Artículo Científico **Rev. Fitotec. Mex. Vol. 31 (1): 27 - 33, 2008**

ADVANCED MATURITY OF 'PERLETTE' TABLE GRAPES BY TRAINING SYSTEMS WHICH INCREASE FOLIAGE EXPOSURE TO SUNLIGHT

MADURACIÓN ADELANTADA DE UVAS DE MESA 'PERLETTE' MEDIANTE SISTEMAS DE CONDUCCIÓN QUE AUMENTAN LA EXPOSICIÓN DEL FOLLAJE AL SOL

Alfonso A. Gardea, José Ramón Noriega, Jesús Antonio Orozco *, Mónica García-Bañuelos, Elizabeth Carvajal-Millán, Elisa M. Valenzuela-Soto and Alfonso Aguilar Valenzuela

Centro de Investigación en Alimentación y Desarrollo, A. C. (CIAD). Km. 0.6 Carr. a La Victoria S/N. 83000, Hermosillo, Son. Tel. y Fax. 01 (662) 280-0146.
**Autor para correspondencia* (avitia65@ciad.mx)

SUMMARY

Although extensive work has been reported on winegrapes (*Vitis vinifera* L.) regarding canopy structure, management and microclimate on berry ripening and composition, scarce information has been devoted to this issue in tablegrapes. Canopy microclimate, photosynthesis and other physiological traits were determined in three year old 'Perlette' vines trained on a T-trellis, in Sonora, México. In the undivided commercial T-trellis UTT) vine canopy, the photosynthetic photon flux densities (PPFD) reaching external, middle and internal leaf layers were 1922, 53 and 34 μmol m^{-2} s^{-1}, respectively. In the same order, net photosynthesis (Pn) rates were 19.0, 1.7 and 1.0 μmol CO_2 m^{-2} s^{-1}, while chlorophyll contents were 1.9, 1.7 and 1.0 mg mL^{-1}. No differences in total protein content were found between leaf layers, but significant differences in rubisco specific activity were found among external, middle and internal leaves, reaching 1.07, 0.65 and 0.25 μmol min^{-1} mg^{-1}, respectively. Four training systems were compared against a commercial undivided T-trellis (UTT): Slanted pergola (Pergola), a specifically designed system (CIAD), Lyre (Lyre) and a divided T-trellis (Divided). Significant differences in PPFD on Lyre, Pergola, CIAD, Divided and UTT yielded 2192, 2076, 1900, 885 and 711 μmol m^{-2} s^{-1}. At véraison, Pn in Pergola, CIAD, Lyre, Divided and UTT was 12.7, 11, 12.5, 10.5 and 5.1 μmol CO_2 m^{-2} s^{-1}, respectively. Five days after harvest, Pn showed a decrease in all training systems, particularly in UTT which showed only 3.7 μmol CO_2 m^{-2} s^{-1}. Stomatal resistance at véraison and postharvest was highest in UTT with 4.2 and 6.8 s cm^{-1} for both periods. Total soluble solids by 27 April were 15.7 °Brix for CIAD, while for UTT was only 12.1 °Brix. A week later, CIAD, Lyre, Pergola and Divided reported 16.3, 15.9, 15.5 and 15.2 °Brix, while UTT reached only 13.1 °Brix. Thus by dividing canopies and applying canopy management techniques the harvest date in the early season seedless grapes can be advanced, by increasing light harvest, photosynthetic rate and berry sugar accumulation.

Index words: *Vitis vinifera*, management systems, photosynthesis, fruit ripening.

RESUMEN

Aunque hay extensos reportes en uvas para vinificación (*Vitis vinifera* L.) sobre el efecto de la estructura, manejo y microclima del dosel en la maduración y composición de las uvas, poca información a este respecto está disponible para uva de mesa. El microclima del dosel, fotosíntesis y otros parámetros fisiológicos fueron determinados en vides 'Perlette' de tres años conducidas en una espaldera en T en Sonora, México. En la espaldera testigo sin división de dosel (UTT), las densidades del flujo de fotones fotosintéticos (PPFD) que alcanzaron a las capas de hojas externas, medias e internas de parras en espalderas en T fueron de 1922, 53 y 34 μmol m^{-2} s^{-1}, respectivamente. En el mismo orden, las tasas de fotosíntesis neta (Pn) fueron de 19, 1.7 y 1 μmol CO_2 m^{-2} s^{-1}, mientras que los contenidos de clorofila fueron de 1.9, 1.7 y 1 mg mL^{-1}. No se encontraron diferencias en el contenido de proteína total entre las tres capas de hojas, pero la actividad específica de rubisco fue significativamente diferente en las capas de hoja externas, medias e internas, con valores de 1.07, 0.65 y 0.25 μmol $min^{-1}mg^{-1}$. Después se establecieron cuatro sistemas de conducción: pérgola inclinada (Pérgola), un sistema diseñado exprofeso (CIAD), el sistema Lira (Lyre) y una espaldera en T dividida (Dividido), para comparación con el sistema comercial de espaldera en T sin división (UTT). Las PPFD presentaron diferencias significativas entre Lyre, Pérgola, CIAD, Dividida y UTT con valores de 2192, 2076, 1900, 885 y 711 μmol m^{-2} s^{-1}. Durante el envero, las tasas de Pn en Pérgola, CIAD, Lira, Dividido y UTT fueron 12.7, 11.0, 12.5, 10.5 y 5.1 μmol CO_2 m^{-2} s^{-1}, respectivamente. Cinco días después de la cosecha, la Pn mostró un decremento en todos los sistemas de conducción, con los valores menores en UTT que asimiló solamente 3.7 μmol CO_2 m^{-2} s^{-1}. La resistencia estomática medida en envero y poscosecha fue estadísticamente mayor en UTT, con 4.2 y 6.8 s cm^{-1} en ambos periodos. En abril 27, los sólidos solubles totales fueron 15.7 °Brix para CIAD mientras que UTT tenía sólo 12.1. Una semana más tarde, CIAD, Lira, Pérgola y Dividido registraron 16.3, 15.9, 15.5 y 15.2 °Brix, aunque UTT sólo subió a 13.1. Por tanto, la apertura del dosel y el uso de técnicas de manejo del mismo sí adelantan la fecha de cosecha en uvas sin semilla de maduración temprana al incrementar la cosecha de luz, las tasas fotosintéticas y la acumulación de azúcares en la baya.

Palabras clave: *Vitis vinifera*, sistemas de manejo, fotosíntesis, maduración del fruto.

Recibido: 4 de abril de 2005.
Aceptado: 28 de agosto de 2007.

INTRODUCTION

It has been widely reported that trellis systems (TS) dividing vine (*Vitis vinifera* L.) canopy increase sunlight penetration, which in turn increase yield and fruit quality (Carbonneau and Casteran; 1987; Reynolds *et al.*, 1996; Smart, 1985). Extensive work has been devoted in a diversity of winegrape varieties like 'Tempranillo' (Baeza *et al.*, 2005), 'Chardonnay' and 'Cabernet franc' (Vanden-Heuvel *et al.*, 2004), 'Chenin blanc' (Volschenk and Hunter, 2001a) and 'Riesling' (Percival *et al.*, 1994) among others. However, no reports were found on table grapes, where harvest is indexed to sugar accumulation in berries. Considering that those sugars are formed by photosynthesis, getting an insight on these events may help in designing more efficient practices.

Benefits from a more efficient use of sunlight, the only energy source freely available to growers, include increases in photosynthetic rates, bud differentiation, berry size, color and sugar content (Archer and Strauss, 1989; Smart, 1985; Vanden-Heuvel *et al.,* 2002). Vineyard productivity is also affected by dividing the canopies because stored reserves increase, while necrotic buds (Hunter and Visser, 1988; Peláez *et al.,* 1994) and cluster susceptibility to fungal infections decrease (Percival *et al.,* 1994).

The Sonoran Desert in northwest México is a Class V region (Winkler *et al.*, 1974), where short-season seedless grapes are grown for the early season market. An early harvest starting in late April or early May increases the probabilities of achieving the highest prices of early season. The industry relays on a wide variety of alternatives to achieve early markets. Canopy management may provide an effective tool to maximize vineyard profitability, since an increased light use efficiency by canopies may advance ripening and lead to early markets. The objective of this study was to determine the effect of canopy division on vine microclimate and physiological factors affecting harvest timing.

MATERIALS AND METHODS

This research was conducted in a three-year old 'Perlette' vineyard, near Pesqueira, Sonora in northwest México (29°21'28'' NL, 110°53'33'' WL, and 317 m of altitude). Rows were planted in an East-West orientation, like most in the region. Planting pattern was 3.2 m between rows and 1 m within vines, although individual vines were trained in an alternate fashion to lateral fruiting wires. 'Perlette' vines were growing in its own roots and an average fertilization of 80N-40P-100K at a dripping rate of 4 L h^{-1} was used at budbreak, bloom, berry set and after harvest. The vines were trained as bilateral cordons and pruned to two-bud spurs, retaining an average of 32 buds per vine, depending on vigor; although crop load was fixed at 15 clusters per vine.

Initial diagnosis. During the first season a preliminary study was conducted in grapevines in a commonly used T-trellis system where the following variables were measured: photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}), net photosynthetic rate (Pn, μmol CO_2 m^{-2} s^{-1}), chlorophyll and total leaf protein contents, and rubisco specific activity (μmol min^{-1} mg^{-1}). Measurements were made at harvest on five plants, at three canopy positions (one leaf per position), namely external, middle and internal layers; these positions were determined perpendicularly to the light beam direction as it penetrates the canopy.

PPFD of the incident light was measured at midday with a LI-191 linear quantum sensor (LICOR Inc. Lincoln, NE, USA), by placing the sensor at 1 m above ground level, parallel to row orientation. Depending on canopy depth, the sensor was placed in the area next to clusters, in the middle of the canopy and in the external side of the foliage, thus resulting in three positions resembling those of internal, middle and external leaves. A LI-6250 non-dispersive CO_2 infrared analyzer was used to measure Pn (LICOR Inc. Lincoln, NE, USA). Once these variables were taken, the same leaves were detached and individually wrapped in aluminum foil, labeled, immersed in liquid nitrogen, and stored at -40 °C for further analyses of chlorophyll content (Arnon, 1949), total protein content (Lowry *et al.*, 1951) and rubisco specific activity (Lilley and Walkers, 1974).

Trellis systems evaluation. Once the preliminary study was completed, four open-canopy TS were installed for comparison with the T-trellis commercially used (thereafter called Undivided T- Trellis, UTT) (Figure 1); this regional control is characterized by a lack of canopy management, resulting in dense canopies. Such systems were slanted pergola (Pergola), the Lyre system (Lyre), and a T-trellis with a divided canopy (Divided). In an E-W row orientation, the canopy side facing South is always exposed to sunlight, while the North side is always shaded and underexposed; therefore the North side was lifted to increase foliage exposure and this TS was called CIAD, after the institution responsible for this project. In the four systems the canopies were managed in order to keep foliage in place by using mobile wires (Figure 1). Each TS was established in three rows 100 m long, and four sampling stations were established in the middle row. On each TS, by opening the canopy two foliage curtains were formed, thus presenting internal and external sides. Sampling was done on eight external and internal leaves for a compound sample of 16 measurements per station, and four replications per TS. The following variables were evaluated at véraison (berry color change) and after harvest:

a) PPFD. Measurements were made as described above. However, total light was computed by adding incident radiation, reflected radiation inside and outside the canopy, and soil reflected radiation (Peláez *et al.,* 1994). An *ad hoc* aluminum frame was built to achieve such goal, allowing placing the linear sensor at specific positions, heights and depths in the canopy, so that the above types of radiation could be measured.

b) Pn and stomatal resistance. These variables were measured as described above, although the latter is computed by default, when measuring Pn.

c) Total soluble solids (TSS). At each sampling station, ten berries were sampled for TSS determination with a temperature-compensated refractometer ATC-1 (Atago, Japan). A compound sample of ten berries from the distal end of 10 clusters was taken. Sampling was done 9 d before expected harvest date, as well as during harvest.

d) Flower differentiation. A compound sample of 20 buds was obtained from fruiting spurs at each TS and immediately transported to our lab wrapped in moist paper. No further replications were considered. Bud differentiation was done by free-hand section cuts of primary and secondary buds examined under a stereoscope, and then classified as: 1) differentiated flowers, 2) no flowers observed, and 3) necrotic buds.

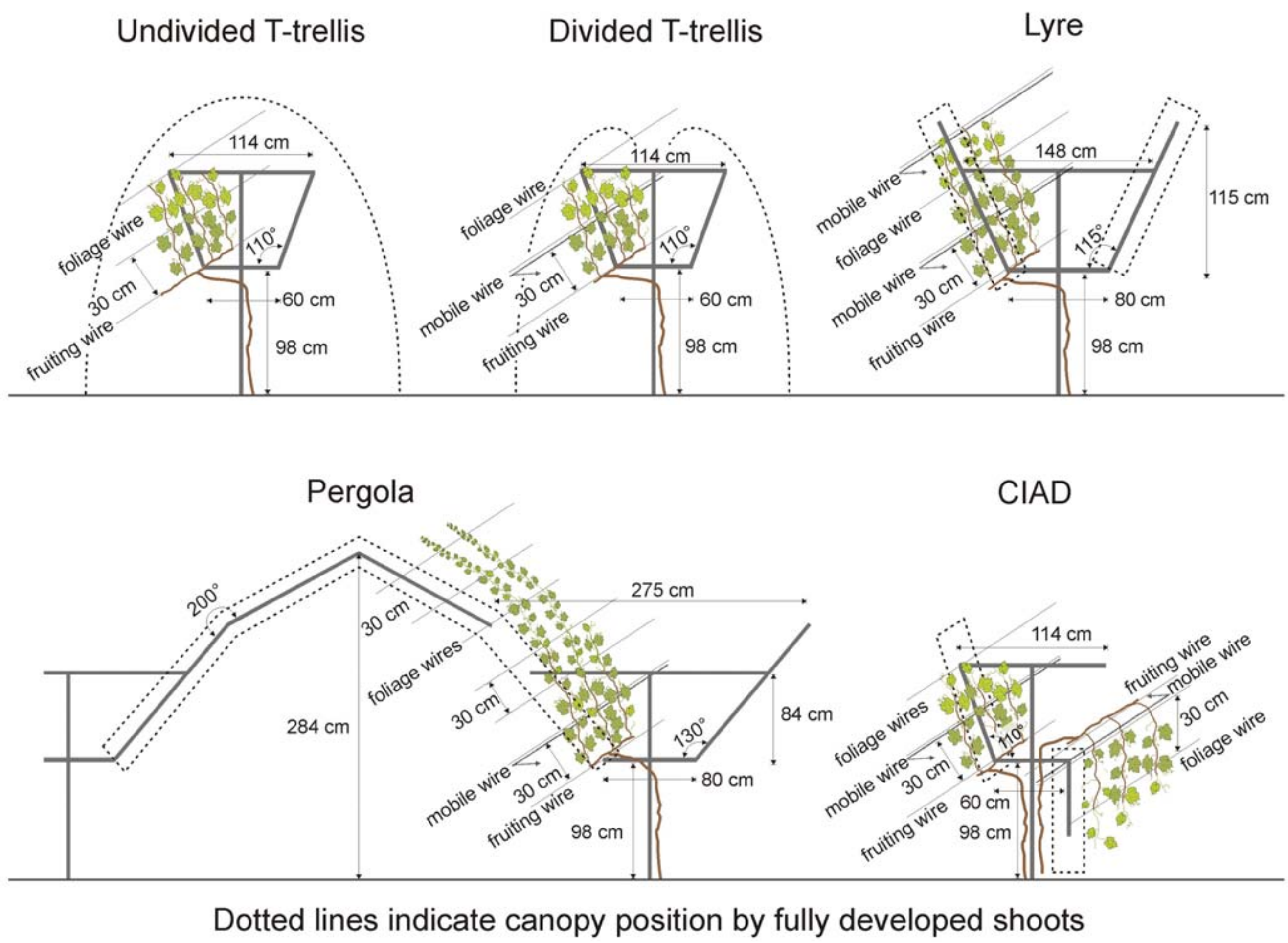

Figure 1. Trellis designs for five vine training systems used to evaluate the performance of 'Perlette' grapevines.

Statistical analyses. A completely randomized design with four replicates was used. Mean separation was done by Tukey ($P \leq 0.05$) (SAS Institute, 1987).

RESULTS AND DISCUSSION

Initial diagnosis of a commercial T-trellis system

PPFD decreased significantly toward the canopy center. External leaves received as much as 90 % of the average 2100 μmol m^{-2} s^{-1} of incident light, whereas internal leaves received only 1.6 % (Table 1). Similar data were reported elsewhere (Smart and Robinson, 1991). Under the last condition net CO_2 fixation is unlikely, since PPFD is below the compensation point, and CO_2 fixed by photosynthesis was less than that lost by respiration (Mullins *et al.,* 1992; Nobel and Long, 1988). A large proportion of interior vs. exterior leaves may be costly with respect to vine carbohydrate budget due to translocation of photoassimilates from light-adapted to dark-adapted shoots (Venden Heuvel *et al*., 2002).

The data also showed that Pn decreased drastically toward the canopy center; *i.e.*, external leaves yielded an activity of 19 μmol CO_2 m^{-2} s^{-1}, while internal leaves reached only 0.9 μmol CO_2 m^{-2} s^{-1} (Table 1). Thus, photosynthetic rate in internal foliage was not enough to account for the carbohydrates lost by respiration (Mullins *et al.,* 1992). Leaf chlorophyll content was significantly lower in internal leaves with only 1.2 mg mL^{-1}, compared to external and middle leaves which presented 1.9 and 1.7 mg mL^{-1}, respectively (Hunter and Visser, 1988; Peláez *et al.,* 1994).

The leaf protein content, however, was independent of light exposure since no differences were found among leaf positions. On the other hand, rubisco specific activity was dependent upon leaf exposure to sunlight, with values of 1.07, 0.65 and 0.25 μmol min^{-1} mg^{-1} for external, middle and internal leaves, respectively. Since protein content did not change, these results imply that photosynthetic rates were dependent upon enzyme activity triggered by increasing light exposure, although other factors might also influence the rubisco activity. Bertamini and Nedunchezhian (2001) reported that chlorophyll content in shaded leaves of grapevines cv. 'Moscato giallo' was 38 to 71 % higher than in light exposed leaves; these authors also found a significantly low rubisco activity in shaded leaves, with values 29 to 46 % lower than in exposed leaves. By then, it was evident that a solution to avoid the shading problem was required, as well as other canopy management strategies.

Comparison of trellis systems

Light incidence. No significant difference was found in the amount of PPFD reaching basal leaves of 'Perlette' vines trained on Divided and Undivided T-trellis, which yielded 771 and 885 μmol m^{-2} s^{-1}, respectively (Table 2). However, treatments including a more expanded canopy such as CIAD, Pergola and Lyre highly increased PPFD with values of 1900, 2076 and 2192 μmol m^{-2} s^{-1}, respectively. The highest light interception reached by Pergola, CIAD and Lyre is a direct result of opening the canopy in two leaf curtains. They increased light penetration simply by separating the foliage, thus allowing sunlight exposure to an increased leaf area and higher photosynthetic rates of exposed leaves. Similar findings have been reported in 'Perlette' vines trained on a Factory Roof System, very similar to a Pergola (Lavee, 1994). 'Riesling' vines trained on divided canopies also had fewer leaf contacts and shaded leaves compared to those with undivided canopies (Reynolds *et al.,* 1996).

Pn and SR. At véraison, no significant differences in photosynthetic rates were found between open or Divided TS (Table 2). Pn ranged from 12.7 to 10.5 μmol CO_2 m^{-2} s^{-1}, rates significantly higher than the 5.1 μmol CO_2 m^{-2} s^{-1} registered in the Undivided TS (UTT). Divided canopies imply an increased leaf area exposed to sunlight (Shaulis and May, 1971; May and Scholefield, 1973; Scholefield *et al.,* 1977).

Table 1. Canopy microclimate and physiological factors in 'Perlette' grapevines trained on a T-trellis with a dense canopy, at Sonora, México.

Leaf layer	PPFD (μmol m^{-2} s^{-1})	Net photosynthesis (μmol CO_2 m^{-2} s^{-1})	Chlorophyll (mg mL^{-1})	Total leaf protein (mg ml^{-1})	Rubisco specific activity (μmol min^{-1} mg^{-1})
External	1922 a	19.0 a	1.9 a	1.7 ns	1.07 a
Middle	53 b	1.7 b	1.7 a	1.7	0.65 ab
Internal	34 b	1.0 b	1.2 b	1.4	0.25 b

* Means (n = 5) within columns followed by different letters are statistically significant (Tukey, 0.05). PPFD= Photosynthetic photon flux density.

Table 2. Overall effect of trellis system on photosynthetic active radiation, net photosynthesis and stomatal resistance of 'Perlette' grapevines in five training systems measured at véraison and following harvest, at Sonora, México.

Trellis system	PPFD (μmol m^{-2} s^{-1})	Net photosynthesis (μmol CO_2 m^{-2} s^{-1})		Stomatal resistance (s cm^{-1})	
		Véraison	After harvest	Véraison	After harvest
Pergola	2076 a	12.7 a	9.0 a	2.6 b	3.5 b
CIAD	1900 a	11.0 a	8.1 a	2.8 b	2.3 b
Lyre	2192 a	12.5 a	9.0 a	3.4 ab	2.5 b
Divided T-trellis	885 b	10.5 a	5.1 a	3.9 a	2.9 b
Undivided T-trellis	771 b	5.1 b	3.7 b	4.2 a	6.8 a

*Means within columns followed by the same letter are statistically the same (Tukey, 0.05).
Each value represents the mean of four compound replicates of 16 samples each. ** PPFD= Photosynthetic photon flux density.

In measurements obtained 5 d after harvest, a decreased response due to the water stress imposed to the vines during harvest was observed, since irrigation is stopped a week before harvest to favor an increase in TSS. An advanced leaf senescence and a decrease in organic amino acids content have been mentioned under such condition (Hunter and Visser, 1988).

Pn values of Pergola, Lyre, CIAD and Divided reached 9.0, 9.0, 8.1 and 5.1 μmol CO_2 m^{-2} s^{-1}, respectively. Pn in UTT went down to 3.7 μmol CO_2 m^{-2} s^{-1}, and it was significantly lower than the above treatments; such drastic decrease is explained by the fact that on this Undivided T-trellis design, the lower arm is only 60 cm from center (Figure 1). Although shoot positioning wires were used on the upper arm to keep shoots in place, in this condition leaves became shaded by the developing laterals during the 20 d interval between readings, because in this region vegetative growth may continue up to the early Fall. In addition, at harvest, labor tends to loose the original shoot arrangement. Therefore, although a marked decrease in Pn was observed in the Divided TT, it was still higher than in the undivided canopies. Hunter *et al*. (1994) pointed out the importance of foliage remaining active after harvest in order to extend the carbohydrate and nitrogen compounds storage period through active photosynthesis and stable nitrate reductase activity.

As mentioned before, the CIAD system was designed to increase light use efficiency in vineyards with an E-W row orientation. In this system the upper and lower leaf curtains are South-exposed to maximize sunlight harvest. However, some adjustments should be added to avoid or diminish the tendency to develop vigorous shoots along the curvature of the lower curtain, since these new shoots shade other areas. Although other researchers have reported diminishing Pn responses on shoots trained downwards, mostly because these shoots reduce water translocation toward the apical parts, and because of reductions in rubisco activity and concentration (Schubert *et al.,* 1995), our results showed a dramatic increase in Pn by splitting the vine foliage for a higher sunlight exposure, regardless of leaf curtain direction.

Stomatal resistance was inversely proportional to Pn. Regardless of sampling period, the open-canopy systems always had lower resistance values as compared to Undivided canopy. Kriedemann (1977) reported maximum photosynthetic rates at stomatal resistance values between 2 and 3.5 s cm^{-1}. In our study, the open canopy systems had values in this range. Since leaf chlorophyll content did not differ among trellis systems (data not shown), it is likely that the explanation must be related to different light exposure and rubisco activity.

Total soluble solids. On April 27, the Undivided canopy had only 12.1 °Brix (Figure 2). Considering that the minimum sugar content required for export of 'Perlette' is set at 15.5 °Brix, this system obviously requires more time before harvest could be started. In such period prices commonly fall down dramatically. Because of the standarized crop load of 15 clusters per vine, open canopies reported a gain in maturity as a result of increased light exposure and photosynthetic rate. At the same date, CIAD had reached 15.7 °Brix and Pergola had 15.3 °Brix. On the second sampling date, 2 d later, ripening in the Undivided controls had advanced only to 13.1 °Brix, while CIAD, Lyre and Pergola reported -in the same order- 16.3, 15.9 and 15.5 °Brix; that is, all of them were ready to be picked.

Consequently, dividing the canopy of a T-trellis (as in Divided) had an effect on berry ripening, since the accumulated sugars accounted for 15.2 °Brix, very close to the commercial harvest index and well in advance of the 13.1 °Brix recorded for UTT. These results imply that, with such an advance in maturity, harvest can be accomplished at an earlier date; therefore, access to the top prices of early season is more likely. The low sugar content attained in Undivided can be attributed to a reduced foliage exposure to sunlight, which in turn caused a reduced photosynthetic rate and a delay in sugar translocation to berries (Volschenk and Hunter, 2001b; Gladstones, 1992; Smart and Smith, 1988). In this particular vineyard harvest did not start but until May 6, so that dividing and managing canopies can advance harvest by 7 to 9 d.

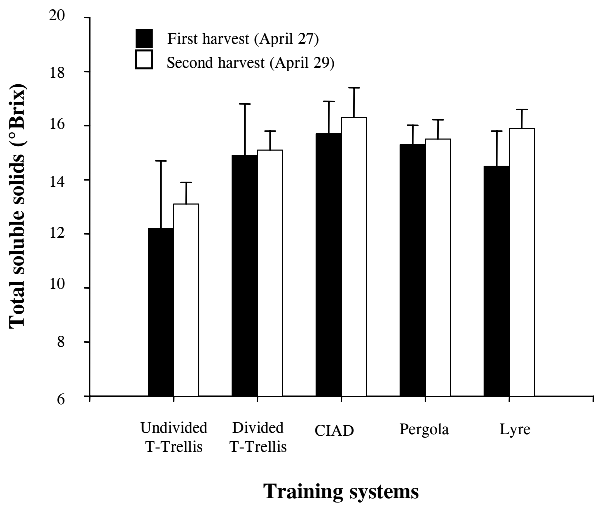

Figure 2. Berry total soluble solids of 'Perlette' vines managed with five trellis systems at Sonora, México. Undivided T- trellis reached commercial maturity (15.5 °Brix) by May 6th. Vertical lines represent the standard deviations (n = 10).

Flower bud differentiation. Flower differentiation and bud necrosis development as a function of the TS were not statistically different. However, there was a tendency for the better exposed canopies to have a higher differentiation and less necrotic buds, both in primary and secondary buds. Such findings are in agreement with previous reports (Pérez and Kliewer, 1990).

CONCLUSIONS

Because of lack of management and canopy structure the Undivided T-Trellis system limits an efficient sunlight distribution within the canopy, thus decreasing the photosynthetic activity. Dividing canopies is a feasible alternative to advance maturity and harvest, mostly due to an increase in berry sugar accumulation, as a result of increasing light harvest and leaf photosynthetic activity. Such physiological responses allow earlier harvest by 7 to 9 d and better opportunities of accessing the highest prices of the early season export market.

BIBLIOGRAPHY

Archer E, H C Strauss (1989) The effect of plant spacing on the water status of soil and grapevines. S. Afr. J. Enol. Vitic. 10:49-58.

Arnon D (1949) Copper enzymes in isolated chloroplasts. Polyphenol oxidase in *Beta vulgaris*. Plant Physiol. 24:1-15.

Baeza P, C Ruiz, E Cuevas, V Sotés, J R Lissarrague (2005) Eco-physiological and agronomic response of Tempranillo grapevines to tour training systems. Am. J. Enol. Vitic. 56:129-138.

Bertamini M, N Nedunchezhian (2001) Decline of photosynthetic pigments, ribulosa-1,5-bisphosphate carboxylase and soluble proteins contents, nitrate reductase and photosynthetic activities, and changes in thylakoid membrane protein pattern in canopy shade grapevine (*Vitis vinifera* L. cv. 'Moscato giallo') leaves. Photosynthetica 39 :529-537.

Carbonneau A P, P Casteran (1987) Interactions TS x soil x rootstock with regard to vine ecophysiology, vigor, yield and red wine quality in the Bordeaux area. Acta Hort. 206:119-140.

Gladstones J (1992) Viticulture and Environment. Winetitles, Adelaide. Australia. 310 p.

Hunter J J, R Skrivan, P Ruffner (1994) Diurnal and seasonal physiological changes in leaves of *Vitis vinifera* L. CO2 assimilation rates, sugar levels and sucrolytic enzyme activity. *Vitis* 33:189-195.

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

Kriedemann P E (1977) Vine leaf photosynthesis. *In*: Proc. Int. Symp. on the Quality of the Vintage. 14-21 February. Capetown, South Africa. pp:67-88.

Lavee S (1994) Training-trellis systems and canopy management of table grapes in Israel. International Symposium of Table Grape Production. Anaheim, California, USA. Amer. Soc. Enol. Vitic. pp:179-188.

Lilley R McC, D A Walker (1974) An improved spectrophotometric assay for ribulosebiphosphate carboxylase. Biochem. Biophys. Acta 358:226-229.

Lowry O H, N J Rosebrough, A L Farr, R J Randall (1951) Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193:265-275.

May P S, P B Scholefield (1973) Effect of various combinations of trellis pruning and rootstock on vigorous 'Sultana' vines. Vitis 12:192- 209.

Mullins M G, A Bouquet, L E Williams (1992) Biology of the Grapevine. Cambridge University Press. Great Britain. 239 p.

Nobel P S, S P Long (1988) Estructura del dosel e intercepción de la luz. *In*: Técnicas en Fotosíntesis y Bioproductividad. J Coombs, D O Hall, S P Long, J M Scurlock (eds). Ed. Futura S. A. México. pp:34-41.

Peláez H, J Yuste, J A Rubio, J R Lissarrague (1994) Balance de radiación fotosintéticamente activa (PAR) en sistemas de conducción del viñedo mediante sensores lineales. 7 Journees d'Etude des Systemes de Conduite de la Vigne. G.E.S.CO. France. pp:236-241.

Percival D C, K H Fisher, J S Sullivan (1994) Use of fruit zone leaf removal with *Vitis vinifera L.* cv. Riesling grapevines. I. Effect on canopy structure, microclimate, bud survival, shoot density, and vine vigor. Am. J. Enol. Vitic. 45:123-132.

Pérez J, W M Kliewer (1990) Effect of shading on bud necrosis and bud fruitfulness of 'Thompson Seedless' grapevines. Am. J. Enol. Vitic. 41:168-175.

Reynolds A G, D A Wardle, A P Naylor (1996) Impact of training system, vine spacing and basal leaf removal on 'Riesling'. I. Vine performance, berry composition, canopy microclimate and vineyard labor requirements. Am. J. Enol. Vitic. 47:63-75.

SAS Institute (1987) Statistical Analysis System. Version 6.03. Cary, NC. 27512-8000, Copyright ©.

Scholefield P B, P May, T F Neales (1977) Harvest-pruning and trellising of Sultana vines. I. Effects on yield and vegetative growth. Sci. Hortic. 7:115-122.

Schubert A, M Restagno, V Novello, E Peterlunger (1995) Effects of shoot orientation on growth, net photosynthesis, and hydraulic conductivity of *Vitis vinifera* L. cv. Cortese. Am. J. Enol. Vitic. 46:324-328.

Shaulis N J, P May (1971) Response of Sultana vines to training on divided canopy and to shoot crowding. Am. J. Enol. Vitic. 22:215-222.

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, M Robinson (1991) Sunlight into Wine. A Handbook for Winegrape Management. Hyde Press, Adelaide, Australia. 88 p.

Smart R E, M S Smith (1988) Canopy management: Identifying the problems and practical solutions. *In*: Proc. Second International Symposium for Cool Climate Viticulture and Oenology. Auckland, New Zealand. R E Smart, R J Thornton, S B Rodriguez, J E Young (eds). New Zealand Soc.Vitic. Oenol. pp:109-115.

Vanden-Heuvel J E, E D Leonardos, J T A Proctor, K H Fisher, J A Sullivan (2002) Translocation and partitioning patterns of ^{14}C photoassimilate from light- and shaded-adapted shoots in greenhouse-grown 'Chardonnay' grapevines (*Vitis vinifera* L.). J. Amer. Soc. Hort. Soc. 127:912-918.

Vanden-Heuvel J E, J T A Proctor, J A Sullivan , K H Fisher (2004) Influence of training/trellising system and rootstock selection on productivity and fruit composition of 'Chardonnay' and 'Cabernet franc' grapevines in Ontario, Canada. Am. J. Enol. Vitic. pp:253-264.

Volschenk C G, J J Hunter (2001a) Effect of trellis conversion on the performance of 'Chenin blanc/99 Richter' grapevines. S. Afr. Enol. Vitic. pp:31-35.

Volschenk C G, J J Hunter (2001b) Effect of seasonal canopy management on the performance of 'Chenin blanc/99 Richter' grapevines. S. Afr. Enol. Vitic. pp:36-40.

Winkler A J, J A Cook, W M Kliewer, L A Lider (1974) General Viticulture. University of California Press. London, England. pp:29-55.