Vitis **40** (4), 175–177 (2001)

Photosynthetic light response curves in relation to illumination of adaxial and abaxial surfaces of sun and shade leaves of *Vitis vinifera* L.

A. Palliotti and A. Cartechini

Dipartimento di Arboricoltura e Protezione delle Piante, Perugia, Italia

Summary

The photosynthetic light response of adaxial (upper) and abaxial (lower) surfaces of sun- and shade-adapted leaves of cv. Grechetto/SO 4 was investigated. Vines were exposed to long-term shade by mounting a black polypropylene cover (40 % light transmittance) over the vines for 6 consecutive years.

The mean leaf blade inclination varied from 81.4° (sun-exposed) to 15.4° (shaded) enabling a high light reception. At light saturation, the maximum rate of photosynthesis of sun and shade leaves were similar if the adaxial or the abaxial leaf surface or both sides were irradiated simultaneously. At lower photon flux density (PFD), the adaxial surface consistently fixed more CO_2 than the abaxial surface in both leaf types. At PFD below saturation, simultaneous illumination of both leaf surfaces led to an increase of the rate of net photosynthesis (Pn) as compared to illumination of only one surface with the same PFD. Bilateral illumination increased the apparent quantum yield and the convexity coefficient (bending rate of the photosynthetic light response curve) as compared to irradiation of only one side of the blade, whereas the light compensation and saturation points were significantly lower. The possible significance of simultaneous irradiation of both leaf surfaces at low PFD on Pn is discussed.

K e y w o r d s : dark respiration, leaf inclination, light compensation, light saturation point, photosynthesis, photon flux density, quantum yield, shade.

Abbreviations: Pn, net photosynthesis; Pn_{sat}, maximum net photosynthesis at light saturation and ambient CO_2 concentration; PFD, photon flux density; PFD_{sat} and PFD_c, photosynthetic light saturation and compensation points; R_d, dark respiration; φ_i, apparent quantum yield; Θ, convexity coefficient.

Introduction

The energy budget and the photosynthetic efficiency of plants are strongly affected by direct illumination of the leaf surfaces. Under natural conditions, the outer leaves of the canopy are differently irradiated on both surfaces, whereas inside the canopy the light intensity at the adaxial (upper) and abaxial (lower) surfaces may be equal, depending on radiation scattering and light reflected from the soil. In fact, different photosynthetic responses to illumination of either the adaxial or abaxial leaf surface have been reported (Syvertsen and Cunningham 1979; Terashima 1986; Postl and Bolhar-Nordenkampf 1992; Proietti and Palliotti 1997).

Since measurements of CO_2 exchange generally involve illumination of the adaxial surface only, the aim of this paper was to investigate the effects of unilateral (adaxial or abaxial) or bilateral illumination on photosynthetic light response curves of leaves of sun- and shade-adapted grapevines.

Material and Methods

E x p e r i m e n t a l c o n d i t i o n s : The experiment was carried out in 1996 and 1997 near Perugia (central Italy, 42° 58' northern latitude, 12° 40' eastern longitude) on 20 7-year-old vines (*Vitis vinifera* L., cv. Grechetto on rootstock SO 4) grown open-air in 40-l plastic pots at a distance of 3 m x 3 m. Pots were filled with a mixture of soil, fine sand and peat (3:1:1, v/v/v) and were fertilized each year using 50 g of Osmocote plus (15 % N, 11 % P, 13 % K and 2 % Mg); they were irrigated weekly to avoid any water stress. All vines were pruned annually to three spurs with two buds each. The 6 shoots retained per vine were oriented upwards.

Since 1991, half the vines were kept under a black polypropylene cover (40 % light transmittance), while the other half was grown in natural light. The screen was mounted 3 m above the ground and covered all sides as well. During veraison, the maximum daily photon flux density (PFD) above and below the screen was 34.5 ± 3.1 and 12.3 ± 0.8 mol photons·m^{-2}·d^{-1}, respectively.

L e a f i n c l i n a t i o n : Leaf inclination was determined as the angle formed between the central long axis of the leaf and the horizontal. Care was taken not to disturb the leaves before measuring. Measurements were taken on all main leaves of three representative sun- and shade-adapted vines.

P h o t o s y n t h e t i c l i g h t r e s p o n s e c u r v e s : During the last week of July 1996 and 1997, photosynthetic light response curves were determined between 9 and 11 a.m. on fully expanded leaves inserted in the medial zone of shoots of shade- and sun-adapted vines by irradiating with various PFDs from above or below or simultaneously from both sides of the leaf. An LCA-3 portable infrared gas analyzer system (Analytical Development Co., Hoddesdon, Herts, UK), and, to obtain bilateral irradiation measurements, a modified leaf chamber (Parkinson PLC-3FM type) with a Plexiglas sheet for transparency in both the upper and lower chamber

Correspondence to: Dr. A. Palliotti, Dipartimento di Arboricoltura e Protezione delle Piante, Università degli Studi di Perugia, Borgo XX Giugno 74, I-06128 Perugia, Italy. Fax: +39-75-5856255. E-mail: palliot@unipg.it

surface were used. During measurements of sun-adapted vines, air temperature and water vapor pressure deficit outside the leaf chamber was 28.6 ±2.1 °C and 2.1 ±0.3 kPa, resp., whereas on shade vines values were 27.1 ±0.9 °C and 1.8 ±0.2 kPa, respectively.

The influence of PFD on Pn was determined by exposing 4 leaves per treatment to decreasing PFD levels by neutral filters. The abaxial leaf surfaces were irradiated by placing a mirror beneath the leaf chamber to reflect the radiation of the sun onto the lower side of the leaves. During the measurements, the intensity of PFD that hit the abaxial leaf surface was approximately the same as at the adaxial surface.

Apparent quantum yield (φ_i) was calculated from the linear portion (0-160 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of the slopes of Pn *vs.* PFD curves. Dark respiration (R_d) was derived from light response curves at PFD = 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The photosynthetic light saturation point (PFD_{sat}) was estimated from light response curves, whereas the light compensation point (PFD_c) was estimated as R_d/φ_i (PALLIOTTI *et al.* 2000). The dimensionless apparent convexity coefficient (Θ), which indicates the bending rate of the photosynthetic light response curve, was estimated according to LIETH and REYNOLDS (1987).

Results were subjected to ANOVA, the Student-Newman-Keuls test was used to compare the means.

Results and Discussion

L e a f i n c l i n a t i o n : Leaves from upward-oriented shoots of sun-adapted vines were oriented almost vertically with an average leaf inclination of 81.4°, whereas leaves from shade-adapted vines were oriented close to horizontal (15.4°). This strong phototropism observed at low PFD improves light reception.

Significant modifications in leaf morphology were also observed: sun-adapted leaves were deeply lobed with an undulating surface while shade-adapted leaves were not lobed and had a flattened surface.

P h o t o s y n t h e t i c l i g h t r e s p o n s e c u r v e s a n d d e r i v e d p h y s i o l o g i c a l p a r a m e t e r s i n r e s p o n s e t o i l l u m i n a t i o n o f l e a f s u r f a c e s : As expected, at mid-morning, the Pn values of shade-adapted leaves were about 50 % lower than those of sun-adapted leaves (Table). PFD_{sat}, PFD_c and R_d were also significantly reduced (by 59, 53 and 44 %, respectively), whereas φ_i and Θ had increased by 21 and 9 %, respectively. In shade-adapted leaves increased Θ values indicate a high light use efficiency for fixing CO_2 at low PFD as compared to sun-adapted leaves. This is probably due to the small gradient of light within the tissues associated with some morpho-anatomical changes in the shade-adapted leaves, which greatly affect the energy balance (*i.e.* lower lamina thickness and epicuticular wax content, higher chlorophyll and carotenoid concentration, change in palisade/spongy parenchyma ratio and number of chloroplasts per palisade cell) (TERASHIMA and SAEKI 1985; PALLIOTTI *et al.* 2000). LEVERENZ (1987) reported that Θ was strongly correlated with both the development of the light gradient inside the leaf and the chlorophyll content. Moreover, photosynthetic adaptation to low PFD involves integrated changes of electron transport pools, enzyme activity and size of the photosynthetic unit (SCHREIBER *et al.* 1977; TERASHIMA and SAEKI 1985; EVANS *et al.* 1993).

In contrast to other species (MOSS 1964; TERASHIMA 1986; POSTL and BOLHAR-NORDENKAMPF 1992; EVANS *et al.* 1993; PROIETTI and PALLIOTTI 1997), in sun- and shade-adapted leaves of grapevine, at PFD values higher than saturation, Pn_{sat} was unaffected if either the adaxial or abaxial or both leaf surfaces were irradiated (Table; Figure). These results also seem to be linked to some leaf anatomical characteristics. In fact, compared with other fruit tree species, both sun- and shade-adapted leaves of grapevines have a lower specific weight, leaf thickness and epicuticular wax content

T a b l e

Influence of different photon flux density (PFD) during vine development and leaf surface illumination on maximum net photosynthesis (Pn_{sat}, $\mu mol\ CO_2\ m^{-2} \cdot s^{-1}$), photosynthetic light saturation and compensation points (PFD_{sat} and PFD_c, μmol photons $m^{-2} \cdot s^{-1}$), dark respiration rate (R_d, mol $CO_2\ m^{-2} \cdot s^{-1}$), quantum yield ($\varphi_i$, mol CO_2/mol PFD) and the dimensionless convexity coefficient (Θ)

	Pn_{sat}	PFD_{sat}	PFD_c	R_d	φ_i	Θ
PFD availability						
Sun-adapted	8.09 b	806 b	60 b	1.90 b	0.034 a	0.823 a
Shade-adapted	4.03 a	332 a	28 a	1.06 a	0.041 b	0.890 b
F	***	***	***	***	**	**
Surface illumination						
Adaxial	6.00	675 b	42 b	---	0.036 b	0.857 b
Abaxial	6.07	730 c	65 c	---	0.026 a	0.751 a
Adaxial + abaxial	6.11	305 a	22 a	---	0.052 c	0.961 c
F	NS	**	***		***	***

, *, NS = significant at $p \leq 0.01$, 0.001 or not significant, respectively. Mean separation within the columns by Student-Newman-Keuls test at 5 %.

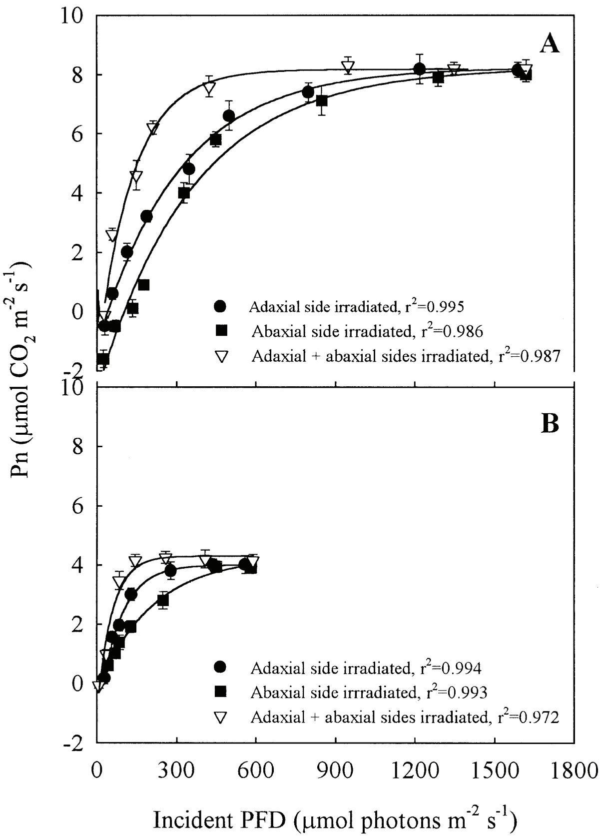

Figure: Photosynthetic light response curves determined during the last week of July in medial leaves of sun- (**A**) and shade-adapted (**B**) grapevines illuminated at the adaxial, abaxial or both surfaces. Each data point is the mean of 4 leaves ± SE.

(SYVERTSEN and SMITH 1984; WOOGE and BARDEN 1987; BONGI *et al.* 1994; PALLIOTTI *et al.* 2000). These characteristics may contribute to reduce light reflectance and to increase light absorption by the leaf; thus all chloroplasts are expected to be saturated with light that hits the adaxial or abaxial surfaces at PFD near saturation. Moreover, the differences between the adaxial and the abaxial leaf side responses confirm the hypothesis of 'sun' and 'shade chloroplasts', respectively, and consequently manifest a significant gradient in the photosynthetic properties of chloroplasts (TERASHIMA and INOUE 1985).

At all PFDs below light saturation in both leaf types adaxial surface consistently fixed more CO_2 than did the abaxial surface. In the latter case, the available light is mainly absorbed by the spongy tissue and only a small amount reaches palisade cells where chloroplasts are probably not fully light-saturated (MOSS 1964).

Below light saturation, the simultaneous illumination of both leaf surfaces enhanced Pn as compared to the illumination of only one surface with the same PFD. Under these conditions, φ_i increased by about 44 %, and 100 %, respectively, as compared to irradiance of only the adaxial or the abaxial surface. PFD_c was reduced significantly as was PFD_{sat}, but Θ increased, indicating both, simultaneous light-saturation of more chloroplasts and a high capacity of light utilization (TERASHIMA 1986).

The increased Pn obtained by additional low PFD on the abaxial leaf surface could be of great importance in the field. This situation can be observed frequently with leaves inside the canopy, where diffuse radiation prevails and strikes both leaf surfaces. In our experiment, diffuse light at the abaxial surfaces contributed significantly to Pn and φ_i and, at the same time, reduced compensation irradiance by about 48 % as compared to illumination of the adaxial surface only. These results indicate that internal leaves can contribute to the CO_2 fixation of vines and they may explain why leaves in the shaded parts of canopies continue to maintain their function.

References

BONGI, G.; PALLIOTTI, A.; ROCCHI, P.; MOYA, I.; GOULAS, Y.; 1994: Blue-green fluorescence excited by UV laser on leaves of different species originates from cutin and is sensitive to leaf temperature. Plant, Cell Environ. **17**, 777-780.

EVANS, J. R.; JAKOBSEN I.; OGREN E.; 1993: Photosynthetic light response curves. 2. Gradients of light absorption and photosynthetic capacity. Planta **189**, 191-200.

LEVERENZ, J. W.; 1987: Chlorophyll content and the light response curve of shade-adapted conifer needles. Physiol. Plant. **71**, 20-29.

LIETH, J. H., REYNOLDS, J. F.; 1987: The nonrectangular hyperbola as a photosynthetic light response model: Geometrical interpretation and estimation of the parameter Θ. Photosynthetica **21**, 363-366.

MOSS, D. N.; 1964: Optimum lighting of leaves. Crop Sci. **4**, 131-136.

PALLIOTTI, A.; CARTECHINI, A.; FERRANTI, F.; 2000: Morpho-anatomical and physiological characteristics of primary and lateral shoot leaves of Cabernet franc and Trebbiano toscano grapevines under two irradiance regimes. Am. J. Enol. Vitic. **51,** 122-130.

POSTL, W. F,.; BOLHAR-NORDENKAMPF, H. R.; 1992: The light response curve of CO_2 gas exchange separated for the abaxial and adaxial leaf surface under different light environments and CO_2 concentrations. In: Research in Photosynthesis, Vol. IV, 369-372. Kluwer Academic Publisher, Netherlands.

PROIETTI, P.; PALLIOTTI A.; 1997: Contribution of the adaxial and abaxial surfaces of olive leaves to photosynthesis. Photosynthetica **33**, 63-69.

SYVERTSEN, J. P.; CUNNINGHAM, G. L.; 1979: The effects of irradiating adaxial or abaxial leaf surfaces on the rate of photosynthesis of *Perezia nana* and *Helianthus annuus*. Photosynthetica **13**, 287-293.

- -; SMITH, M. L. jr.; 1984: Light acclimation in citrus leaves. I. Changes in physical characteristics, chlorophyll, and nitrogen content. J. Am. Soc. Hortic. Sci. **109**, 807-812.

TERASHIMA, I.; 1986: Dorsiventrality in photosynthetic light response curves of a leaf. J. Exp. Bot. **37**, 399-405.

- -; INOUE, Y.; 1985: Vertical gradient in photosynthetic properties of spinach chloroplasts dependent on intra-leaf light environment. Plant Cell Physiol. **26**, 781-785.

- -; SAEKI, T.; 1985: A new model for leaf photosynthesis incorporating the gradients of light environment and of photosynthetic properties of chloroplasts within a leaf. Ann. Bot. **56**, 489-499.

WOOGE, J. D.; BARDEN, J. A., 1987: Seasonal changes in specific leaf weight and leaf anatomy of apple. HortScience **22**, 292-294.

Received June 11,2001