

The Effect of Irradiating Adaxial or Abaxial Side on Photosynthesis of Rose Leaves

R. Paradiso
Department of Agricultural Engineering and Agronomy
University of Naples Federico II
Via Università, 100, 80055 Portici, Naples
Italy

L.F.M. Marcelis
Wageningen UR Greenhouse Horticulture
PO Box 644, 6700 AP, Wageningen
The Netherlands

Keywords: *Rosa hybrida* L., intra canopy lighting, absorption, transmission, reflection

Abstract

In many cropping systems most of the light irradiates the adaxial side of leaves. However, in cropping systems with intra canopy lighting a reasonable fraction of light may irradiate even the abaxial side of the leaves. The aim of this study was to investigate the effect of irradiating the abaxial leaf side compared to irradiating the adaxial side, in rose plants grown in glasshouse with the bending technique. The instantaneous effects on the optical properties and the light response of photosynthesis were analysed in intact leaves. Results demonstrated that the rate of net photosynthesis was higher when leaves were lighted from the adaxial side compared to the abaxial side. This was the consequence of both a higher light absorption and higher quantum yield (photosynthesis per unit absorbed light) in adaxial-lighted leaves.

INTRODUCTION

In many greenhouse crops, manipulations of the plant architecture are applied to increase the light interception and to optimize the photosynthesis efficiency of the different leaf layers (Buck-Sorlin et al., 2011). For instance, in cut rose crops, the shoot bending results in increased photosynthetically active surface per plant, by forming an extended horizontal canopy (Kim et al., 2004). Bent canopy has proven to function as a source of assimilates for the growth of upright flower shoots, mainly in low light intensity conditions (Baille et al., 2006; González-Real et al., 2007). This technique can result in increases of the plant growth rate and the number and length of flower stems (Kool and Lenssen, 1997).

According to Aikman (1989), plant productivity can be enhanced if light is uniformly provided along the vertical profile of the plant and penetration of light into the canopy is increased, preventing the lower and inner leaves being below the light compensation point and the upper and outer leaves approaching the saturation point. However, the final effect of the vertical light distribution on crop photosynthesis may depend on the season (Sarlikioti et al., 2011). Inter-lighting, performed by putting lamps in the row in between the canopy, leads to higher light intensities in the lower part of the canopy. This has been successfully used in a number of vegetable crops (Hovi-Pekkanen et al., 2006; Hovi-Pekkanen and Tahvonen, 2008; Trouwborst et al., 2009). This lighting strategy irradiates both the adaxial (upper) and abaxial (lower) leaf sides.

In most of the plant species with upright growth, the adaxial and the abaxial leaf surfaces develop and function in different environments, with respect to the light intensity (Photosynthetic Photon Flux Density, PPFD) and quality (wavelength composition). Adaxial sides are exposed to more direct radiation (from solar or artificial lighting), with higher light intensity and broader spectra. Abaxial sides are shaded by the leaf blade itself and receive only about 10% of the light incident to the adaxial ones. This light reaches the

abaxial side after it has been transmitted through the mesophyll (self-transmitted light) or reflected from the surroundings (mainly by leaves), and contains relatively much green light (Pospíšilová and Solárová, 1987). However, when inter-lighting is used a considerable amount of direct light may reach the abaxial side of the leaves.

Measurements of photosynthesis on plant crops mainly concern lighting from the adaxial leaf side. Most of the studies on the response to light stimuli to the different leaf sides have been carried out on C4 metabolism plants (Driscoll et al., 2006; Soares et al., 2008) more than on C3 species (Morr and O'Leary, 1984; Wang et al., 2008). Although, several researches have been reported on field grown plant species (Terashima, 1986; Postl and Bolhar-Nordenkamp, 1992), only little information seems to be available on greenhouse crops. In some hypostomatic species, like rose is (Pandey et al., 2007), under equal light intensity, photosynthesis is higher when light is provided from the adaxial rather than the abaxial side and the difference increases as the irradiance increases (Syvertsen and Cunningham, 1979; Proietti and Palliotti, 1997). However, as far as we know, no data on abaxial lighting of leaves is available on rose, particularly in greenhouse grown plants.

The aim of the experiment was to investigate the optical properties and the light response of photosynthesis (instantaneous effects) in intact leaves of rose, hydroponically grown with the bending technique, in relation to the leaf side lighted (adaxial vs. abaxial).

MATERIALS AND METHODS

Plant Material and Growth Conditions

The experiment was carried out in Wageningen (The Netherlands, 51°97'N; 5°67'E), in a heated experimental glasshouse. Rose plants (*Rosa hybrida* L.) cultivar 'Akito' for cut flowers were grown on rockwool slabs. Cuttings were transplanted on 25 February in double rows, at the plant density of 6.5 plants m⁻².

Plants were structured following the bent shoot technique, bending the weaker or blind stems down into the paths and leaving the harvestable flower stems to form the upright canopy (Kool, 1997).

During the experimental period, from the beginning of October to the end of November, the temperature inside the greenhouse was 21.1°C on average during the day (heating set point 21°C) and 18.2°C during the night (heating set point 17.5°C). Supplemental lighting by HPS lamps (Philips SON-T Green Power 600 W; Koninklijke Philips Electronics N.V., The Netherlands) provided a light intensity of 150 μmol m⁻² s⁻¹ at the canopy level (switching off threshold 250 W m⁻² of outside global radiation), extending the natural day-length to 16 hours (3:00 till 19:00). During the daytime, the relative humidity was kept around 70%, by using a mist system, and the air CO₂ concentration was enriched to 500 ppm approximately.

Water and fertilizers 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

Photosynthesis measurements were carried out during the sixth week of the growing cycle (starting from October, 6 when upright shoots were cut back), on stems with 13 to 16 leaves, with small flower bud already visible. Middle age leaves, penta-foliolate, from the 6th to the 8th from the top of the upright stem, were considered.

Net photosynthesis was measured on the top leaflet, with a portable photosynthesis open system (LCpro⁺ - ADC, UK), connected to a 6.25 cm² leaf chamber. The leaf chamber was lighted by a LED array of about 15% blue (around 465 nm) and about 85% red light (around 655 nm). Light saturation curves were performed at decreasing levels of light intensity, at the following theoretical PPFD values: 1500, 1000, 500, 250, 100, 50 and 0 μmol m⁻² s⁻¹, by using a LED array. The actual values recorded in the leaf chamber were: 1395, 930, 465, 232, 93, 46, 0 μmol m⁻² s⁻¹. Measurements lasted

10 min at 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 5 min in all the intermediate light levels and 15 min in the darkness and 1 measure per minute was logged. From each series of data, only the last 3 values (after 7, 2 and 12 min of adaptation, respectively) were selected in order to obtain reliable average values. The conditions inside the leaf chamber were kept constant (temperature 25°C, CO₂ concentration 400 ppm, RH 62%). Measurements on adaxial- and abaxial- lighted leaves were performed on the same leaf, on 4 plants randomly chosen, and the sequence of the side lighted was randomized.

After the photosynthesis measurements, the top leaflet was removed and transmission (Tr) and reflection (Ref) spectra for the two leaf sides were measured in the 400-700 nm range of wavelengths (bandwidth 1 nm), with a spectrophotometer (Lambda 950 UV/NIR, Perkin Elmer Inc. Waltham, Massachusetts, USA). Tr and Ref values were expressed as percentage of the incident light and leaf absorption (Abs) was calculated as $\text{Abs}=100-(\text{Tr}+\text{Ref})$. Photosynthesis measurements were referred to the average absorbed light of the Ad- and Ab- lighted leaves.

Photosynthesis light response curves were fitted by non-rectangular hyperbola (Cannell and Thornley, 1998):

$$P = \frac{I\alpha + P_{MAX} - \sqrt{[I\alpha + P_{max}]^2 - 4I\alpha\theta P_{max}}}{2\theta} - R_D \quad (1)$$

where P is the net photosynthesis, I is incident or absorbed PAR, α the initial quantum yield of CO₂ assimilation, P_{max} the maximum photosynthesis rate, R_D dark respiration and θ determines the curvature of the relationship.

RESULTS

Middle age leaves of rose lighted from the adaxial side transmitted 4.9% and reflected 5.9%, while absorbed 89.2% of the incident visible light (Table 1). Lighting from the abaxial side increased the average transmission to 5.7% (+16%) and the reflection to 11.7% (+98%), resulting in a decrease of the absorption to 82.6% of the incident visible light (-7%) (Table 1).

Light absorption of green light decreased in both adaxial- and abaxial- lighted leaves to 83.4 and 76.5% of the incident light, respectively (Table 1).

The absorption of the blue-red light of the LCpro⁺ LED array of the photosynthesis system was slightly higher compared to the white light, with average values of 92.0 and 85.2% in adaxial- and abaxial-lighted leaves, respectively (Table 1).

The rate of net photosynthesis increased with the level of the supplied light, regardless of the direction of lighting (Fig. 1A). Net photosynthesis saturated at around 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light intensity for both adaxial and adaxial lighted leaves.

Rates of net photosynthesis at all light intensities were lower when leaves were lighted from the abaxial side (Fig. 1B; Table 2). Maximum net photosynthesis in abaxial lighted leaves was 15% lower than in adaxial lighted leaves (Table 2). When net photosynthesis was plotted versus absorbed light, the rate of net photosynthesis was still lower for leaves lighted from abaxial side (Fig. 1B). However the differences between adaxial and abaxial were a little smaller (compare Fig. 1A and B). The initial quantum yield of CO₂ assimilation as estimated from fitting the non-rectangular hyperbola, suggested the initial quantum yield of adaxial leaf side was twice that of abaxial leaf side (0.11 versus 0.05 $\mu\text{mol CO}_2 \text{ mol absorbed quanta}^{-1}$).

DISCUSSION AND CONCLUSIONS

The rate of net photosynthesis in leaves of rose ‘Akito’ was higher when light was provided on the adaxial rather than on the abaxial surface, as observed on other species with leaf bifacial anatomy (Syvertsen and Cunningham, 1979; Proietti and Palliotti, 1997). Originally, this difference was reported to depend on different efficiency in light absorption and transport to chloroplasts, in the two leaf sides. In this leaf anatomy, typical

arrangement of tissues consists of palisade mesophyll (PM), underneath the epidermis of the adaxial side, and spongy mesophyll (SM), adjacent to the epidermis of the abaxial side (Vogelmann et al., 1996; Evans, 1999). Palisade cells are columnar shaped, vertically oriented and tightly packed: this regular array enables light to penetrate deeply into the leaf, spreading light more evenly among chloroplasts of palisade cells (where most the chloroplasts are concentrated). By contrast, spongy cells are irregular shaped and distributed and loosely packed, with more intercellular air space that scatter and reflect light, lengthening the photon paths to the chloroplasts. As 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 through the palisade cells (sieve effect; Vogelmann, 1993), and does contribute significantly to the leaf photosynthesis (40% in *Vicia faba*; Nishio et al., 1993). Conversely, under abaxial lighting, light penetration to the PM is limited because of the high scattering and absorption in SM, including a considerable absorption by photosynthetically inactive materials (Terashima and Saeki, 1985). Sun and Nishio (2001) summarized 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 to the adaxial side, was due to both a lower light absorption as well as a lower quantum yield (photosynthesis per unit absorbed light). In fact, the PM has a more efficient structure than the SM 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, it was found that 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 PM than in SM (Sun and Nishio, 2001). In addition, the rate of photosynthesis within the leaf is affected by light gradient and quality (Terashima and Saeki, 1985; Vogelmann, 1993) and variable CO₂ concentration (Farquhar et al., 1980). The intra-leaf light gradient generates sun- and shade-type chloroplasts (Terashima, 1986).

In conclusion, our data support the notion that light utilization for photosynthesis in rose leaves is more efficient under adaxial rather than abaxial lighting of rose leaves.

Our results on photosynthetic performances of rose leaves lighted from the abaxial side represent useful data 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 (Buck-Sorlin et al., 2011; Paradiso et al., 2011). Indeed, if crop models would assume similar efficiency for light on abaxial and adaxial leaf side, they would overestimate crop photosynthesis.

However, care is needed to draw conclusions from the instantaneous effects studied in our experiment. Indeed, whether the contribution of leaves lighted from the abaxial side can result in similar behaviour in the practise depends on the extent at which the short-term effect of abaxial lighting will sustain on the long term, since it is possible that leaves lighted for a longer period may acclimate and perform differently.

ACKNOWLEDGEMENTS

We thank Jan Snel and Benno Burema for their skilful assistance. R. Paradiso acknowledges the financial support of the University of Naples Federico II - Short Mobility Programme for Teachers and Researchers - Year 2008. The contribution of L.F.M. Marcelis was partly supported by Powerhouse.

Literature Cited

- Aikman, D.P. 1989. Potential increase in photosynthetic efficiency from the redistribution of solar radiation in a crop. *J. Exp. Bot.* 40:855-864.
- Baille, A., Gutiérrez Colomer, R.P. and González-Real, M.M. 2006. Analysis of intercepted radiation and dry matter accumulation in rose flower shoots. *Agr. Forest Meteorol.* 137:68-80.

- Buck-Sorlin, G., de Visser, P.H.B., Henke, M., Sarlikioti, V., van der Heijden, G.W.A.M., Marcelis, L.F.M. and Vos, J. 2011. Towards a functional-structural plant model of cut-rose - simulation of light environment, light absorption, photosynthesis and interferences with the plant structure. *Ann. Bot.* 108:1121-1134.
- Cannell, M.G.R. and Thornley, J.H.M. 1998. Temperature and CO₂ response of leaf and canopy photosynthesis: a clarification using the non-rectangular hyperbola model of photosynthesis. *Ann. Bot.* 82:883-892.
- Driscoll, S.P., Prins, A., Olmos, E., Kunert, K.J. and Foyer, C.H. 2006. Specification of adaxial and abaxial stomata, epidermal structure and photosynthesis to CO₂ enrichment in maize leaves. *J. Exp. Bot.* 57:381-390.
- Evans, J.R. 1999. Leaf anatomy enables more equal access to light and CO₂ between chloroplasts. *New Phytologist* 143:93-104.
- Farquhar, G.D., von Caemmerer, S. and Berry, J.A. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149:78-90.
- González-Real, M.M., Baille, A. and Gutiérrez Colomer, R.P. 2007. Leaf photosynthetic properties and radiation profiles in a rose canopy (*Rosa hybrida* L.) with bent shoots. *Sci. Hortic.* 114:177-187.
- Hovi-Pekkanen, T., Näkkilä, J. and Tahvonen, R. 2006. Increasing productivity of sweet pepper with interlighting. *Acta Hort.* 711:165-169.
- Hovi-Pekkanen, T. and Tahvonen, R. 2008. Effects of interlighting on yield and external fruit quality in year-round cultivated cucumber. *Sci. Hortic.* 116:152-161.
- Kim, S.H., Kenneth, A.S. and Lieth, J.H. 2004. Bending alters water balance and reduces photosynthesis of rose shoots. *J. Am. Soc. Hort. Sci.* 129(6):896-901.
- Kool, M.T.N. and Lenssen, E.F.A. 1997. Basal-shoot formation in young rose plants. Effects of bending practices and plant density. *J. Hortic. Sci.* 72:635-644.
- Morr, K.A. and O'Leary, J.W. 1984. Stomatal behavior and CO₂ exchange characteristics in amphistomatous leaves. *Plant Physiol.* 74:47-51.
- Nishio, J.N., Sun, J. and Vogelmann, T.C. 1993. Carbon fixation gradients across spinach leaves do not follow internal light gradients. *Plant Cell* 5:953-961.
- Pandey, R., Chacko, P.M., Choudhary, M.L., Prasad, K.V. and Pal, M. 2007. Higher than optimum temperature under CO₂ enrichment influences stomata anatomical characters in rose (*Rosa hybrida*). *Sci. Hortic.* 113:74-81.
- Paradiso, R., Meinen, E., Snel, J.F.H., De Visser, P., Van Ieperen, W., Hogewoning, S.W. and Marcelis, L.F.M. 2011. Spectral dependence of photosynthesis and light absorptance in single leaves and canopy in rose. *Sci. Hortic.* 127:548-554.
- Pospíšilová, J. and Solárová, J. 1987. Adaptations and acclimations of dorsiventral leaves to irradiance: epidermal diffusive conductance and net photosynthetic rate. *Photosynthetica* 21:349-356.
- Postl, W.F. and Bolhar-Nordenkampf, H.R. 1992. The light response curve of the CO₂ gas exchange separated for the abaxial and adaxial leaf surface under different light environments and CO₂ concentrations. p.369-372. In: N. Murata (ed.), *Research in Photosynthesis*. Vol. IV. Kluwer Academic Publ., Dordrecht - Boston - London.
- Proietti, P. and Palliotti, A. 1997. Contribution of the adaxial and abaxial surfaces of olive leaves to photosynthesis. *Photosynthetica* 33(1):63-69.
- Sarlikioti, V., de Visser, P.H.B., Buck-Sorlin, G.H. and Marcelis, L.F.M. 2011. How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional-structural plant model. *Ann. Bot.* 108(6):1065-1073.
- Soares, A.S., Driscoll, S.P., Olmos, E., Harbinson, J., Arrabaça, M.C. and Foyer, C.H. 2008. Adaxial/abaxial specification in the regulation of photosynthesis and stomatal opening with respect to light orientation and growth with CO₂ enrichment in the C₄ Species *Paspalum dilatatum*. *New Phytol.* 177:186-198.
- Sun, J. and Nishio, J.N. 2001. Why abaxial illumination limits photosynthetic carbon fixation in spinach leaves. *Plant Cell Physiol.* 42(1):1-8.
- Syvertsen, J.P. and Cunningham, G.L. 1979. The effects of irradiating adaxial and abaxial

- leaf surface on the rate of net photosynthesis of *Perezia nana* and *Helianthus annuus*. *Photosynthetica* 13:287-293.
- Terashima, I. 1986. Dorsiventrality in photosynthetic light response curves of a leaf. *J. Exp. Bot.* 37:399-405.
- Terashima, I. and Saeki, T. 1985. A new model for leaf photosynthesis incorporating the gradients of light environment and of leaf photosynthetic properties of chloroplasts within a leaf. *Ann. Bot.* 56:489-499.
- Trouwborst, G., Oosterkamp, J., Hogewoning, S.W., Harbinson J. and Van Ieperen, W. 2010. The responses of light interception, photosynthesis and fruit yield of cucumber to LED-lighting within the canopy. *Physiol. Plant.* 138(3):289-300.
- Vogelmann, T.C. 1993. Plant tissue optics. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 44:233-251.
- Vogelmann, T.C., Nishio, J.N. and William, K.S. 1996. Leaves and light capture: light propagation and gradients of carbon fixation within leaves. *Trends in plant science - Review.* February 1(2).
- Wang, Y., Noguchi, K. and Terashima, I. 2008. Distinct light responses of the adaxial and abaxial stomata in intact leaves of *Helianthus annuus* L. *Plant Cell Environ.* 31:1307-1316.

Tables

Table 1. Percentage leaf absorption (Abs), transmission (Tr) and reflection (Ref) of rose leaves for the whole visible region of the spectrum (400-700 nm), the green light region and the LED array of the LCpro⁺ photosynthesis system, as a function of lighting from the adaxial and abaxial leaf sides.

Leaf side lighted	Visible spectrum (400-700 nm)			Green region (500-580 nm)			LCpro ⁺ LED array
	Abs	Tr	Ref	Abs	Tr	Ref	Abs
Adaxial	89.2	4.9	5.9	83.4	8.5	8.1	92.0
Abaxial	82.6	5.7	11.7	76.5	9.8	13.6	85.2

Table 2. Light saturated net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of rose leaves as a function of lighting with $1395 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from the adaxial (Ad) and abaxial (Ab) leaf sides (Mean value \pm Standard error of mean; n=4).

	Adaxial	Abaxial	% Difference (Ab vs Ad)
Net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	12.4 ± 0.5	10.5 ± 0.9	15

Figures

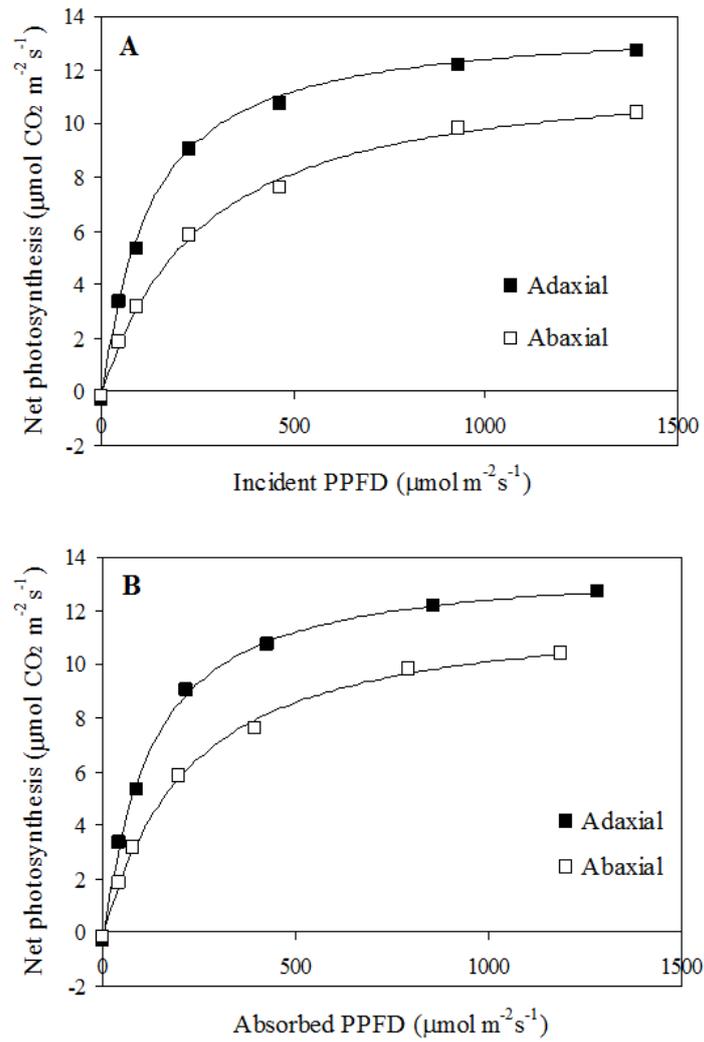


Fig. 1. Light response curves of net photosynthesis of rose leaves in adaxial- and abaxial-lighted leaves, as a function of incident light (A) and absorbed light (B) (Mean value + Standard error; n=4). Data are fitted by non-rectangular hyperbola.

