GAS EXCHANGE OF FIELD-GROWN *VITIS VINIFERA* L. cv. ZWEIGELT LEAVES IN RELATION TO LEAF AGE AND POSITION ALONG THE STEM

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Abstract

Aims: The study aimed to investigate the effects of leaf age and position along the stem on the seasonal evolution of photosynthesis and water use efficiency (WUE) of primary leaves of field-grown grapevines (*Vitis vinifera* L. cv. Zweigelt) under natural growing conditions in the Pannonian climate.

Methods and results: Single-leaf gas exchange measurements were carried out in three vineyards with different planting densities, training systems and canopy management in the Neusiedlersee region (Burgenland, Austria). From the beginning of leaf development until flowering, basal leaves in the fruiting zone showed the highest photosynthetic activity. After flowering until ripening, the zone with the highest photosynthetic activity continuously moved in the apical direction. Leaves reached their maximum photosynthetic activity 30 to 40 days after emergence, depending on investigation site and vineyard management. Due to sufficient water supply, photosynthesis of old leaves decreased slowly; thus 100 days after unfolding leaves still retained 65% to 75% of their maximum photosynthetic activity.

Conclusion: The development of single-leaf photosynthesis in the Zweigelt grapevine corresponded to the results of prior investigations on other grape varieties. However, vineyard management strongly influenced the evolution of gas exchange during the growing period. Leaves from vines stressed by high crop load or poor canopy management showed early leaf senescence and a strong decline in photosynthetic activity after reaching maximum level. Well-watered leaves from shoot-thinned vines with moderate crop load and equal light exposure throughout the canopy exhibited high photosynthesis with a much slower decrease in older leaves.

Significance and impact of the study: The results indicate that under favourable growing conditions ensured by adequate water supply and canopy management, basal leaves maintain good photosynthesis and WUE over a long period of time. Thus old leaves, as well, can contribute to the photosynthesis of the entire vine.

Key words: photosynthesis, water use efficiency, leaf age, leaf insertion height, Zweigelt

Résumé

Objectifs : L'objectif était d'étudier l'évolution saisonnière de la photosynthèse et de l'efficience de l'utilisation de l'eau (WUE : *water use efficiency*) des feuilles de pousses principales de la vigne Zweigelt (*Vitis vinifera*. L. cv. Zweigelt), en condition de plein champ et dans un climat pannonique.

Méthodes et résultats : Les mesures des échanges gazeux ont été effectuées sur des feuilles isolées de trois vignobles différents dans la région du Neusiedlersee (Burgenland, Autriche) avec différents espacements, différents systèmes de conduites et différents types de gestion du feuillage. La plus grande activité photosynthétique a été observée chez les feuilles basales de la zone fructifère entre le début du développement du bourgeon de feuille et la floraison. Après la floraison et jusqu'à la maturité du raisin, la zone avec la plus grande activité photosynthétique se déplaçait de façon continuelle en direction apicale. L'activité maximale photosynthétique des feuilles a été atteinte 30 à 40 jours après leur développement, en fonction du site de l'expérience et de la gestion du vignoble. Suite à une irrigation suffisante, la photosynthèse des feuilles âgées n'a diminué que lentement, de sorte que 100 jours après leur émergence, les feuilles présentaient toujours 65% à 75 % de leur activité photosynthétique maximale.

Conclusion : L'évolution de la photosynthèse de feuilles isolées de la vigne Zweigelt correspond à celle déjà observée lors d'études antérieures sur d'autres cépages. Il s'est pourtant avéré que la gestion du vignoble a un impact considérable sur le processus d'échanges gazeux pendant la période de végétation. Les feuilles des vignes soumises au stress, à cause d'une mauvaise gestion du feuillage ou d'un rendement supérieurement fructifère, ont présenté des signes de sénescence plus tôt ainsi qu'une plus forte réduction de l'activité photosynthétique après l'atteinte du niveau maximum. Les feuilles des vignes bien irriguées, écimées, moyennement fructifères et exposées à la lumière de façon homogène sur toute leur surface foliaire ont quant à elles montré une forte activité photosynthétique avec une diminution lente chez les feuilles âgées.

Signification et impact de l'étude : Les résultats de l'étude indiquent que les feuilles âgées, sous des conditions favorables de croissance (une irrigation et une gestion du feuillage adéquates), sont capables de maintenir dans la zone basale de leur pousse et sur une longue durée une activité photosynthétique et WUE importante, et peuvent ainsi contribuer de façon positive à la photosynthèse du cep entier.

Mots clés : photosynthèse, efficience de l'utilisation de l'eau, âge de la feuille, hauteur du point d'insertion de la feuille, Zweigelt

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INTRODu CTION

The interactions between leaf age and grapevine photosynthesis have been widely studied. Grape leaves reach adult size and maximum photosynthetic activity 30-40 days after appearance, then a gradual and constant decline in photosynthesis occurs (reviewed by Poni and Intrieri, 2001). However, these investigations have been carried out on different grape varieties under various climatic conditions, using both potted plants (Alleweldt *et al.*, 1982 ; Intrieri *et al.*, 1992 ; Kriedemann *et al.*, 1970 ; Patakas *et al.*, 1997 ; Zufferey *et al*., 2000) and field-grown grapevines (Bertamini and Nedunchezhian, 2003 ; Poni *et al.*, 2008 ; Schubert *et al.*, 1996 ; Schultz *et al.*, 1996). Hence, it appeared that the speed and intensity of the drop in photosynthesis after reaching the maximum rate differ between the studies. Especially under dry conditions, leaves tend to a faster decline in photosynthesis with increasing leaf age than in cool climates with sufficient water supply (Bertamini and Nedunchezhian, 2003 ; Schultz *et al.*, 1996). Photosynthesis of a single leaf within the canopy can be influenced by various factors : the amount of sunlight received determines not only actual photosynthesis but also photosynthetic efficiency. Leaves grown in shade show a permanent adaptive reduction in single-leaf photosynthesis (Palliotti *et al.*, 2000). Unfavourable light conditions in the lower part of the canopy cause earlier reduction in photosynthesis with increasing leaf age than under optimal light conditions (Hunter and Visser, 1989). Zufferey *et al.* (2000) showed that temperatures below and above an optimum of 27-32°C reduced photosynthetic activity of bunch leaves. Among climatic factors, water vapour deficit in the ambient air also has a high impact on gas exchange. With increasing leaf-to-air vapour pressure deficit, stomata close and photosynthesis is reduced (Düring, 1987). Furthermore, photosynthesis is related to leaf chlorophyll content. Bertamini and Nedunchezhian (2003), Hunter and Visser (1989) and Schubert *et al*. (1996) showed that the development of chlorophyll content from leaf emergence to senescence mostly corresponds to photosynthetic activity. Single-leaf photosynthesis is also influenced by fruit-to-leaf ratio. Leaf removal enhances single-leaf photosynthesis of remaining leaves (Hunter and Visser, 1988b ; Poni *et al*., 2008).

Austria's Neusiedlersee wine-growing region (Burgenland) has a Pannonian climate. It distinguishes itself as the warmest region of all Austrian grape-growing regions ; in particular, the midday temperatures during wine-growing periods are higher than in other regions. Concomitantly to the high temperature, precipitation is usually low during growing periods (ZAMG, 2002). These climatic conditions clearly favour the production of red wine, with the traditional Austrian variety Zweigelt being the most important variety. In this region it is often common practice to remove leaves positioned in the fruiting zone at the beginning and during the ripening period, because the farmers consider them to be unnecessary or even detrimental to the development of the grape. The main reasons for the defoliation of basal leaves in cool climates are prevention against bunch rot and improvement of colouring and aroma compounds (Koblet, 1987 ; Percival *et al.*, 1994 ; Reynolds and Vanden Heuvel, 2009 ; Zoecklein *et al.*, 1992). But it should be questioned if this viticultural practice is advisable for the Neusiedlersee region. In most years, the risk for severe botrytis infection is low because of the warm summer temperatures and early harvest, not later than the middle of September. It is doubtful if the direct exposure of grapes to the sun, caused by late defoliation in the fruiting zone, is always beneficial to fruit and wine quality (Bavaresco *et al.*, 2008 ; Bergqvist *et al.*, 2001 ; Guidoni *et al.*, 2008 ; Reynolds *et al.*, 2005). Furthermore, through late defoliation in the fruiting zone, photosynthetically active leaves that positively contribute to whole vine photosynthesis are suddenly removed (Petrie *et al.*, 2003), thereby reducing sugar accumulation in the berries (Iacono *et al.*, 1995 ; Petrie *et al.*, 2003) and carbohydrate reserve accumulation in roots and trunks (Bennet *et al.*, 2005).

So far, there are no specific data about the progress of single-leaf photosynthesis in Zweigelt grapevines. Such data would facilitate a better evaluation of defoliation in relation to photosynthetic activity. Therefore, the aim of the study was to clarify whether leaves in the basal part of the shoot are still photosynthetically active during ripening, compared to other leaf positions, and thus useful for grape ripening. The photosynthetic activity of single leaves at different positions along the shoot was investigated during the growing period. The gas exchange measurements were performed under natural conditions on field-grown Zweigelt grapevines from three different vineyards with similar soil and climatic conditions but different canopy management.

MATERIALS AND METHODS

1. Plant material and growing conditions

The field studies were conducted in 2005 in three vineyards (termed A2, B3, B4) in the Austrian wine-growing district of Neusiedlersee (Burgenland). The region belongs to the Pannonian climate with a mean annual rainfall of 574 mm and an average temperature of 10.1°C (ZAMG, 2002). All three vineyards have black steppe soils (with a humic A-horizon and a directly adjacent C-horizon), which is characteristic for the region. Vineyard A2 has a calcareous, sandy clay soil with a high portion of gravel in the subsoil (40 cm and deeper), classified as Tschernosem (Nestroy *et al.*, 2000). Vineyard B4 has a calcareous, sandy clay soil without stones in the topsoil

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(0-50 cm) and a moderate portion of stones in the subsoil (50-60 cm and deeper), also classified as Tschernosem (Nestroy *et al.*, 2000). Vineyard B3 has a sandy clay soil with a very high portion of gravel in the topsoil and a layer of gravel only in the subsoil (40 cm and deeper), resulting in a very dry soil with poor water holding capacity. This soil is classified as Paratschernosem.

All vineyards were planted with *Vitis vinifera* L. cv. Zweigelt. The rootstock was *Vitis riparia* x *Vitis berlandieri* 161-49 C in vineyard A2 (with a high plant density of 6,900 plants per ha) and the commonly used *Vitis riparia* x *Vitis berlandieri* Kober 5BB in vineyards B3 and B4. Plant density (distance between rows x distance between vines) was 1.8 x 0.8 m in A2, 2.8 x 1.0 m in B3 and 2.7 x 1.0 m in B4. In A2 and B4 the vines were trained to a single cane and one small spur. After shoot thinning, 6 (A2) and 7 (B4) shoots per vine were retained, whereas in B3 13 shoots were present per vine without shoot thinning. Vineyards B3 and B4 were equipped with a drip irrigation system, and irrigation was carried out by the winegrowers according to observation of the vineyards, natural precipitation and personal experience. Due to sufficient precipitation during most of the growing season, irrigation was carried out only two times in vineyard B3 (at flowering: DOY 170, and at the beginning of ripening: DOY 214) and only one time in vineyard B4 (at flowering: DOY 169).

Shortly after budburst, one vine was randomly selected in each vineyard. Three shoots per vine, positioned at the proximal, the middle and the distal position of the fruiting cane, were tagged. All shoots were bearing fruit, with up to 3 inflorescences between node 3 and 6 on each shoot. Measurements of leaf area and gas exchange were performed on the tagged shoots on 7 dates during the growing season 2005; the phenological stages (BBCH) were measured according to Lorenz *et al.* (1995): DOY 132 (BBCH 14), DOY 143 (BBCH 17), DOY 150 (BBCH 19), DOY 162 (BBCH 61), DOY 175 (BBCH 69), DOY 194 (BBCH 77) and DOY 217 (BBCH 81). On the first two dates (DOY 132 and 143), when only 4 and 7 leaves, respectively, were unfolded, all leaves were sun leaves (fully exposed to the sun). From the third date on (DOY 150), leaves positioned on the outside of the canopy and therefore directly exposed to sunlight (photosynthetic photon flux density (PPFD) $\geq$ 300 µmol m^{-2} s^{-1}) were grouped in "sun leaves" and those positioned inside of the canopy and therefore never subjected to full sunlight (PPFD < 300 µmol m^{-2} s^{-1}) were grouped in "shade leaves".

2. Climatic conditions

Meteorological data were recorded using meteorological stations positioned in vineyards A2 and B3. The data obtained from the station in vineyard B3 were also used for vineyard B4, which was located near (~ 1 km) B3. In vineyard A2, a Unidata Starlogger (Kroneis, Vienna, Austria) equipped with sensors for temperature, relative humidity and precipitation was used. A meteorological station from Adcon Telemetry (Klosterneuburg, Austria) with sensors for temperature, relative humidity and precipitation was installed in vineyard B3.

3. Leaf gas exchange measurements

Single-leaf gas exchange (photosynthesis A, µmol CO_2 m^{-2} s^{-1}, transpiration E, mmol H_2O m^{-2} s^{-1} and stomatal conductance gs, mol H_2O m^{-2} s^{-1}) was measured on all primary leaves of the tagged shoots with a LCpro photosynthesis system (ADC, Hoddesdon, York, UK) equipped with a broad leaf chamber (area = 6.25 cm^2). Measurements were performed between 10 a.m. and 2 p.m. All measurements were performed using a LED-light unit (light intensity = 1750 µmol m^{-2} s^{-1}) on the leaf chamber to ensure a constant saturated light supply for every leaf. Measurements were taken using ambient air, which was aspirated nearby the canopy through a flexible tube. Ambient conditions were used for CO_2, temperature and humidity inside the cuvette, and the airflow was set to 250 µmol s^{-1}. Intrinsic water use efficiency (WUE_i) was calculated as A/gs (µmol CO_2 m^{-2} s^{-1}/mol H_2O m^{-2} s^{-1}), according to Jones (2004).

4. Growth parameters and vine water status

On each date, single-leaf area of every primary leaf on each tagged shoot was measured using a LI-3000A portable area meter (LI-COR, Nebraska, USA). Shoot length of the tagged shoots was measured for determination of shoot growth. At harvest a sample of 20 vines per vineyard was harvested, and grape yield (average number of clusters per vine, average yield (kg) per vine and occurrence of berry shrivel (%)) was determined.

Predawn leaf water potential was measured in vineyard B3, which represented the vineyard with the driest soil conditions. Measurements were taken on irrigated and non-irrigated vines (4 leaves per variant), with a plant water status console (Soilmoisture Equipment Corp., Santa Barbara, USA) according to Scholander *et al.* (1965). Measurements were taken on 5 dates between flowering and ripening: DOY 171, DOY 186, DOY 199, DOY 210 and DOY 224.

5. Data analysis

Means of predawn water potential and single-leaf area were analysed with ANOVA (SPSS statistics 15.0). Polynomial regression curves (quadratic or cubic) were fitted to photosynthesis against leaf insertion height using SigmaPlot 10.0 (Systat Software Inc.). For the evaluation

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of gas exchange against leaf age, data were grouped in classes of 3 to 6 days. Means and standard deviation of leaf age and gas exchange were analysed using SPSS statistics 15.0. Nonlinear regression curves were fitted with SigmaPlot 10.0 (Systat Software Inc.). For all regression curves ANOVA statistic was performed with SigmaPlot. Significance levels for ANOVA were *, **, and *** at 0.05, 0.01, and 0.001, respectively.

RESULTS

The yearly mean temperature in 2005, measured in vineyards A2 and B3, was higher than the long-term average of Neusiedl am See (1971-2000) (Table 1). In April, May, June, July and September the monthly mean temperature was approximately 1 °C higher than the long-term average ; only in August was the temperature lower. Precipitation was high during the growing season (April-September), especially in August, when the monthly precipitation was threefold higher than the long-term average. There were only slight differences in climatic conditions between the two vineyards.

Due to high precipitation, the predawn water potential of single leaves in vineyard B3 was only slightly negative, ranging between -0.01 and -0.18 MPa (Table 2). The lowest predawn water potential was measured on DOY 186 and 224. There were no significant differences between irrigated and non-irrigated vines.

Vegetative development of selected vines differed between the three vineyards. From DOY 143 on, shoot growth in vineyard B3 was lower than in A2 and B4. On DOY 175, shortly before shoots were topped, shoots in A2 were the longest, followed by B4 and B3 (Table 3). Single-leaf area of mature leaves (basipetal leaf position 4 to 10) also differed between the three vineyards (Table 4). From the beginning of flowering (DOY 162) to DOY 194, single-leaf area was significantly smaller in B3 than in A2 and B4. At ripening (DOY 217), single-leaf area was largest in A2, followed by B4 and B3.

Analysis at harvest showed differences in grape yield (Table 5). B3 had the highest number of clusters per vine and highest fruit yield per vine. It also had the highest occurrence of *Traubenwelke* (berry shrivel). A2 had the lowest number of clusters per vine, but median fruit yield and lowest occurrence of *Traubenwelke*.

Figures 1, 2 and 3 show the development of single-leaf photosynthesis (A) as a function of basipetal leaf position along the stem for vineyards A2, B3 and B4, respectively. On site A2, A was low (max. 7.00 µmol CO_2) in all leaves during the first measurement, when 4 leaves were unfolded (Figure 1, DOY 132), owing to the low temperature on that day (max. temperature : 17.6°C)

Table 1 - Monthly mean temperature (°C) and precipitation (mm) measured in vineyards A2 and B3 in the year 2005 compared to the long-term average (1971-2000) of the ZAMG Station in Neusiedl am See (ZAMG, 2002).

	Monthly mean temperature (°C)			Monthly precipitation (mm)		
	A2	B3	Average 1971-2000 Neusiedl am See	A2	B3	Average 1971-2000 Neusiedl am See
Jan	1.5	1.4	-0.5	35	14	32
Feb	-1.2	-1.1	1.1	57	35	29
Mar	4.4	4.3	5.4	17	16	37
Apr	11.9	11.8	10.6	49	55	42
May	16.5	16.6	15.2	62	49	61
Jun	19.9	19.7	18.3	33	27	65
Jul	21.7	21.5	20.4	77	87	64
Aug	19.3	19.0	20.1	174	192	63
Sep	17.3	17.4	15.5	61	34	50
Oct	11.6	11.8	9.9	2	2	44
Nov	4.6	4.4	4.2	53	46	48
Dec	1.3	1.1	1.1	40	61	40
2005	10.7	10.7	10.1	660	618	574

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Table 2 - Predawn leaf water potential (MPa) measured in vineyard B3 in the year 2005 on five different dates on non-irrigated and irrigated vines. Each value is a mean (n = 4).

Predawn leaf water potential (Ψ_{PD}, MPa)			
Date (DOY)	non-irrigated (mean ± SD)	irrigated (mean ± SD)	significance[a]
171	-0.08 ± 0.021	-0.05 ± 0.013	0.050ns
186	-0.15 ± 0.025	-0.12 ± 0.014	0.134ns
199	-0.01 ± 0.022	-0.01 ± 0.014	0.801ns
210	-0.07 ± 0.026	-0.07 ± 0.013	0.906ns
224	-0.18 ± 0.058	-0.18 ±.0.037	0.834ns

Table 3 - Average shoot length (cm) of tagged shoots measured in the three vineyards on five different dates before shoot topping. Each value is a mean (n = 3).

DOY	Average shoot length (cm)		
	vineyard A2	vineyard B3	vineyard B4
132	22.7	20.0	22.3
143	41.7	35.0	41.7
150	66.3	46.7	64.0
162	86.7	68.3	81.7
175	117.7	93.3	97.3

Table 4 - Average single-leaf area of primary leaves (basipetal position 4 to 10) on the tagged shoots measured on four different dates from flowering (DOY 162) to ripening (DOY 217). Each value is a mean (n = 3 shoots); values with the same letters are not statistically different according to Student Newman-Keuls test (P ≤ 0.05).

DOY	Average single-leaf area (cm^2) of primary leaves positioned between node 4 and 10			
	vineyard A2	vineyard B3	vineyard B4	significance[a]
162	190.0b	142.2a	206.7b	0.001***
175	216.9b	154.2a	202.1b	0.000***
194	230.3b	173.8a	211.1b	0.010**
217	191.3b	155.6a	179.1ab	0.030*

and because the leaves were not yet fully developed. On DOY 143, 7 leaves were already present and A of the 5 basal leaves was markedly higher (with up to 15.00 µmol CO_2). The apical leaves (nodes 6 and 7), with a maximum chronological leaf age of 7 days, had very low or even negative A. One week later (Figure 1, DOY 150) A was highest in basal sun leaves (leaf position 1-5) with 15.00-20.00 µmol CO_2, whereas young apical leaves had very low or negative A. Shade leaves had lower A than sun leaves. Low temperature (max. temperature 21.2°C) again caused low A at the beginning of flowering (Figure 1, DOY 162). Nevertheless, the highest values (12.00 µmol CO_2 for sun leaves, on average) were still found in the basal part of the shoot (nodes 1-7), and they declined gradually towards the shoot apex. On the first date after full bloom (Figure 1, DOY 175) A of basal leaves (nodes 1-7) was lower than in the middle of the shoot (nodes 8-12), where a maximum of 17.00 µmol CO_2 was reached. On DOY 194 (corresponding to BBCH 77) the zone with the highest A moved to nodes 10-15. At this date, up to 25 leaves were unfolded on untopped shoots. On the last date (Figure 1, DOY 217, BBCH 81)

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the highest A was performed by leaves with basipetal leaf position 15 to 25 (17.00 µmol CO_2). A of sun leaves in the basal part of the shoot (nodes 4-10) was diminished by ~ 30 % compared to maximum A. Apical leaves also had high rates of A with 12.00-17.00 µmol CO_2.

On site B3 (Figure 2) the photosynthetic performance was similar to A2 on the first two dates (DOY 132 and 143). Beginning with DOY 150, a higher variation occurred between single leaves than on site A2, as reflected by the low regression coefficient of the fitted curve. Already at the beginning of bloom (Figure 2, DOY 162), which occurred one week earlier than in A2, A of basal leaves was lower compared to leaves of position 3 to 6 on the shoot. After full bloom (Figure 2, DOY 175) the zone with the highest A was already found in leaves inserted between node 7 and 13. At the same time the proportion of shade leaves was high in the basal part of the shoot. On DOY 194, when the majority of berries were touching, the highest A was performed by apical leaves inserted between nodes 15 and 20. At the beginning of ripening (Figure 2, DOY 217), A was lower (10.00 µmol CO_2 m^{-2} s^{-1} on average) compared to site A2 across the whole shoot, and dependency of photosynthesis on insertion height no longer followed a curve progression, as had been observed in A2.

On site B4 (Figure 3), A was also similar to A2 and B3 on DOY 132 and DOY 143, when 5 and 7 leaves were unfolded. At the beginning of bloom (DOY 150) A of the first two basal leaves began to decrease compared to leaves in the middle of the shoot, where a maximum of 12.00 µmol CO_2 were reached. From DOY 175 to 217 the variation in photosynthesis between single leaves along the shoot as well as between the shoots became too large for the identification of a zone with maximum A. Nevertheless, there was a trend that A of basal leaves decreased moderately compared to leaves in the middle of the shoot.

Figures 4, 5 and 6 show A, WUE_i and gs, respectively, in relation to leaf age for the three vineyards A2, B3 and B4. For this overview, the results from all dates and

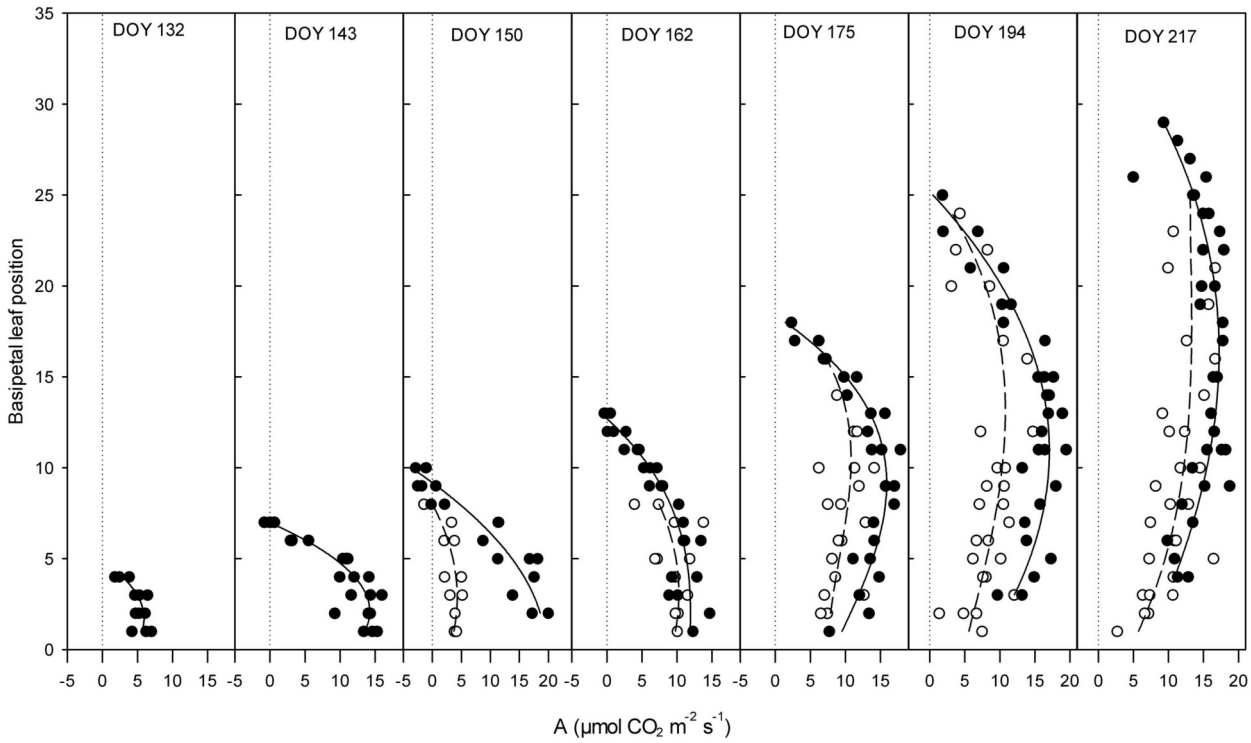


Figure 1 - Single-leaf photosynthesis (A) plotted as a function of basipetal leaf position along the stem for vineyard A2 measured at different dates (DOY 132, DOY 143, DOY 150, DOY 162, DOY 175, DOY 194 and DOY 217). Each point is an individual measurement. Closed symbols and continuous lines indicate sun leaves; open symbols and dashed lines indicate shade leaves.

Regression equations are: DOY 132 sun leaf: $y = 4.2767 + 1.9527x - 0.576x^2$ ($r^2 = 0.610$*); DOY 143 sun leaf: $y = 11.590 + 2.5212x - 0.6005x^2$ ($r^2 = 0.890$***); DOY 150 sun leaf: $y = 19.5272 - 0.0042x - 0.2316x^2$ ($r^2 = 0.882$***), shade leaf: $y = 2.9443 + 0.9284x - 0.1623x^2$ ($r^2 = 0.569$*); DOY 162 sun leaf: $y = 11.7776 + 0.1400x - 0.199x^2 - 0.0051x^3$ ($r^2 = 0.893$***), shade leaf: $y = 9.1639 + 0.7244x - 0.1173x^2$ ($r^2 = 0.164$ns); DOY 175 sun leaf: $y = 8.2747 + 1.2474x + 0.0012x^2 - 0.0051x^3$ ($r^2 = 0.874$***), shade leaf: $y = 7.5253 + 0.00497x + 0.0808x^2 - 0.0053x^3$ ($r^2 = 0.244$ns); DOY 194 sun leaf: $y = 7.6606 + 1.6978x - 0.0744x^2 - 0.0002x^3$ ($r^2 = 0.835$***), shade leaf: $y = 4.9030 + 0.6897x - 0.0023x^2 - 0.0012x^3$ ($r^2 = 0.379$*); DOY 217 sun leaf: $y = 6.5176 + 1.2228x - 0.0294x^2 - 0.0003x^3$ ($r^2 = 0.533$***), shade leaf: $y = 4.5049 + 1.2931x - 0.0620x^2 + 0.0010x^3$ ($r^2 = 0.458$***). *P ≤ 0.05, **P ≤ 0.01 and ***P ≤ 0.001, respectively.

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Table 5 - Yield parameters for the three vineyards at harvest 2005 (DOY 262): number of clusters per vine, kg of fruit yield per vine and incidence of clusters showing berry shrivel.

	Vineyard A2	Vineyard B3	Vineyard B4
Clusters/vine (no.)	6.6	21.0	7.6
Fruit yield/vine (kg)	2.04	3.50	1.53
Clusters with berry shrivel (%)	17.1	34.3	23.7

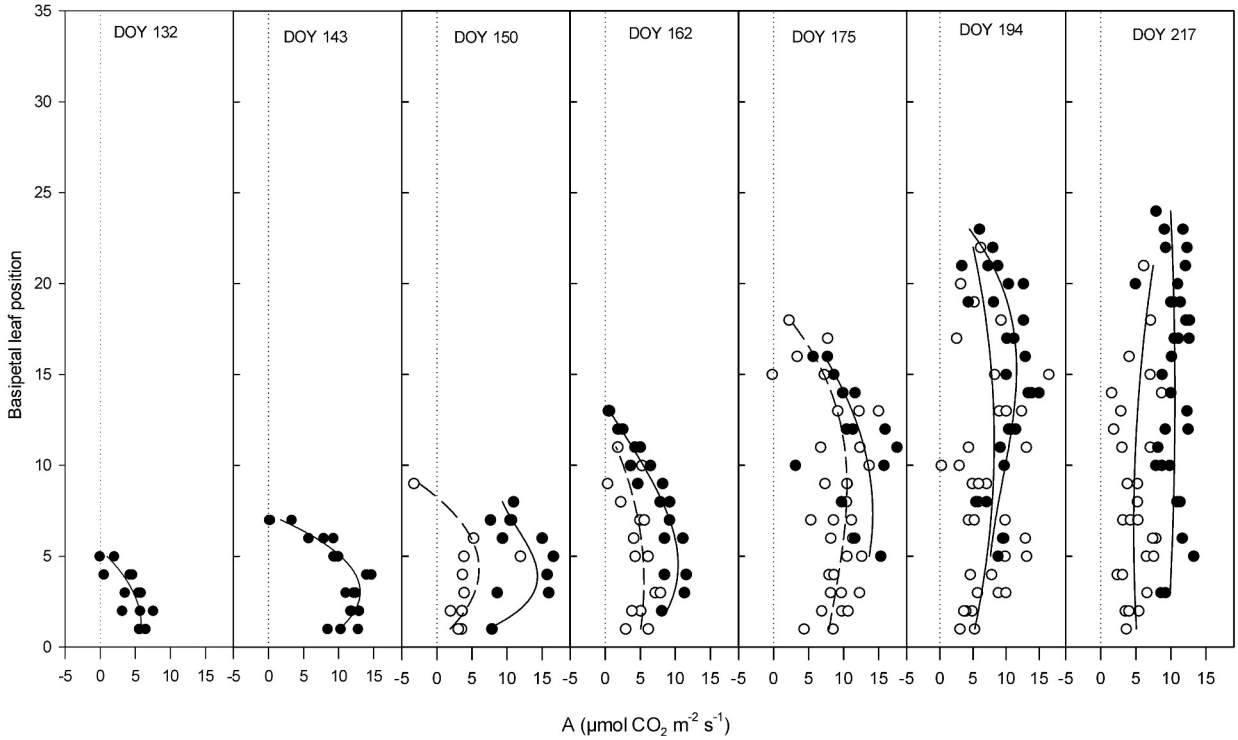


Figure 2 - Single-leaf photosynthesis (A) plotted as a function of basipetal leaf position along the stem for vineyard B3 measured at different dates (DOY 132, DOY 143, DOY 150, DOY 162, DOY 175, DOY 194 and DOY 217). Each point is an individual measurement. Closed symbols and continuous lines indicate sun leaves; open symbols and dashed lines indicate shade leaves.

Regression equations are: DOY 132 sun leaf: $y = 5.3936 + 0.7755x - 0.3328x^2$ ($r^2 = 0.603$*); DOY 143 sun leaf: $y = 6.4469 + 4.3672x - 0.7207x^2$ ($r^2 = 0.872$***); DOY 150 sun leaf: $y = 0.3325 + 8.3881x - 1.5373x^2 + 0.0787x^3$ ($r^2 = 0.407$ns), shade leaf: $y = 5.2404 - 3.0710x + 1.951x^2 - 0.1067x^3$ ($r^2 = 0.642$ns); DOY 162 sun leaf: $y = 4.8556 + 2.6244x - 0.3621x^2 + 0.0102x^3$ ($r^2 = 0.898$***), shade leaf: $y = 4.6055 + 0.5092x - 0.0716x^2$ ($r^2 = 0.330$ns); DOY 175 sun leaf: $y = 9.2281 + 1.3416x - 0.0916x^2$ ($r^2 = 0.264$ns), shade leaf: $y = 7.5074 + 0.4170x + 0.0197x^2 - 0.0033x^3$ ($r^2 = 0.315$*); DOY 194 sun leaf: $y = 8.2293 - 0.6281x + 0.1252x^2 - 0.0046x^3$ ($r^2 = 0.390$*), shade leaf: $y = 4.6878 + 0.6243x - 0.0277x^2$ ($r^2 = 0.072$ns); DOY 217 sun leaf: $y = 9.4691 + 0.1601x - 0.0058x^2$ ($r^2 = 0.012$ns), shade leaf: $y = 5.2454 - 0.1714x + 0.0132x^2$ ($r^2 = 0.098$ns). *$P \leq 0.05$, **$P \leq 0.01$ and ***$P \leq 0.001$, respectively.

insertion heights were combined. The development of photosynthetic activity plotted against leaf age was characterised by a sharp increase, followed by a maximum and a slow decrease in older leaves (Figure 4). In vineyard A2 (Figure 4A) A of sun leaves strongly increased for approximately 20 days after emergence. The maximum A of sun leaves was reached 40 days after emergence (with average photosynthesis of 15.30 µmol CO_2). Afterwards A declined to 71 % of maximum activity when leaves were 100 days old. In vineyard B3 (Figure 4B) A strongly increased for 12 days after emergence. Maximum A was already observed 30 days after leaf emergence and was lower than in A2 (11.70 µmol CO_2). A was reduced to 67 % of its maximum 100 days after leaf emergence. Photosynthetic performance in B4 (Figure 4C) was situated between A2 and B3. After the increase of A, which lasted for 17 days, a maximum with 12.80 µmol CO_2 on average was observed 34 days after leaf emergence. A of 100-day-old leaves was still 68 % of their maximum. Maximum A of shade leaves was 65 % of the maximum sun leaf A, independent of the vineyard. The decrease in A of old leaves was lower than in sun leaves in all three vineyards.

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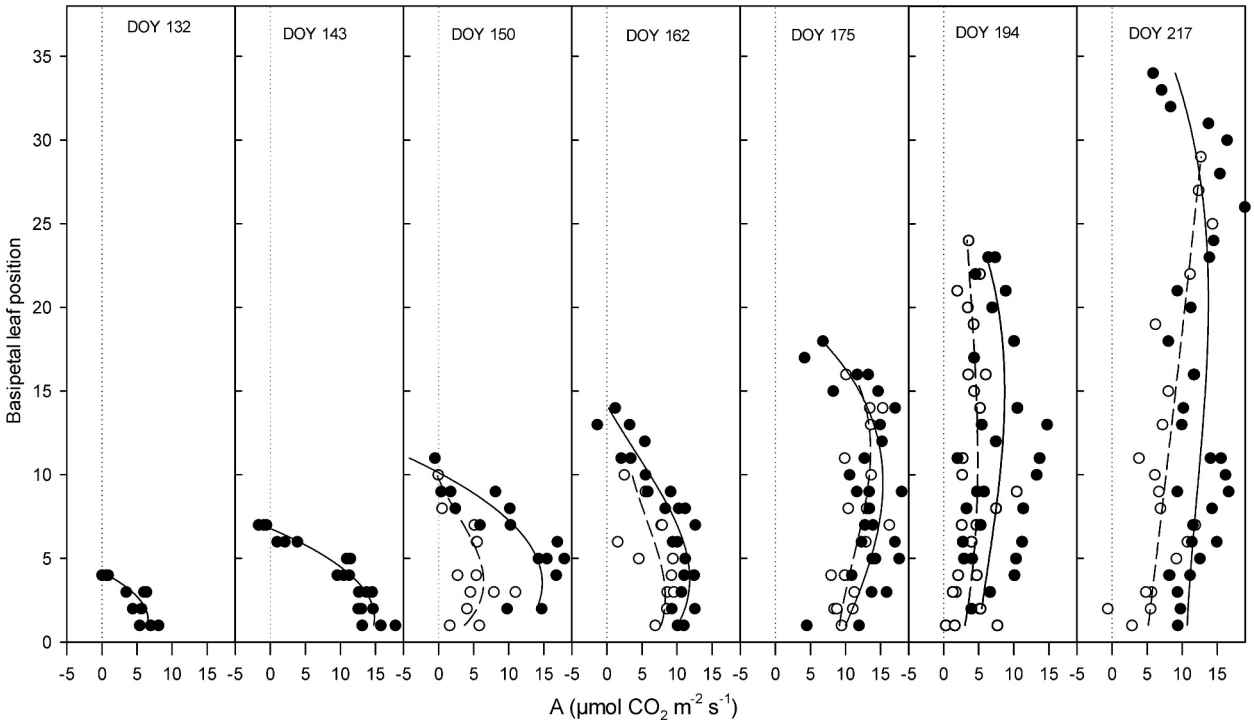


Figure 3 - Single-leaf photosynthesis (A) plotted as a function of basipetal leaf position along the stem for vineyard B4 measured at different dates (DOY 132, DOY 143, DOY 150, DOY 162, DOY 175, DOY 194 and DOY 217). Each point is an individual measurement. Closed symbols and continuous lines indicate sun leaves; open symbols and dashed lines indicate shade leaves.

Regression equations are: DOY 132 sun leaf: $y = 5.1783 + 2.1120x - 0.8000x^2$ ($r^2 = 0.790$***); DOY 143 sun leaf: $y = 13.7681 + 1.5045x - 0.5205x^2$ ($r^2 = 0.907$***); DOY 150 sun leaf: $y = 10.5410 + 2.3987x - 0.3399x^2$ ($r^2 = 0.840$***), shade leaf: $y = 0.7983 + 3.4791x - 0.6327x^2 + 0.0274x^3$ ($r^2 = 0.448$ns); DOY 162 sun leaf: $y = 8.4526 + 1.9056x - 0.3027x^2 + 0\ 0089x^3$ ($r^2 = 0.838$***), shade leaf: $y = 9.7471 + 1.2790x - 0.2992x^2 + 0.0133x^3$ ($r^2 = 0.347$ns); DOY 175 sun leaf: $y = 8.9327 + 1.0957x - 0.0181x^2 - 0.0028x^3$ ($r^2 = 0.378$*), shade leaf: $y = 8.8573 + 0.2232x + 0.0696x^2 - 0.0046x^3$ ($r^2 = 0.412$ns); DOY 194 sun leaf: $y = 4.7618 + 0.3125x + 0.0111x^2 - 0.0010x^3$ ($r^2 = 0.073$ns), shade leaf: $y = 2.6028 + 0.4712x - 0.0290x^2 + 0.0004x^3$ ($r^2 = 0.074$ns); DOY 217 sun leaf: $10.6235 + 0.0871x + 0.0140x^2 - 0.0005x^3$ ($r^2 = 0.145$ns), shade leaf: $y = 4.8910 + 0.2878x - 0.0006x^2$ ($r^2 = 0.398$*). *P ≤ 0.05 , **P ≤ 0.01 and ***P ≤ 0.001, respectively.

WUE_i plotted against leaf age showed a different development than A (Figure 5). Unlike A, little or no decrease in WUE_i was observed after reaching the maximum in both sun and shade leaves. Regarding the three vineyards, differences similar to those observed in the development of A could be detected. Highest average WUE_i (90 µmol CO_2/mol H_2O) was observed in A2 (Figure 5A). Leaves in vineyard B3 showed the lowest average WUE_i (83 µmol CO_2/mol H_2O, Figure 5B) and leaves in vineyard B4 had slightly lower WUE_i than in A2 (88 µmol CO_2/mol H_2O, Figure 5C). WUE_i in shade leaves was slightly lower than in sun leaves, especially in young leaves, but the differences were far smaller than observed in A. In old leaves no clear differences in WUE_i between sun and shade leaves could be detected, because sun leaves showed higher WUE_i than shade leaves in one vineyard and lower in the other.

Figure 6 shows gs in relation to leaf age for the three vineyards. Generally the results had higher variation which made curve fitting difficult, particularly for shade leaves where no statistically significant regression curves could be found in vineyard A2 (Figure 6A) and vineyard B4 (Figure 6C). In all three vineyards gs was low in young sun leaves and reached a maximum afterwards. After this, maximum gs declined again. In vineyard A2 (Figure 6A) gs increased in young leaves to an average maximum of 0.178 mol H_2O m^{-2} s^{-1}, when leaves were between 42 and 44 days old. In B3 (Figure 6B) maximum gs was reached between day 24 and day 36 and was lower (0.143 mol H_2O). In B4 (Figure 6C) gs increased to 0.149 mol H_2O at the leaf age of 27 to 30 days.

DISCUSSION

Gas exchange measurements on leaves of field-grown Zweigelt grapevines under natural growing conditions confirmed the results of prior investigations by various authors (Alleweldt *et al.*, 1982; Intrieri *et al.*, 1992; Patakas *et al.*, 1997; Poni *et al.*, 1994; Kriedemann *et al.*, 1970; Schultz *et al.*, 1996). The progress of photosynthetic activity against leaf age was generally characterised by a sharp increase after leaf emergence for 12 to 20 days as observed by Poni *et al.* (1994) and Intrieri *et al.* (1992).

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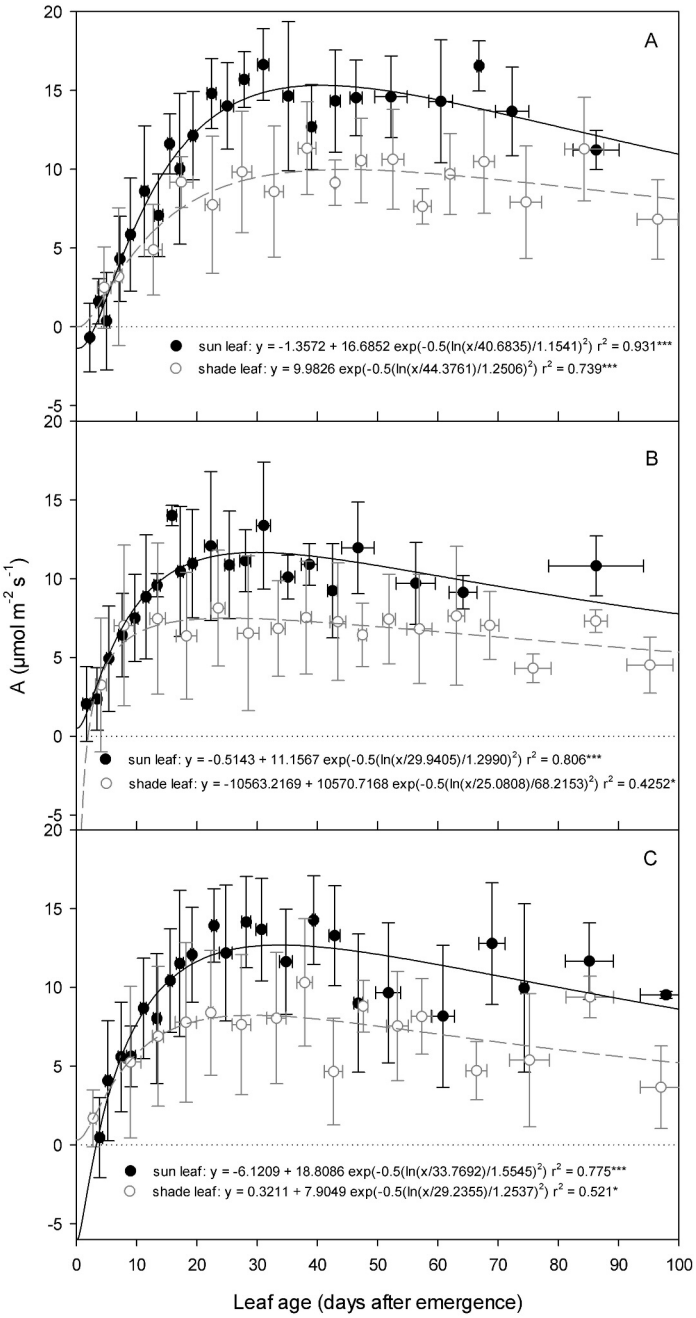


Figure 4 - Single-leaf photosynthesis (A) plotted as a function of leaf age (days after emergence) for the three vineyards (A = vineyard A2, B = vineyard B3 and C = vineyard B4). Each point is a mean, and the error bars show the standard deviation. Closed symbols and continuous lines indicate sun leaves; open symbols and dashed lines indicate shade leaves. *P ≤ 0.05 , **P ≤ 0.01 and ***P ≤ 0.001, respectively.

In accordance with prior investigations, the curve flattened until the maximum photosynthesis was reached, i. e., between 30 and 40 days after leaf emergence. This was followed by a slow decrease, so that old leaves maintained a relatively high photosynthetic activity of 65 % to 70 %, as reported by Intrieri *et al.* (1992) and Patakas *et al.* (1997). Schultz *et al.* (1996) observed that leaves can maintain 100 % of maximum photosynthesis for up to 100 days. Grapevine leaves undergo a number of changes during development, from young to mature and finally to senescent leaf, causing alterations in gas exchange. In young, still growing leaves, the rates of A are small or even negative, because the photosynthetic apparatus is not yet fully developed. The contents of chlorophyll and carotenoids increase with leaf development (Bertamini and Nedunchezhian, 2003 ; Keller *et al.*, 2001 ; Schubert *et al.*, 1996). Furthermore, the content of total soluble proteins increases during leaf ontogeny, indicating an increase in Rubisco content (Bertamini and Nedunchezhian, 2003 ; Keller *et al.*, 2001). Because of the low Rubisco content, carboxylation efficiency is low in young leaves. Schultz *et al.* (1996) demonstrated that young leaves have a high concentration of internal CO_2, indicating that the intrinsic capacity for assimilation is still small and photosynthesis is mainly limited by non-stomatal factors. Moreover, growing leaves exhibit higher rates of photoinhibition and photorespiration than mature leaves (Iacono and Sommer, 1996). Mature leaves show highest photosynthesis, correlating with highest contents of leaf pigments and total nitrogen. After leaf maturation gas exchange declines, but the rates are variable. One factor is the availability of nitrogen, which is positively correlated to chlorophyll and Rubisco content. With increasing leaf age, leaf chlorophyll content decreases. The degradation of leaf chlorophyll is accelerated if nitrogen availability is limited (Keller *et al.*, 2001). Leaf aging in the lower parts of the canopy is further promoted by shading, which causes re-mobilization of nitrogen to upper canopy levels (Niinemets, 2007). Both effects, lower contents of nitrogen and shading, can explain the stronger reduction in A of old leaves in vineyard B3 compared to vineyards A2 and B4. Lower contents of total nitrogen correspond to a loss in Rubisco activity, which is coupled to a reduction in Ribulose-1,5-bisphosphate (RuBP) regeneration capacity. Therefore carboxylation efficiency decreases with leaf senescence and non-stomatal limitation of A becomes more important (Schultz *et al.*, 1996).

Furthermore, drought stress is one of the main reasons for reduced photosynthetic activity in old leaves, causing early leaf senescence (Schultz *et al.*, 1996). In the investigation year of the present study, there was good water supply due to unusually high precipitation. During the growing period, predawn water potential did not fall below -0.20 MPa, a number that is generally considered

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a threshold value for drought stress (Santesteban *et al.*, 2011). Given that the measurements were taken on site B3, which represented the vineyard with the driest soil conditions, we may assume that none of the three vineyards was drought stressed during the investigations.

Under saturated light conditions A of shade leaves reached 65 % of the maximum sun leaf A, which agrees with Schultz *et al.* (1996). Palliotti *et al.* (2000) found that shade leaf A was about 50 % of sun leaf A under saturated light conditions, which was reached at lower light intensities. In the present study gas exchange measurements on both sun and shade leaves were carried out under saturated light conditions. A LED-light source mounted on the leaf chamber provided a PPFD value of 1750 µmol m^{-2} s^{-1} for every leaf. Therefore the reduction in photosynthetic activity in shade leaves (by 35 %) compared to sun leaves was caused by adaptation to low light conditions and not by differences in current irradiance. When leaves develop under low PPFD availability, they acclimate to shade by various morphological alterations, e.g., reduced leaf area ratio, reduced leaf weight ratio and increased individual area per leaf, in order to enlarge light intercepting surface (Palliotti *et al.*, 2000; Schultz and Matthews, 1993). Corresponding to the lower leaf area ratio, shade leaves are thinner due to thinner epidermis, palisade and spongy tissue. Their epicuticular wax content and hair density are reduced, causing lower boundary layer resistance and light reflectance (Palliotti *et al.*, 2000). Furthermore, the development of the vessel system is changed by low light, so that petioles from shade leaves have fewer xylem conduits compared to sun leaves (Schultz and Matthews, 1993). Due to these modifications shade leaves have lower hydraulic conductivity, which probably caused the lower gs values in shade leaves of the present study. However, photosynthetic activity of shade leaves is less limited by stomata than A of sun leaves. The reduction of A in shade leaves is mainly caused by a decrease in carboxylation efficiency, which indicates a loss in Rubisco activity (Schultz *et al.*, 1996). Upon shading, leaves generally re-allocate photosynthetic nitrogen from Rubisco and electron transport components to light harvesting proteins and chlorophyll, thereby enhancing light harvesting (Niinemets, 2007). Palliotti *et al.* (2000) found increased concentrations of chlorophyll a + b, as well as carotenoids per area in shade-adapted grapevine leaves. As a result of these adaptations, shade leaves show a modified photosynthetic activity compared to sun leaves, which ensures maximal utilisation of low light intensities but inhibits the exploitation of high light intensities. Photosynthetic light response curves have shown that shade leaves have increased quantum yield at low light conditions, lower light compensation point, reduced dark respiration, but also a lower light saturation point (Palliotti *et al.*, 2000; Prieto *et al.*, 2010). The reduction of A in shade leaves in the present study was possibly further intensified by photoinhibition caused by high PPFD values during the measurements. Iacono and Sommer (1996) pointed out that shade-adapted grapevine leaves grown inside the canopy are more likely to suffer photoinhibition when exposed to high light intensities than sun leaves. Prieto *et al.* (2010) demonstrated that differences in

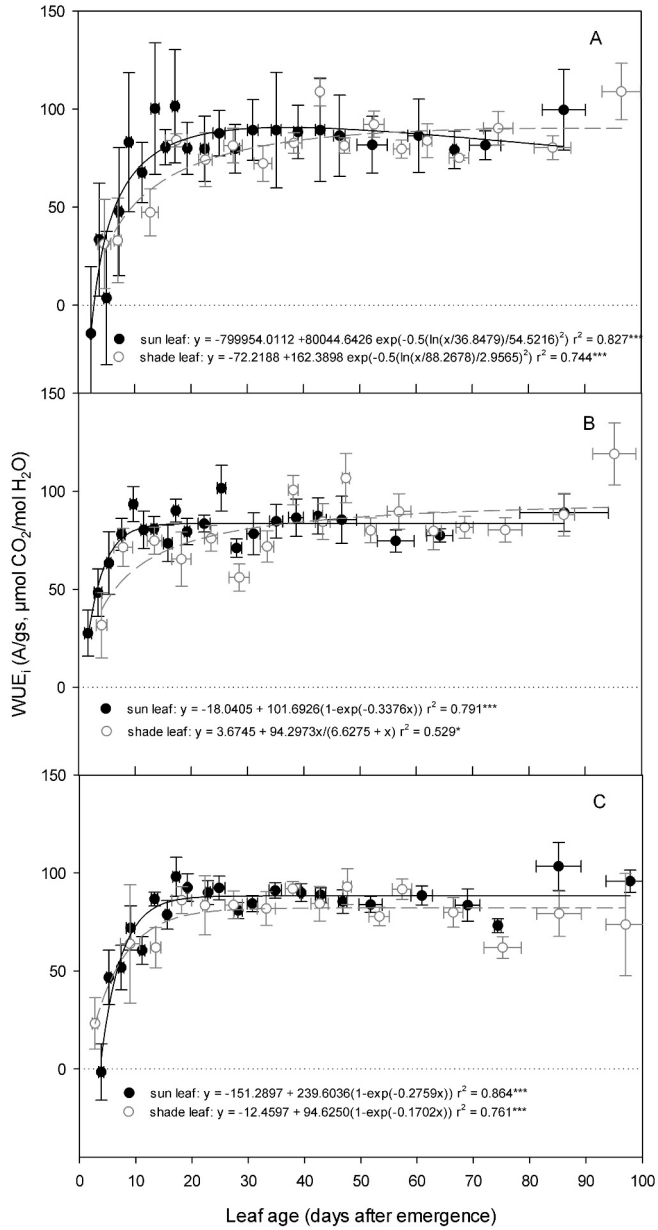


Figure 5 - Intrinsic water use efficiency (Wu E_i) plotted as a function of leaf age (days after emergence) for the three vineyards (A = vineyard A2, B = vineyard B3 and C = vineyard B4). Each point is a mean, and the error bars show the standard deviation. Closed symbols and continuous lines indicate sun leaves; open symbols and dashed lines indicate shade leaves. *P ≤ 0.05 , **P ≤ 0.01 and ***P ≤ 0.001, respectively.

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maximal A of sun- and shade-adapted leaves decreased from bloom until harvest with increasing leaf age. In the present study maximum photosynthesis in shade leaves was reached at the same time or earlier than in sun leaves, as observed by Schultz *et al.* (1996). On the contrary, Schubert *et al.* (1996) found that leaves reached maximum A 20 days later when they were exposed to low light intensities than when they were exposed to high light intensities. However, unlike our study, the results were not obtained from shade-adapted leaves but from leaves that were shaded only for the measurement. Like A, gs was also reduced in shade leaves, as in Schultz *et al.* (1996). WUE_i was similar in mature sun and shade leaves (older than 30 to 40 days) because A and gs were reduced to the same degree.

Nevertheless, our own results indicate that grape growers have the option to influence photosynthetic activity through vineyard management practices. One important factor is canopy and shoot management, which affects light exposure of single leaves (Smart, 1985). Canopies with vertically positioned shoots, as those in all three vineyards of the present study, tend to have an increased number of leaf layers in the fruiting zone (Reynolds and Vanden Heuvel, 2009). This can be avoided by reducing the shoot number per vine to a reasonable number through winter pruning and shoot thinning (Smart, 1988; Reynolds *et al.*, 2005), as in vineyards A2 and B4. Without shoot thinning dense canopies are formed and leaves positioned in the basal part of the shoot often receive lower light intensities than apical leaves, causing lower rates of photosynthesis (Hunter and Visser, 1988b; Iacono and Sommer, 1996). Such an effect was visible in vineyard B3, where 13 shoots per meter caused self-shading in the basal leaves and a high proportion of shaded leaves. Underdeveloped shoots were also present in B3 because no shoot thinning was performed, which tends to lower values of A and gs (Cloete *et al.*, 2008). A high percentage of shaded leaves in the canopy should be avoided because leaves in the interior of the canopy receive only a small portion of light (Smart, 1985) and therefore only marginally contribute to total vine assimilation (Intrieri *et al.*, 1997).

Another factor to be considered is the fruit load. While in vineyard B3 each vine had 21 clusters, only 6.6 clusters were present on each vine in vineyard A2. Several studies have shown that under excessive growth a modification of the source-to-sink ratio towards a stronger sink by either increased fruit load (Edson *et al.*, 1993, 1995; Naor *et al.*, 1997) or reduced leaf area (Hunter and Visser, 1988b; Intrieri *et al.*, 1997; Poni *et al.*, 2008) generally enhances single-leaf A. But in the case of vineyard B3 the contrary effect, i. e., lower A, despite higher cluster number, was visible compared to the other two vineyards. In order to explain this behaviour the situation of the whole vine and not only cluster number has to be considered. Vines in B3 had reduced shoot growth and single-leaf area and highest occurrence of berry shrivel (*Traubenwelke*) compared to A2 and B4. High crop load reduces vegetative growth (Edson *et al.*, 1993; Miller *et al.*, 1993),

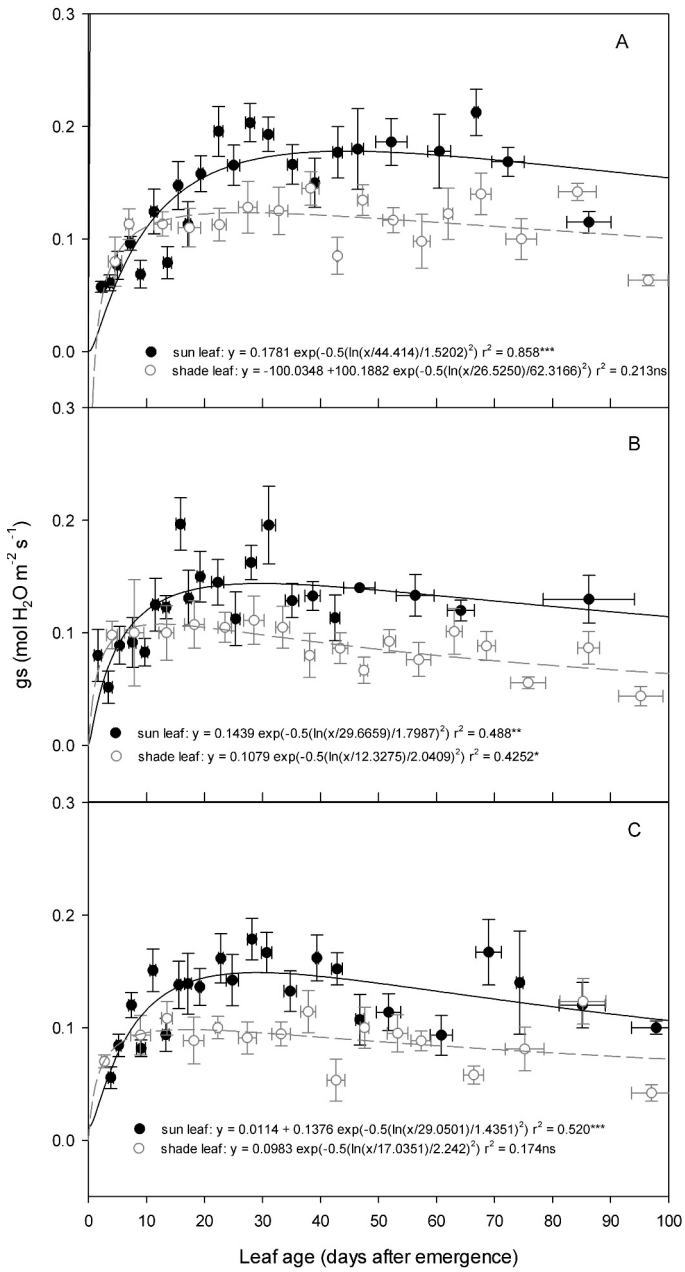


Figure 6 - Stomatal conductance to water vapour (gs) plotted as a function of leaf age (days after emergence) for the three vineyards (A = vineyard A2, B = vineyard B3 and C = vineyard B4). Each point is a mean, and the error bars show the standard deviation. Closed symbols and continuous lines indicate sun leaves; open symbols and dashed lines indicate shade leaves. *P ≤ 0.05 , **P ≤ 0.01 and ***P ≤ 0.001, respectively.

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but on the other hand reduced leaf size may increase single-leaf A as a compensatory effect (Edson *et al.*, 1995). One possible explanation for the absence of an increase in single-leaf A is a limitation in water or nutrient supply, owing to unfavourable soil conditions and poor root development. The high yields, which were achieved not only in the year of investigation but also in the preceding years, may have caused a shift in dry matter partitioning from storage organs towards reproductive sinks (Edson *et al.*, 1995 ; Miller *et al.*, 1993 ; Petrie *et al.*, 2003). It is likely that root development was impaired by yearly high crop load. As mentioned before, vineyard B3 was planted on a very dry soil with gravel in the subsoil 40 cm and deeper. This soil had a very poor water holding capacity and restricted capacity for nutrient supply. Even though precipitation was sufficient, and no drought stress could be recorded as based on values of predawn leaf water potential, water supply was inferior to that in vineyards A2 and B4. Therefore, it is possible that the combination of poorly developed roots and unfavourable soil reduced water nutrient uptake by the vine. Keller *et al.* (2001) pointed out that nitrogen deficiency in grapevine may cause reduced carboxylation efficiency, because of reduced Rubisco synthesis in grapevine leaves.

The development of WUE_i of grapevine leaves against leaf age is of great importance, particularly with regard to economic use of water. The results of our study indicate that WUE_i in Zweigelt leaves does not decrease after reaching the maximum value, due to the fact that gs and A decreased to the same extent. This agrees with Poni *et al.* (1994), who described a positive correlation between A and gs for mature leaves. Also Schultz *et al.* (1996) and Schubert *et al.* (1996) found that gs declines similarly (or even more rapidly) to A with increasing leaf plastochron index or leaf age. Exhibiting only a slight reduction in photosynthesis and WUE equal to that of mature leaves, old leaves in the fruiting zone can still play an important role during fruit growth. They positively contribute to the whole vine photosynthesis (Petrie *et al.*, 2003), and extensive leaf removal of primary leaves in the fruiting zone should therefore be avoided. Especially under warm conditions leaf removal in the fruiting zone, resulting in bunches directly exposed to sunlight, may negatively affect fruit quality (Reynolds and Vanden Heuvel, 2009). Increased occurrence of sunburn (Guidoni *et al.*, 2008), considerably increased berry temperature (Bergqvist *et al.*, 2001), decreased titratable acidity and soluble solids (Bergqvist *et al.*, 2001 ; Vasconcelos and Castagnoli, 2000) and even lower anthocyanin concentrations (Bergqvist *et al.*, 2001) have been observed in dry climates after defoliation in the bunch zone. Even though the effect of defoliation on fruit quality is dependent on yearly climatic conditions (Bavaresco *et al.*, 2008) and grape cultivar (Kliewer, 1977), it has already become apparent that in Austrian viticulture the removal of 1 or 2 basal leaves per shoot is highly efficient (Redl *et al.*, 1984). Therefore the focus should be placed on improvement of canopy management in order to increase the efficiency of basal leaves (Hunter and Visser, 1988a), which are able to produce photosynthetates even after harvest, which is important for reserve accumulation (Hunter *et al.*, 1994).

The insertion height on the shoot where leaves had the highest photosynthetic activity moved from the basal part to the apex during the growing season. Before bloom, the zone with highest photosynthesis remained in and beneath the fruiting zone. After bloom there was a sudden advance, most pronounced in A2, after which the zone with highest photosynthetic activity moved continuously up the shoot. This result is in accordance with Poni *et al.* (1994), who found that under constant radiation basal leaves had high rates of photosynthesis until bloom. In their study, median leaves showed highest photosynthesis from bloom to veraison, and not until veraison did photosynthesis of apical leaves grow larger than that of median and basal leaves. In contrast, Hunter and Visser (1988b) reported that in excessively vigorous Cabernet-Sauvignon vines photosynthesis of bunch leaves, basal leaves and median leaves declined from berry set until ripening, and only in apical leaves did photosynthesis increase during this period. Hunter and Visser (1988a) concluded from further experiments that leaves in the bunch zone are not important for the vine from veraison until the ripening stage.

Significantly, the development shown in the present study resembles the course of assimilate transport direction along the shoot shown by Koblet (1969) for the early-ripening cultivar Müller-Thurgau. He determined the insertion height in the grape shoot above which assimilates are transported apically, and below which they are mainly transported in basipetal direction. Although his experiments were performed in a controlled environment, our study shows an analogy between the movements of the zone separating the directions of assimilate transport and the zone with highest photosynthetic activity during growing period. This development was not confirmed by Hunter and Visser (1988a), who did not find much assimilate import to apical leaves, even when they were not fully developed, but pointed out the importance of leaves positioned above the bunches for the nourishment of the bunch during all stages.

CONCLUSION

The results of the present study confirm that leaves of field-grown Zweigelt grapevines positioned in the basal part of the shoot are photosynthetically active during the ripening period of the grapevine. Therefore, extensive leaf removal cannot be recommended. Considering that measurements were taken in a year with unusually high

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precipitation it is likely that in dry years photosynthesis of basal leaves will not be able to reach equally high values without irrigation. In any case, actual drought stress will be an exception, because most of the vineyards in the Neusiedlersee region are equipped with irrigation systems that are used extensively. Therefore, it can be concluded that farmers should focus on canopy management practices in the early growing stage to avoid dense canopies; this will increase solar radiation through the canopy and reduce the risk of bunch rot.

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REFERENCES

Alleweldt G., Eibach R. and Rühl E., 1982. Investigations on gas-exchange in grapevine. I. Influence of temperature, leaf age and daytime on net photosynthesis and transpiration. *Vitis*, **21**, 93-100 (in German).

Bavaresco L., Gatti M., Pezzutto S., Fregoni M. and Mattivi F., 2008. Effect of leaf removal on grape yield, berry composition, and stilbene concentration. *Am. J. Enol. Vitic.*, **59**, 292-298.

Bennett J., Jarvis P., Creasy G.L. and Trought M.C.T., 2005. Influence of defoliation on overwintering carbohydrate reserves, return bloom, and yield of mature Chardonnay grapevines. *Am. J. Enol. Vitic.*, **56**, 386-393.

Bergqvist J., Dokoozlian N. and Ebisuda N., 2001. Sunlight exposure and temperature effects on berry growth and composition of Cabernet-Sauvignon and Grenache in the central San Joaquin Valley of California. *Am. J. Enol. Vitic.*, **52**, 1-7.

Bertamini M. and Nedunchezhian N., 2003. Photosynthetic functioning of individual grapevine leaves (*Vitis vinifera* L. cv. Pinot noir) during ontogeny in the field. *Vitis*, **42,** 13-17.

Cloete H., Archer E., Novello V. and Hunter J.J., 2008. Shoot heterogeneity effect on Shiraz/Richter 99 grapevines. II. Physiological activity. *S. Afr. J. Enol. Vitic.*, **29**, 1-8.

Düring H., 1987. Stomatal responses to alterations of soil and air humidity in grapevines. *Vitis*, **26**, 9-18.

Edson C.E., Howell G.S. and Flore J.A., 1993. Influence of crop load on photosynthesis and dry matter partitioning of Seyval grapevines I. Single leaf and whole vine response pre- and post-harvest. *Am. J. Enol. Vitic.*, **44**, 139-147.

Edson C.E., Howell G.S. and Flore J.A., 1995. Influence of crop load on photosynthesis and dry matter partitioning of Seyval grapevines. II. Seasonal changes in single leaf and whole vine photosynthesis. *Am. J. Enol. Vitic.*, **46**, 469-477.

Guidoni S., Oggero G., Cravero S., Rabino M., Cravero M.C. and Balsari P., 2008. Manual and mechanical leaf removal in the bunch zone (*Vitis vinifera* L. cv. Barbera): Effects on berry composition, health, yield and wine quality, in a warm temperature area. *J. Int. Sci. Vigne Vin*, **42**, 49-58.

Hunter J.J. and Visser J.H., 1988a. Distribution of 14C-photosynthetate in the shoot of *Vitis vinifera* L. cv. Cabernet-Sauvignon. I. The effect of leaf position and developmental stage in the vine. *S. Afr. J. Enol. Vitic.*, **9**, 3-9.

Hunter J.J. and Visser J.H., 1988b. The effect of partial defoliation, leaf position and developmental stage of the vine on the photosynthetic activity of *Vitis vinifera* L. cv. Cabernet-Sauvignon. *S. Afr. J. Enol. Vitic.*, **9**, 9-15.

Hunter J.J. and Visser J.H., 1989. The effect of partial defoliation, leaf position and developmental stage of the vine on leaf chlorophyll concentration in relation to the photosynthetic activity and light intensity in the canopy of *Vitis vinifera* L. cv. Cabernet-Sauvignon. *S. Afr. J. Enol. Vitic.*, **10**, 67-73.

Hunter J.J., Skrivan R. and Ruffner H.P., 1994. Diurnal and seasonal physiological changes in leaves of *Vitis vinifera* L.: CO_2 assimilation rates, sugar levels and sucrolytic enzyme activity. *Vitis*, **33**, 189-195.

Iacono F., Bertamini M., Scienza A. and Coombe B.G., 1995. Differential effects of canopy manipulation and shading of *Vitis vinifera* L. cv. Cabernet-Sauvignon. Leaf gas exchange, photosynthetic electron transport rate and sugar accumulation in berries. *Vitis*, **34**, 201-206.

Iacono F. and Sommer K.J., 1996. Photoinhibition of photosynthesis and photorespiration in *Vitis vinifera* under field conditions – effects of light climate and leaf position. *Aust. J. Grape Wine Res.*, **2**, 1-11.

Intrieri C., Poni S., Silvestroni O. and Filippetti I., 1992. Leaf age, leaf position and photosynthesis in potted grapevines. *Adv. Hort. Sci.*, **6**, 23-27.

Intrieri C., Poni S., Rebucci B. and Magnanini E., 1997. Effects of canopy manipulations on whole-vine photosynthesis: Results from pot and field experiments. *Vitis*, **36**, 167-173.

Jones H., 2004. What is water use efficiency? In: Bacon M.A. *Water use efficiency in plant biology*. Blackwell Publishing Ltd; CRC Press, Oxford, UK; Boca Raton, USA, pp. 27-41.

Keller M., Kummer M. and Vasconcelos M.C., 2001. Soil nitrogen utilisation for growth and gas exchange by grapevines in response to nitrogen supply and rootstock. *Aust. J. Grape Wine Res.*, **7**, 2-11.

Kliewer W.M., 1977. Influence of temperature, solar radiation and nitrogen on coloration and composition of Emperor grapes. *Am. J. Enol. Vitic.*, **28**, 96-103.

Koblet W., 1969. Wanderung von assimilaten in rebtrieben und einfluss der blattfläche auf ertrag und qualität der trauben. *Wein-Wissenschaft*, **24**, 277-319.

Koblet W., 1987. Effectiveness of shoot topping and leaf removal as a means of improving quality. *Acta Hort.*, **206**, 141-156.

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Kriedemann P.E., Kliewer W.M. and Harris J.M., 1970. Leaf age and photosynthesis in *Vitis vinifera* L. *Vitis*, **9**, 97-104.

Lorenz D.H., Eichhorn K.W., Bleiholder H., Klose R., Meier U. and Weber E., 1995. Phenological growth stages of the grapevine (*Vitis vinifera* L. ssp. *vinifera*) – Codes and descriptions according to the extended BBCH scale. *Aust. J. Grape Wine Res.*, **1**, 100-103.

Miller D.P., Howell G.S. and Striegler R.K., 1993. Reproductive and vegetative response of mature grapevines subjected to differential cropping stresses. *Am. J. Enol. Vitic.*, **44**, 435-440.

Naor A., Gal Y. and Bravdo B., 1997. Crop load affects assimilation rate, stomatal conductance, stem water potential and water relations of field-grown Sauvignon blanc grapevines. *J. Exp. Bot.*, **48**, 1675-1680.

Nestroy O., Danneberg O.H., Englisch M., Geßl A., Hager H., Herzberger E., Kilian W., Nelhiebel P., Pecina E., Pehamberger A., Schneider W. and Wagner J., 2000. Systematische Gliederung der Böden Österreichs (Österreichische Bodensystematik 2000). *Mitt. Österr. Bodenkundl. Ges.*, **60,** 123pp**.**

Niinemets Ü., 2007. Photosynthesis and resource distribution through plant canopies. *Plant Cell Environ.*, **30**, 1052-1071.

Palliotti A., Cartechini A. and 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.

Patakas A., Noitsakis B. and Chartzoulakis K., 1997. Changes in W.U.E. in *Vitis vinifera* as affected by leaf age. *Acta Hort.*, **449**, 457-460.

Percival D.C., Fisher K.H. and Sullivan J.A., 1994. Use of fruit zone leaf removal with *Vitis vinifera* L. cv. Riesling grapevines. II. Effect on fruit composition, yield, and occurrence of bunch rot (*Botrytis cinerea* Pers.:Fr.). *Am. J. Enol. Vitic.*, **45**, 133-140.

Petrie P.R., Trought M.C.T., Howell G.S. and Buchan G.D., 2003. The effect of leaf removal and canopy height on whole-vine gas exchange and fruit development of *Vitis vinifera* L. Sauvignon Blanc. *Funct. Pant Biol.*, **30**, 711-717.

Poni S., Intrieri C. and Silvestroni O., 1994. Interactions of leaf age, fruiting, and exogenous cytokinins in Sangiovese grapevines under non-irrigated conditions. I. Gas exchange. *Am. J. Enol. Vitic.*, **45**, 71-78.

Poni S. and Intrieri C., 2001. Grapevine photosynthesis: effects linked to light radiation and leaf age. *Adv. Hort. Sci.*, **15**, 5-15.

Poni S., Bernizzoni F. and Civardi S., 2008. The effect of early leaf removal on whole-canopy gas exchange and vine performance of *Vitis vinifera* L. Sangiovese. *Vitis*, **47**, 1-6.

Prieto J.A., Galat Giorgi E. and Perez Pena J., 2010. Modelling photosynthetic-light response on Syrah leaves with different exposure. *Vitis*, **49**, 145-146.

Redl H., Weindlmayer J., Pleil J., Weiser J. and Resch E., 1984., Untersuchungsergebnisse über den einfluss von laubbehandlungsmaßnahmen auf traubenertrag, traubenqualität und krankheitsauf-treten in hochkulturanlagen. *Mitt. Klosterneuburg*, **34**, 185-193.

Reynolds A.G., Molek T. and De Savigny C., 2005. Timing of shoot thinning in *Vitis vinifera*: Impacts on yield and fruit composition variables. *Am. J. Enol. Vitic.*, **56**, 343-356.

Reynolds A.G. and Vanden Heuvel J.E., 2009. Influence of grapevine training systems on vine growth and fruit composition: A review. *Am. J. Enol. Vitic.*, **60**, 251-268.

Santesteban L.G., Miranda C. and Royo J.B., 2011. Suitability of pre-dawn and stem water potential as indicators of vineyard water status in cv. Tempranillo. *Aust. J. Grape Wine Res.*, **17**, 43-51.

Scholander P.F., Bradstreet E.D., Hemmingsen E.A. and Hammel H.T., 1965. Sap pressure in vascular plants. *Science*, **148**, 339-346.

Schubert A., Restagno M. and Lovisolo C., 1996. Net photosynthesis of grapevine leaves of different age exposed to high or low light intensities. *Adv. Hort. Sci.*, **10**, 163-169.

Schultz H.R. and Matthews M.A., 1993. Xylem development and hydraulic conductance in sun and shade shoots of grapevine (*Vitis vinifera* L.): evidence that low light uncouples water transport capacity from leaf area. *Planta*, **190**, 393-406.

Schultz H.R., Kiefer W. and Gruppe W., 1996. Photosynthetic duration, carboxylation efficiency and stomatal limitation of sun and shade leaves of different ages in field-grown grapevine (*Vitis vinifera* L.). *Vitis*, **35**, 169-176.

Smart R.E., 1985. Principles of grapevine canopy microclimate manipulation with implications for yield and quality. A review. *Am. J. Enol. Vitic.*, **36**, 230-239.

Smart R.E., 1988. Shoot spacing and canopy light microclimate. *Am. J. Enol. Vitic.*, **39**, 325-333.

Vasconcelos M.C. and Castagnoli S., 2000. Leaf canopy structure and vine performance. *Am. J. Enol. Vitic.*, **51**, 390-396.

Zamg, 2002. Klimadaten von Österreich: 1971-2000. Klimadaten von über 200 Stationen in ganz Österreich, Zentralanstalt für Meteorologie und Geodynamik, Wien.

Zoecklein B.W., Wolf T.K., Duncan N.W., Judge J.M. and Cook M.K., 1992. Effects of fruit zone leaf removal on yield, fruit composition, and fruit rot incidence of Chardonnay and White Riesling *(Vitis vinifera* L.) grapes. *Am. J. Enol. Vitic.*, **43**, 139-148.

Zufferey V., Murisier F. and Schultz H.R., 2000. 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. *Vitis*, **39**, 19-26.

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