stomatal conductance showed different reactions to the light intensity in the different leaf layers of the canopy (Fig. 5). When leaves were lighted from the adaxial side, stomatal conductance was lower and similar in the leaves of the bent shoots and of the lower part of the upright shoot (Fig. 5). Specifically, stomatal conductance increased from $0.32 \text{ mmol m}^{-2} \text{s}^{-1}$ (PPFD $100 \mu\text{mol m}^{-2} \text{s}^{-1}$) to $0.53 \text{ mmol m}^{-2} \text{s}^{-1}$ (PPFD $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) on the average of BS and US-BL, while it raised to 0.46 (PPFD $100 \mu\text{mol m}^{-2} \text{s}^{-1}$) and to 1.02 (PPFD $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) on average in US-ML and TL (Fig. 5).

Stomatal conductance was always lower in leaves lighted from the abaxial side (Fig. 5). In this case, leaves in the middle part of the upright shoot showed higher values than those in the other positions ($0.616 \text{ mmol m}^{-2} \text{s}^{-1}$ in US-ML compared with 0.319 in BS, 0.233 in US-BL, and $0.391 \text{ mmol m}^{-2} \text{s}^{-1}$ in US-TL) (Fig. 5).

Differences in stomatal conductance between adaxial- and abaxial-lighted leaves were smaller in leaves the lower plant positions, and they increased from the bent shoot to the top of the upright shoot (Fig. 4).

Specific leaf weight of the top leaflet of rose leaves changed with the leaf position, with higher value in the youngest leaves

Table 1. Average values of leaf absorption (Abs), transmission (Tr) and reflection (Ref) of rose cultivar ‘Akito’ in the visible portion of the spectrum (400 – 700 nm) and estimated absorption of red-blue light under the LcPro LED lamp (85% red, 15% blue), as a function of lighting from the adaxial (Ad) and the abaxial (Ab) sides, in the canopy layers: bent shoot (BS) and upright shoot (US), top leaves (TL), middle leaves (ML) and bottom leaves (BL)

Values are means ($n = 3$); different letters indicate significant differences at $P < 0.05$ within each column

		Visible spectrum 400–700 nm			Green region 500–580 nm			LED array LcPro ⁺
		Tr	Ref	Abs	Tr	Ref	Abs	Abs
BS	Ad	4.40ab	5.68b	89.92a	7.38a	7.39b	85.23a	92.01a
	Ab	5.61ab	10.75a	83.64b	9.54a	11.01ab	79.45ab	84.99b
US BL	Ad	4.14b	5.75b	90.11a	7.17a	7.58b	85.25a	92.35a
	Ab	5.20ab	11.8a	83.01b	9.17a	13.17a	77.66b	85.09b
US ML	Ad	4.90b	5.86b	89.25a	8.52a	8.12b	83.36ab	92.01a
	Ab	5.67ab	11.71a	82.62b	9.83a	13.62a	76.55b	85.16b
US TL	Ad	4.64b	5.78b	89.58a	6.18a	6.92b	86.90a	90.92a
	Ab	5.93a	11.12a	82.95b	7.68a	11.28a	81.04ab	83.01b

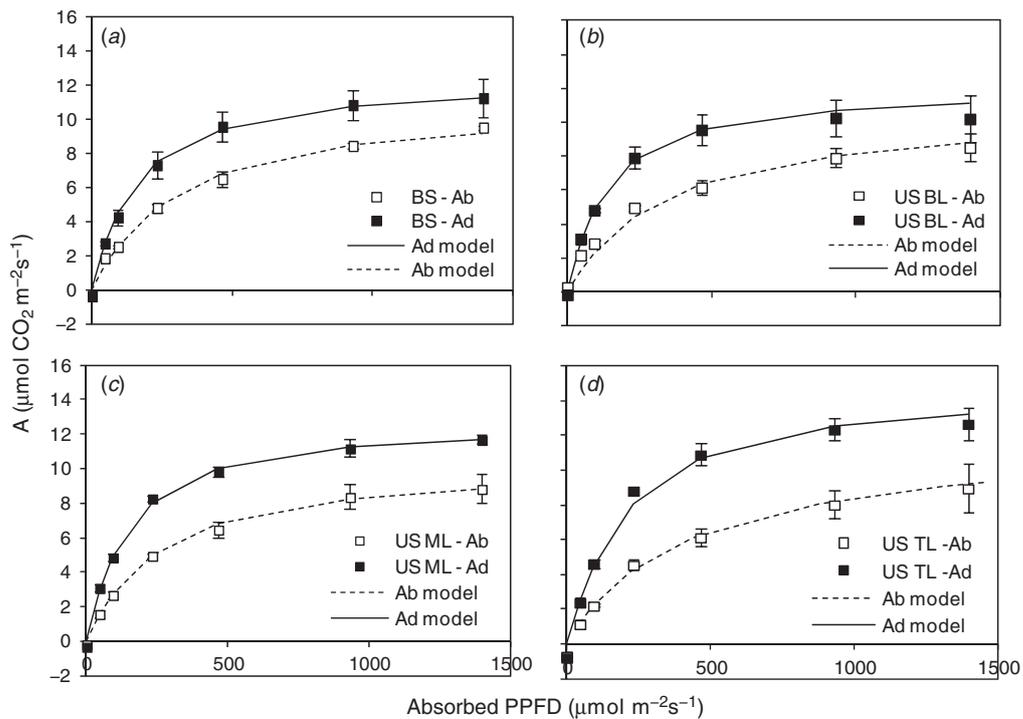


Fig. 3. Light response curves of net photosynthesis of rose cultivar ‘Akito’ as a function of lighting from the adaxial (Ad) and the abaxial (Ab) leaf sides in the canopy layers: (a) bent shoot (BS), (b) upright shoot bottom leaves (US-BL), (c) upright shoot middle leaves (US-ML), (d) upright shoot top leaves (US-TL) (means \pm s.e., $n = 4$).

on the top of the upright shoot (16.28 vs 12.63 mg cm⁻² on the average of all the other positions) (Fig. 6).

Modelling the consequences of leaf optical and photosynthetic properties on photosynthesis at canopy level

According to the simulations, the contribution of light reflected from the greenhouse floor to absorbed light of the crop increased from ~3.5% at LAI 3 to 15% at LAI 1

(Table 3). This resulted in a higher impact of incorporating abaxial properties in the simulation model at lower LAI.

When the observed optical and photosynthesis abaxial characteristics were used for the modelled abaxial leaf surface (adaxial and abaxial) instead of applying the adaxial properties to both leaf sides (adaxial and adaxial) the simulated photosynthesis dropped (Table 3). At 100 μmol PAR m⁻² s⁻¹ this drop was bigger the lower the LAI (5.4% at LAI 1, see Table 3). At 500 μmol PAR m⁻² s⁻¹, photosynthesis only

Table 2. Average values of photosynthesis parameters as a function of lighting from the adaxial (Ad) and the abaxial (Ab) leaf sides, in the canopy layers: bent shoot (BS) and upright shoot top leaves (US-TL), middle leaves (US-ML), bottom leaves (US-BL), of rose cultivar ‘Akito’ grown with shoot bending technique (means, $n = 4$) Maximum rate of electron transport (J_{\max} , $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$); linear electron transport efficiency (α , $\mu\text{mol electrons per } \mu\text{mol photons}$); curvature factor of light response curve (θ , unitless); light saturated net CO_2 assimilation (A_{\max} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$). For A_{\max} , mean values, $n = 3$; different letters indicate significant difference at $P < 0.05$ within each column

Leaf	Surface	J_{\max} ($\mu\text{mol electrons m}^{-2} \text{s}^{-1}$)	α ($\mu\text{mol electrons per } \mu\text{mol photons}$)	θ	A_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$)
BS	Ad	71.14	0.26	0.42	11.32a
	Ab	62.92	0.18	0.21	9.53b
US BL	Ad	69.66	0.42	0.28	10.47a
	Ab	60.39	0.16	0.27	8.55b
US ML	Ad	73.31	0.42	0.28	11.36a
	Ab	58.71	0.20	0.21	8.90b
US ML	Ad	90.45	0.33	0.33	12.79a
	Ab	62.08	0.31	0.35	8.52b

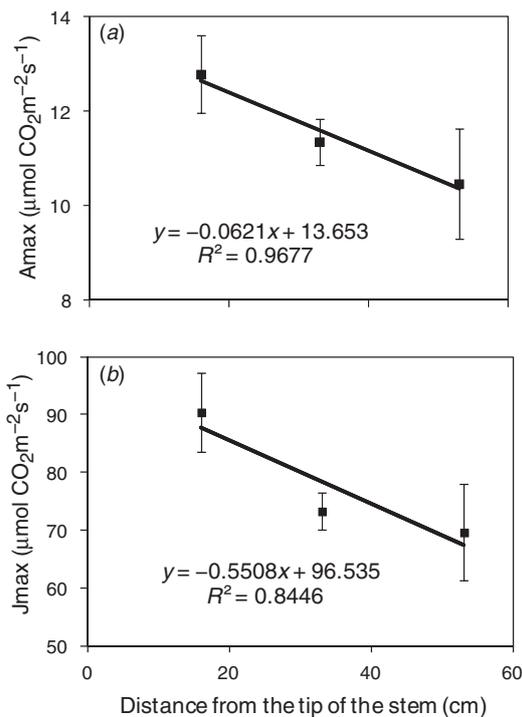


Fig. 4. Maximum capacity of net CO_2 assimilation (A_{\max} ; a) and electron transport rate (J_{\max} ; b) of rose cultivar ‘Akito’ as a function of the distance from the top of the canopy (leaf lighted from the adaxial side; means \pm s.e., $n = 4$). Values at 16, 33, and 53 cm correspond to top leaves (TL), middle leaves (ML) and bottom leaves (BL) of the upright shoot respectively.

slightly decreased (1–2%). At LAI 1 the absorption of floor reflected light is considerable: 10% of the total incoming light and 15% of total crop absorption; at LAI 3 only 3% of incoming light was absorbed via floor reflection. The photosynthesis in absolute amounts is most negatively affected by applying adaxial and abaxial instead of adaxial and adaxial properties: at lower light intensity for smaller LAI (-0.20 in LAI 1 vs $-0.11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ at LAI 3), whereas

the larger LAI is more sensitive at higher light levels (LAI 3: -0.24 vs $-0.07 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ at LAI 1) (Table 3).

Discussion

In leaves lighted from the adaxial side, light response curves revealed a tendency to increasing values of photosynthesis from the basal to the top positions of the upright shoot at the higher light intensities, even though the differences among the leaf layers were found to be not significant. It may be hypothesised that such tendency may be ascribed to increasing leaf nitrogen content as found by Gonzalez-Real and Baille (2000).

Accordingly, the maximum photosynthetic capacity and the rate of electron transport showed a tendency to increasing values from the basal to the top leaves. In rose plants grown with the bent shoot technique, González-Real *et al.* (2007) found similar gradient in photosynthetic capacity along the flower shoot, with lower values of maximum net CO_2 assimilation and maximum photosynthetic Rubisco capacity in the basal compared with the uppermost leaves, in parallel to the decrease in the light extinction. Differences of photosynthesis in leaves in diverse positions along the stem depend on the different photosynthetic performance due to the different age of leaf tissues, and also to the different light environment to which leaves are exposed during their development. Indeed, young top leaves exhibit higher photosynthetic rate compared the old basal ones because they perform photosynthesis more efficiently, but also because they are always exposed to higher irradiance level. Depending on position in the canopy, leaves are exposed to a different light spectrum, with top leaves receiving a higher fraction of blue and red light compared with those positioned at the lower layers, which excite the photosynthetic apparatus more efficiently than at other visible wavelengths (Arena *et al.* 2016; Amitrano *et al.* 2018).

In the present experiment, bent shoot leaves did not show lower photosynthesis compared with upright shoot leaves. This result can be ascribed to the young age of the bent shoot leaves due to the recent pruning and to the good exposition to light of

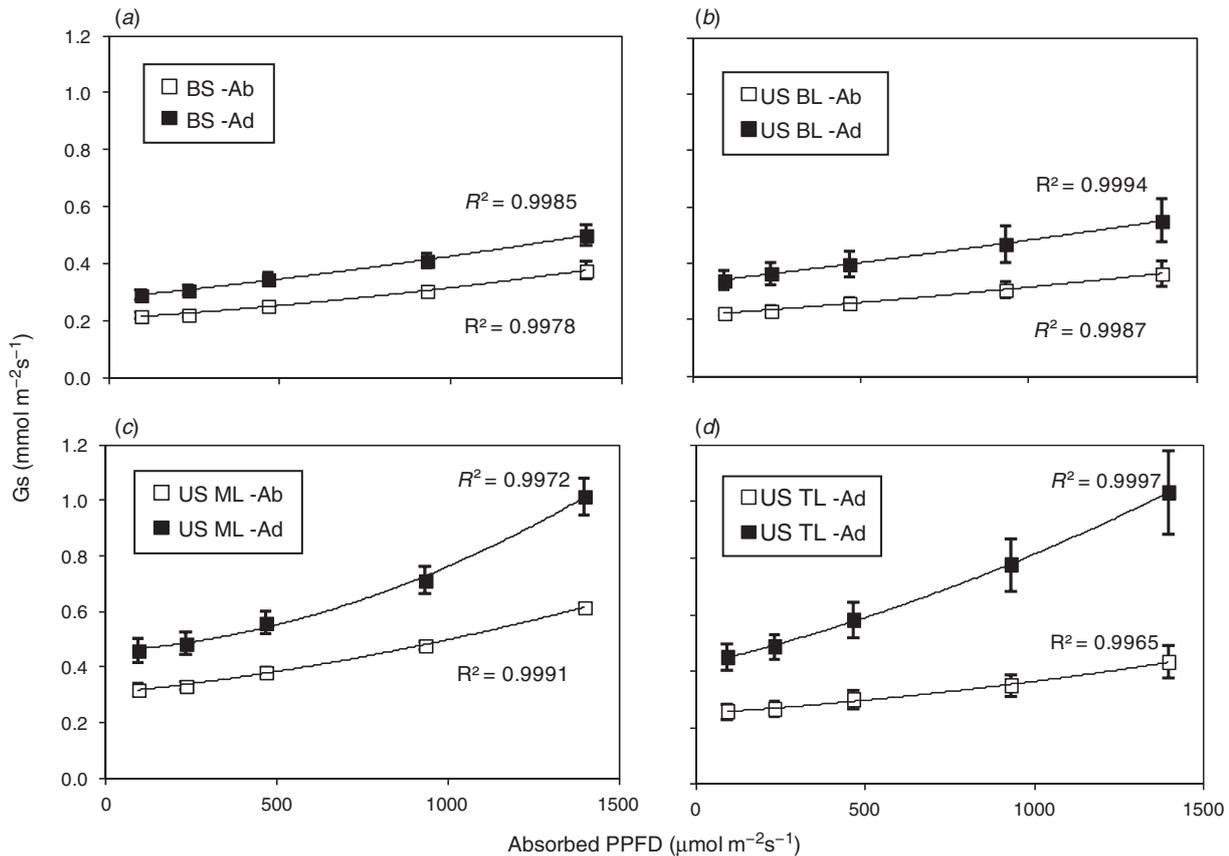


Fig. 5. Light response curves of stomatal conductance of rose cultivar 'Akito' as a function of lighting from the adaxial (Ad) and the abaxial (Ab) leaf sides in the canopy layers: (a) bent shoot (BS), (b) upright shoot bottom leaves (US-BL), (c) upright shoot middle leaves (US-ML), (d) upright shoot top leaves (US-TL) (means \pm s.e., $n = 4$).

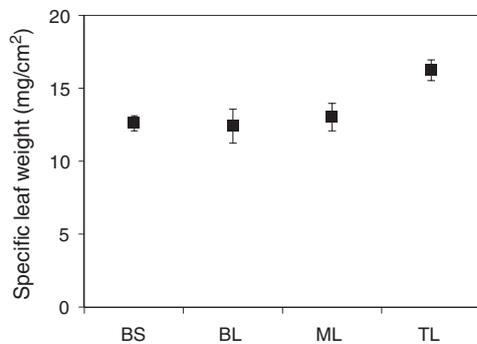


Fig. 6. Average values of specific leaf weight (SLW, mg FW cm^{-2} leaf) in the canopy layers: bent shoot (BS) and upright shoot (US), bottom leaves (BL), middle leaves (ML) and top leaves (TL) (means \pm s.e., $n = 10$).

the bent canopy in the first weeks after bending, when this canopy was still regularly shaped. In addition, Kim *et al.* (2004) found that differences in photosynthesis were no longer observed 3 weeks after bending. However, we found significant differences in the specific leaf weight with leaves in the basal and middle part of the plant lighter than those in the top part. This agrees with the decline of specific leaf weight of the bent shoots and older leaves of rose during fall and winter, which suggests a partial remobilisation of assimilates from the

leaf lamina to the young developing leaves and flowers (González-Real *et al.* 2007).

The rate of net photosynthesis in rose leaves was higher when light was applied to the adaxial rather than on the abaxial side, as observed in other species with leaf bifacial anatomy (Syvertsen and Cunningham 1979; Proietti and Palliotti 1997). In the comparison among leaf layers, it may be hypothesised that in leaves lighted from the adaxial side photosynthesis is higher because the photosynthetic apparatus is naturally predisposed to receive a large amount of light of a certain percentage of red and blue useful for photosynthesis. In addition, the different photosynthetic response to the light direction may also depend on different efficiency in light absorption and transport to chloroplasts, in leaves lighted on the two sides. Indeed, in leaf bifacial anatomy, typical arrangement of tissues consists of palisade mesophyll, underneath the epidermis of the adaxial side, and spongy mesophyll, adjacent to the epidermis of the abaxial side (Vogelman *et al.* 1996; Evans 1999). In palisade mesophyll, cells are columnar shaped, vertically oriented and tightly packed: this regular arrangement enables light to penetrate deeply into the leaf, spreading light more evenly among palisade cells, where most the chloroplasts are concentrated. In contrast, in spongy mesophyll, cells are irregular shaped and distributed and loosely packed, with more intercellular air

Table 3. Momentary crop light absorption and gross photosynthesis modelled for three leaf areas indices (LAIs) and two light levels

Optical and photosynthetic properties of adaxial and abaxial leaf sides were based on observed adaxial (Ad and Ad) or adaxial and abaxial (Ad and Ab) properties respectively. The difference in photosynthesis indicates the percentage change in photosynthesis when in the model ad and ab was used instead of Ad and Ad. PAR, photosynthetically active radiation

LAI	Light level ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$)	PAR abs ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)		Gross crop photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)		
		From above	Reflected	Ad and Ad	Ad and Ab	Difference (%)
1	100	53	10	3.71	3.51	-5.4
1	500	268	46	8.70	8.63	-0.8
2	100	77	6	5.33	5.15	-3.4
2	500	389	31	14.59	14.39	-1.4
3	100	89	3	5.99	5.88	-1.8
3	500	443	16	18.00	17.76	-1.3

space that scatter and reflect light, lengthening the photon paths to the chloroplasts. As a consequence, when the leaf is lighted adaxially, photosynthesis takes place in the palisade mesophyll, but also the spongy mesophyll receives a substantial amount of light filtering through the palisade cells (sieve effect; Vogelmann 1993), and does contribute relevantly to the leaf photosynthesis (40% in *Vicia faba*; Nishio *et al.* 1993). Conversely, under abaxial lighting, light penetration to the palisade mesophyll is limited because of the high scattering and absorption in spongy mesophyll, including a considerable absorption by photosynthetically inactive materials (Terashima and Saeki 1985). Sun and Nishio (2001) summarised that under adaxial lighting palisade cells act as a light guide to the underlying spongy cells, while under abaxial lighting spongy cells acts like a light trap. The lower photosynthesis of leaves when lighted from the abaxial side compared with the adaxial side was due to both a lower light absorption and a lower quantum yield (photosynthesis per absorbed light unit). Further, the palisade mesophyll has a more efficient structure than the spongy mesophyll for photosynthesis, because of the combination of better light penetration and higher photosynthetic capacity, due to the higher chloroplast and Rubisco concentration (Evans 1999). In spinach bifacial leaves, the rate of CO₂ fixation across the leaf profile reflects the Rubisco concentration and activity and, even more, the Rubisco/chlorophyll ratio, which is higher in palisade mesophyll than in spongy mesophyll (Sun and Nishio 2001). In addition, the rate of photosynthesis within the leaf is affected by light gradient and quality (Terashima and Saeki 1985; Vogelman *et al.* 1996) and variable CO₂ concentration (Farquhar *et al.* 1980). The intra-leaf light gradient generates sun- and shade-type chloroplasts (Terashima 1986).

The difference in photosynthesis between the illumination provided at adaxial and abaxial is reduced when moving along the canopy layer from top to bottom. This may be due to the fact that the bent shoots receive less light during the growth compared with upper and middle leaves and are thus acclimated to low light. This is consistent with the lower electron transport in BS compared with US-TL leaves. In fact, it is well known that as canopy develops, the leaves in the lower positions adapt an acclimation strategy in which various leaf traits are adjusted to optimise resource use with increasing shade (Niinemets *et al.*

2015). More specifically, compared with sun-adapted leaves, shade-adapted leaves exhibit some morpho-anatomical and physiological modifications such as lower lamina thickness, higher chlorophylls and carotenoids content, lower ribulose biphosphate carboxylase concentration (Terashima and Takenaka 1990; Yamori *et al.* 2010), as well as a higher light use efficiency for fixing CO₂ at low light intensity (Palliotti and Cartechini 2001; Pignou *et al.* 2017).

In middle and top leaves lighted adaxially, stomatal conductance increased with the irradiance level, whereas the same leaves were less responsive to the increasing light when lighted abaxially. Conversely, in bent shoot and basal leaves stomatal conductance was lower and much less responsive to increasing light, and differences between the directions of lighting on the adaxial or abaxial side were smaller. We hypothesise that this dissimilar response is presumably due to the different capacity to utilise in photochemistry the absorbed light by leaves occupying different canopy layers. It has been demonstrated that plant architecture may significantly affect the light absorption and photosynthesis in tomato (Sarlikioti *et al.* 2011), thus the leaf position into the canopy may be a strong determinant in enhancing or reducing the amount of intercepted light that will drive the light reactions of photosynthesis.

Moreover, the increase of stomatal conductance with light in both middle and top leaves lighted adaxially, favouring a higher CO₂ diffusion to the carboxylation sites, promotes the photosynthetic performance in these leaves compared with the others.

It is also important to consider that, within the canopy, not only the light intensity but also its spectral composition may vary, influencing significantly the photosynthesis (Théry 2001). Under our experimental conditions, leaves from the upper layers of the canopy receive not only more light compared with the basal leaves, but also a light regime rich in red and blue wavelengths, that stimulates the stomatal opening in leaves at the upper positions more than the green enriched light which act on leaves at the lower positions (Arená *et al.* 2016; Izzo *et al.* 2019). In contrast, the different leaf structure of middle and top leaves compared with basal leaves (sun- v. shade- adapted leaves) also concurs to explain the apparent diverse photosynthetic behaviour of the upper leaves.

Stomatal conductance mimics net photosynthesis, with values in leaves lighted from the adaxial side always higher than those of leaves lighted from the abaxial side, indicating no stomatal limitation to gas exchanges in our experimental conditions.

It should be noted that all plants were grown in the same conditions and that illumination direction was only varied during the gas exchange measurements. When plants would have been grown for a prolonged period with illumination from below or above the leaves might have acclimated and hence might have shown a different response than instantaneous measurements of the present study.

Mechanistic crop growth models have been in use for several decades, yet their focus on physiological processes has gone at the expense of architectural functionality. Recently, functional–structural plant (FSP) models have addressed structure explicitly, and are able to involve optical properties for their 3D objects (Vos *et al.* 2010). The disadvantage of FSP models is their requirement of extensive datasets for calibration. Thus, we used our current mechanistic functional model and used its possibility to activate or inactivate the up- and downward flux of light. In this way the impact of abaxial leaf properties were estimated to affect crop photosynthesis to a limited extent (0–5% decrease relative to applying adaxial properties for both leaf sides). Moreover, at higher LAI and light level the model showed that the impact was less, in relative terms, as might be explained by the smaller relative differences between adaxial and abaxial photosynthesis according to the measured light response curves. However, the modelling results should be verified by measurement of up- and downward light gradients in the crop. Moreover, Beer's law, which was used to compute the light gradient, may be too simplistic given the inhomogeneous structure of the rose crop, having a broad basis of horizontally bent leaves and a hedge structure on top of erect flowering shoots. A next step to an FSP model of rose has already been made (Buck-Sorlin *et al.* 2011) and merging of these models would enable a further study on the impact of optical properties of plant components even more.

Our results on photosynthetic response of rose leaves lighted from the two leaf sides support the notion that light utilisation for photosynthesis in rose bifacial leaves is more efficient under adaxial than under abaxial lighting. However, it should be noted that in our experiment we measured only the instantaneous effects. In the case of exposure to a prolonged period of lighting from both leaf sides, the physiological behaviour might change due to light acclimation processes and this aspect should be investigated in future studies. The presented data represent useful knowledge in the view of new lighting strategies for greenhouse crops (inter-lighting, inner canopy lighting), as well as useful input for modelling crop photosynthesis under different lighting systems. Indeed, if crop models assume similar efficiency for lighting on the abaxial and the adaxial leaf side and similar contribution from the leaf layers, the overall crop photosynthesis would be overestimated.

Introducing abaxial optical and photosynthetic properties in the crop model to replace the generally used adaxial properties showed a decrease in crop photosynthesis in the magnitude of 1–5%, depending on LAI and light level. Discrimination of adaxial and abaxial properties is therefore advocated to

improve accuracy of the current crop models. Moreover, detailed functional structural plant models that incorporate architectural, optical and photosynthetic properties are recommended to better evaluate crop response to a specific lighting strategy.

Conflict of interest

The authors declare no conflict of interest.

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