SHOOT HETEROGENEITY EFFECTS IN A SHIRAZ/R99 VINEYARD

H Cloete[1], E Archer[2], V Novello[3] & JJ Hunter[4]

[1] Department of Viticulture and Oenology, Private Bag X1, Matieland, University of Stellenbosch, 7602 Stellenbosch, South Africa. hcloete@sun.ac.za
[2] Lusan Premium Wines, PO Box 104, 7599 Stellenbosch. earcher@distell.co.za
[3] Dipartimento di Colture Arboree, I 10095 Grugliasco, Italy. vittorino.novello@unito.it
[4] ARC Infruitec-Nietvoorbij, Private Bag X5026, 7599 Stellenbosch, South Africa. kobush@arc.agric.za

Acknowledgements: The authors wish to thank the personnel of the viticulture and grapevine physiology laboratory of the ARC Infruitec-Nietvoorbij, Stellenbosch, for technical assistance. We thank Dr. Martin Kidd for his assistance in analysing the data.

Key words: shoot heterogeneity; physiology; vegetative growth; reproductive growth; grape composition

Abstract
The effect of shoot heterogeneity on vegetative and reproductive growth parameters, vine physiology and grape composition was investigated in a Shiraz/Richter 99 vineyard. Comparisons between underdeveloped (typically shorter and less ripened at véraison) and normally developed shoots in both shaded and well-exposed canopies were made. Compared to underdeveloped shoots, normal shoots had a larger total leaf area, due to the higher occurrence of secondary shoots as well as larger leaves on primary and secondary shoots. Since the physiological activity of the leaves from normal shoots was higher than that from underdeveloped shoots, higher levels of total carbohydrates were produced and stored in the former. Starch was more evenly distributed over the whole shoot length in the longer and thicker normally developed shoots compared to the underdeveloped shoots. The larger clusters of the normally developed shoots were evidence of their more favourable total leaf area per gram berry mass. Berries from the normally developed shoots were smaller at five weeks after véraison than those from underdeveloped shoots, displaying a higher skin to pulp ratio and therefore higher anthocyanin and total phenolic extraction potential for winemaking. The peculiar absence of large differences in grape composition between normally and underdeveloped shoots indicated that assimilates needed for berry ripening of the latter originated in organs other than the leaves [e.g. from adjacent normal shoots and the rest of the permanent structure of the vine (cordon, trunk, roots)]. The larger differences in berry size that occurred between shoot types in the shaded compared to the well-exposed canopies may be evidence for this. The photosynthetic activity of shoots was lower in shaded than in exposed canopies. The total carbohydrate production of the normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of their own clusters and of the shoot itself as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This was illustrated by the lower levels of starch that accumulated in the normal shoots from shaded compared to that of exposed canopies. Vine shoot heterogeneity clearly led to visible and physiological imbalances that would impact negatively on grape and wine quality as well as production costs and should therefore be avoided on any terroir.

Résumé
Nous avons fait des recherches sur l’effet de l’hétérogénéité des bourgeons sur les paramètres de la croissance végétative et reproductive, la physiologie de la vigne et la composition du raisin dans une parcelle de Shiraz/Richter 99. Des bourgeons sous-développés (typiquement plus courts et moins mûrs à la véraison) ont été comparés avec des bourgeons normaux dans un couvert ombragé ou exposé à la lumière. Comparés aux bourgeons sous-développés, les normaux ont eu une plus grande surface feullière totale à cause du plus grand nombre de entre-cœurs aussi bien que des feuilles plus grandes portées par les bourgeons principaux et entre-cœurs. Vu que l’activité physiologique des feuilles des

bourgeons normaux était supérieure à celle des bourgeons sous-développés, une quantité d'hydrates de carbone supérieure a été produite et mise en réserve par les premiers. L'amidon se distribuait plus régulièrement le long des sarments normaux, plus épais et longs en comparaison avec les sarments sous-développés. Les grappes plus grosses des sarments normaux ont montré que la surface feuillère totale par gramme de raisin était plus favorable. Cinq semaines après la véraison les baies des sarments normaux étaient plus petites que celles des sarments sous-développés, montrant un rapport entre peau et pulpe plus grand et un plus grand potentiel d'extraction des anthocyanes et de phénols pour l'élaboration du vin. L'étrange absence d'une grosse différence de composition du raisin entre les deux types de bourgeons a montré que les assimilés nécessaires pour mûrir les raisins des bourgeons sous-développés dérivent d'autres organes que leurs feuilles [p.ex. des bourgeons normaux adjacents et du reste de la structure permanente de la vigne (le cordon, le tronc, les racines)]. Cette hypothèse est supportée par la différence de dimensions de la baie entre les deux types de bourgeons qui était supérieure à l'ombre par rapport au feuillage exposé à la lumière. L'activité photosynthétique était inférieure à l'ombre que dans le feuillage exposé. La production totale d'hydrates de carbone des bourgeons normaux ombragés apparaissait insuffisante aux besoins de maturation de leurs propres grappes et du bourgeon même aussi bien que pour la maturation du sarment et des grappes des bourgeons sous-développés. Cela était démontré par le niveau d'amidon accumulé dans les sarments normaux, qui était inférieur à l'ombre par rapport aux sarments dans le feuillage exposé. Puisque l'hétérogénéité des bourgeons de la vigne a porté à un déséquilibre physiologique qui peut avoir une influence négative sur la qualité du raisin et du vin aussi bien que sur le coût de production, il faut l'éviter sur tout terroir.

Introduction

The eventual objective of canopy management is to obtain a photosynthetic efficient, homogeneous canopy with uniformly and well distributed shoots of similar vigour, producing healthy, high quality grapes of similar bunch and berry size and with a uniform level of ripeness (Hunter & Archer, 2001). Canopy management practices during the growth season are therefore aimed at changing the magnitude, position, and/or orientation of canopy components (shoots, leaves and clusters), improving the microclimate (light, humidity, air flow, temperature) and balancing the vegetative (including the roots) and reproductive development and functioning (Hunter & Archer, 2001). Research done on the effect of canopy management showed that, compared to untreated, treated vines had a more uniform interception of sunlight throughout the whole canopy, which led to a more homogeneous ripening of all the clusters (Volschenk & Hunter, 2001). Apart from the effects of irregular sunlight exposure, asynchronous ripening may be enhanced by the varying leaf area:fruit ratio of individual shoots (Jackson & Lombard, 1993). Short shoots may have insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975). Koblet (1977) found that short shoots imported more assimilate from adjacent shoots than did normally developed shoots. It can be assumed that the presence of short shoots may lead to a decrease in the grape quality of other, stronger shoots on the same vine. Different shoot lengths in a vine would thus impair the overall quality, as well as increasing the variation in composition of individual clusters.

The purpose of this study was to investigate the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard on vegetative and reproductive growth parameters, vine physiology and grape composition.

Materials and Methods

Experimental vineyard

A seven-year-old *Vitis vinifera* L. cv. Shiraz, grafted onto Richter 99, vineyard was used for this study. The vineyard is situated at the experiment farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij, Stellenbosch, in the Western Cape (Mediterranean climate). The vines are spaced 2.75 m × 1.5 m on a Glenrosa soil with a western aspect (26^{o} slope) and trained onto a 7-wire lengthened Perold trellising system (VSP) with movable canopy wires. Rows were orientated in a North-South direction.

Micro sprinkler irrigation was applied at pea size berry and at véraison. Pest and disease control was applied during the growth season according to the standard program of the ARC. Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning were applied in order to create well-exposed canopies. Selection of underdeveloped shoots was based on length and comparative lack of lignification at véraison.

Vegetative measurements
Primary and secondary shoot length (cm) and mass (g), degree of lignification of primary shoots, number of primary and secondary leaves per shoot, leaf area (cm^2) and leaf mass (g) of primary and secondary leaves, as well as the starch content (mg/g dry mass) of the basal, middle and apical parts of the main shoots were measured. The degree of lignification of the shoots was scored from one to five – five being completely lignified and one being still completely green. The leaf area was measured with a LICOR LI-3100 area meter (Lincoln, Nebraska, USA). The starch content of shoots/shoot parts was analysed by hydrolysing the starch and determining the glucose formed by reading the absorbancies at 420 nm (Hunter *et al.*, 1995). Measurements were taken at one, three, four and five weeks after véraison.

Physiological parameters
The photosynthesis and transpiration measurements were determined as described by Hunter & Visser (1988). The different chlorophyll concentrations in fresh leaves were measured as described by Hunter & Visser (1989). The photosynthesis and transpiration measurements were taken at two, three and five weeks after véraison. Chlorophyll concentration was determined five weeks after véraison.

Reproductive measurements
Cluster size (length, shoulder width and volume), berry size (mass and volume), number of berries per cluster and the skin:pulp (including seeds) ratio were determined. Volume measurements were done by water displacement in a measuring cylinder. Berry mass and volume were measured by determining the average of 100 randomly selected berries. The skin:pulp ratio was obtained by dividing skin fresh mass (average of 100 berries) by the mass per berry after the skin fresh mass was subtracted. The mass of the seeds was included in the calculation. Measurements were taken at one, three, four and five weeks after véraison.

Berry composition measurements
Sugars (glucose and sucrose) and organic acids (malic and tartaric acid) were extracted and analysed by gas liquid chromatography (GLC) after silylation, as described by Hunter & Ruffner (2001). Soluble solids (^{o}B), pH and total titratable acidity were determined using standard laboratory methods. The anthocyanin and phenol content of the berry skins were measured using the method described by Hunter *et al*. (1991). All measurements were carried out at one, three, four and five weeks after véraison, except for the glucose and sucrose measurements that were only done five weeks after véraison.

Results and Discussion
Vegetative measurements
The longer primary shoots of the normally developed shoots matured earlier in the season than the shorter, underdeveloped shoots (Fig. 1). Since reserves were more uniformly distributed in the normal shoots and the total starch content over the whole shoot was higher, it appeared as if reserve accumulation of underdeveloped shoots was impaired by grape ripening (Fig. 2). Primary leaves of normal shoots were larger and thicker than those of underdeveloped shoots, while no difference in the number of primary leaves per shoot was found (data not shown). More and longer secondary shoots occurred on normal shoots, whereas the secondary shoot leaves were found to be larger and thicker (data not shown). The normally developed shoots seemed to have a higher potential for producing a higher yield with better quality than the underdeveloped shoots. The former had a more desirable leaf area composition (almost equal contribution of primary and secondary leaves to the total leaf area of the shoot) in addition to the larger total leaf area per shoot (Fig. 3).

Physiological parameters
Up to the third week after véraison, it seemed as if the total effective leaf area per shoot rather than the physiological functioning per unit leaf area should be considered more important (Fig. 4). Differences in physiological activity between leaves from normally and underdeveloped shoots only became apparent in the third week after véraison. From then on, normal shoots displayed significantly higher rates of photosynthesis and transpiration than underdeveloped shoots (Figs. 4 & 5). Likely reasons are the lower source:sink ratio found on underdeveloped shoots as well as a possible physical resistance against gas transfer in the leaves on those shoots. Although not constantly significant, normal shoots further received higher PPFD levels, while higher stomatal conductance and lower internal CO_2 levels of the leaves were measured compared to underdeveloped shoots (data not shown). A higher WUE ratio was also calculated for the normal shoots (data not shown). Photosynthetic activity and the chlorophyll concentration of the leaves were not positively correlated five weeks after véraison (Figs. 4 & 6). Equal amounts of chlorophyll.cm^{-2} and a non-significant difference in the assimilation number were calculated for the leaves from normally and underdeveloped shoots (Figs. 6 & 7). It was thus rather the effective area per leaf or per shoot than the chlorophyll concentration or activity that was responsible for any differences in the photosynthetic productivity of the leaves from normally and underdeveloped shoots. From the physiological data it was expected that the size and quality of the yield from normally developed shoots would be higher than that from underdeveloped shoots.

Reproductive measurements
Clusters on normal shoots were significantly larger than those on underdeveloped shoots (data not shown). The crop load of underdeveloped shoots could have been excessive in relation to their fruit ripening potential. This was probably compensated for by a decrease in the cluster size. Significantly more berries were found in the clusters on normal shoots compared to those on underdeveloped shoots (data not shown). The larger leaf area of normal shoots (Fig. 3) as well as the stronger sink strength of their larger clusters would have resulted in a larger carbohydrate flow to the clusters on these shoots. The better carbohydrate supply possibly increased berry set. The growth and ripening curves of the berries from underdeveloped shoots seemed delayed because of overcropping. Together with the larger berries and lower skin:pulp ratio found for underdeveloped shoots, it was expected that berries from normal shoots would be better ripened with more intense flavour and colour.

Berry composition measurements
No statistically significant differences in the sugar concentration (^oB), glucose or sucrose levels, total acidity or pH, malic or tartaric acid, phenol content or the colour intensity and density measurements were found between the berries from normally and underdeveloped shoots at five weeks after véraison (Table 1). It was assumed that the assimilates needed for berry ripening in the latter shoots originated in other organs than leaves, such as adjacent shoots and the rest of the permanent structure of the vine (cordon, trunk, roots). The larger differences in berry size found between shoot types in the shaded compared to the well-exposed canopies may be evidence of this. As normal shoots had thicker skins and a higher skin:pulp ratio, extractability potential of these compounds during winemaking would be higher for these shoots. Since the photosynthetic activity of shoots was lower in shaded than in exposed canopies, the total carbohydrate production of normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of the shoot itself, their own clusters as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This was illustrated by the lower levels of starch that accumulated in the normal shoots from shaded compared to that of exposed canopies (Fig. 2). Underdeveloped shoots probably decreased the grape quality of adjacent normal shoots and affected reserve accumulation and shoot ripening negatively.

Conclusions
Even though large differences in the total effective leaf area, crop load and physiological activity per unit leaf area were found between normally and underdeveloped shoots, no statistically significant differences in the berry composition were found at five weeks after véraison. As it was found that lignification of underdeveloped shoots occurred later in the season than that of normally developed shoots, competition between shoot and berry ripening most probably occurred. Lower levels of starch

formation and accumulation also occurred in the underdeveloped shoots, while the reserves were more evenly distributed over the whole length of normal shoots. In order to maintain longevity of the vine (and also the individual spurs), grape ripening should occur without any detrimental effect on other processes in the vine, such as reserve accumulation. This did not happen in the case of the underdeveloped shoots, as reserve accumulation seemed to be impaired by grape ripening processes; the latter appeared to have been favoured to the detriment of vegetative growth and cluster size. Except for the competition between berry ripening and reserve storage, the assimilates used by the underdeveloped shoots for cluster ripening may have originated in other organs than the leaves, such as adjacent shoots and the rest of the permanent structure of the vine (cordons, trunk or roots). The larger differences in berry size found between shoot types in the shaded compared to the well-exposed canopies could be evidence for this. Since the photosynthetic activity of shoots was lower in shaded than in exposed canopies, the total carbohydrate production of the normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of the shoot itself, their own clusters, as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This was illustrated by the lower levels of starch that accumulated in the normal shoots of shaded compared to those of exposed canopies. The study clearly showed that shoot heterogeneity results in uneven vegetative and reproductive growth, physiological activity as well as reserve accumulation in the vine. Underdeveloped shoots seemed to act as parasites in the canopies by importing assimilates from adjacent normally developed shoots and the permanent vine structure in order to ripen their clusters. Berry and shoot ripening of normal shoots as well as starch accumulation were thus detrimentally affected. Shoot heterogeneity should therefore be avoided in commercial vineyards and at any given terroir.

Literature cited

Archer, E., 2001. Die verband tussen stokvormingspraktyke en druifgehalte. Wynland Augustus 2001, 111-112.

Hunter, J.J. & Archer, E., 2001. Short-term cultivation strategies to improve grape quality. Viticulture and Enology Latin-American Congress. 12-16 Nov., Montevideo, Uruguay. VIII (on cd).

Hunter, J.J., De Villiers, O.T. & Watts, J.E., 1991. The effect of partial defoliation on quality characteristics of *Vitis vinifera* L. cv. Cabernet Sauvignon grapes II. Skin colour, skin sugar and wine quality. Am.J.Enol.Vitic. 42, 13-18.

Hunter, J.J. & Ruffner, H.P., 2001. Assimilate transport in grapevines – effect of phloem disruption. Aust. J. of Grape and Wine Research 7, 118-126.

Hunter, J.J., Ruffner, H.P. & Volschenk, C.G., 1995. Starch concentrations in grapevine leaves, berries and roots and the effect of canopy management. S.Afr.J.Enol.Vitic., 16(2), 35-40.

Hunter, J.J. & Visser, J.H., 1988. The effect of partial defoliation, leaf position and developmental stage of the vine on the photosynthetic activity of *Vitis vinifera* L. cv. Cabernet Sauvignon. S.Afr.J.Enol.Vitic. 9:2, 9-15.

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

Jackson, D.I. & Lombard, P.B., 1993. Environmental and management practices affecting grape composition and wine quality – a review. Am.J.Enol.Vitic. 44, 409-430.

Koblet, W., 1977. Translocation of photosynthate in grape vines. Proc. Int. Symp. on the Quality of the Vintage. 14-21 Feb., Cape Town, 45-51.

Peterson, J.R. & Smart, R.E., 1975. Foliage removal effects on "Shiraz" grapevines. Am.J.Enol.Vitic. 26, 119-124.

Volschenk, C.G. & Hunter, J.J., 2001. Effect of seasonal canopy management on the performance of Chenin blanc/99 Richter grapevines. S.Afr.J.Enol.Vitic. 22, 36-40.

Tables and Figures

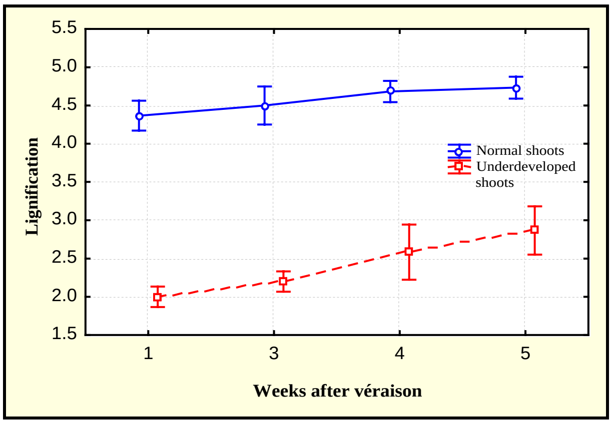


Fig. 1 Degree of lignification of normally and underdeveloped primary shoots at different ripening stage after véraison. Different ripening stages indicate the numbe of weeks after véraison. Error bars indicate 95 % confidenc intervals.

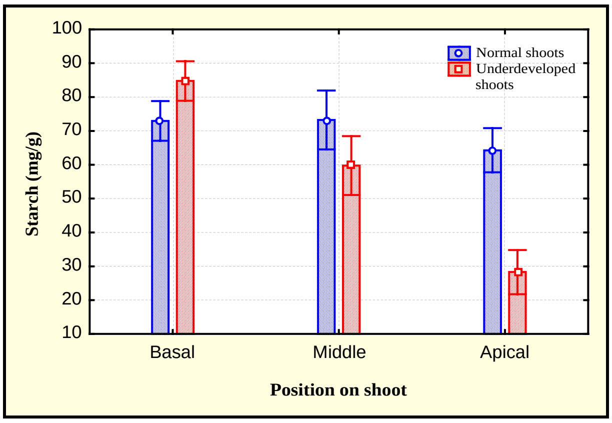


Fig. 2 Average starch concentration in different positions on normally and underdeveloped shoots. Error bars indicate 95 % confidence intervals.

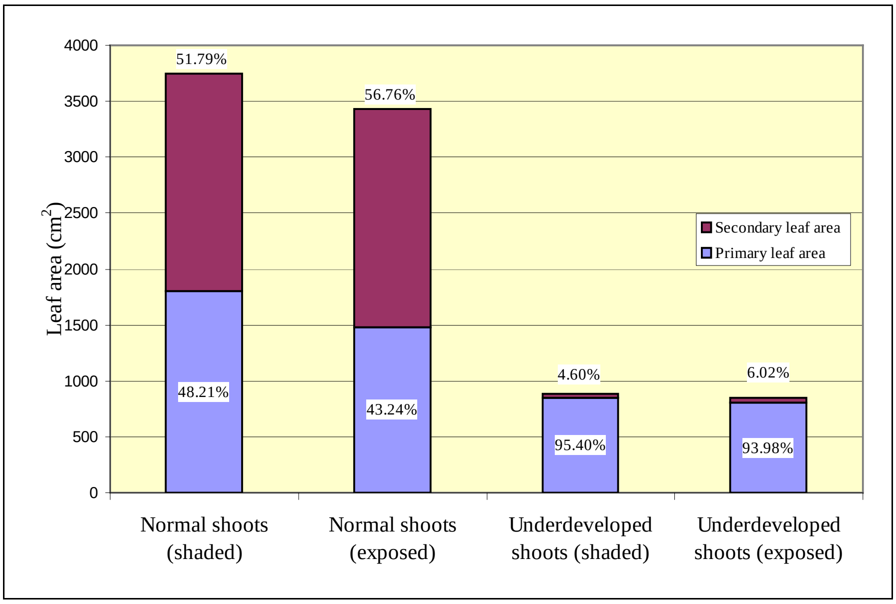
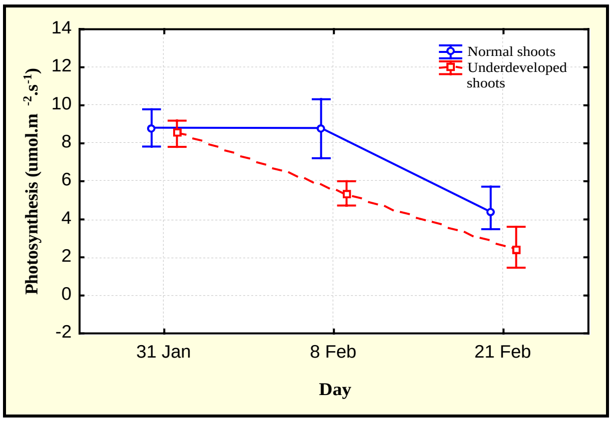


Fig. 3 Average contribution of the primary and secondary leaves to the total leaf area per shoot.



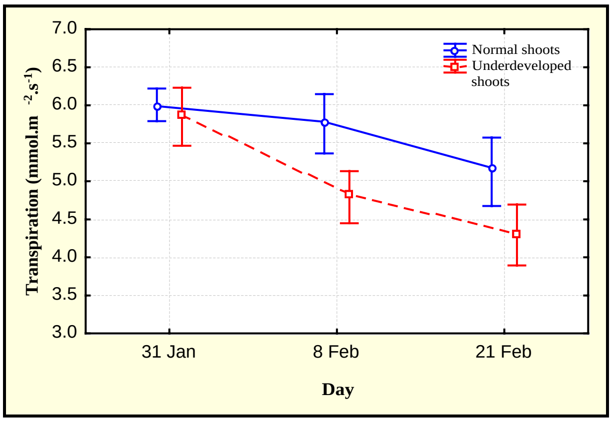
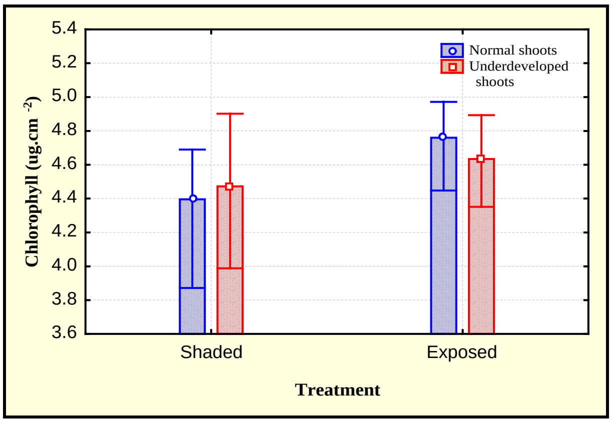


Fig. 4 Photosynthetic rates of basal leaves from normally and underdeveloped shoots measured in the second, third and fifth week after véraison. Error bars indicate 95 % confidence intervals.

Fig. 5 Transpiration rates of basal leaves from normally and underdeveloped shoots in the second, third and fifth week after véraison. Error bars indicate 95 % confidence intervals (bootstrap analysis).



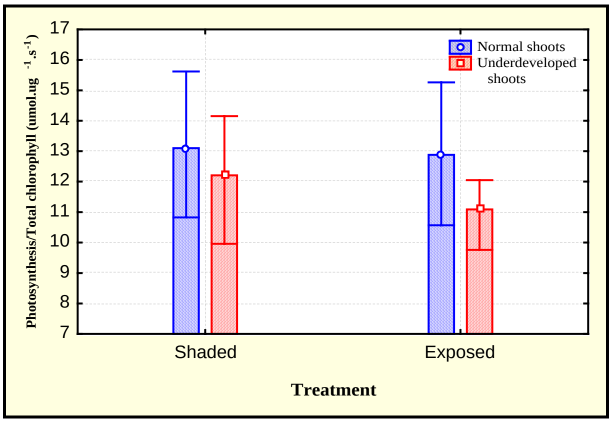
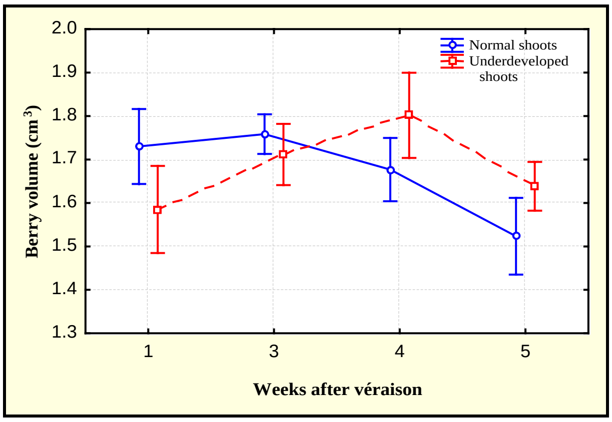


Fig. 6 Total chlorophyll.cm^{-2} of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison in **2003**. Error bars indicate 95 % confidence intervals (bootstrap analysis).

Fig. 7 Photosynthetic rates per ug of chlorophyll of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison in **2003**. Error bars indicate 95 % confidence intervals (bootstrap analysis).



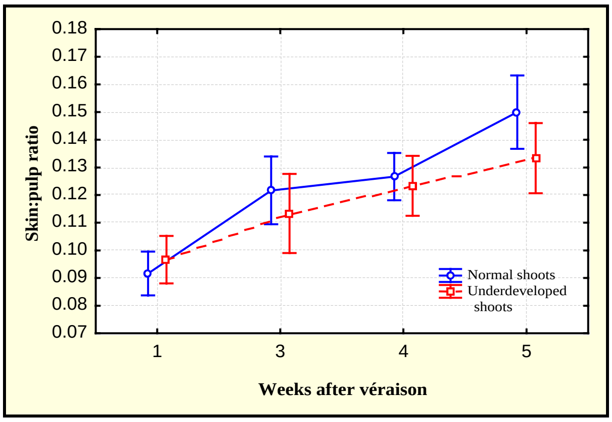


Fig. 8 Berry volume of normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95 % confidence intervals.

Fig. 9 Berry skin:pulp ratio of clusters from normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95 % confidence intervals.

Table 1: Grape composition of normal and underdeveloped shoots under shaded and exposed canopy conditions.

	NORMAL SHOOTS			UNDERDEVELOPED SHOOTS			COMMENTS
	SHADED	EXPOSED	*AVERAGE*	SHADED	EXPOSED	*AVERAGE*	
Degrees Balling	20.2	20.6	*20.4*	21.1	21.2	*21.2*	NS
Glucose (mg/g)	89.03	86.02	*87.53*	80.91	84.51	*82.71*	NS
Sucrose (mg/g)	3.20	3.62	*3.41*	3.35	3.65	*3.50*	NS
pH	3.36	3.34	*3.35*	3.32	3.30	*3.31*	Underdeveloped shoots had lower pH
Titratable acid (g/L)	7.1	8.5	*7.8*	8.0	8.5	*8.3*	NS
Malic acid (mg/g)	2.21	2.29	*2.25*	2.41	2.66	*2.54*	Underdeveloped shoots had higher malic acid. Exposure favoured acid content.
Tartaric acid (mg/g)	7.07	8.41	*7.74*	7.04	7.83	*7.44*	Underdeveloped shoots had lower tartaric acid. Exposure favoured acid content.
Tartaric:malic acid ratio	3.20	3.71	*3.46*	2.95	3.02	*2.99*	Underdeveloped shoots had lower ratio. Exposure favoured acid ratio.
Colour intensity (520nm)	0.482	0.464	*0.473*	0.526	0.502	*0.514*	Underdeveloped shoots had higher intensity*
Colour density (520nm+420nm)	0.588	0.570	*0.579*	0.640	0.614	*0.627*	Underdeveloped shoots had higher density*
Phenolics (280nm)	0.496	0.519	*0.508*	0.540	0.554	*0.547*	Underdeveloped shoots had higher phenol concentration*

*Anthocyanin and phenolic contents of the skins were measured in absorbancy units.