CANOPY PHOTOSYNTHETIC ACTIVITY AND WATER RELATIONS OF SYRAH/R99 AS AFFECTED BY ROW ORIENTATION ON A PARTICULAR TERROIR
INFLUENCE DE L'ORIENTATION DES RANGS SUR L'ACTIVITE PHOTOSYNTHETIQUE ET LES RELATIONS HYDRIQUES EN SYRAH/R99 DANS UN TERROIR PARTICULIER

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Key words: terroir, row orientation, vegetative growth, reproductive growth, water relations, photosynthesis.

Abstract
The photosynthetic activity and water relations of a Syrah/R99 vineyard, situated in the Stellenbosch region, were investigated approximately one month after véraison. Vines were vertically trained, spur pruned, and spaced 2.75 x 1.5 m in North-South orientated rows on a terroir with Glenrosa soil and a West-facing slope. Microsprinkler-irrigation was applied at pea berry size and at véraison stages. The 1.4 m high canopies were suckered, shoot-positioned and topped and accommodated by means of three sets of double wires. Photosynthetic activity and water potential were measured on leaves in apical, middle and basal positions on both primary and secondary shoots. Lateral shoots in apical, middle and basal positions were measured. Both East and West sides of the canopy were measured in the morning and in the afternoon. In addition, photosynthesis and water potential of interior and exterior leaves on primary (apical, middle and basal leaves) and secondary (middle leaves in apical, middle and basal positions) shoots were compared.

The canopy typically increased in number of leaf layers from top to bottom. Light penetration decreased in tandem. On primary shoots, photosynthetic activity of leaves on sunny and shaded sides of the canopy was higher in the morning than in the afternoon. Photosynthesis of sun-exposed leaves decreased from the apical to basal position. On the shaded part of the canopy, photosynthesis of middle leaves was reduced compared to apical and basal leaves. The photosynthetic activity of the canopy was therefore higher in the morning than in the afternoon. Water potential of leaves on the sunny side of the canopy was also consistently lower than that of leaves on the shaded side. Although the sunny side is expected to display lower water potential, the differences were, however, not in line with the large differences found for photosynthetic activity. The sun-exposed side of the canopy had slightly lower water potential in the morning than in the afternoon.

Basally positioned secondary shoots on the sunny side of the canopy had higher photosynthetic activity in the morning than in the afternoon; that of secondary shoots in apical and middle positions was, however, similar in the morning than in the afternoon. Photosynthetic patterns of leaves on the sunny side of the canopy *versus* the shaded side of the canopy were similar to those on the primary shoot. Water potential patterns of leaves on secondary shoots (morning *versus* afternoon and sunny side *versus* shaded side) were similar to those of leaves on primary shoots.

Comparing the photosynthetic activity and water potential of exterior and interior leaves in different positions on either primary or secondary shoots, similar patterns than those found for sunny and shaded sides of the canopy occurred. In the morning, large differences between the exterior and interior leaves occurred when measured from the sunny side. However, when measured from the shaded side, values were similar to those of interior leaves measured from the sunny side and no marked differences between exterior and interior leaves were found.

The results are useful for application to terroirs forcing different row orientations. It provides an indication of the photosynthetic performance and water relations that can be expected with a particular row orientation.

Résumé

L’activité photosynthétique et les relations hydriques de plantes de Syrah sur R99 un mois après la véraison ont été étudiées dans un vignoble de la région de Stellenbosch. Le vignoble, planté à 2,75 entre rangs et 1,5 m sur le rang, sur un sol de type Glenrosa, était en pente et exposé a l’ouest: pour les rangs on avait adopté une orientation nord –sud. Les plantes, conduites selon un système de type en cordon de Royat, avaient donc un port ascendant de la végétation, palissée dans un plan vertical à l’aide de trois paires de fils. Une irrigation à micro-jets était appliquée dans la phase comprise entre la nouaison et la fermeture de la grappe et à la véraison. Le tronc était ébourgeonné et la végétation rognée à 1,4 m de hauteur. On a mesuré la photosynthèse et le potentiel hydrique de feuilles en position basale, médiane et apicale soit des bourgeons principaux, soit des entre-cœurs. On a considéré des entre-cœurs en position apicale, médiane et basale le long du bourgeon principal. Soit le matin, soit l'après-midi on a examiné le coté est et le coté ouest du rang.. On a comparé la photosynthèse et le potentiel hydrique de feuilles situées à l’extérieur ou à l’intérieur de la végétation: on a considéré séparément les feuilles apicales, médianes et basales des bourgeons principaux et les feuilles médianes des bourgeons anticipés, situés en position apicale, médiane et basale.

Le nombre de couches du feuillage augmente typiquement du sommet à la base de la végétation et la pénétration de la lumière baisse en proportion. Sur les bourgeons principaux l’activité photosynthétique de toutes les feuilles était plus élevée le matin que l’après midi, soit pour la face au soleil soit pour celle à l'ombre. La photosynthèse des feuilles exposées directement au soleil diminuait du sommet vers la zone basale. Sur le côté à l'ombre la photosynthèse des feuilles médianes était plus limitée en comparaison aux feuilles apicales et basales. L’activité photosynthétique de la plante entière était donc plus importante le matin que pendant l’après-midi. Le potentiel hydrique des feuilles exposées au soleil était beaucoup plus bas que celui des feuilles ombragées. Même si on s’attendait un potentiel hydrique inférieur pour le côté ensoleillé, les différences n’ont pas été en ligne avec les différences importantes trouvées pour l’activité photosynthétique. Le côté ensoleillé du rang avait un potentiel hydrique légèrement plus bas le matin que l’après midi. Les bourgeons secondaires de la zone basale sur le coté exposé au soleil avaient une activité phothosynthétique plus élevée le matin par rapport à l’après midi, tandis que pour les bourgeons secondaires en position apicale et médiane l’activité était à peu prés la même pendant toute la journée. Dans le cas des bourgeons secondaires l’activité photosynthétique des feuilles exposées par rapport aux feuilles ombragées et leur potentiel hydrique suivaient un comportement (matin contre après midi et côté soleil contre côté ombragé) analogues à celui des feuilles des bourgeons principaux.

Si l’on compare l'activité photosynthétique et le potentiel hydrique des feuilles externes et internes du couvert en position différente on trouve le même modèle de comportement pour les deux types de bourgeons que l'on avait observé pour le côté exposé ou non exposé du couvert. Pendant la matinée des grandes différences se produisaient entre les feuilles internes et externes de la végétation sur la face ensoleillée du rang, tandis que, si l’on prend ces mesures du côté

ombragé, les valeurs de toutes les feuilles sont pareilles à celles des feuilles internes du côté ensoleillé.

Ces résultats fournissent des indications sur les performances photosynthétiques et sur les relations hydriques que l'on peut s'attendre, en rapport à un terroir particulier, si l'on choisit une orientation donnée des rangs.

Introduction

On a particular terroir, the choice of vine row orientation is very important, since it can influence the total vine light interception and, as a consequence, the vineyard productivity and the grape enological aptitude. This is particularly true for vertically trained canopies which may result in partial shade when parameters such as canopy width and height, vine spacing and row distance are not optimal (Hunter, 1998). Phenological phase and latitude will also affect the expression of row orientation on the grapevine and its products.

In Europe, North-South (N-S) row orientation collects more solar energy than East-West (E-W) orientation from flowering to véraison; after that, the latter performs better (Champagnol, 1982; Magnanini & Intrieri, 1987; Zufferey & Murisier, 1997; Zufferey *et al.*, 1998). This influence becomes less pronounced at higher latitude, due to the flatter solar track (Champagnol, 1982; Magnanini & Intrieri, 1987). The daily balance of total net CO_2 uptake per vine was higher in N-S oriented than in the E-W oriented rows, until the beginning of September (Zufferey *et al.*, 1999). The whole canopy net CO_2 assimilation of potted and field grown grapevines was not affected by N-S or E-W row orientation (Intrieri *et al.*, 1998); nevertheless, N-S oriented vines showed a marked decrement in whole canopy transpiration at midday, resulting in a higher water use efficiency. This could be of paramount importance for the choice of row orientation on warm-arid areas (Champagnol, 1982; Intrieri *et al.*, 1998). East-West row orientation reduced growth, yield, total dry matter production (Intrieri *et al.*, 1997) and *Botrytis* incidence (Murisier & Zufferey, 1999). Bud fertility was not affected by row orientation (Murisier & Zufferey, 1999).

Sauvignon blanc berry composition was more variable when vines were grown in E-W rows and more uniform when rows were N-S oriented (Naylor *et al.*, 2003); in contrast, Intrieri *et al.* (1997) did not find any effect of row orientation on fruit composition of Chardonnay. According to Murisier (1983) wines from vines grown in N-S oriented rows have been preferred in comparison to those obtained from E-W oriented rows; however, no effect on wine sensory descriptors was found by Intrieri *et al.* (1997).

This investigation was prompted given the fact that row orientation is an integral part of grapevine cultivation and because little information is available regarding its effect on physiological parameters, particularly in the Southern Hemisphere. In addition, knowledge on the physiological behaviour of different parts of the canopy when simultaneously exposed to varying sunlight under field conditions is scarce.

Materials and Methods

Vineyard

A seven-year-old Syrah/R99 vineyard, situated in the Stellenbosch region, was used. The trial was carried out during the 2004 growth season approximately one month after véraison. Vines were vertically trained, spur pruned, and spaced 2.75 x 1.5 m in North-South oriented rows on a terroir with Glenrosa soil and a West-facing slope. Microsprinkler-irrigation was applied at pea berry size and at véraison stages. The 1.4 m high canopies were suckered, shoot-positioned and topped (Hunter, 2000) and accommodated by means of three sets of double wires.

Measurements

Photosynthetic activity and water potential were measured on leaves situated in apical, middle and basal positions on both primary and secondary shoots. Secondary shoots in apical, middle and basal positions of the primary shoot were measured. Measurements were taken at both East and West sides of the canopy in the morning, between 10:00 and 12:00, and in the afternoon, between 14:00 and 16:00, which are, respectively, the hours of maximum East or West canopy side illumination. In addition, at the same hours, photosynthesis and water potential of interior and exterior leaves on primary (apical, middle and basal leaves) and secondary (middle leaves on shoots in apical, middle and basal positions) shoots were compared. Each set of measurements was repeated in two different weeks. Photosynthetic activity was measured on four leaf replicates by means of a portable infra red gas analyzer equipped with leaf chamber (ADC-LCA2, Analytical Development Co, Hoddesdon, UK). Leaf water potential was measured on four leaf replicates by means of a pressure chamber according to Scholander *et al*. (1965). Light intensity in the top, middle, and bottom part of the canopy, and outside of the canopy was measured by means of a quantum line sensor.

Canopy leaf layers were counted from top to bottom. Moreover, canopy vegetative parameters were measured on five shoots sampled either at the East or at the West side of the canopy. On each shoot, main and secondary leaves were counted; the leaf area per shoot was measured by means of a LICOR LI-3100 area meter (Lincoln, Nebraska, USA). Moreover, berry number, berry mass and rachis mass of the two bunches per shoot were assessed.

Statistical analyses

Data were statistical analyzed by using the GLM procedure of the SAS statistical package (SAS Institute, Cary, NC, USA).

Results and Discussion

Canopy vegetative parameters showed no statistical differences between East and West sides (Table 1); however, shoots of the East side, when compared with shoots of the West side, showed a tendency to produce a lower primary leaf area and a higher secondary leaf area. Although cluster characteristics did not differ significantly between the two canopy sides, the clusters of the West side tended to have a higher mass and more berries. According to Smart *et al*. (1990), this could be due to a better fruit set depending on a higher light interception at the cluster zone.

The canopy typically increased in number of leaf layers from top (4 layers) to bottom (6 layers), and in foliage width from 0.25 m to 0.6 m. Light penetration decreased in tandem; in comparison to the irradiance intercepted by the exterior leaves, mean values of light intercepted by the interior leaves was 25 % at the top of the canopy and 13 % at the bottom of the canopy, without any significant difference between East and West sides.

On primary shoots, net photosynthetic rates of leaves at all the positions were higher at the canopy side that received maximum irradiance, that is, at the East side in the morning and at the West side in the afternoon (Table 2). The photosynthetic rate of leaves on the sun-illuminated canopy side decreased from the apical to basal position. On the shaded side of the canopy, photosynthesis of middle leaves was lower than that of apical and basal leaves. However, on average (data not shown), leaves of the East canopy side, fully illuminated in the morning, showed a tendency to a total higher net CO_2 uptake than leaves of the West canopy side, fully illuminated in the afternoon. Similar results were found by Zufferey *et al*. (1999) in a cool Alpine area. Water potential of leaves on the sunny side of the canopy was also consistently lower than that of leaves on the shaded side (Table 3). Although the sunny side is expected to display lower water potential, the differences were, however, not in line with the large differences found for photosynthetic activity. The sun-exposed side of the canopy generally had slightly lower water potential in the morning than in the afternoon. As light interception differed only slightly between the two illuminated canopy sides at the time of measurement in the morning and in the afternoon, the lower fruit set and cluster mass at the East side may be explained by the combined effects of photosynthetic activity and water potential, forcing physiological and morphological changes.

Regarding the photosynthetic activity of secondary shoots, leaves of basally positioned shoots on the sunny side of the canopy had higher rates in the morning than in the afternoon (Table 2); leaves of shoots positioned in the middle showed a similar activity in the morning than in the afternoon; leaves of shoots in the apical canopy position had rates varying with the leaf allocation within the shoot. Photosynthetic patterns of leaves on the sunny side of the canopy *versus* the shaded side of the canopy were similar to those observed on the primary shoot. The contribution of the secondary shoots to the total vine CO_2 uptake is of great importance, as stated by Novello (1996) and Hunter (2000), provided that their leaves are well sun-exposed. Water potential patterns of leaves on secondary shoots (morning *versus* afternoon and sunny side *versus* shaded side) were similar to those of leaves on primary shoots (Table 3).

Comparing the photosynthetic activity (Table 4) and water potential (Table 5) of exterior and interior leaves, in different positions, on either primary or secondary shoots, patterns were similar to those observed for sunny and shaded sides of the canopy. In the morning, large differences between the exterior and interior leaves occurred when measurements were taken from the sunny side. However, when measured from the shaded side, values were similar to those shown by interior leaves from the sunny side, and no marked differences between exterior and interior leaves were found. Similar results were observed in the afternoon (Table 5). Even though the water potential of exterior leaves from the shaded side did not differ from that of internal leaves of the sunny side, the photosynthetic activity was higher in the former than in the latter.

Overall, the rate of leaf net CO_2 uptake at the West side in the afternoon was 88 % of that measured at the East canopy side in the morning, whereas the photosynthetic rate at the East side in the afternoon was 74 % of that measured at the West side in the morning. Since the light interception at the leaf level was almost the same at the East side in the morning and at the West side in the afternoon, this reduction of photosynthetic activity may be related to the inhibitory effect of the 'photosynthetic feedback' built up during the day and/or other biochemical factors acting at the mesophyll level (Chaumont *et al.*, 1994; Düring, 1991; Zang *et al.*, 1991).

The results found in this trial are useful for explaining the performance of vines on different terroirs and planted to different row orientations. It provides an indication of the photosynthetic performance and water relations, with implications for yield and grape composition, that can be expected when a particular row orientation is considered during planting.

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Table 1. Canopy vegetative parameters and cluster characteristics (data ± SE).

Parameter	Canopy side	
	East	West
Main leaf number/shoot	14 ± 1.86	14 ± 1.17
Main leaf area (cm^2)	127.96 ± 7.34	133.2 5± 9.2
Main leaf area/shoot (cm^2)	1710.41 ± 165.67	1788.00 ± 92.1
Secondary leaf number/shoot	33 ± 0.8	29 ± 3.0
Secondary leaf area (cm^2)	12.85 ± 0.64	12.77 ± 0.96
Secondary leaf area/shoot (cm^2)	417.67 ± 14.9	326.04 ± 26.19
Total leaf area/ shoot (cm^2)	2128.08 ± 160.36	2149.66 ± 71.12
Cluster number/shoot	2.0 ± 0.0	2.0 ± 0.0
Cluster mass (g)	278.8 ± 0.21	310.4 ± 9.4
Berry number/cluster	141.0 ± 13.8	150.2 ± 8.1
Berry mass (g)	2.00 ± 0.21	2.08 ± 0.07
Rachis mass (g)	10.0 ± 0.63	11.4 ± 0.46

Table 2. Photosynthetic rate (μmol m^{-2} s^{-1}) of primary and lateral shoots in sun and shade side of the canopy in the morning (AM) and afternoon (PM). (NS non significant; * significant per P≤ 0.05; ** significant per P≤ 0.01).

Shoot type	Lateral position	Leaf position	AM			PM		
			East	West	Sign.	East	West	Sign.
Primary		**Top**	7.84	2.16	*	1.90	7.61	*
		Middle	8.12	1.74	*	1.13	6.10	NS
		Basal	4.56	1.88	*	1.50	3.32	NS
Lateral	**Top**	**Top**	6.97	2.97	NS	0.97	7.56	**
		Middle	7.83	2.55	**	2.04	8.50	**
		Basal	9.57	2.11	**	2.36	6.66	NS
Lateral	**Middle**	**Top**	9.72	2.67	**	1.76	7.84	*
		Middle	8.60	3.18	NS	1.30	8.55	**
		Basal	7.77	1.90	**	1.83	8.05	**
Lateral	**Bottom**	**Top**	8.67	2.01	*	2.11	6.83	NS
		Middle	9.23	2.03	**	1.22	7.59	*
		Basal	5.65	1.31	*	1.45	4.35	NS

Table 3. Leaf water potential (MPa) of primary and lateral shoots in sun and shade side of the canopy in the morning (AM) and afternoon (PM). (NS non significant; * significant per P≤ 0.05; ** significant per P≤ 0.01).

Shoot type	Lateral position	Leaf position	AM			PM		
			East	West	Sign.	East	West	Sign.
Primary		**Top**	-1.27	-1.05	**	-1.22	-1.16	NS
		Middle	-1.16	-0.92	*	-0.99	-1.15	NS
		Basal	-1.20	-1.04	*	-1.05	-1.19	NS
Lateral	**Top**	**Top**	-1.24	-1.09	NS	-1.23	-1.23	NS
		Middle	-1.16	-0.99	NS	-1.09	-1.19	NS
		Basal	-1.21	-1.01	*	-1.08	-1.11	NS
Lateral	**Middle**	**Top**	-1.25	-0.99	*	-1.07	-1.16	NS
		Middle	-1.25	-0.96	*	-1.04	-1.19	*
		Basal	-1.16	-0.91	**	-0.94	-1.21	NS
Lateral	**Bottom**	**Top**	-1.33	-0.97	**	-1.06	-1.20	*
		Middle	-1.20	-0.97	**	-1.02	-1.17	NS
		Basal	-1.21	-0.99	*	-0.99	-1.16	NS

Table 4. Photosynthetic rate (µmol m^{-2} s^{-1}) of primary and lateral shoots in external (EX) and internal (IN) portion of the canopy in the morning (AM) and afternoon (PM). (NS non significant; * significant per P≤ 0.05; ** significant per P≤ 0.01).

Shoot Type	**Lateral Position**	**Leaf position**	**AM**						**PM**					
			East			**West**			**East**			**West**		
			EX	**IN**	**Sig.**	**EX**	**IN**	**Sig.**	**EX**	**IN**	**Sig.**	**EX**	**IN**	**Sig.**
Primary		**T**	9.55	3.73	**	3.55	2.73	*	3.29	2.27	*	8.13	2.48	**
		M	8.76	2.30	**	2.57	2.58	NS	2.56	2.01	NS	7.83	2.38	**
		B	6.03	2.18	**	2.24	1.87	NS	2.54	1.86	*	4.75	2.49	**
Lateral	**T**	**M**	7.38	3.16	**	3.22	2.80	NS	3.14	2.52	NS	6.45	3.07	**
	M	**M**	8.45	2.36	**	2.98	2.16	*	2.53	2.22	NS	7.41	2.50	**
	B	**M**	7.47	2.60	**	2.29	1.57	*	2.64	1.56	**	5.98	2.10	**

Table 5. Leaf water potential (MPa) of primary and lateral shoots in external (EX) and internal (IN) portion of the canopy in the morning (AM) and afternoon (PM). (NS non significant; * significant per P≤ 0.05; ** significant per P≤ 0.01).

Shoot Type	**Lateral position**	**Leaf position**	**AM**					
			East			**West**		
			EX	**IN**	**Sig.**	**EX**	**IN**	**Sig.**
Primary		**T**	-0.98	-0.86	N S	-0.94	-0.85	N S
		M	-1.05	-0.82	* *	-0.90	-0.83	N S
		B	-1.00	-0.85	* *	-0.90	-0.81	* *
Lateral	**T**	**M**	-1.03	-0.84	* *	-0.96	-0.90	N S
	M	**M**	-1.01	-0.81	* *	-0.89	-0.85	N S
	B	**M**	-0.96	-0.77	* *	-0.88	-0.73	* *
Shoot Type	**Lateral position**	**Leaf position**	**PM**					
			East			**West**		
			EX	**IN**	**Sig.**	**EX**	**IN**	**Sig.**
Primary		**T**	-0.96	-0.90	N S	-1.10	-0.96	* *
		M	-0.94	-0.90	N S	-1.06	-0.90	* *
		B	-0.96	-0.88	N S	-1.11	-0.87	* *
Lateral	**T**	**M**	-0.95	-0.89	N S	-1.04	-0.92	*
	M	**M**	-0.93	-0.79	* *	-1.04	-0.81	* *
	B	**M**	-0.93	-0.83	* *	-1.09	-0.84	* *