Shoot Heterogeneity Effects on Shiraz/Richter 99 Grapevines. I. Vegetative Growth

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In this study the vegetative growth parameters of normally developed and underdeveloped shoots were compared in an attempt to quantify shoot heterogeneity in a Shiraz/Richter 99 vineyard. A field trial was performed in the Stellenbosch area, Western Cape, South Africa. Comparisons based on certain vegetative growth parameters were made between normally developed and underdeveloped shoots from both shaded and well-exposed canopies. The longer primary shoots of the normally developed shoots matured earlier in the season, with less apparent competition between shoot lignification and grape ripening. Reserves were more evenly distributed in these shoots. Total starch content over the whole shoot was found to be higher in the normally developed shoots, particularly when well exposed. More and longer secondary shoots occurred on the normally developed shoots than on the underdeveloped shoots. No difference was found in the number of primary leaves (leaves on primary shoots) between normally developed and underdeveloped shoots, although the leaf area was much larger in the case of the former. Normally developed shoots had more and larger secondary leaves (leaves on secondary shoots), while all the leaves that developed in the shaded canopies were found to be larger than those in the well-exposed canopies with a higher leaf area:mass ratio. The normally developed shoots seemed to have a greater potential for producing a higher yield, with better quality, than the underdeveloped shoots, as they have a more desirable leaf area composition in addition to a larger total leaf area per shoot.

Wine industries worldwide are committed to producing grape and wine quality suited to meet the challenges of ever-increasing national and international market competition and requirements (Hunter & Archer, 2001a). This often requires an increase in grape and wine quality without a decrease in the yield or longevity of the vine. Carbon allocation to the clusters should therefore be optimised without detrimentally affecting the growth and development of other parts of the vine (Hunter, 2000). A skilful and comprehensive management strategy, which includes long and short-term cultivation practices, is needed (Hunter & Archer, 2001a).

According to Carbonneau (1995), the yield, berry maturation and wine quality are dependent on the canopy structure, as it defines the microclimate and thus the photosynthetic activity and carbon output of the canopy. Well-positioned shoots, with leaves optimally exposed to maximise sunlight interception and photosynthesis, are essential to obtain a canopy in which each individual leaf contributes to the photosynthetic capacity of the vine (Archer, 1988; Hunter & Visser, 1990a; Kliewer & Dokoozlian, 2000).

The size and quality of a commercial harvest seem to depend on the proportion of assimilates partitioned towards cluster development rather than vegetative growth (Kriedemann, 1977). According to Hunter (1991) it is very important to maintain balances between vegetative growth, reproductive growth and reserve accumulation, as it was found that physiological processes and the ultimate wine quality decreased in the case of unbalanced vines.

In a balanced vineyard, shoot growth ceases around véraison (Archer, 2001). After elongation, shoot maturation (formation of periderm) and reserve accumulation commence, with a sharp increase towards post-harvest (Hunter *et al.*, 1995a). According to Coombe (1992), Eichhorn & Lorenz (1977) regard wood maturation to be completed after harvest. Thus, lignification and reserve accumulation occur mainly at the same time as grape ripening, which could result in competition between the vegetative and reproductive organs of the vine.

This balance is also important on a shoot-to-shoot basis. According to Archer (2001), the quality of each individual cluster is directly proportional to the physiological output of its shoot. Flavour and concentration are expected to be optimum when there is an optimum relationship between the active leaves and the clusters per individual shoot. It is accepted that 10 cm^2 to 12 cm^2 leaf area is generally required to ripen one gram of fruit (Hunter & Visser, 1990b, and references therein). Short shoots may therefore have insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975), which may lead to the increased import of assimilates from adjacent shoots and the rest

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of the permanent vine structure (Koblet, 1977), and a decrease in overall quality of the yield.

The purpose of this study is to quantify the differences between normally and underdeveloped shoots in a Shiraz/Richter 99 vineyard regarding certain vegetative growth parameters.

MATERIALS AND METHODS

Experimental vineyard

A seven-year-old *Vitis vinifera* L. cv. Shiraz, clone SH1A, grafted onto Richter 99 (*Vitis Berlandieri* x *Vitis rupestris*), clone RY2A, vineyard was used for this study. The vineyard is situated at the experimental farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij near 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° slope) and trained onto a 7-wire lengthened Perold trellising system with movable canopy wires (VSP). Rows were orientated in a North-South direction.

Micro-sprinkler irrigation was applied at pea berry size and at véraison. Pest and disease control was applied during the growth season according to the standard programme of the ARC.

Experimental design

The experiment was laid out as a completely randomised 2×4×2 factorial design. The three factors were: degree of canopy exposure (well-exposed and shaded canopies); ripening stages (one, three, four and five weeks after véraison); and level of shoot development (normally developed and underdeveloped shoots). There were three replications for each of the 16 treatment combinations.

Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning (at berry set and pea berry size on the basal half of the shoot) were applied in order to create well-exposed canopies. Selection of underdeveloped shoots was based on comparative length and lack of lignification at véraison.

Measurements

Vegetative parameters: A total of five normally developed shoots from 15 randomly selected vines were used for each treatment replicate at each ripening stage. Ten underdeveloped shoots under the same conditions were used, to ensure a large enough berry sample to perform all the necessary analyses. Measurements included the following: 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.

The degree of lignification of the shoots was visually scored from one to five – five being completely lignified and one still completely green. The leaf area was measured with a LICOR LI-3100 area meter (Lincoln, Nebraska, USA).

Shoots sampled at five weeks after véraison were divided into three parts, namely basal, middle and apical, whereafter only the internodes were analysed for starch. Both the nodes and the internodes were used for the determination of the fresh and dry mass of the shoots. Calculation of the total starch content per shoot was based on the assumption that the starch content of the nodes was the same as that of the internodes.

The internodes were frozen at -20°C prior to freeze-drying with a Chriss Alpha freeze-drying unit. The shoots were then ground and milled with a Tecator Cyclotec 1093 Sample mill. Sucrose, hexoses and organic acids were extracted as described by Hunter *et al*. (1995b). The residue was then freeze-dried and used for starch extraction and analysis (Hunter *et al*., 1995a).

Light intensity measurements: The photosynthetic photon flux density (PPFD) was measured in the vineyard with an ADC portable photosynthesis meter (The Analytical Development Co., England) specified in Hunter & Visser (1988). Measurements were taken at 10:00 on the scheduled day (31 January, 8 February and 21 February 2002). Sun leaves in the basal (first three leaves above the clusters) position on the shoot were measured in all cases. Results were expressed as $\mu mol.m^{-2}.s^{-1}$. Three leaves per replicate were measured.

Statistical analyses

For statistical analyses, a factorial ANOVA was used. A 5% level of significance was applied. Depending on the data, non-parametric bootstrap analyses were used. Differences were considered significant when no overlapping of the 95% confidence intervals occurred.

RESULTS AND DISCUSSION

Primary and secondary shoot growth

The normally developed primary shoots had an average length of 112 cm and were significantly longer ($p \leq 0.01$) than the underdeveloped shoots with an average length of 50 cm (Fig. 1). Significantly more ($p \leq 0.01$) (Fig. 2) and longer (Fig. 3) secondary shoots developed on normal shoots compared with underdeveloped shoots. Although normally developed shoots from exposed vines were somewhat shorter than those from shaded vines (Fig. 1), longer (Fig. 3) and heavier (Fig. 4) secondary shoots were found on normally developed shoots in well-exposed canopies. This is in accordance with the findings of Hunter & Visser (1990a); they found a non-significant decrease of the primary shoot length as a result of defoliation. This apparent decrease may indicate the diversion of photosynthetates to other parts of the vine.

Canopy management did not affect the primary shoot growth of underdeveloped shoots (Fig. 1). Defoliation on these shoots would also have been restricted, since a large proportion of these shoots are found in canopy interiors (Smart *et al*., 1988). The non-significant higher number of lateral shoots on underdeveloped shoots in the well-exposed canopies, compared with shaded canopies (Fig. 2), is in agreement with the findings of Hunter (2000). It was found in earlier studies that the development of lateral shoots is promoted by partial defoliation *per se* (Hunter & Visser, 1990a).

Secondary shoots of underdeveloped shoots in shaded canopies had a longer average length (albeit larger variation) with no difference in mass compared with those in exposed canopies (Fig. 4). This difference in shoot length could be ascribed to the stimulating effect of shading on shoot growth (Keller & Hrazdina, 1996) or a reduction in growth as a result of photomorphogenesis. As the mass of these secondary shoots did not differ between the canopy treatments, the well-exposed canopies induced thicker secondary shoots with probably a higher translocatory potential.

Although the exact position of the secondary shoots on the primary shoots was not noted, it could be assumed that in the case of the underdeveloped (thus untopped) shoots, the majority of the secondary shoots developed in the basal part of the canopy and in the cluster region. This assumption is based on the average length of the shoots (±50 cm) and the statement of Carbonneau *et al.* (1997) that “the first basal third of the foliage ... corresponds to the zone of frequent occurrence of laterals”. This was also reported by Pisciotta (2004). Therefore secondary shoots of underdeveloped shoots may contribute to the development of a denser and more shaded cluster region.

With normally developed shoots, the topping treatment stimulated the formation of secondary shoots in the apical part of the primary shoot due to the removal of apical dominance caused by the inhibitory effect of growth regulators such as auxin (Hunter, 2000). Secondary shoots were therefore most probably positioned over the whole length of the primary shoot. This is regarded as important for the optimal efficiency of the canopy and contribution to the clusters (Hunter, 2000).

Although the primary shoot length did not increase after véraison (data not shown), the mass of the normally developed shoots peaked at four weeks after véraison, whereafter it decreased. Underdeveloped shoots showed a similar pattern, but far less pronounced ($p \leq 0.05$) (Fig. 5).

The increase in primary shoot mass after véraison could be ascribed to shoot maturation and reserve accumulation. Since the mass of the underdeveloped primary shoots did not increase to the same extent as the normal shoots, it seems evident that the above-mentioned processes did not occur to the same degree. Canopy exposure seemed to contribute to shoot maturation and reserve accumulation, since the shoot mass of normally and underdeveloped shoots tended to be higher in well-exposed canopies, compared with shaded canopies (data not shown).

The decrease in primary shoot mass between four and five weeks after véraison is possibly due to the translocation of water from the shoots to other parts of the vine, such as the clusters and permanent structure. The normal seasonal development of the underdeveloped shoots seemed to be delayed, which may explain the higher water percentage found in these shoots five weeks after véraison (data not shown).

The balance between vegetative and reproductive growth in underdeveloped shoots was obviously disrupted, resulting in a delay in the ripening (starch accumulation and lignification) of vegetative tissue. The strength of the reproductive sink tissue was

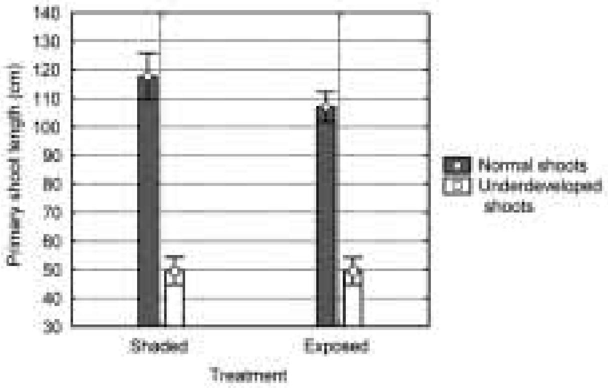

FIGURE 1
Average primary shoot length of normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

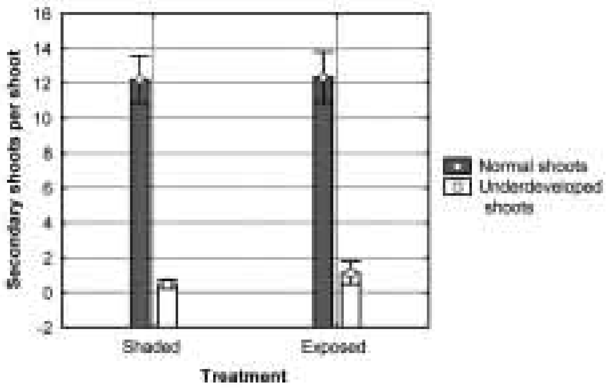

FIGURE 2
Average number of secondary shoots of normally developed and underdeveloped primary shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

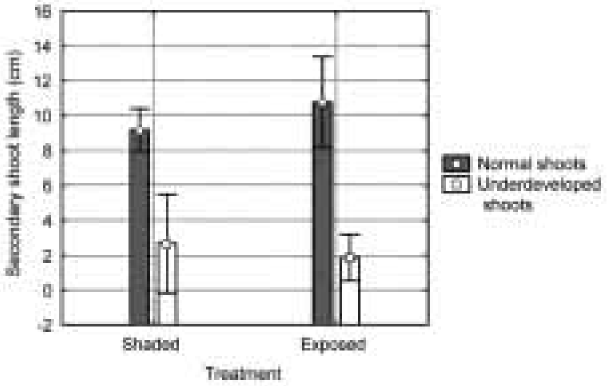

FIGURE 3
Average secondary shoot length of normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

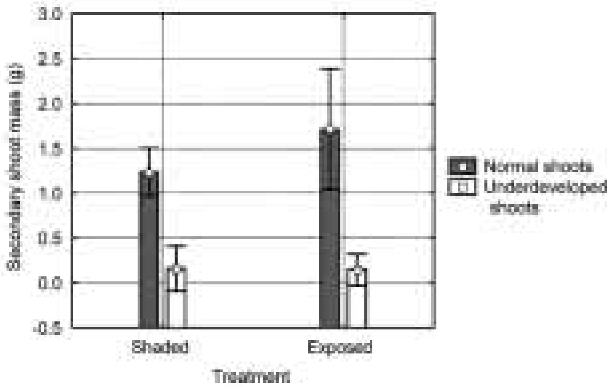

FIGURE 4
Average fresh mass of secondary shoots of normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

increased on these shoots compared with normally developed shoots. This would, however, seriously affect growth and production of the whole vine in the following seasons, particularly if these shoots were to be used as spurs.

Lignification and starch content

It was found that lignification of the normally developed shoots was far more advanced at véraison than that of the underdeveloped shoots ($p \leq 0.01$); at five weeks after véraison the difference in maturity remained very pronounced (Fig. 6). Therefore it was assumed that a stronger competition occurred in underdeveloped shoots between shoot and grape ripening, and that both processes were negatively affected. In order to maintain longevity, grape ripening should occur without any detrimental effect on growth and development in other parts of the vine (Hunter & Archer, 2001b), such as shoot maturation and reserve accumulation.

The degree of lignification tended to be higher in the well-exposed canopies (Fig. 7). This is in accordance with Reynolds *et al*. (1986) who found that periderm formation seemed to be a function of shoot density, as a higher percentage of poorly ripened shoots occurred in shaded canopies.

After cessation of vegetative growth, both supply and demand for photosynthetates decreased (Hunter & Visser, 1990a), which explains the very slow rate of assimilate translocation noted by De la Harpe (1983) and Hunter *et al*. (1995a) at ripeness. According to De la Harpe (1983) not even the storage organs, such as the trunk, cordon arms and roots, constituted very strong sinks during this time. The persisting CO_2 assimilation by basal leaves during ripening (Hunter *et al*., 1994) contributed to sustained carbohydrate supply while demand decreased. This resulted in an increase in the supply:demand ratio in the vine (Hunter *et al*., 1995a). Since the apical sink demand in particular decreased during this time, sucrose probably accumulated in the basal parts of the shoot where it is metabolised to starch and stored. This may partly explain the higher starch content of the basal part of the shoot compared to the rest of the shoot (Figs. 8 & 9).

It should also be taken into account that the leaves from the middle and, in particular, the apical parts of the shoots, are still actively transporting sucrose to the ripening clusters at five weeks after véraison, which further explains why less assimilate is available for reserve accumulation in those parts of the shoot. In the case of normally developed shoots, the assimilate supply from the leaves could have been enough to adequately ripen the clusters and accumulate starch simultaneously, which could be the reason

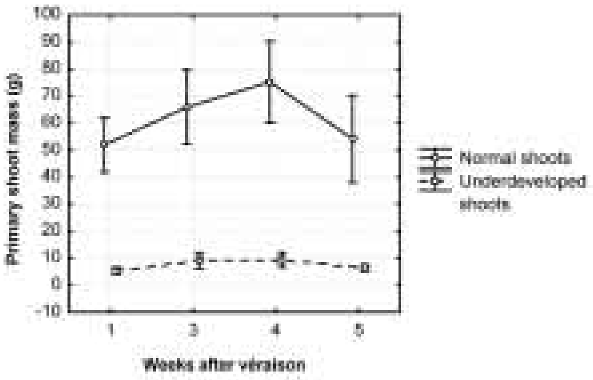

FIGURE 5

Average fresh mass of normally developed and underdeveloped primary shoots at one, three, four and five weeks after véraison.
(Error bars indicate 95% confidence intervals).

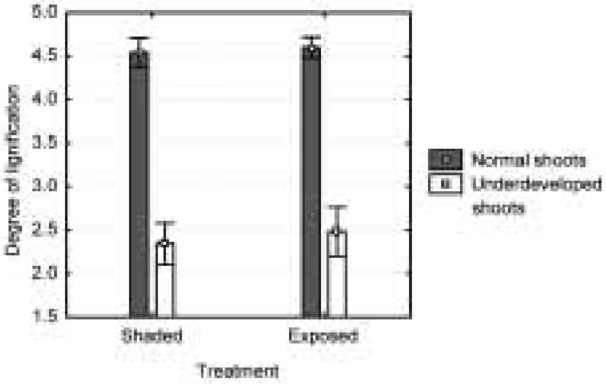

FIGURE 7

Degree of lignification of normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

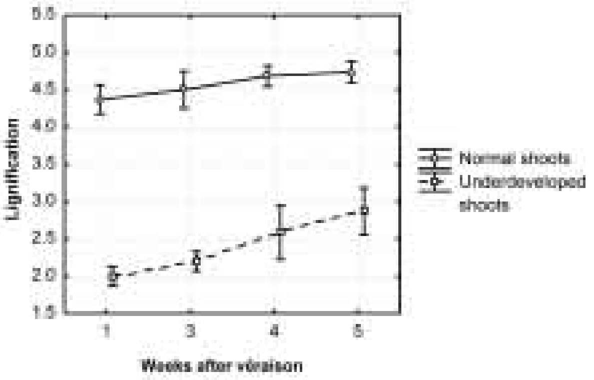

FIGURE 6

Degree of lignification of normally developed and underdeveloped primary shoots at one, three, four and five weeks after véraison.
(Error bars indicate 95% confidence intervals).

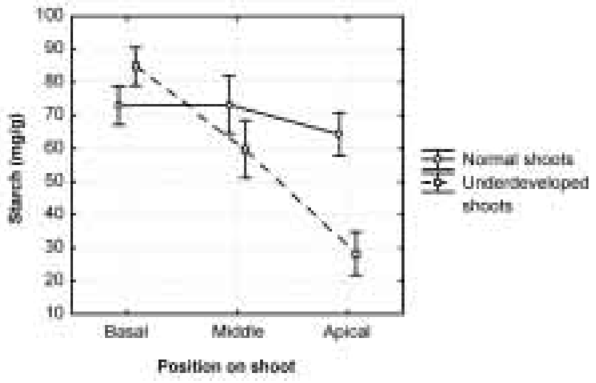

FIGURE 8

Average starch concentration in different positions on normally developed and underdeveloped shoots.
(Error bars indicate 95% confidence intervals).

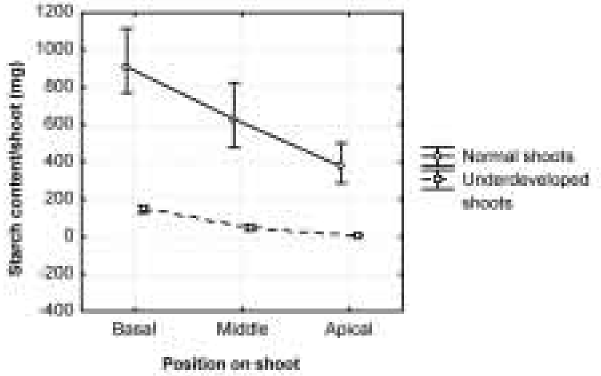

FIGURE 9

Average starch content in different positions on normally developed and underdeveloped shoots.
(Error bars indicate 95% confidence intervals).

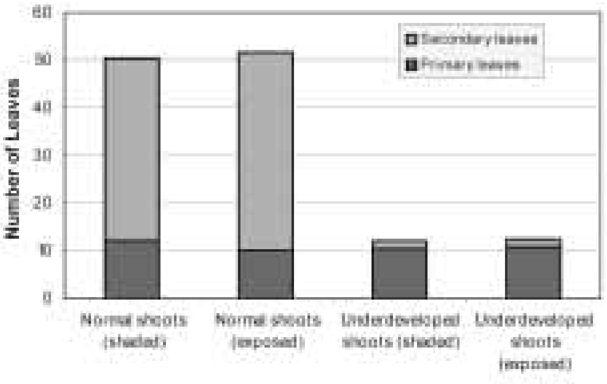

FIGURE 10

Average contribution of primary and secondary leaves to the total number of leaves per shoot.

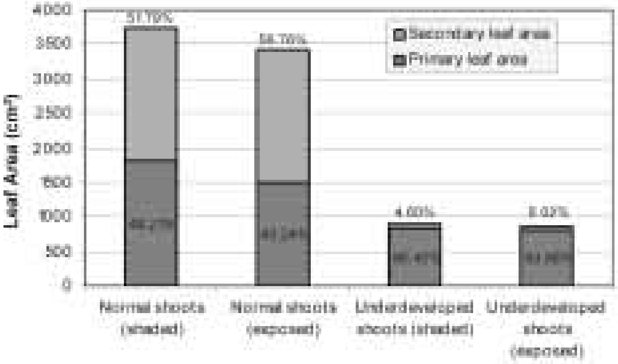

FIGURE 11

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

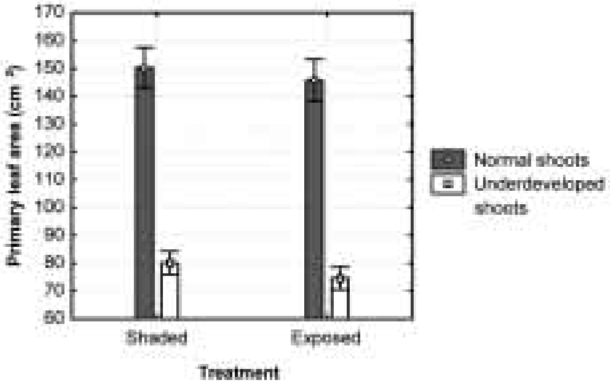

FIGURE 12

Average area of primary leaves from normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

for the more uniform starch concentration found in these shoots (Fig. 8). On the other hand, the supply of the leaves of the underdeveloped shoots was probably not enough to satisfy the demand of the ripening clusters as well as the shoots, resulting in less uniform ripening.

Although the basal starch concentration of the underdeveloped shoots was significantly higher than that of the normally developed shoots (Fig. 8), the total starch content should also be taken into account (Fig. 9). Normally developed shoots accumulated significantly more total starch reserves in the basal parts than the underdeveloped shoots, while exposure of the canopy ostensibly led to the former shoots having a higher total starch content. The stored reserves in the basal part of the shoot play an important role in growth and development of vegetative as well as reproductive tissue in the following season (Hunter *et al*., 1995a), particularly when a spur pruning system is used.

Primary leaf development and growth

Although the normally developed and underdeveloped shoots had similar numbers of primary leaves per shoot (Fig. 10), the primary leaves of the normal shoots comprised a much larger percentage of the total leaf area per shoot (Fig. 11). This is explained by the significantly larger primary leaves found on the normally developed shoots (Fig. 12).

The non-significantly higher number of primary leaves found on normal shoots in shaded compared with well-exposed canopies (Fig. 10) was attributed to the longer shoot lengths found in the former. It was further found that the primary leaves of the normally developed shoots in the shaded canopies comprised a larger percentage of the total leaf area per shoot than in the exposed canopies (Fig. 11), due to the higher number of leaves per shoot as well as the larger mean primary leaf area (Fig. 12). This is in accordance with Keller and Hrazdina (1996) who found that low light intensity stimulated individual leaf area expansion.

Primary leaves from underdeveloped shoots in shaded canopies also seemed to have a larger mean area than those in the exposed canopies (Fig. 12). The result of this phenomenon is a non-significant larger contribution of the primary leaves to the total leaf area per underdeveloped shoot in the shaded canopies (Fig. 11), since there was no significant difference in the number of primary leaves per shoot between the canopy treatments (Fig. 10).

Secondary leaf development and growth

The significantly higher number of secondary leaves on normal shoots compared with underdeveloped shoots ($p \leq 0.01$) (Fig. 10) was to be expected, due to the significantly more and longer secondary shoots found on the normally developed shoots. The canopy treatment did not affect the number of secondary leaves on underdeveloped shoots, while it seemed as if a higher number of leaves occurred on normal shoots in exposed canopies compared with shaded canopies (Fig. 10). The longer secondary shoots in the exposed canopies as well as the stimulating effect of the partial defoliation applied to create the exposed canopies may have contributed to this.

The significantly larger secondary leaves found on the normal shoots compared with the underdeveloped shoots ($p \leq 0.01$) (Fig. 13) made an important contribution to the total leaf area per shoot (Fig. 11). Hunter (2000) stated that the activity of secondary leaves in the canopy makes an important contribution to the attainment of maximum yield and grape quality. Not only the total leaf area as such but also the composition of the leaf area should be taken into account, as it plays a critical role in the efficiency of the canopy and the nourishing of the clusters. Therefore, the normally developed shoots may have a greater potential for producing a higher yield with better quality than the underdeveloped shoots, as they have a more desirable leaf area composition in addition to the larger total leaf area per shoot.

Regardless of the canopy treatment, the secondary leaves made similar contributions to the total leaf area on normally developed shoots (Fig. 11). Although more secondary leaves per shoot were found for the exposed vines (Fig. 10), the leaves had a larger mean area in the shaded canopies (Fig. 13). This supports the statement of Keller and Hrazdina (1996), namely, that low light intensities stimulate individual leaf expansion. In contrast, secondary leaves of the underdeveloped shoots in the well-exposed canopies tended to be somewhat larger than those in the shaded canopies (Fig. 13), which could possibly be explained by the better development of the secondary shoots under those conditions. It was, however, not statistically significant and did not make any difference in the composition of the total leaf area per underdeveloped shoot.

According to Poni and Giachino (2000) the assimilation rate of the secondary leaves increased with the lateral shoot size and decreased when the more primary leaves were retained with trimming. If their findings were to be true in this case as well, it could be expected that the secondary leaves on the normally developed shoots from the vines with exposed canopies will have the highest assimilation rates of all the shoot-canopy treatment combinations and will therefore make a large contribution to the total photosynthetic activity of the shoot.

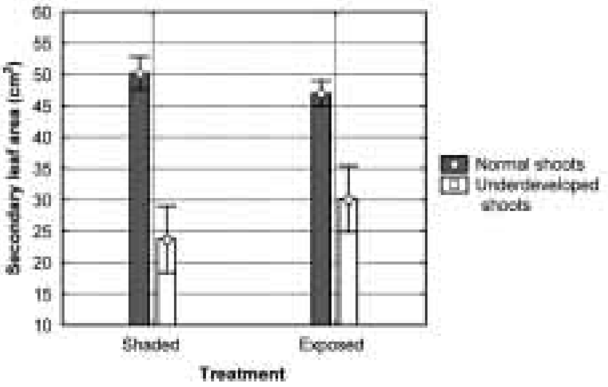

FIGURE 13

Average area of secondary leaves from normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

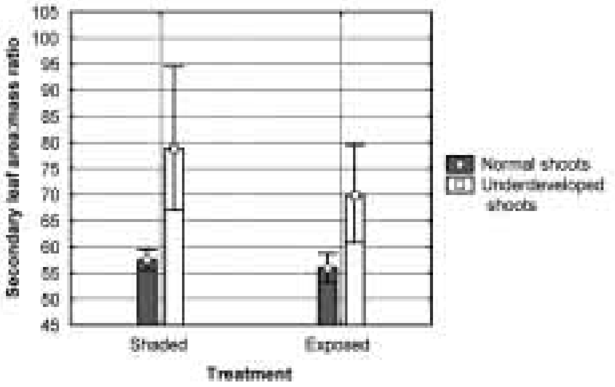

FIGURE 15

Leaf area:mass ratio of secondary leaves from normally developed and underdeveloped shoots in shaded and well-exposed canopies.
Error bars indicate 95% confidence intervals (bootstrap analysis).

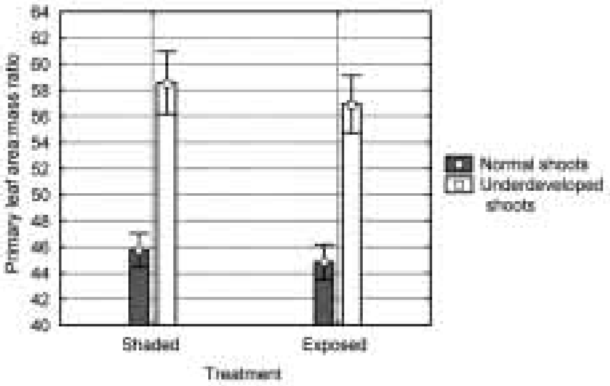

FIGURE 14

Leaf area:mass ratio of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

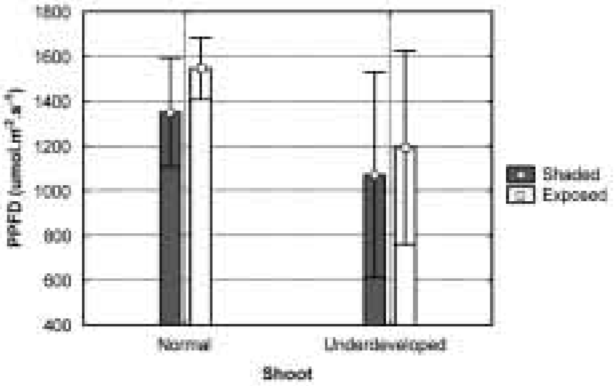

FIGURE 16

PPFD received by basal leaves of normally developed and underdeveloped shoots in shaded and well-exposed canopies.
(Error bars indicate 95% confidence intervals).

Leaf area:mass ratio

Primary (Fig. 14) as well as secondary leaves (Fig. 15) from well-exposed canopies were thicker (lower leaf area:mass ratio) than those from shaded canopies, and this ratio was significantly lower ($p \leq 0.01$) for the normal shoots compared with the underdeveloped shoots. Higher levels of PPFD were measured in the well-exposed canopies compared with the shaded canopies (Fig. 16). Basal leaves of normally developed shoots were also more exposed to sunlight than those of underdeveloped shoots. According to Marini & Marini (1983), a strong correlation exists between the specific leaf mass and the PPFD in the canopy, while Keller and Hrazdina (1996) found stimulated individual leaf area expansion under low light intensities.

While studying beans (*Phaseolus vulgaris* L.), Crookston *et al*. (1975) found that shading decreased the thickness of leaves as well as the photosynthetic activity per unit leaf area. This was ascribed to the sharp increase in mesophyll resistance, which they linked to the decreased enzymatic activity and alterations in leaf anatomy and chloroplast ultrastructure also found. It could therefore be expected that the difference in the leaf area:mass ratio between the shoot types and the canopy treatments will have an important effect on the physiological activity of the individual shoots as well as the efficiency of the respective canopies.

CONCLUSIONS

Compared with the underdeveloped shoots, the normally developed shoots were longer and thicker, with more and longer secondary shoots distributed over the whole length of the shoot. The latter was found to be important for the optimal efficiency of the canopy. Within canopy treatments, normally developed shoots from the shaded canopies were longer and thinner than those in the exposed canopies. More and longer secondary shoots developed on the normal shoots in the more exposed canopies. Secondary shoots on the shoots that were underdeveloped also seemed to be thicker in the exposed canopies. The thicker shoots can possibly be an indication of a higher physiological potential, within limits.

Periderm development (lignification) in normal shoots occurred earlier in the season, and maturation of the shoots was thus not in such strong competition with grape ripening than seemed to be the case of underdeveloped shoots. Higher levels of starch formation and accumulation occurred in the normally developed shoots, while reserves were also more evenly distributed over the whole length of the shoot. The total starch content of the shoots from the well-exposed canopies was also higher on a per shoot basis, which may have a significant effect on the initial growth of the following season. The leaves of the normally developed shoots were better able to supply assimilates to both the shoots and grapes for their ripening, especially in the well-exposed canopies. In order to maintain longevity of the vine (and also the functionality of individual spurs) grape ripening should occur without any detrimental effect on other processes in the vine, such as reserve accumulation. This was however not achieved in the case of the underdeveloped shoots – reserve accumulation seemed to be impaired by grape ripening processes.

Significantly larger primary leaves were found on normally developed shoots compared with underdeveloped shoots, although no difference in the number of leaves per shoot was found. Secondary leaves on the normally developed shoots were found to be more numerous and larger than on the underdeveloped shoots, while more secondary leaves were found on normal shoots from the exposed compared with the shaded canopies. Primary as well as secondary leaves were found to be larger in the shaded compared with the well-exposed canopies, whereas the leaf area:mass ratio was lower in the exposed canopies.

The primary and secondary leaves of the normally developed shoots made an almost equal contribution to the total leaf area per shoot, whereas the primary leaves of the underdeveloped shoots made a noticeably higher contribution. Therefore, the normally developed shoots may have had a greater potential for producing a sustainable higher yield of better quality than the underdeveloped shoots, without impairing the longevity of the vine.

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