

## A model analysis of the photosynthetic response of *Vitis vinifera* L. cvs Riesling and Chasselas leaves in the field: I. Interaction of age, light and temperature

V. ZUFFEREY<sup>1, 2)</sup>, F. MURISIER<sup>1)</sup> and H. R. SCHULTZ<sup>3)</sup>

<sup>1)</sup> Station Fédérale de Recherches en Production Végétales de Changins, Centre Viticole du Caudoz, Pully, Suisse

<sup>2)</sup> Eidgenössische Technische Hochschule Zürich, Institut für Pflanzenwissenschaften, ETH Zentrum, Zürich, Schweiz

<sup>3)</sup> Institut für Weinbau und Rebenzüchtung, Forschungsanstalt, Geisenheim, Deutschland

### Summary

The photosynthetic activity (A) of leaves of different ages on primary and secondary shoots of Riesling and Chasselas vines was measured under field conditions in relation to photon flux density (PFD) at various leaf temperatures. The data sets from 4 years and two locations (Geisenheim, Germany; Changins, Switzerland) were analysed using non-linear regression models to determine possible genetic and/or climate-induced differences in the light and temperature response between different leaf ages. A non-rectangular hyperbola with physiologically meaningful parameters was found to adequately describe the response to photon flux density. For both varieties, maximum photosynthetic rates were observed on leaves of primary shoots, opposite to the clusters, at a leaf temperature of 27–32 °C and at light saturation. Young leaves showed a less pronounced temperature optimum. The light response curves of photosynthesis of the two cultivars were similar over a temperature range of 20–30 °C. Below this temperature, Riesling showed higher values of A than Chasselas in most cases, whereas it was the reverse when leaf temperature exceeded 30 °C. This was particularly evident for leaves on secondary shoots and was related to differences in the photorespiration rate. Mature Riesling leaves had higher apparent quantum yields ( $\alpha$ ) and lower light saturation indices ( $I_s$ ) than Chasselas at leaf temperatures below 30–35 °C. Dark respiration ( $R_D$ ) and the light compensation point ( $I_C$ ) responded strongly to temperature with differences between leaf ages but no consistent difference between varieties. Leaves on secondary shoots of both cultivars had the highest photosynthetic activity during the ripening period of the fruit.

**Key words:** photosynthesis, photon flux density, light compensation and saturation point, leaf age, leaf temperature, primary and secondary shoots, empirical model, apparent quantum yield, photorespiration.

**Abbreviations:** A = photosynthetic rate,  $A_{\max}$  = maximum photosynthetic rate at ambient CO<sub>2</sub> concentration, PFD = photon flux density,  $\alpha$  = quantum yield,  $I_s$  = light saturation index,  $I_C$  = light compensation point,  $R_D$  = dark respiration, PR = photorespiration, LPI = leaf plastochron index,  $c_i$  = intercellular CO<sub>2</sub> concentration.

### Introduction

The photosynthetic activity of a canopy is conditioned by many climatic and physiological factors. Light intensity, temperature and age of the leaves have a great impact on gas exchange of leaves and consequently on the production of dry matter. Since light represents the primary factor for photosynthesis, it is important to know how leaves respond to light intensity in the photosynthetic active range (PFD,  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). However, PFD varies permanently over space and time in grapevine canopies because of climate, position in the canopy, and diversity of leaf angles and directions of the leaf surfaces with respect to the solar angle. Additionally, grapevines are heterogeneous in age structure (SCHULTZ 1995) and can have complex vegetation forms (CARBONNEAU 1995). These factors influence the photosynthetic potential of the leaves during their development and maturity (JURIK *et al.* 1979; SCHULTZ 1989; CARTECHINI and PALLIOTTI 1995).

Since light intensity is coupled to the energy balance of leaves, the light response curves of photosynthesis are modulated by temperature and leaf age (BERRY and BJÖRKMANN 1980; CATSKY and TICHÁ 1980; CHAVES *et al.* 1987; SCHULTZ 1989), where leaf age acts through stomatal development and leaf size, and thus boundary layer conditions (FIELD and MOONEY 1983). Photosynthesis and respiration can adapt to the temperature prevailing at a given time. This so-called modulative temperature adaptation (LARCHER 1995) occurs within a few days, or sometimes hours. Possible mechanisms involved are: changes in substrate concentrations, alterations of enzyme activities such as ribulose-bisphosphate-carboxylase/oxygenase (Rubisco) or fructose bis-phosphate phosphatase (BERRY and BJÖRKMANN 1980), replacement of certain enzymes by isoenzymes with the same action but different temperature optima; and by chemical and structural alterations in the biomembranes, such as fatty acid composition (BERRY and DOWNTON 1982). All these factors can influence the shape of the photosynthetic response curve to light (THORNLEY 1976) and since ambient temperature conditions vary constantly in the field, this shape will vary too. Thus, there is no light saturation point *per se* for plants, although from the literature, one could get the impression that this value is fixed around 700–800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PFD for grapevines (GEISLER 1963; KRIEDEMANN 1968; RÜHL *et al.* 1981; SMART 1984; DÜRING 1988), although these light values only apply to leaf temperatures between 25 and 30 °C and

to adult, non-senescent leaves. A few response curves of grapevine photosynthesis to light for a wider range of temperatures have been presented previously (KRIEDEMANN 1968; SCHULTZ 1989); however no systematic analysis of light response curves with respect to the effect of temperature and leaf age has been performed, although this is essential for modelling vine photosynthesis. Additionally, there is some evidence that different cultivars may react differently to temperature (CHAVES *et al.* 1987) and thus there may be a genetic factor modifying the light and temperature response. Therefore, the objectives of the present study were: 1) to determine the photosynthetic response in relation to light at various leaf temperatures and for different types and ages of leaves for two cultivars grown in their respective environment; 2) to analyse the resulting data sets from a total of 4 years from two sites in Germany and Switzerland, with an empirical model in order to discern possible physiological differences (part I); 3) to quantify the effect of ambient temperature on local modulative temperature adaptation (part II).

### Material and Methods

**Plant material and experimental sites: Geisenheim, Germany:** Experiments were conducted in 1987 and 1988 on 9-year-old, field-grown Riesling grapevines (clone 198 Gm on 5 C rootstocks) at the State Research Institute in Geisenheim, Germany (50.0° North, 8.0° East). Plants were grown at 2.8 m x 0.85 m spacing and trained to an Espalier-type, cane-pruned canopy system. Details of growing conditions and soil analyses are given elsewhere (SCHULTZ 1989). Vines were dormant pruned to 10 buds·m<sup>-2</sup> in January. Vineyard management was according to commercial practices with the exception that shoots remained unhedged throughout the season. The experiment was conducted on sun shoots growing on the canopy exterior, well exposed to light throughout most of the day.

**Changins, Switzerland:** Experiments were conducted in 1997 and 1998 on 14-year-old, field-grown Chasselas grapevines (clone 14/33-4 on 3309 C rootstocks) at the experimental viticultural estate of the Swiss Federal Research Station for Plant Production in Changins (Viticultural Centre in Pully), Switzerland (46.5° North, 6.7° East). Vines were trained to a Guyot system at 1.85 m x 0.8 m spacing. A bud load of 7 buds per vine was retained after pruning. The experimental plot was south-exposed with a 15 % slope. The rest of the experimental protocol was the same as in Germany. The climatic data (temperature and rainfall) of the two experimental sites can be found in Tabs. 1 and 2.

**Determination of physiological leaf age:** The age of the leaves was expressed in plastochrons. The leaf plastochron index (LPI) was used to define the position of the leaf on the shoot according to the concept defined by ERICKSON and MICHELINI (1957). The details of the calculation of the LPI have been outlined previously (SCHULTZ 1993).

Table 1

Monthly mean temperatures (°C) at the two experimental sites, Geisenheim (D) and Changins (CH), during the 4 study years in comparison to the long-term averages (1951-1980)

	D		long-term	long-term	CH	
	1987	1988			1997	1998
January	-3.2	4.6	1.1	1.1	1.8	3.7
February	1.5	3.5	2.2	1.7	5.8	5.5
March	2.6	5.0	5.6	5.5	8.8	7.3
April	11.4	9.7	9.6	8.7	9.7	9.4
May	11.2	15.9	13.9	13.3	14.6	15.9
June	15.3	16.7	17.1	16.5	17.0	18.3
July	18.5	17.8	18.5	18.4	18.4	21.0
August	17.2	18.8	17.8	17.6	21.1	20.4
September	16.1	14.3	14.6	14.5	17.4	15.5
October	10.4	11.0	9.7	9.6	11.2	11.8
November	5.9	4.2	5.2	4.9	7.2	4.3
December	3.3	5.5	2.3	2.0	4.4	2.7
Year	9.2	10.6	9.8	9.5	11.5	11.3

Table 2

Monthly rates of precipitation (mm) at the two experimental sites, Geisenheim (D) and Changins (CH), during the 4 study years in comparison to the long-term averages (1951-1980)

	D		long-term	long-term	CH	
	1987	1988			1997	1998
January	25	62	43	72	59	85
February	40	66	35	68	63	21
March	45	76	30	135	20	39
April	10	23	37	76	71	165
May	41	35	54	93	190	34
June	94	43	56	112	220	42
July	92	65	54	107	135	51
August	77	12	60	121	85	68
September	63	41	44	110	68	222
October	72	57	39	91	62	144
November	52	34	42	88	71	140
December	16	65	42	93	105	33
Year	627	579	536	1105	1149	1044

Vine leaves were classified into 6 age or plastochron classes. The determination of the age classes was based on individual leaf surface development and maximum photosynthetic rate,  $A_{max}$  (Fig. 1). The first age class, consisting of 4 plastochrons (LPI 3-6), corresponds to very young growing leaves with a rapid development. The age category from 6-10 represents a developmental stage in which 90-95 % of the photosynthetic potential has been attained

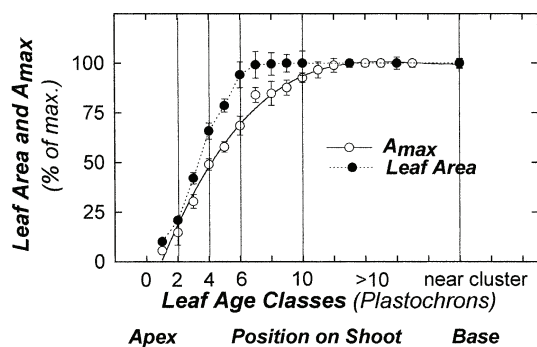


Fig. 1: Schematic presentation of leaf age classes, expressed in plastochrons, on primary shoots. Selection of age classes was based on development of leaf area and maximum photosynthetic activity,  $A_{\max}$ . Cultivar: Chasselas, measured in Pully, 1998.

and leaf area expansion is completed. Leaves with a LPI  $>10$  were pooled into one class since  $A_{\max}$  was relatively constant along single shoots. Not included in this class were leaves (within 1-2 leaves in close proximity) to the fruit which formed a separate category (Fig. 1) since their photosynthetic activity is highest on the shoot (SCHULTZ 1989). The leaves on the secondary shoots were grouped into apical and basal lateral leaves only, since the plastochron concept was not applicable because of their irregular growth. At the end of vegetative development, the LPI simply represents the position of the leaf on the shoot.

**M e a s u r e m e n t s o f g a s e x c h a n g e :** The gas exchange of Riesling vines was measured using a portable open gas exchange system without climatic control ( $\text{CO}_2/\text{H}_2\text{O}$  porometer, Walz, Effeltrich, Germany), which uses a Binoss infrared gas analyser (Leybold Hereaus, Hanau, Germany). Air and leaf temperature was measured using a NTC thermistor and thermocouple (Chromel-Alumel), respectively. The cuvette was equipped with a ventilator to keep the boundary layer resistance low and to avoid over-temperatures.

Photosynthesis of Chasselas vines was measured using an ADC-LCA 3 (ADC, Hoddesdon, England) open gas exchange system equipped with a Parkinson leaf chamber. Both, air and leaf temperatures were measured with thermistors.

All measurements were conducted on well-watered plants (pre-dawn water potential  $>-0.2$  MPa) during 6 phenological stages as outlined in the protocol given by SCHULTZ *et al.* (1996). Most of the measurements were conducted during the phenological stages 27-35 (bloom to end of berry growth phase I) defined by EICHORN and LORENZ (1977). All gas exchange parameters were calculated using the equations of VON CAEMMERER and FARQUHAR (1981).

**M e a s u r i n g a n d m o d e l l i n g t h e l i g h t r e s p o n s e :** Photon flux density (PFD) impinging on the leaf surface was measured parallel to the measurements of gas exchange with a quantum sensor. After exposing the leaves to full light intensity ( $>1600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), PFD was progressively lowered until complete darkness by using transmission filters (Schott, Mainz, Germany). The time the leaves needed to reach a new steady state after each

change of PFD was between 2 and 8 min (the higher the air and leaf temperature, the longer the time needed to reach an equilibrium). The leaf temperature typically decreased by 2 to 3 °C after being submitted to darkness when the ambient temperature was very high ( $>32$  °C). At cooler air temperatures, the variation in leaf temperature was only 1 °C or less. Measurements were conducted at low leaf to air vapour pressure deficits to avoid negative effects of low humidity on A.

In order to model the photosynthetic response to light, we used the equation proposed by MARSHALL and BISCOE (1980). For details see Appendix.

**E s t i m a t i n g t h e r a t e o f p h o t o r e s p i r a t i o n :** The rate of photorespiration (PR) at light saturation in leaves was calculated from the rate of net  $\text{CO}_2$  assimilation and the partial pressures of  $\text{CO}_2$  and  $\text{O}_2$  according to SHARKEY (1988). Intercellular  $\text{CO}_2$  concentrations, necessary for the calculations, were inferred from measurements of A and stomatal conductance to  $\text{CO}_2$  above  $I_s$ .

## Results

Figs. 2 and 3 represent a comparison of the photosynthetic light response of Riesling and Chasselas leaves of different age classes at different temperatures during mid-summer and Fig. 4 presents the estimated parameter values from these curves. For young growing leaves of primary shoots (LPI 3-6),  $A_{\max}$  varied little with temperature but more so for Riesling than for Chasselas (Fig. 2 A-E, Fig. 4 A, F).  $A_{\max}$  remained stable  $>25$  °C for Chasselas but decreased for Riesling (Fig. 2 A-E). The photosynthetic activity of Riesling leaves of this age class was superior to that of Chasselas independent of intercepted radiation, when leaf temperature was below 30 °C (Fig. 2 A-C), and it became somewhat lower at temperatures  $>30$  °C (Fig. 2 D-E). For apical leaves of secondary shoots this response was strongly accentuated above 25 °C, when photosynthesis of Riesling leaves became clearly inferior to that of Chasselas, this is also reflected in the parameter estimates of  $A_{\max}$  (Fig. 4 F).

The light response of photosynthesis of adult leaves (LPI 6-10, LPI $>10$ , leaves opposite the cluster, basal lateral leaves) showed a strong temperature response (Figs. 2-4). There was a clear thermal optimum for all these leaves (Figs. 3, 4). Photosynthetic activity of the two cultivars was almost identical for temperatures between 20 and 30 °C. When temperatures exceeded 30 °C, A was more reduced for Riesling than for Chasselas, especially for the basal leaves on secondary shoots, indicating less thermal stability for Riesling than for Chasselas (Fig. 3 O), whereas at low temperatures (15-20 °C) Riesling had higher values of maximum A than Chasselas (Figs. 3, 4 C-E). Leaves opposite the clusters showed the highest maximum photosynthetic rates with  $16.9 \mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$  for Chasselas and  $18.4 \mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$  for Riesling between 25 and 32 °C (Fig. 4 D).

There were substantial differences in dark respiration rates between leaf ages (Fig. 4 Y-AD), but no clear differ-

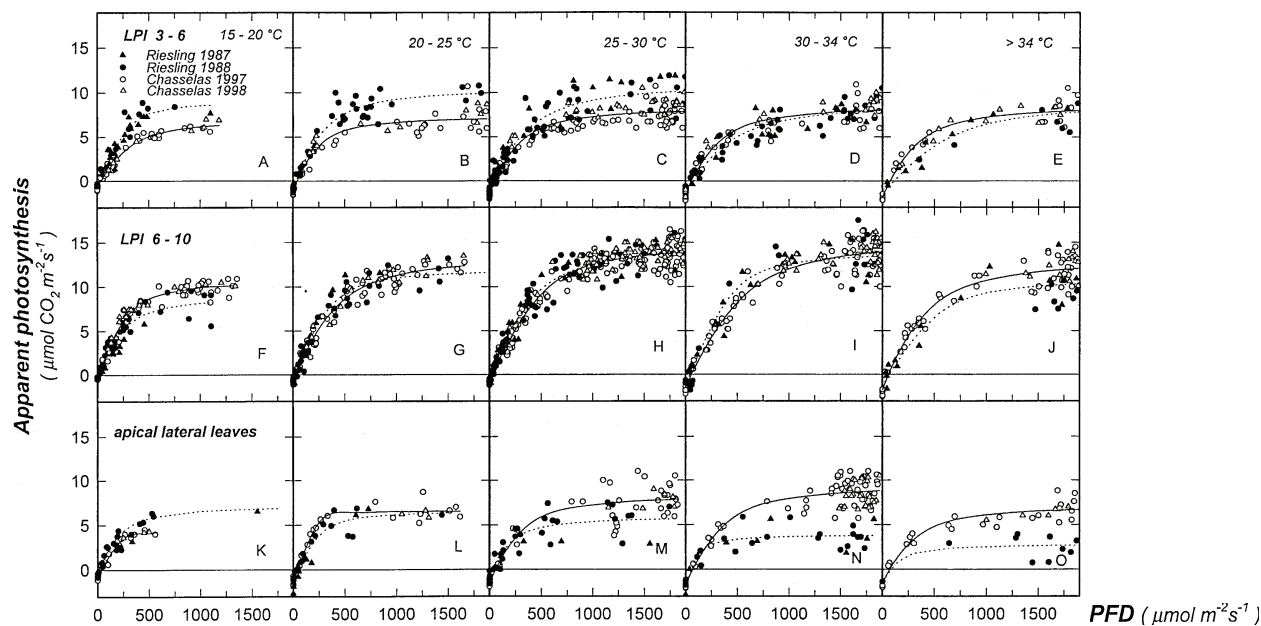


Fig. 2: Influence of photon flux density (PFD) on apparent photosynthesis of growing leaves of primary and secondary shoots (LPI 3-6 (A-E)), apical lateral leaves (K-O) and adult leaves (LPI 6-10 (F-J)) at various temperature intervals and low leaf to air vapour pressure difference. The measurements were conducted during the phenological stages 27-35 (bloom to the end of berry growth phase I) in 1987 and 1988 for Riesling and in 1997 and 1998 for Chasselas. The model curves were calculated according to equation (1) (see Appendix).

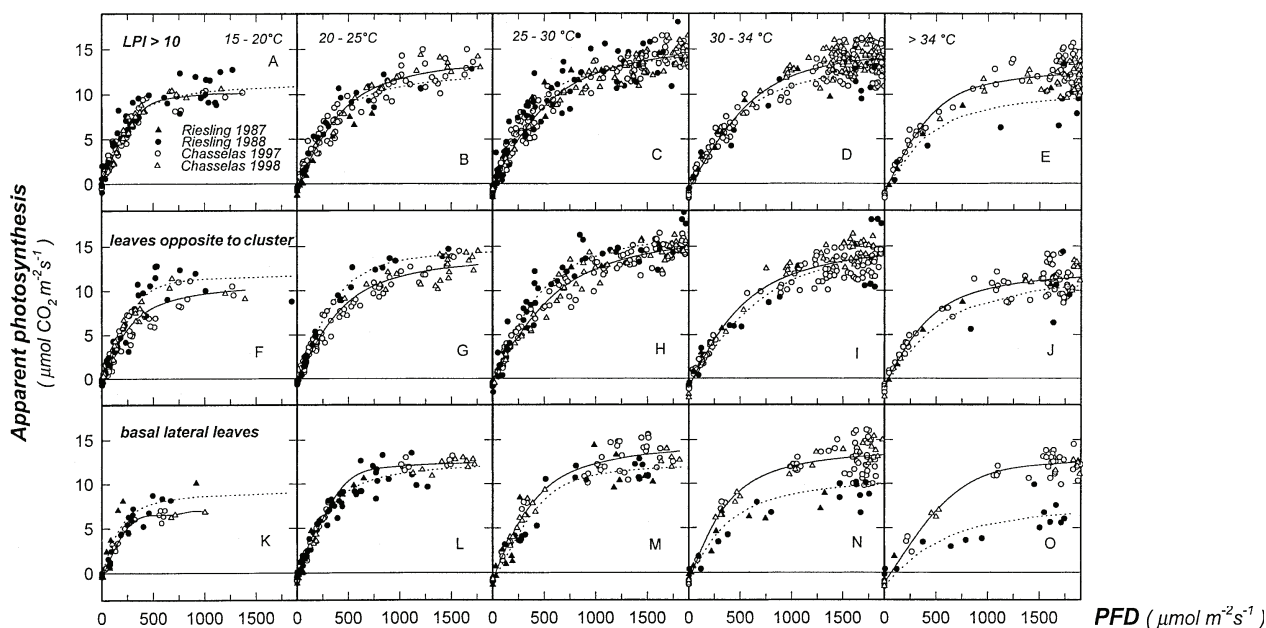


Fig. 3: Influence of photon flux density (PFD) on apparent photosynthesis of adult leaves of primary and secondary shoots (LPI>10 (A-E)), leaves opposite to the cluster (F-J), basal lateral leaves (K-O) at various temperature intervals and low leaf to air vapour pressure difference. The measurements were conducted during the phenological stages 27-35 (bloom to the end of berry growth stage I) in 1987 and 1988 for Riesling and in 1997 and 1998 for Chasselas. The model curves were calculated according to equation (1) (see Appendix).

ences between cultivars. The  $R_D$  for both varieties increased with temperature and induced a shift in the light compensation point ( $I_c$ ) towards higher values of light intensity (Fig. 4 S-X). For young leaves (LPI 3-6),  $I_c$  was near  $25 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at  $15-20^\circ\text{C}$  (Fig. 4 S) but increased to nearly  $95 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at temperatures superior to  $34^\circ\text{C}$ . This increase in  $I_c$  was observed for all leaf types and ages of both cultivars (Fig. 4 S-X), but was most pronounced for basal lateral leaves of Riesling (Fig. 4 W) which was probably related to the high values of  $R_D$  found for this age class (Fig. 4 AC).

With increasing temperature, the increase in A as a function of PFD was more gradual (Figs. 2, 3), which is also reflected in the increasing light saturation indices,  $I_s$ . For leaf ages LPI 3-6, the  $I_s$  increased with temperature from about  $700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at  $15-20^\circ\text{C}$  for both Riesling and Chasselas to  $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at temperatures  $>34^\circ\text{C}$  for Riesling and  $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for Chasselas (Fig. 4 M). For adult leaves,  $I_s$  was lower for Riesling than for Chasselas for most temperatures except for the highest (Fig. 4 N-P). There was a decrease in  $I_s$  for Chasselas  $>30^\circ\text{C}$  which was also noted for Riesling but less consistent with respect to



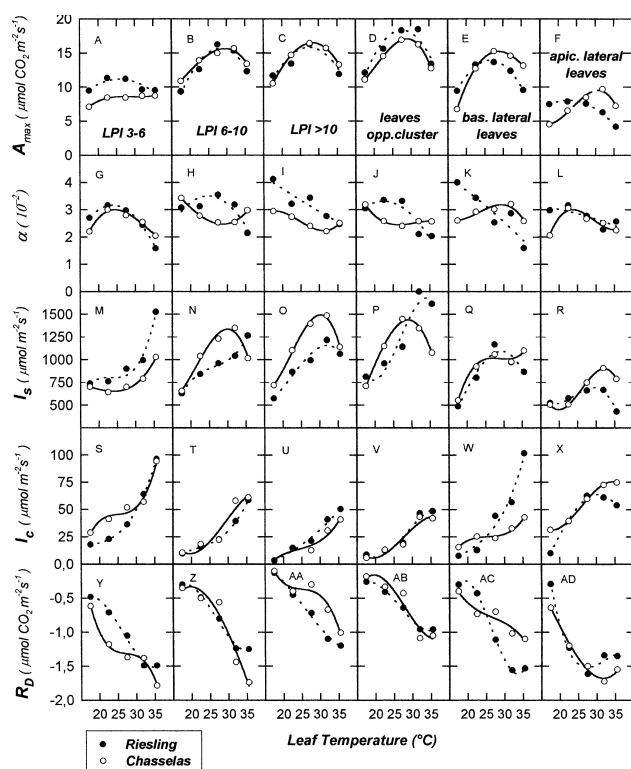


Fig. 4: Equation parameters  $A_{\max}$  (A-F),  $\alpha$  (G-L),  $R_D$  (Y-AD) of the light response curves of photosynthesis of Riesling and Chasselas leaves presented in Figs. 2 and 3. Parameters were calculated with the model of MARSHALL and BISCOE (1980). The light compensation points,  $I_c$  (S-X), and the light saturation indices,  $I_s$  (M-R), are calculated from equations (2) and (3) (see Material and Methods resp. Appendix).

the temperature threshold (Fig. 4 N-R). Fig. 4 also displays the values of the parameter  $\alpha$ , denoting the slope of the response curve according to the model of MARSHALL and BISCOE (1980) (Fig. 4 G-L). This parameter is roughly equal to the apparent quantum yield ( $\text{mol CO}_2$  fixed per  $\text{mol incident photons}$ ) at low light intensities ( $<100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), and has some important implications since it defines the productivity of a plant under limiting light, respectively the utilisation efficiency of light quanta. In general,  $\alpha$  diminished with increasing temperature regardless of the age class and type of leaves, with the exception of the basal lateral leaves of Chasselas (Fig. 4 K). The adult leaves had  $\alpha$  values superior to those of growing leaves. The  $\alpha$  of Riesling was generally higher than that of Chasselas at temperatures between 15 and 30 °C, but was penalised  $>32$  °C, indicating that there was an adaptation to a more efficient use of quanta at cooler temperatures for Riesling.

The light response curves of apparent photosynthesis flattened out considerably for both varieties with increasing temperature, but this effect was more striking for Riesling leaves.

Since the rate of photorespiration (PR) plays a large role in determining the shape of the light response curve, we estimated PR for three leaf age classes (Fig. 5). The PR strongly increased with temperature for both varieties, but was lower for adult Riesling leaves as compared to Chasselas except when temperature exceeded 32 °C (Fig. 5 B, C). More

important, the ratio of PR to A was lower for Riesling than for Chasselas for most temperatures except for the very highest, where there was a strong increase in PR/A and PR represented more than 50 % of A for all leaf age classes tested (Fig. 5 D-F). Thus PR may have contributed to the observed differences in the shape of the light response curves between varieties.

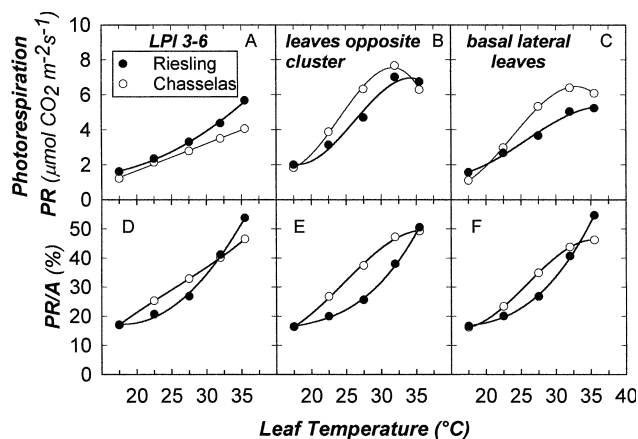


Fig. 5: Calculated values of photorespiration (PR) (SHARKEY 1988) and the photorespiration and net photosynthesis (A) ratio PR/A in relation to leaf temperature for growing leaves of primary shoots (LPI 3-6, A, D), adult leaves (opposite cluster, B, E) and leaves of secondary shoots (basal lateral leaves, C, F) of Riesling and Chasselas.

In addition to analysing the light response curves in detail during a fixed period, it was of interest to investigate the seasonal dynamics of this response at 25-30 °C. Early in the season (near day 150, beginning of June, flowering), photosynthetic activity on primary shoots was highest for both cultivars (Fig. 6 A, C). From the end of flowering until mid-August (day 220), the shape of the light response remained almost constant for leaves of primary shoots of Riesling and Chasselas. The photosynthesis of leaves of secondary shoots of both varieties increased regularly. Before veraison (day 235), a slight decline in A was noted for Riesling, which coincided with the cessation of vegetative growth and the lag-phase in berry development. After veraison the photosynthetic activity of the primary and secondary leaves increased somewhat for Riesling but also for leaves on secondary shoots of Chasselas (Fig. 6 B-D). During fruit ripening (after day 235) A decreased for primary leaves of both cultivars, but less so for Riesling, whereas A of lateral shoots remained constant (Riesling) or even increased (Chasselas) (Fig. 6 B, D).

## Discussion

The analysis of a large data set of photosynthesis measurements over 4 years in two locations with two varieties showed that the effect of light intensity on the apparent photosynthesis was modulated by temperature, age and type of leaf, as well as stage of the growing season. Increasing leaf temperature modified the response curves of A to light causing an increase in  $I_c$ ,  $I_s$ , and  $R_D$ .

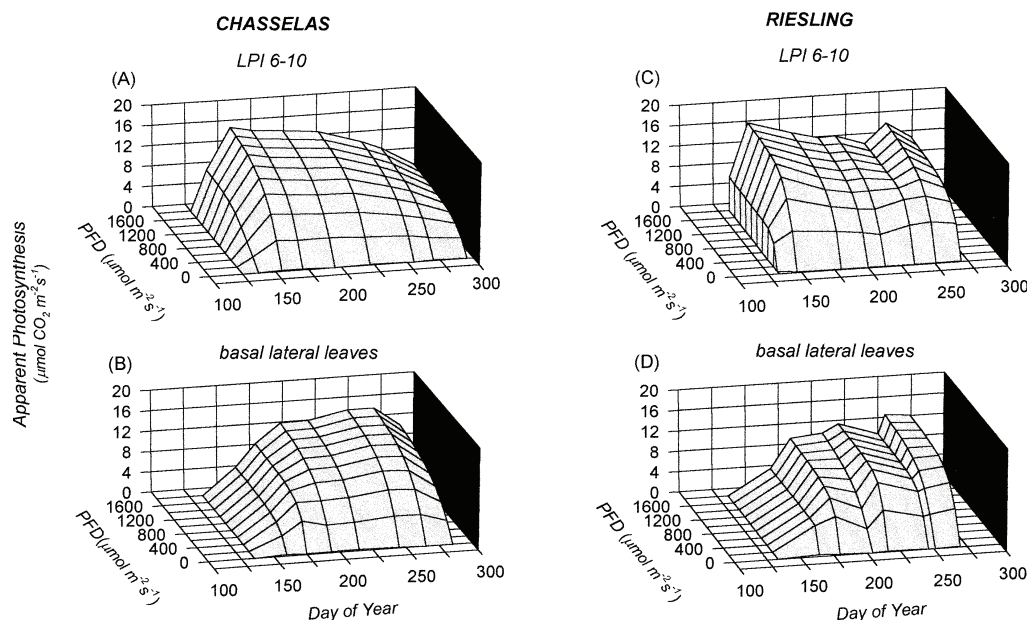


Fig. 6: Influence of photon flux density on the apparent photosynthesis of leaves of primary shoots (LPI 6-10, A, C) and secondary shoots (basal lateral leaves, B, D) at different times during the growing season for Riesling and Chasselas. Measurements were conducted at leaf temperatures of 25-30 °C and at low leaf to air vapour pressure difference. The curves were calculated from equation (1) (see Appendix).

In general,  $I_s$  of young growing leaves was inferior to that of adult leaves. Certain authors also noted that  $I_s$  often diminishes with progressing senescence of the leaves (HODANOVA 1979; CATSKY and TICHÁ 1980; CONSTABLE and RAWSON 1980; SCHULTZ 1989). The  $I_s$  was near 700  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at leaf temperatures between 20 and 25 °C in adult Riesling and Chasselas leaves comparable to the results of many studies under so-called optimum conditions (GEISLER 1963; KRIEDEMANN 1968; RÜHL *et al.* 1981; SMART 1984; DÜRING 1988). However, when leaf temperature was between 25 and 30 °C,  $I_s$  was approaching 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and reached about 1200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for adult Riesling leaves and 1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for Chasselas leaves between 30 and 34 °C. The increase in  $I_s$  with temperature is confirmed by similar results from other studies on grapevines (KRIEDEMANN and SMART 1971; CHAVES *et al.* 1987; SCHULTZ 1989) and other cultivated plants (FLORE and LAKSO 1989). Thus, on very hot summer days, only a limited number of leaves situated at the circumference of the canopy and exposed to direct light reach  $I_s$ .

In the present study, the light response curves of photosynthesis became distinctly flatter with increasing temperature due to a significant increase in PR relative to A typical for  $C_3$  plants (BADGER and COLLATZ 1977; CATSKY and TICHÁ 1980; OGREN 1984) including grapevines (ALBUQUERQUE-REGINA and CARBONNEAU 1995; DÜRING 1991). The absolute levels of PR measured and estimated in various studies differ largely because of differences in the methods used (SHARKEY 1988). OGREN (1984) estimated the level of PR at 15 % of A, while ZELITCH (1975) placed PR closer to 40-50 % for most  $C_3$  plants. For grapevines, reported PR values were 15-20 % of A at 25 °C (DÜRING 1988) and increased to 30-40 % for temperatures between 25 and 30 °C (IACONO and SOMMER 1996) with some possible varietal variations (DÜRING 1988, 1991; ALBUQUERQUE-REGINA and CARBONNEAU 1995). The PR data reported for Riesling and Chasselas are within the range

described above and differences between varieties may have been more a result of adaptive responses to the prevailing temperature conditions with possible modifications of substrate concentration or Rubisco activity and structural alterations in the biomembranes (BERRY and DOWNTON 1982) rather than a "true" genetic difference. Since stomatal conductance ( $g$ ) plays a mayor role in determining intercellular  $\text{CO}_2$  concentration ( $c_i$ ) and thus the ratio of  $\text{CO}_2/\text{O}_2$ , differences in  $g$  are another possible explanation (OGREN 1984). However, since calculated  $c_i$  concentrations are problematic due to possible heterogeneous stomatal opening, which can also be induced by changes in PFD (DÜRING and LOVEYS 1996), the results obtained are difficult to evaluate.

The  $I_c$  increased more strongly with temperature for young, growing leaves of primary and secondary shoots than for adult leaves due to differences in  $R_D$ . This finding is confirmed by the results of many previous studies (HODANOVA 1979; JURIK *et al.* 1979; CONSTABLE and RAWSON 1980; BYKOV *et al.* 1981; PASIAN and LIETH 1989; SCHULTZ 1989). Since an important part of the leaf surface of the canopy is composed of these young leaves at certain times of the season, daily vine carbon balance at high temperatures and at times of low light intensity (cloudy weather, dense canopy) may be strongly reduced.

The slope of the light response curve  $\alpha$  denotes the utilisation efficiency of the incident light energy for fixing  $\text{CO}_2$ . In general, young, growing leaves are less efficient than adult leaves (CATSKY and TICHÁ 1980; CONSTABLE and RAWSON 1980; PASIAN and LIETH 1989) mainly due to a yet incomplete photosynthetic machinery. However, in our study, the  $\alpha$  values calculated for young, growing and adult Chasselas leaves were almost identical at temperatures between 20 and 32 °C. PASIAN and LIETH (1989) and FIELD and MOONEY (1983) noted that there was no significant correlation between  $\alpha$  and leaf age except for a progressive decrease in senescent leaves. Nevertheless,

$\alpha$  decreased with increasing temperature and more so, albeit from higher levels, for Riesling than for Chasselas which was probably related to the differences in PR (BERRY and DOWNTON 1982; EHLERINGER and PEARCY 1983).

However, the physiological interpretation of the parameter  $\alpha$  remains difficult for several reasons. Since  $\alpha$  is related to incident radiation, rather than absorbed radiation, it may be quite different from the actual quantum yield, in particular because substantial absorption changes occur with leaf age and time of season in *Vitis vinifera* (SCHULTZ 1996). Additionally, the parameters  $\alpha$ ,  $\theta$ , and  $A_{\max}$  used in the equation proposed by MARSHALL and BISCOE (1980) are not completely independent. They can interact so that in some cases  $\alpha$  and  $\theta$  can influence each other and can lead to unrealistic results (LEVERENZ 1988). When estimating the parameter values by fitting the model to data sets with few data  $>700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , sometimes negative values for  $\theta$  resulted. This was due to the fact that  $\theta$  determines the shape of the curve so that, when data for high PFD levels were lacking, the exact shape cannot be discerned, resulting in considerable uncertainty in the value of  $\theta$ . Since most  $\theta$  values were between 0.7 and 0.95, we consequently fixed a lower threshold of 0.7 for the fittings. The  $\theta$  values did not suggest a pattern with age or temperature and were on the average  $0.788 \pm 0.107$  for Riesling and  $0.763 \pm 0.098$  for Chasselas. These values for  $\theta$  indicate that the curves lie between a Blackman response curve ( $\theta = 0$ ) and the rectangular hyperbola ( $\theta = 1$ ). The interaction between  $A_{\max}$  and  $\alpha$  can lead to a relative increase in  $\alpha$  at low values of  $A_{\max}$  and thus to a certain extent could have masked differences between leaf ages.

During the season, the photosynthetic potential of the leaves in relation to PFD is not stable and changes are not only related to a decrease in photosynthetic capacity by increasing leaf age (KRIEDEMANN 1968; FLORE and LAKSO 1989; SCHULTZ *et al.* 1996). For both varieties, basal leaves on lateral shoots had assimilation rates that were 20-30 % below those of leaves on primary shoots during the phenological stage of berry set to veraison, but they became more effective than the latter ones at the end of the fruit ripening period. This is consistent with results from other studies using direct and indirect methods to assess for  $A$  or assimilate transport from various leaf classes (STOEV *et al.* 1966; KOBLET and PERRET 1971; CANDOLFI-VASCONCELOS and KOBLET 1991; SCHULTZ *et al.* 1996) and underlines the importance of secondary shoots for sugar accumulation in the berries during ripening.

Is there a varietal effect in the interaction between age, light and temperature? There are several factors differing between the two data sets used in this study. Measurements were conducted 10 years apart in two different locations with two varieties and different equipment. Although, at first glance, varietal differences seem to exist, we will show in a forthcoming paper that these differences were entirely caused by modulative temperature adaptation, that is local acclimation to the prevailing temperature conditions. In this respect, the presented data sets provide a unique source for characterizing grapevine photosynthesis for the purpose of modelling and should be viewed as such.

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## Appendix

The model of the photosynthetic response to light is a mathematical derivative of the "Blackman response curve" and contains 4 parameters and thus permits a large degree of flexibility with respect to the shape of the light response.

$$A_{\text{PFD}} = \frac{\alpha \text{ PFD} + A_{\text{max}} + R_{\text{D}} - ((\alpha \text{ PFD} + A_{\text{max}} + R_{\text{D}})^2 - 4 \alpha \text{ PFD} \theta (A_{\text{max}} + R_{\text{D}}))^{1/2}}{2 \theta} - R_{\text{D}} \quad (1)$$

where:

- $A_{\text{PFD}}$  = apparent photosynthesis at a certain PFD,  
 $A_{\text{max}}$  = maximum apparent photosynthesis at light saturation for a given temperature,  
 $\alpha$  = initial slope of the curve, apparent quantum yield (mol CO<sub>2</sub>-mol photons<sup>-1</sup>),  
 PFD = photon flux density (μmol m<sup>-2</sup>s<sup>-1</sup>),  
 $R_{\text{D}}$  = dark respiration at a given temperature,  
 $\theta$  = dimensionless parameter, describes the convexity of the light response (LEVERENZ 1988).

By rearranging equation (1), the PFD compensation point ( $I_c$ ) was estimated using the equation:

$$I_c = R_{\text{D}} (R_{\text{D}} + A_{\text{max}}) / (\alpha (R_{\text{D}} - A_{\text{max}})) \quad (2)$$

The PFD saturation point is difficult to quantify, since the onset of saturation occurs gradually. We therefore used the equation proposed by PASIAN and LIETH (1989) to calculate a "saturation index" ( $I_s$ ), which corresponds to light levels close to maximum photosynthetic rates:

$$I_s = 2 (A_{\text{max}} + R_{\text{D}}) / \alpha \quad (3)$$

Parameter estimates for equations (1) - (3) were obtained by least square non-linear regression analyses using the program "Derivative Free Non-Linear Regression" of BMDP (DIXON 1985). For the parameter estimates of equation (1),  $\theta$  was only allowed to vary between 0.7 and 1.0 to ensure that convergence criteria were met.