Light interception, gas exchange and carbon balance of different canopy zones of minimally and cane-pruned field-grown Riesling grapevines

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Summary

Leaf area development, pre-dawn leaf water potential, spatial and temporal patterns of light interception and photosynthesis (A) of minimal pruned (MP) and cane-pruned vertical shoot positioned (VSP) field-grown Riesling grapevines were monitored in 2002 and 2003. In order to quantify the contribution of different canopy segments to whole vine carbon gain, diurnal single leaf gas exchange measurements were conducted several times during the season in 8 different canopy segments keeping leaves in their natural position. Carbon losses due to nocturnal respiration (DR) were estimated with a model describing the dependence of DR on temperature. MP vines had about 17 times more but less vigorous shoots with smaller leaves. Leaf area (LA) development was faster for MP than for VSP vines and LA was 2.5-3-fold higher for most of the season. Spatial and temporal patterns of average daily light interception were related to LA development and canopy dimensions for both MP and VSP vines during the first part of the season, but increased independent of LA until mid-October and more so for VSP than MP. Diurnal gas exchange measurements showed differences between canopy segments, measuring dates and systems. Differences between segments were related to light interception in the absence of water deficit, high leaf temperature and vapour pressure deficit. The higher light interception of MP vines caused pre-dawn water potential to decrease faster and to remain at lower levels during most of the season. This limited A more severely for leaves of MP vines in canopy segments which were well exposed to light. The estimated seasonal carbon gain per canopy segment was highest in the apical canopy zones for both canopy systems but carbon assimilation was higher for MP than for VSP vines in all segments with the exception of the interior canopy. Respiratory losses by leaves depended on night temperature and time during the season but generally varied between 3 and 7 % of the amount of carbon gained during the day. MP vines had slightly higher relative respiration losses than VSP vines. On a whole-plant basis, carbon gain of MP vines was between 5.7 (beginning of the season) and 2.2 times (end of season) higher than for VSP vines.

K e y   w o r d s : minimal pruning (MP), cane-pruned vertically shoot positioned (VSP), light interception, gas exchange, carbon gain.

Introduction

Since the early investigations on the "capacity" of unpruned *versus* pruned vines (WINKLER 1954, 1958), and the adoption of minimal- and non-pruning systems for the commercial production of wine grapes mainly in warm, irrigated grape districts of Australia (CLINGELEFFER 1983, CLINGELEFFER and POSSINGHAM 1987, SOMMER and CLINGELEFFER 1993, CLINGELEFFER *et al.* 2005), many aspects of these systems have been studied with different varieties and in locations varying in climate and soil. Investigations in cool climate grape production areas with sometimes late ripening varieties and with soils or rootstocks inducing high vigor have generally shown, that MP systems can be used, if supplementary crop size control is ensured (CLINGELEFFER 1993, SOMMER *et al.* 1993, POOL *et al.* 1993, POSSINGHAM 1996, FENDINGER *et al.* 1996). However, depending on the variety, mechanical thinning can be very problematic and alternative thinning methods have not yet been sufficiently tested (SCHULTZ 2002, WEYAND and SCHULTZ 2005).

Apparent contradictory results with respect to yield and quality in European trials (negative tendency: CARBONNEAU 1991, OLLAT *et al.* 1993, positive tendency: MARTÍNEZ DE TODA and SANCHA 1998, SCHULTZ *et al.* 2000, INTRIERI *et al.* 2001), where thinning was not applied, may be related to differences in the growth habit of the varieties tested and/or the growing conditions causing differences in light interception and consequently whole-vine carbon balance. There have been a few studies dealing with the subject of light interception and estimated or directly measured carbon balance of MP as compared to conventional production systems (DOWNTON and GRANT 1992, LAKSO *et al.* 1996, PONI *et al.* 2000, INTRIERI *et al.* 2001, LAKSO and EISSENSTAT 2005, LAKSO and PONI 2005). Somewhat surprising is that with the exception of the study by INTRIERI *et al.* (2001), maximum leaf area index or total leaf area per vine were similar for MP and conventionally pruned vines in all these studies. Thus, the main differences in carbon balance between these systems were attributed to early season leaf area development and canopy filling which is faster for MP as compared to pruned vines due to the larger amount of buds retained (DOWNTON and GRANT 1992, LAKSO *et al.* 1996, PONI *et al.* 2000, LAKSO and EISSENSTAT 2005).

However, many studies in warm but also in cool climates, including Germany (SCHULTZ *et al.* 2000), with a wide array of varieties show, that MP systems often develop substantially increased maximum leaf areas (CLINGELEFFER and POSSINGHAM 1987, CLINGELEFFER 1989, SOMMER *et al.* 1993, SCHMID and SCHULTZ 2000, INTRIERI *et al.* 2001).

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This may not improve light interception and subsequent whole-vine carbon balance if most of this leaf area is shaded (Intrieri *et al.* 2001); but the degree of shading is a function of canopy structure which also depends on growth conditions and variety.

Apart from potential differences in general light interception and carbon balance of the whole-vine canopy, differences may also exist between different canopy zones (Escalona *et al.* 2003) due to the large spatial and temporal variations in the within-canopy radiation regime. Different segments contribute differently to the carbon balance of a vine and to identify those of low "productivity" can be useful in improving canopy structure and thus over-all performance (Shaulis *et al.* 1966). Under a given set of conditions and saturating light, the outer leaf layers of fully developed canopies of MP vines have similar gas exchange rates as conventionally pruned vines (Downton and Grant 1992, Sommer and Clingeleffer 1993, Sommer *et al.* 1993, Lakso *et al.* 1996, Poni *et al.* 2000, Intrieri *et al.* 2001). However, since the structure of the canopy can modify leaf position and leaf environment, carbon gain in a natural situation in the field may be very different (Ross 1981). Additionally, environmental constraints such as low rainfall in combination with high yields and large leaf areas and thus increased water consumption (Schmid and Schultz 2000) may also affect total carbon gain of MP vines.

The objectives of the present study were: (1) to quantify light interception and it's spatial variation for an MP and a conventional pruned canopy system throughout the season in a cool climate region; (2) to determine the contribution of different canopy segments to whole-vine photosynthesis under non-irrigated conditions; (3) to estimate carbon fixation and respiratory losses and calculate a seasonal carbon balance of different canopy segments.

Material and Methods

E x p e r i m e n t a l   d e s i g n : Field experiments were conducted with *Vitis vinifera* L. cv. Riesling (clone: Gm 198/ rootstock: 5C, planted in spring 1977) in 2002 and 2003 in Geisenheim (50° N, 8° E), Germany. Compared to other locations with cool climates where MP systems have been tested, such as Coonawarra (Australia), this site has about 300 heat units (summation of degree days above 10 °C with a 19 °C cut-off) less over the growing season (1045 as compared to 1337) with an annual precipitation of 534 mm (as compared to 638 mm for Coonawarra) (Gladstones 1992). The experimental vineyard had a South to South-West exposure and a loam to clay-loam soil. We compared a vertically shoot positioned (VSP) pruning system with a minimal pruning treatment (MP). The VSP was trained as a Sylvoz-system with a cordon at a height of 1.1 m bearing 3-4 short canes (5-6 buds each) which were tied to a wire 0.6 m above the ground.

The minimal pruned plots were converted from the Sylvoz-trellis during the winter 1995-1996 by wrapping all one-year-old canes around the highest catch wire (1.8 m above ground). Every two to three years, a light mechanical winter pruning was applied about 0.5 m above the soil surface to prevent shoots from reaching the ground. Both, the MP- and VSP-system were arranged in three replicated randomized blocks of 3-5 rows each, in a row by vine spacing of 2.8 m x 0.85 m. The VSP was pruned to an average of 5.9 buds per m² (14.2 buds per vine) and on the MP system, 71.6 buds per m² (171.8 buds per vine) were retained (Table).

T a b l e

Average number of buds, shoots, percent bud break and average yield per unit surface area and per vine during the seasons of 2002 and 2003. Data are means ± SD. Bud and shoot number were determined on 10 vines for VSP and 4 planting distances for the MP system

2002 - 2003	VSP	MP
Buds (number m^{-2})	5.9 ± 1.2	71.6 ± 13.7
Buds (number vine^{-1})	14.2 ± 2.9	171.8 ± 32.9
Shoots (number m^{-2})	5.6 ± 1.1	57.0 ± 10.9
Shoots (number vine^{-1})	13.4 ± 2.6	136.8 ± 26.2
Bud break (%)	95.62 ± 4.6	78.81 ± 3.8
Yield (t ha^{-1})	11.7 ± 0.2	26.4 ± 0.2
Yield (kg vine^{-1})	2.8 ± 0.05	6.3 ± 0.05

L e a f   g a s   e x c h a n g e   m e a s u r e m e n t s : Measurements of photosynthetic rate (A, µmol m^{-2} s^{-1}), stomatal conductance (g, mmol m^{-2} s^{-1}), photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}) and leaf temperature (T$_{leaf}$, °C) were conducted with a portable photosynthesis system (LCA4, ADC BioScientific, Hoddeston, UK) on leaves positioned in 8 different canopy zones according to the segmentation profile proposed by Lebon and Schultz (1996; Fig. 1). Irrespective of absolute width and height, canopies were divided into an apical, central, and basal part on the two vertical canopy sides and one segment on top of the canopy and in the canopy interior (Fig. 1). Segments 1, 2, and 3 were facing South-East, and 6, 7, and 8 were facing North-West (Fig. 1). For MP and VSP canopies, height and width were on average about 2.1 m and 1,2 m, and 1.35 m and 0.45 m, respectively (Fig. 1). The top segment was about 0.15 m in height for both systems.
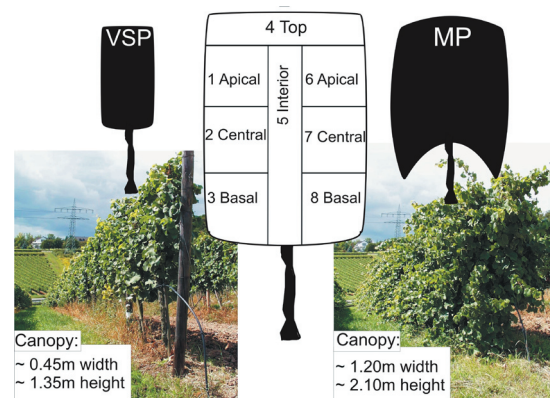

Fig. 1: Schematic presentation of the canopy segmentation profile used for measuring photosynthesis and estimating respiration and carbon balance. VSP: vertical shoot positioning, MP: minimal pruning.

Segments on the canopy exterior were about 0.65 m in height and 0.4 m in width for the MP system and 0.40 m in height and 0.15 m in width for the VSP system, the rest was defined as canopy interior (segment 5). The measurements were conducted on 3-6 randomly selected leaves per canopy zone in their natural position (azimuth and inclination angle) on 24 plants per treatment distributed over all field replicates.

Measurements were conducted throughout mostly clear and sunny days during different developmental stages designated by the BBCH code of EICHHORN and LORENZ (1977) (28th May 2002 (BBCH 17), 2nd June 2003 (BBCH 57), 29th July 2002 (BBCH 77), 15th August 2003 (BBCH 81) 24th September 2002 (BBCH 85), 13th October 2003 (BBCH 89)). Since the canopy was still incomplete for the VSP system on the 28th May, only basal and central segments could be measured.

L i g h t   i n t e r c e p t i o n : Total canopy light interception was measured on 4 dates in 2002 (8th May, 18th June, 15th August, 1st October) with a ceptometer (AccuPAR, Decagon Devices, Pullman, Washington, USA). The ceptometer, equipped with 80 single cosine-corrected sensors at 1 cm spacing, was moved on a below-vine canopy grid covering the entire distance across the row (2.8 m, 1.4 m on each side of the vines) and 1.25 m along the row. Two grids per system were installed in the vineyard. Across the row, PPFD was measured and automatically recorded at 1 cm intervals. Along the row, measurements were conducted every 20.8 cm, giving 3920 data points per measurement. Measurement time per grid was approximately 10 min, and at each repositioning of the ceptometer (28 times per grid), total incident PPFD above the canopy (100 %) was measured with an external, horizontally positioned, sensor (Li-190SZ, LiCOR, Lincoln, Nebraska, USA). Total light interception was calculated as 100 minus the fractional light transmission to the vineyard ground. Light readings were recorded 6 (15th August) to 9 times · d⁻¹ (18th June) giving a total of 23,520 to 35,280 data points · d⁻¹ and system.

L e a f   a r e a   d e t e r m i n a t i o n : Leaf area (LA) development was determined on 4 dates in 2002 and 2003 for both systems. For the VSP, 4 plants per date were chosen at random, while for MP, 4 strips of a canopy length of 0.85 m each (= planting distance) were sampled because it was impossible to separate individual vines in this treatment. In 2002 all leaves were stripped off the plants and individual leaf length was measured and correlated to individual LA (SCHULTZ 1992). Measurements were simplified in 2003. For each plant or planting distance sampled, the leaf length of 10 leaves was measured for the VSP (total n = 40 samplings date⁻¹) and 60 for the MP treatment (total n = 240 samplings date⁻¹). Leaves were then dried at 65 °C and individual leaf dry weight was determined. Individual leaf area was then plotted as a function of leaf weight which gave linear regression coefficients, R^2, between 0.69 and 0.86 depending on the sampling date. The remaining populations of leaves on the plants were harvested, split in 4 groups per plant or planting distance and dried. Established regressions were extrapolated to these dry weight values to calculate LA. This method somewhat overestimates total LA at the beginning of the season when leaves

are growing but results in general agreed well with LA's determined during the previous year for the same phenological stages.

Leaf area allocated to different segments in the canopy was calculated from the results of a detailed LA distribution study conducted in the same vineyard with the same canopy systems (ZIMMER 1998). In that study, the canopy was segmented into cylinders of 0.15 x 0.15 x 0.1 m (width by length by height) using a cage-like structure as previously described (SCHULTZ 1995). For each segment, all leaves were removed, the length of the leaf lamina measured and LA calculated according to SCHULTZ (1992). From these data we calculated a percent LA distribution for our size segments. We assumed this distribution pattern to be stable for MP vines throughout the season because of the lack of directed growth (Fig. 1, ZIMMER 1998). For VSP vines, where canopy geometry is maintained by frequent hedging, this distribution was assumed to be stable after bloom. For the one measurement date of gas exchange before bloom (28th May), percent LA distribution was estimated from the results of a shoot growth model, which simulates single leaf sizes and shoot length (SCHULTZ 1992) assuming only variations with height but not across the canopy width.

C a r b o n   g a i n ,   d a r k   r e s p i r a t i o n ,   c a r b o n   b a l a n c e : Carbon fixation per segment was estimated by fitting polynomial regressions to the diurnal patterns of measured A per canopy zone and integrating A over the day. A was then multiplied by the estimated LA of that particular zone to get an approximation of the contribution of a particular zone to whole plant assimilation. Four LA measurement dates were close to days where gas exchange was measured (within 2-9 d) but two differed by 3-4 weeks. For these days, we estimated LA by extrapolating from the previous LA data point to the one following closest to the date of measurement of gas exchange using a 3rd order polynomial regression.

In order to get an estimation of the carbon balance of a canopy zone over the course of a 24 h day/night cycle, leaf dark respiration (DR) over the night period was calculated with an empirical respiration model (SCHULTZ 1991). The model uses a simple exponential relationship of DR to temperature and was parameterized for 6 phenological phases based on a large data set covering the entire season (SCHULTZ 1991).

$$DR = a \, e^{(k \, T)} \qquad (1)$$

where a = base coefficient (= DR if T =0), k = temperature coefficient of DR, and T = leaf temperature. For the tested day/night periods, we simply assumed that DR occurred during the interval between sunset and sunrise and that leaf temperature would be equal to air temperature during that period for all segments. Nocturnal hourly temperature data were obtained from a station of the National German Weather Service (Deutscher Wetterdienst, DWD), Geisenheim, located about 1.5 km away from the experimental vineyard. Integrated carbon losses were multiplied with LA per segment and subtracted from diurnal carbon gain to yield an estimation of carbon balance per canopy segment or per vine.

W a t e r   p o t e n t i a l   m e a s u r e m e n t s : Pre-dawn leaf water potential (Ψ_{pd}) was measured with a

Scholander pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, CA, USA) (Scholander *et al.* 1964) several times during the 2002 and 2003 seasons. Six to eight adult leaves were sampled across all segments of both systems.

S t a t i s t i c s : Analyses of variance (ANOVA, Holm-Sidak-method) were calculated with SigmaStat 3.1 (Systat Software Inc., Point Richmond, CA, USA).

Results and Discussion

V e g e t a t i v e   g r o w t h : In spring, leaf area development was more rapid for MP than for VSP vines due to the much larger shoot number despite reduced bud break (Table) confirming many previous studies (e.g. Clingeleffer 1984, Downton and Grant 1992, Sommer *et al.* 1993, Poni *et al.* 2000) (Fig. 2). In 2002 near veraison maximum leaf area was 15.2 m^2 vine^{-1} for the MP and 5.2 m^2 vine^{-1} for the VSP system. This degree of vigour of MP vines is comparable to data from other studies in cool climates (Sommer 1995, Lakso *et al.* 1996) but the differences in LA with respect to the conventional pruned systems reported are often much smaller due to reduced or absent shoot trimming (Lakso *et al.* 1996, Intrieri *et al.* 2001). MP vines retained about a 3-fold higher LA throughout most of the season in both years with a slight decline in this ratio during September and October due to some leaf losses (Fig. 2). Accelerated senescence of leaves from the canopy interior of MP vines has been reported previously and is thought to be related to a larger degree of water deficit experienced as a

result of the larger leaf area (Downton and Grant 1992, Sommer *et al.* 1993, Sommer 1995, Martínez de Toda and Sancha 1998, Schmid and Schultz 2000). This may have been also the cause of pre-mature leaf shedding in the present study, since MP vines had generally lower pre-dawn water potentials throughout the two seasons (Fig. 3) and earlier and larger losses in LA in 2003 were correlated with earlier and stronger levels of water deficit (Figs 2 and 3). In studies where water stress was absent, leaf longevity of MP vines was not negatively affected (Lakso *et al.* 1996, Poni *et al.* 2000, Intrieri *et al.* 2001).

L i g h t   i n t e r c e p t i o n : The analysis of light interception from the measurements on the grid systems showed that MP vines exhibited very different spatial and temporal light interception patterns as compared to VSP vines (Fig. 4). The spatial distribution and temporal development of daily average light interception per grid point reflected the more rapid leaf area development and the larger canopy dimensions of MP as compared to VSP vines between shortly after bud break (Fig. 4 A), bloom (Fig. 4 B) and veraison (Fig. 4 C). Thereafter, light interception continued to increase for both systems without further increases in leaf area (compare Figs 2 and 4 C, D). MP and VSP vines reached a maximum average light interception across all grid points of 76 % and 63 %, respectively, at the end of the season (Fig. 4 D). Intrieri *et al.* (2001) in a study with Sangiovese found a correlation between leaf area development and average light interception for a conventional pruning system up to about 18 m^2 m^{-1} row length (= maximum leaf area attained) and for MP vines up to about 14 m^2 m^{-1} row length attained already 35 d after bud break (maximum leaf
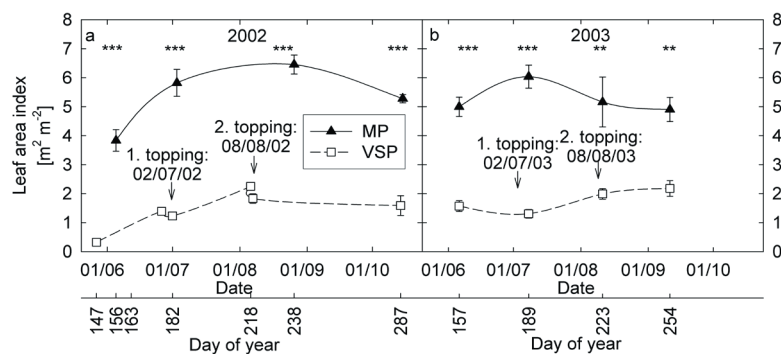

Fig. 2: Leaf area indices of MP and VSP vines during the 2002 (**a**) and 2003 (**b**) seasons. Data are means ± SE with n = 3 - 4; *: p ≤ 0.05, **: p ≤ 0.01,***: p ≤ 0.001.
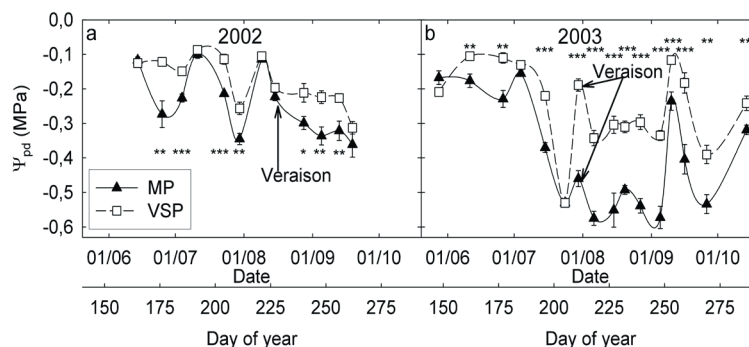

Fig. 3: Pre-dawn leaf water potential during the growing seasons in 2002 (**a**) and 2003 (**b**) for MP and VSP vines. Data represent the mean of 6 - 8 leaf samples ± SE; *: p ≤ 0.05, **: p ≤ 0.01,***: p ≤ 0.001.
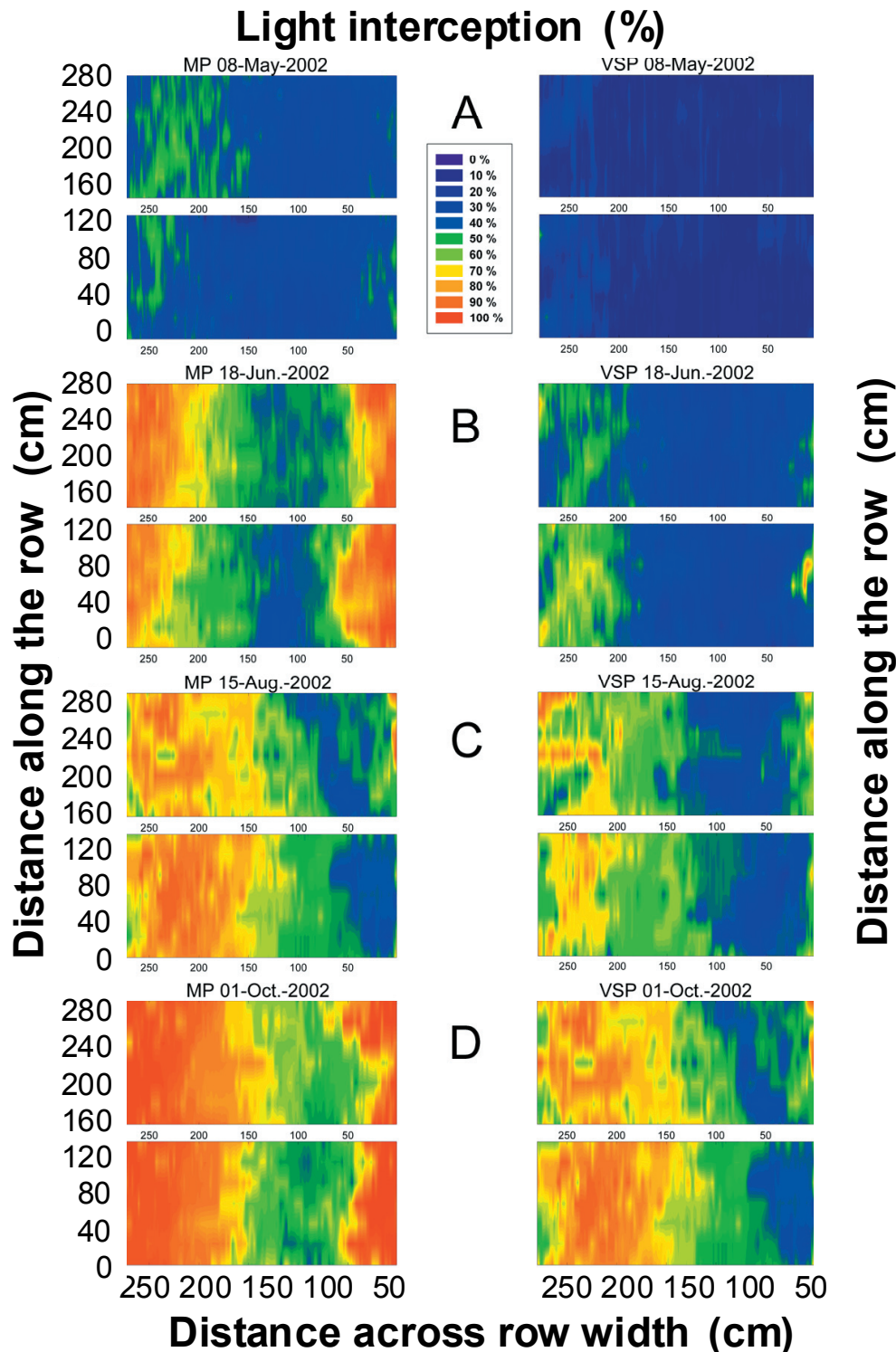
Fig. 4: Spatial and temporal variation in average daily light interception profiles across 2 grid systems per canopy type each covering the entire row width and 125 cm distance along the row in 2002 (left panel MP, right panel VSP). Data are averages of light readings recorded 6 (15th August) to 9 times per day (18th June) giving a total of 23520 to 35280 data points per day and system.

area = 29 m^2 m^{-1}). They suggested, that the difference between the canopy systems was related to the more open canopy structure of the conventional system with a maximum light interception near 78 %, whereas leaf areas in access of 14 m^2 m^{-1} for the MP vines only contributed to mutual shading and light interception was only 65 % (INTRIERI *et al.* 2001). In the present study with less vigorous Riesling vines, maximum leaf areas of VSP and MP vines were reached much later during the season and were equiv-

alent to about 5.6 and 16.8 m^2 m^{-1} row length, respectively, suggesting that for VSP, LA was insufficient to maximize light interception and for MP, that canopy structure must have been superior to that of the Sangiovese study.

There was a distinct seasonal shift in the frequency distribution of light interception classes for both canopy systems (Fig. 5). At all times during the season, MP canopies had a larger proportion of higher light interception classes than VSP canopies (Figs 4 and 5). Apart from the

differences in canopy dimensions, this may also be related to higher local leaf area density values (leaf area per unit canopy volume) (Zimmer 1998, Schmid and Schultz 2000) and/or differences in the distribution of leaf inclination angles and azimuth (Mabrouk *et al.* 1997 a). Recently Louarn (2005) has shown large differences with respect to the latter two parameters between a VSP type canopy system and one with free hanging shoots.

As the season progressed and whole-canopy light interception continued to increase for both systems despite unchanged or decreased leaf areas, the differences between the two systems became smaller (Figs 4 and 5). This indicated an increase in the radiation interception efficiency
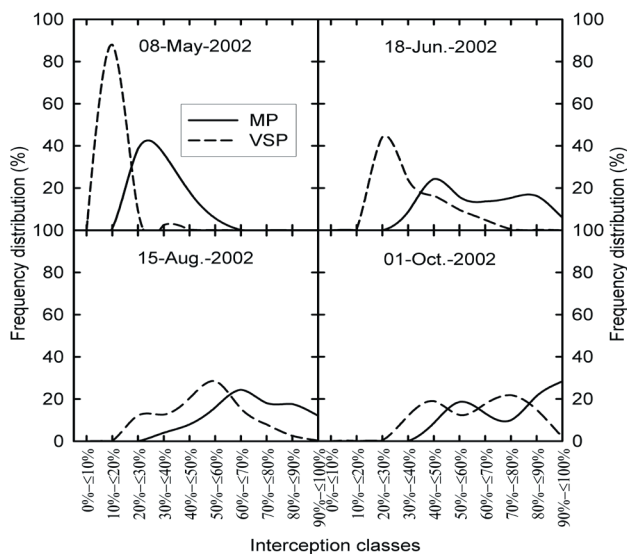

Fig. 5: Frequency distribution of daily light interception classes for 4 d throughout the 2002 season for MP and VSP canopies. The presentation is based on data shown in Fig. 4.

caused by decreasing solar angles at a high latitude location (50° North in the present case) (Varlet-Grancher *et al.* 1989), which was more pronounced for the thin vertical VSP canopies due to a different angle between sun azimuth and canopy surface (Mabrouk *et al.* 1997 b). Since light interception has been correlated with whole-canopy CO_2 exchange rates (Poni *et al.* 2003) this characteristic may be important for the achievement of full grape maturity in Northern temperate viticultural areas.

Canopy light interception has also been related to whole vine water consumption (Riou *et al.* 1994, Williams and Ayars 2005) and can explain the stronger decrease in Ψ_{pd} for MP as compared to VSP vines during the season. The decrease in the difference in light interception between MP and VSP vines during the course of the season may therefore also explain why differences in whole plant water use between both systems also diminish (Schmid and Schultz 2000).

G a s   e x c h a n g e : Former studies on the gas exchange of MP as compared to conventional pruned systems which were conducted on representative, well exposed mature leaves showed no or only small differences in photosynthetic rate (Downton and Grant 1992, Sommer and Clingeleffer 1993, Sommer *et al.* 1993, Intrieri *et al.* 2001). In some cases, there were reports about higher A

values very early and very late during the season for leaves on MP vines (Downton and Grant 1992, Intrieri *et al.* 2001) which may influence the CO_2 exchange rate of the entire canopy during these periods (Lakso *et al.* 1996, Poni *et al.* 2000). In order to better characterize the effect of local differences in leaf age and sun exposure caused by differences in the canopy structure on leaf gas exchange, we measured A in the natural leaf position in different canopy segments. This system, originally proposed by Lebon and Schultz (1996), has been used to quantify differences in light interception related to the canopy zone (Zufferey and Murisier 1997) and to estimate the contribution of different canopy zones to whole plant photosynthesis during drought (Escalona *et al.* 2003).

We found important diurnal variations in A among canopy locations and observed a clear seasonal trend in the relative contribution of different canopy zones to whole-vine photosynthesis (Figs 6-9). The top segment of both canopy systems received the highest light intensities throughout the season (up to 50 mol PPFD d^{-1}). Due to the South-West exposure of the vineyard, more light was intercepted by the South-East (S-E) oriented canopy walls in the morning until mid-afternoon (Figs. 6-9). There were small differences in the amount of PPFD received by the different canopy segments on this side throughout the season, with the apical and central parts being exposed to higher PPFD values longer during the day (e.g. Figs 6 and 7). Despite the larger variation in our data due to varying leaf position, this is similar to what models on radiation interception would predict (Riou *et al.* 1989, Zufferey and Murisier 1997). The North-West (N-W) oriented canopy side received full PPFD only from mid-afternoon on and there were strong
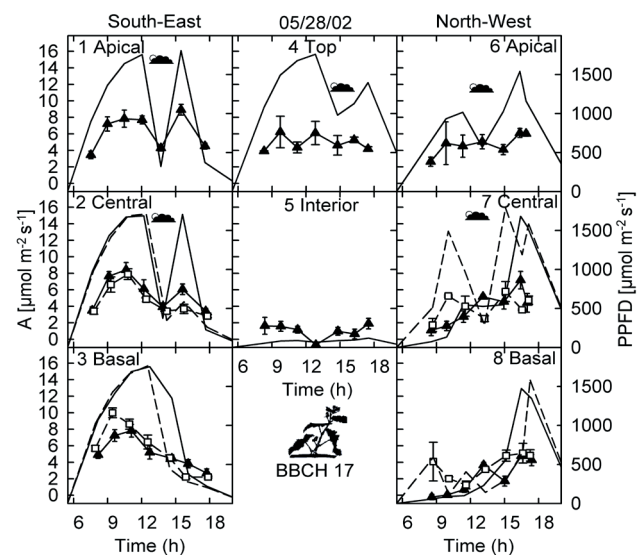

Fig. 6: Net-photosynthesis (A) and photosynthetic photon flux density (PPFD) of canopy segments of MP and VSP vines on 28 May 2002. Data represent means of 3 - 6 leaves ± SE. Measurements were conducted in the natural position of the leaves. Closed symbols (▲) and continuous lines are for MP vines, open symbols (□) and dashed lines are for VSP. Due to the early measuring date, there were no leaves present in segments 1, 4, 5 and 6 for the VSP vines. The phenological phase is presented in picture code (BBCH) according to the developmental scale of Eichhorn and Lorenz (1977).

differences between canopy segments (Figs 6-9). During the course of the season, PPFD received by the central and basal canopy zones decreased progressively, which also reduced A in these segments (Figs 6-9). In general, the top and apical segments on both canopy sides had the highest diurnal values of A confirming previous studies with this segmentation system (LEBON and SCHULTZ 1996, ESCALONA *et al.* 2003). Early in the season, these segments only had leaves in the MP canopies (Fig. 6). A responded to PPFD in all segments at the beginning and at the end of the season (end of May, Fig. 6, mid October, Fig. 9). This response was masked by water deficit, high temperatures and high vapour pressure deficits influencing A for mid-season measurement dates (end of July, Fig. 7, mid August, Fig. 8) for all canopy segments except those receiving low light during most of the day (central and basal zones on the N-W side and interior zone). For the days in question, Ψ_{pd} values were -0.26 MPa and -0.3 MPa for the VSP system and -0.35 MPa and -0.55 MPa for the MP system (see also Fig. 3). Also, leaves of MP as compared to VSP vines generally show lower diurnal Ψ values even at similar soil water status due to hydraulic constraints in the water transport system (GRUBER and SCHULTZ 2005). These differences can explain the lower photosynthetic rate of the MP leaves as compared to VSP leaves on the top and S-E exposed canopy segments, since stomatal conductance, g, (data not shown) responds to leaf water status and limits A (ESCALONA *et al.* 1999). However, at the lower Ψ_{pd} values, direct effects on photosynthetic quantum efficiency (DÜRING 1998, FLEXAS *et al.* 1998) and electron transport rate can not be excluded (DÜRING 1998, FLEXAS *et al.* 2002). Additionally, for measurements on July 29th (Fig. 7), leaf temperatures at mid day exceeded 40 °C in these same segments (data not shown), which, even in the absence of water deficit can substantially reduce maximum Rubisco acitivity and electron transport rates in grape (SCHULTZ 2003). The stronger relative reduction in A in high light-exposed canopy sections as compared to low light segments, which has also been observed in a water stress study with different varieties in Spain (ESCALONA *et al.* 2003), is related to a stronger limitation of light-saturated as compared to light-limited photosynthesis by water deficit (ESCALONA *et al.* 1999). This is also reflected by the fact, that leaves located in the canopy interior showed no response to changes in environmental factors and had only very low photosynthetic rates (Figs 6-9).

In the absence of environmental constraints, A of MP and VSP leaves was similar in all canopy sections (Figs 6 and 9) confirming previous results (DOWNTON and GRANT 1992, SOMMER and CLINGELEFFER 1993, SOMMER *et al.* 1993, INTRIERI *et al.* 2001). MP leaves retained comparable A values to VSP leaves in the apical canopy segments until mid-October (Fig. 9), despite being much older (they are the basal leaves on the shoot) than those in the same segment of the upright growing VSP canopies (they are the youngest on the shoot). This seems to support some data concluding that leaves in MP systems have superior longevity than leaves on conventional pruned vines (DOWNTON and GRANT 1992, INTRIERI *et al.* 2001). Despite yield increases of MP vines in our study of 225 % as compared to VSP
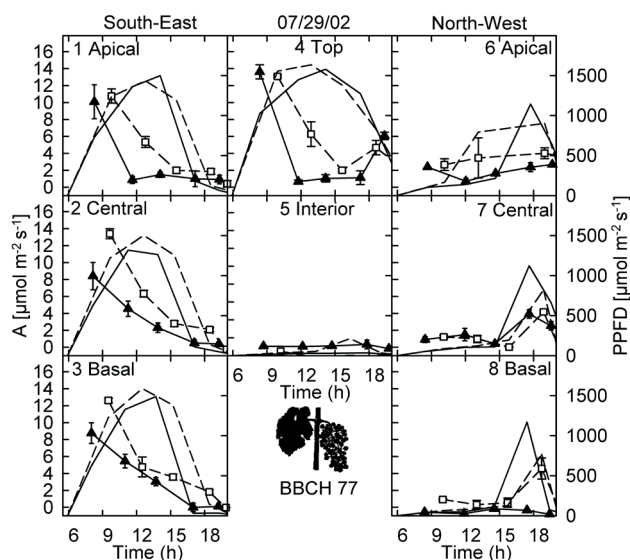

Fig. 7: Net-photosynthesis (A) and photosynthetic photon flux density (PPFD) of canopy segments of MP and VSP vines on 29 July 2002. Data represent means of 3 - 6 leaves ± SE. Closed symbols (▲) and continuous lines are for MP vines, open symbols (□) and dashed lines are for VSP. For explanation of picture code see Fig. 6.
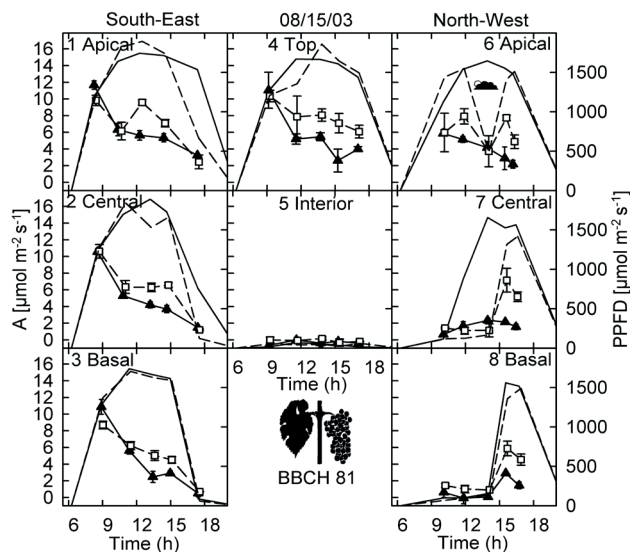

Fig. 8: Net-photosynthesis (A) and photosynthetic photon flux density (PPFD) of canopy segments of MP and VSP vines on 15 August 2003. Data represent means of 3-6 leaves ± SE. Closed symbols (▲) and continuous lines are for MP vines, open symbols (□) and dashed lines are for VSP. For further details see Fig. 6.

vines (Table), a stimulating effect on photosynthesis due to the increased sink size (DOWNTON *et al.* 1987) was probably small since an increase in LA paralleled the increase in yield.

C a r b o n   b u d g e t : In order to evaluate the balance between daily CO_2 uptake and nocturnal CO_2 release for the two canopy systems and different canopy positions, the measured values of A were integrated over the light period for all canopy segments and 6 measurement days (only 4 are shown in Figs 6-9). Since night respiration was not measured on the same days, we used a model to estimate DR based on nocturnal data of air temperature (SCHULTZ
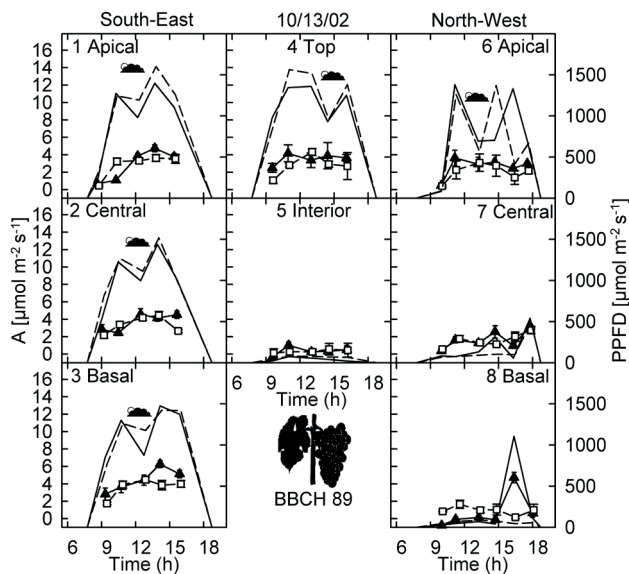
Fig. 9: Net-photosynthesis (A) and photosynthetic photon flux density (PPFD) of canopy segments of MP and VSP vines on 13 October 2003. Data represent means of 3 - 6 leaves ± SE. The picture code represents the phenological stage. Closed symbols (▲) and continuous lines are for MP vines, open symbols (□) and dashed lines are for VSP. For further details see Fig. 6.
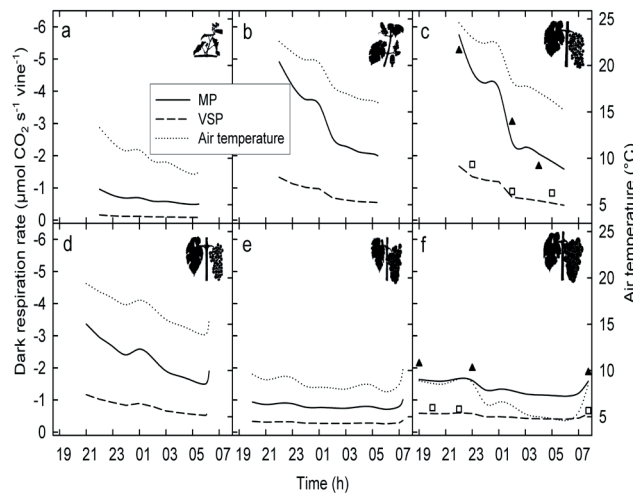

Fig. 10: Estimated night respiration rates for those 6 days/nights for which photosynthesis was measured (a = May 28, 2002; b = June 2, 2003; c = July 29, 2002; d = August 15, 2003; e = September 24, 2002; f = October 13, 2003). Dotted lines represent air temperature values. Continuous and dashed lines are simulated dark respiration values for MP and VSP vines, respectively, which were multiplied by the average leaf area per vine at each phenological stage (presented in picture code). Symbols in c and f are data on dark respiration for the two canopy systems measured outside the 2002-2003 season but during the same phenological stages.

1991). The model has been parameterized separately for different phenological stages (*i.e.* changes in the temperature response factor, Q_{10}, SCHULTZ 1991). We assumed, that temperature distribution was equal within the canopy. Fig. 10 shows the estimated dark respiration rate per vine for the 6 days/nights in question, where calculated DR values were multiplied with the total vine LA. A few values from respiration measurements on MP and VSP vines outside the 2002 and 2003 seasons were available and added in Fig. 10 to show, that the estimated values seem realistic. Our analysis was based on the assumption, that there were no specific canopy system-related differences in DR. PONI *et al.* (2000) reported similar DR rates of MP and VSP vines in a whole canopy study, but LAKSO *et al.* (1996) found that DR rates of MP vines were increased early in the season as a response to the accelerated canopy development. An additional source of error in the estimation of DR may be the response to water deficit which is not included in the model. AL-HAZMI *et al.* (1996) found a small decrease in DR of potted Cabernet Sauvignon vines during water stress, suggesting that there may have been an effect which would influence the calculations of total vine carbon budget. However, depending on plant type and size, DR may also increase as a response to water deficit (FLEXAS *et al.* 2005).

Carbon gain estimations per canopy segment ((diurnal integrated A – nocturnal integrated DR) multiplied by (LA per segment)) showed that for both canopy systems, the top segment contributed the most to the whole-vine carbon budget throughout the season (maximum of 9.2 g C segment^{-1} d^{-1} for MP and 4 g C segment^{-1} d^{-1} for VSP) (Fig. 11). With the exception of the canopy interior, total acquired C was always higher for MP as compared to VSP vines in all segments, reflecting the differences in LA. For VSP vines

carbon gain increased from the beginning of the season to about veraison (BBCH code 81) in all S-E and apical canopy segments and decreased thereafter (Fig. 11). MP vines had high rates of carbon assimilation already early in the season (Fig. 11). These rates remained relatively stable until veraison in the S-E and apical canopy sections despite a more than doubling in leaf area. During this period limitations of A caused by water deficit and high temperatures prevented higher rates of carbon assimilation (Figs 7 and 8). Carbon acquired by the central and basal parts of the canopy on the N-W side decreased continuously after bloom (BBCH code 57) for the MP canopy. In general N-W sections gained less C than S-E sections for both systems which was related to the amount of intercepted PPFD (ZUFFEREY and MURISIER 1997, ESCALONA *et al.* 2003). The interior segment showed relatively high positive C assimilation (up to 1.7 g C segment^{-1} d^{-1}) only at stages before canopy filling was complete for both pruning treatments (BBCH 17 and 57) but had rates which were negative or close to zero thereafter (Fig. 11). This was also the segment where pre-mature leaf senescence was observed.

The general decline in carbon gain after veraison was related to the rapidly shortening photoperiod and a concomitant progressive ageing of the canopy (LAKSO *et al.* 1996, PONI *et al.* 2000). The seasonal pattern and distribution between single canopy positions of the present study is roughly comparable to results obtained by ESCALONA *et al.* (2003). Their estimates of daily carbon gain ranged from about 0.5 to more than 7 g C m^{-2} d^{-1}, whereas in our study when data were converted to a per unit leaf area basis, we obtained a range from negative values to about 4.3 g C m^{-2} d^{-1} which included the deduction of respiration.
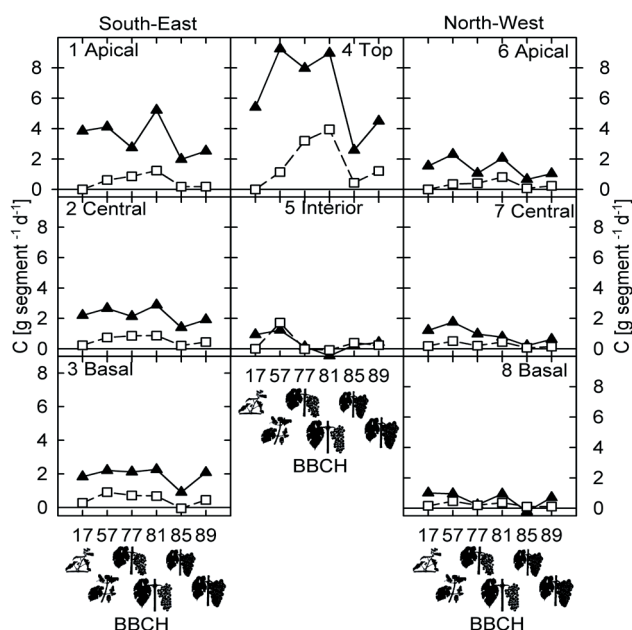
Fig. 11: Integrated carbon gain of 8 canopy segments for 6 d during the 2002 – 2003 seasons. Phenological stages are indicated by picture code. Closed symbols (▲) and continuous lines are for MP vines, open symbols (□) and dashed lines are for VSP.

Calculating carbon gain for entire vines gave superior values for MP throughout the season. For example, at BBCH 17 (28th May 2002), MP fixed 18.5 g C vine^{-1}·day^{-1} which was about 5.7 fold more than VSP (3.29 g C vine^{-1}·day^{-1}) due to its faster canopy filling and essentially more mature LA per vine. Maximum values were reached for both systems close to veraison (BBCH 81, 15th August 2003) with a gain of 22.43 g C vine^{-1}·day^{-1} for MP and 10.28 g C vine^{-1}·day^{-1} for VSP and decreased again thereafter despite the continued increase in average light interception (Fig. 4). This indicates that the increase in light interception efficiency could not compensate for the decrease in day length and the loss of photosynthetic capacity of older leaves.

Calculated respiratory losses were between 4 and 7 % for most of the season (maximum losses on the 29th July were 1.18 g and 0.34 g for MP and VSP vines, respectively), which is about 10-15 % lower than those values obtained from whole-vine gas exchange measurements (Lakso *et al.* 1996, Poni *et al.* 2000). However, those values include respiratory activity from stems and fruit which were not included in the present study. Nevertheless, in general our data on carbon gain even when extrapolated over the entire season are comparable to those found in the literature (Downton and Grant 1992, Lakso *et al.* 1996, Poni *et al.* 2000) and agree well with calculated carbon requirements for vines when respiratory costs for growth and maintenance of other vegetative organs and fruit are deducted (Williams 1996).

Despite a carbon balance which was superior for MP as compared to VSP vines, it was not sufficient to counter balance the large differences in yield (Table) with respect to sugar concentration in the fruit. During the two years of observation, VSP vines reached 21.8 and 23.2 °Brix in 2002 and 2003, respectively, whereas MP vines reached 20.8 ° Brix in both years.

Conclusion

In a two-year study, MP Riesling vines exhibited higher rates of carbon gain than pruned VSP vines. This carbon was mostly invested into yield formation, whereas sugar concentration in the fruit was lower. Since managing costs are substantially lower for MP vines than for VSP vines, there is a possibility to develop a highly economic viticultural system for quality wine production if yield can be controlled to a level comparable to VSP vines.

Acknowledgements

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