# PHOTOTROPIC AND GEOTROPIC SHOOT ORIENTATION: EFFECT ON PHYSIOLOGICAL, VEGETATIVE AND REPRODUCTIVE PARAMETERS

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**Key words:** Merlot, shoot orientation, vegetative growth, photosynthetic activity, water potential, light interception, grape composition.

## Abstract

The effect of shoot orientation during two growth seasons (2002/2003 and 2003/2004) on physiological, vegetative and reproductive parameters was investigated in the Stellenbosch area in a Merlot/R99 vineyard with a vertical trellising system. Vines were spaced 2.7 X 1.5 m in north-south orientated rows. Micro-sprinkler irrigation was applied at pea size berry and at vèraison stages. Observations were done on vines with a natural distribution and orientation of phototropically (upward) and geotropically (downward) shoots on the same cordon.

Soil water typically varied according to the progress in the season and with soil depth, decreasing towards the end of the season and increasing with depth. Geotropic orientation reduced the primary and lateral shoot length as well as the primary and secondary shoot leaf area. With phototropic shoot position, secondary shoots were more evenly distributed along the primary shoots. Basal and apical stem and leaf water potential was lower with geotropic orientation than with phototropic orientation. This was particularly pronounced during the ripening period. In spite of this, basal and apical leaf photosynthetic activity of the phototropically orientated shoots was higher than that of the geotropically orientated shoots, most probably because of more favourable microclimatic conditions experienced by the former. Bunch mass and volume and length of bunches were not significantly affected by shoot orientation. Phototropic orientation of shoots noticeably increased glucose and tartaric acid contents of the berries, whereas sucrose, malic acid and citric acid contents were virtually unaffected. In phototropically orientated shoots, less water was lost by the skins, favouring skin colour intensity. The results have important implications for bunch and berry composition uniformity and for trellising system selection on different terroirs.

## Resumè

On a étudié l'effet de l'orientation des rameaux sur les paramètres physiologiques, végétatifs et reproductif durant deux saisons de croissance (2002/2003 et 2003/2004) dans la région de Stellenbosch dans une vignoble du cépage Merlot sur 99R conduite en espalier et taillé à cordon coursonné. Les vignes étaient espacées 2.7 x 1.5 m. L'irrigation a été appliquée quand la baie avait la dimension d'un pois et à la véraison. La végétation a été manipulé pour avoir les rameaux sur le même cordon orientés une partie vers le haut (phototropiques) et l'autre vers le bas (géotropiques).

L'orientation vers le bas a réduit la longueur et la surface foliaire du rameau principal et des entre cœurs. Quand le rameau est orienté vers le bas les entre cœurs sur le même rameau sont plus homogènes. Le potentiel hydrique foliaire et de tige à midi évalué sur la feuille basale et apicale était inférieur dans l'orientation vers le bas au confronte de l’orientation vers le haut. Cela était particulièrement prononcé pendant la période de maturation du raisin. L'activité photosynthétique des feuilles basale et apicale des rameaux orientés vers le haut était plus haute que celle des rameaux orientés vers le bas, probablement, à cause des conditions microclimatiques plus favorables. Le poids, le volume et la longueur des grappes n'ont pas été sensiblement influencés par orientation du rameau. L'orientation vers le haut a sensiblement augmenté le glucose et l'acide tartrique des baies, le saccharose, l'acide malique et l’acide citrique étaient pratiquement inchangés. Moins d'eau a été perdue par les peaux des baies et cela a favorisé l'intensité de la couleur. Les résultats ont des implications importantes pour l'uniformité de composition de la baie et pour le choix du système de conduite dans les différents terroirs.

## Introduction

There is worldwide interest in developing canopy management practices that improve canopy microclimate and grape and wine quality. High shoot vigour is a major concern (Kliewer *et al.*, 1989; Calò *et al.*, 1999). Vigour can be affected by genotype (scion-rootstock combination), different management practices (trellising system, vine spacing, bud load per vine, fertilisation, irrigation, etc.) as well as by soil type and climatic conditions (Kramer, 1983; Gifford *et al.*, 1984; Archer & Strauss, 1985; Hunter *et al.*, 1995; Hunter, 1998a, 1998b; Hunter & Volschenk, 2001). The trellising system has a pivotal role in the positioning and efficient accommodation of shoots. Several trellising systems have been described that changed the arrangement and direction of shoot growth. The Geneva double curtain, introduced by Shaulis *et al.* (1966), was based on the idea of dividing grapevine canopies and positioning shoots to grow downwards. Other training systems promoted the vertical growth of shoots, e.g. the Lyre (Carbonneau & Huglin, 1982), Te Kauwhata two tier (Smart, 1984) and Bordeaux traditional (Carbonneau & Huglin, 1982); the horizontal growth of shoots, e.g. the Tendone and Lincoln trellis (Jackson & Nguyen, 1983); or the growth of shoots at an inclined angle, e.g. the Tatura (Van den Ende, 1984) and South African Y slanting arm trellis (Zeeman, 1978). Orientation affects shoot growth, upward orientation inducing higher vigour than downward orientation (May, 1966; Shaulis *et al.*, 1966; Kliewer *et al.*, 1989; Tassie & Freeman, 1992; Schubert *et al.*, 1995; Lovisolo & Schubert, 2000).

Training systems are constantly being altered and newly developed with the purpose of adapting grapevine growth to climatic and cultural conditions. The positioning of shoots is, however, the basis of all training systems in viticulture. Although the implications of shoot orientation as induced by trellis structure, height and size on grapevine growth and yield have been extensively investigated (Freeman *et al.*, 1992, and references therein), few studies dealt with the effects (Volschenk & Hunter, 2001; Pisciotta *et al.*, 2003) and particularly the seasonal timing of shoot orientation, examined independently of trellis structure, and with special reference to physiological processes. The purpose of this investigation was therefore to study the effect of shoot orientation at different stages during the growth season on physiological, vegetative and reproductive parameters.

## Materials and Methods

### Vineyard

Seven-year-old Merlot vines, grafted onto 99 Richter, were studied in the Western Cape on the experiment farm of the ARC Infruitec-Nietvoorbij, Stellenbosch, during two growth seasons. Vines were spaced 2.7 x 1.5 m in north-south orientated rows and trained to a vertical trellis system. They were pruned to two-bud spurs, spaced approximately 14 cm apart on the split cordon. Suckering was applied (removing at 30 cm length all shoots not situated on two-bud spurs). Micro-sprinkler irrigation was applied at pea size berry and at vèraison stages (12 hours @ 32L/hour).

### Treatments and experiment design

Two treatments were applied: 1) Geotropic, where shoots were positioned in a slanted downward orientation and 2) Phototropic, where shoots were positioned in an upward orientation. Treatments and four replications (comprising either 10 or 15 vines each) were completely randomised.

Measurements were performed at five development stages (berry set, pea size, vèraison, three weeks after vèraison and ripeness).

### Vegetative measurements

Primary and secondary shoot length (cm), leaf area ($cm^2$), number of secondary shoots, and total shoot length (cm) in the two different orientations were measured at berry set, pea size, vèraison, three weeks after vèraison and ripeness stages. The Absolute Growth Rate per day of the total shoot (Primary + Secondary shoots) was determined (A.G.R.). At ripeness (2003/04 season), the secondary shoot node number per secondary shoot were counted at each primary shoot node position. Twelve shoots per treatment were randomly selected and used to obtain the bunch mass:shoot mass ratio, shoot length (primary and secondary shoots) and leaf area (primary and secondary shoots). Leaf area was determined with a LI-COR LI 3000 portable area meter.

### Yield and grape composition

Bunches of twelve randomly selected shoots per treatment were harvested and the mass (g), volume ($cm^3$), length (cm) and rachis mass (g) determined. Berries were stored at –20°C until required for further analyses. For phenolic and anthocyanin determination in grape skins, 100 berries were sampled and the skins separated from the pulps by gentle squeezing between thumb and forefinger. Any pulp adhering to skins was removed. Skins were then rinsed in distilled water, blotted dry and their fresh mass determined. Dried skins were weighed, ground in a Sorvall Omni-mixer and stored at room temperature. Phenolics and anthocyanins were extracted and determined spectrophotometrically as described by Hunter *et al*. (1991). Extraction and determination of sugars and organic acids by gas liquid chromatography were done at ripeness stage as described by Hunter & Ruffner (2001).

### Physiological measurements

Rate of photosynthesis ($\mu mol/m^2/s$), rate of transpiration ($mmol/m^2/s$), stomatal conductance ($mmol/m^2/s$), and leaf and stem water potential (kPa) were measured on basal leaves (3rd to 4th nodium) and apical leaves (12th nodium). Rate of photosynthesis, rate of transpiration and stomatal conductance were measured using an ADC portable photosynthesis meter (The Analytical Development Co., England). The photosynthesis apparatus consisted of an infra-red $CO_2$ analyser, a data logger, a Parkinson broad leaf chamber (volume = 16 $cm^3$, area = 6,25 $cm^2$) and an air supply unit (length of sample tube = 4 m). The air flow rate through the open system was adjusted to 300 $cm^3/min$. Measurements were carried out between 10:30 and 11:30 on the day scheduled. Leaf and stem water potential were measured at mid-day (13:30). Leaves used for determination of stem water potential were wrapped in a double layer bag (inside plastic and outside aluminium foil). Stem and leaf water potential was measured using a Scholander-type pressure chamber. Ambient light intensity between the vine rows as well as light intensity just above and below the cordon were determined with a LI-COR Line Quantum Sensor during late morning. Light intensity was expressed as percentage of the ambient light level.

### Statistical analyses

Data of all variables at each measurement stage were submitted to a two-way analysis of variance (year, treatment). No significant differences were found for the interaction (year x treatment). Data represent the means of two years. Differences between treatment means were tested at $p<0,05$ * and $p<0,01$ **.

## Results and Discussion

### Soil water

Soil water typically varied according to the season, the progress in the season and with soil depth, decreasing towards the end of the season and increasing with depth (Figs.1 & 2).

### Vegetative growth

Primary and secondary shoot length (Table 1a) and the number of primary nodes per shoot (data not shown) were lower with geotropic than with phototropic orientation of shoots. A reduction in the length of geotropically orientated shoots is commonly observed in plants (Wareing & Nasr, 1958; Prasad & Cline, 1985) and is in agreement with the findings of Kliewer *et al*. (1989), Schubert *et al*. (1999) and Lovisolo & Schubert (2000) on the grapevine. These differences were not pronounced at berry set stage when the shoot orientation was not yet completely differentiated. The differences in growth between the two orientation treatments are explained by the values of A.G.R. (Table 1a). The higher secondary shoot length of phototropically orientated shoots was due to their higher number of secondary shoots (Table 1a). With phototropic shoot orientation, secondary shoots were more evenly distributed along the primary shoots (Fig. 2). The results are in agreement with those of Kliewer *et al*. (1989) that geotropic orientation generally produced stronger laterals near the shoot base and weaker secondary shoots at all other node positions than did phototropic orientation. The reduced radial development of vessels is only one component of a generalized depression of the shoot growth process in the apex (Schubert *et al*., 1999), in this particular case induced by geotropic shoot orientation. The primary and particularly secondary shoot leaf area was higher with phototropic orientation (Table 1b). However, the leaf area of individual primary and secondary leaves was not significantly different between the two orientations (data not shown), due to the higher number of particularly young leaves per shoot.

### Yield and grape composition

Bunch and berry mass and the volume and length of bunches were not significantly affected by shoot orientation. Due to their higher leaf area per shoot, the total leaf area per shoot:bunch mass ratio ($cm^2$:g) of phototropically orientated shoots was slightly higher than that of geotropically orientated shoots (Tables 1b & 2). Grapes of geotropically orientated shoots were most probably overly exposed, whereas those of phototropically orientated shoots were protected against excessive radiation (Fig. 3). Except for the post-véraison stage, phototropically orientated shoots contained less water in their grape skins (Fig. 4), which favoured the concentration of secondary compounds such as skin anthocyanins and phenolics (Fig. 5). The pattern of anthocyanin and total phenolic development is in accordance with the finding of Somers (1976), i.e. that the highest anthocyanin concentration occurred from 20-30 days after vèraison and then decreased with further ripening. Glucose and tartaric acid concentrations were significantly higher in the grapes of phototropically orientated shoots. It seemed that phototropic shoot orientation significantly affected glucose content (Fig. 6), probably as a result of increased photosynthetic activity and the transport of sucrose to the berry (Table 3). Higher tartaric acid contents are favourable for grape quality (Hunter & Ruffner, 2001, and references therein). No significant differences were found for sucrose, malic acid and citric acid contents (Fig.6).

### Leaf gas exchange and water potential

Except for the berry set stage, leaves in the apical part of the canopy (12th nodium) had higher photosynthetic activity, stomatal conductance and transpiration rate than those in the basal part of the canopy (3rd to 4th nodia) for both shoot orientations (Table 3). This is in accordance with the results of Schubert *et al*. (1995) and Lovisolo & Schubert (2000). The results also followed the seasonal pattern reported by Alleweldt *et al.* (1982) and Hunter *et al*. (1994). Apical and basal leaf photosynthetic activity was significantly higher for phototropically orientated shoots compared to that of geotropically orientated shoots at all measurement dates (Table 3), most probably because of higher stem and leaf water potential (Table 3) and more favourable microclimatic conditions (Fig.3) experienced by the former. This was particularly pronounced during the ripening period. In general, leaf water potential of apical leaves was lower than that of basal leaves from berry set to vèraison stage; from post vèraison to ripeness an opposite tendency occurred (Table 3). Stem water potential of apical leaves stayed lower than that of basal leaves until the post-véraison stage, after which they followed an opposite pattern. For both shoot orientations, relationships with leaf transpiration rate were therefore only evident until véraison, when leaf water potential is considered, and until post-véraison, when stem water potential is considered. During the late ripening stages the vine most probably regained water because of rainfall and a decrease in day and night ambient temperatures. The reduction in canopy (source) photosynthetic activity during this time would have decreased sucrose production and together with the decline in demand for sugar from the berries (sinks), this would have impacted on xylem and phloem water potential and pressure gradients in the plant.

## Conclusions

Results in this study indicated that geotropic (downward) orientation reduced shoot vigour of Merlot. Compared to phototropic (upward) orientation, geotropically orientated shoots induced a reduction in growth rate, physiological activity and berry composition. It is clear that the phototropic orientation of shoots should receive priority and form an integral part of decisions on which long and short term practices are to be followed at a particular terroir. Phototropic orientation of shoots should always be accompanied by shoot positioning. This is very important under both moderate and vigorous growth conditions.

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Table 1a.  Vegetative parameters as affected by shoot orientation.

| Measurement stage | Berry set | | | Pea size | | | Veraison | | | Post veraison | | | Ripeness | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | down | | up | down | | up | down | | up | down | | up | down | | up |
| **Primary shoot length (cm)** | 105.2 | * | 102.4 | 110.70 | ns | 124.1 | 111.8 | ns | 120.0 | 116.9 | ns | 126.2 | 115.1 | ns | 135.4 |
| **Total lateral shoot length (cm)** | 80.2 | * | 86.3 | 85.6 | * | 96.1 | 86.2 | * | 105.2 | 91.1 | * | 108.0 | 104.5 | * | 112.1 |
| **Total shoot length (cm)** | 191.4 | * | 188.7 | 196.3 | ns | 220.2 | 198.0 | ns | 225.2 | 208.0 | ns | 234.2 | 219.6 | ns | 247.5 |
| **Total number of lateral shoot** | 11.4 | * | 9.0 | 11.8 | ns | 12.6 | 12.8 | ns | 14.8 | 13.0 | * | 16.2 | 14.2 | * | 17.0 |
| **P+L AGR per day (cm)** | | | | 0.2 | | 1.2 | 0.1 | | 0.1 | 0.5 | | 0.4 | 0.4 | | 0.5 |

Table 1b.  Vegetative parameters as affected by shoot orientation.

| Measurement stage | Berry set | | | Pea size | | | Veraison | | | Post veraison | | | Ripeness | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | down | | up | down | | up | down | | up | down | | up | down | | up |
| **Total primary leaf area (cm$^2$)** | 2079.3 | ns | 2157.0 | 2382.4 | ns | 2406.0 | 2214.4 | ns | 2410.9 | 2239.6 | ns | 2280.9 | 2293.8 | ns | 2450.2 |
| **Total lateral leaf area (cm$^2$)** | 1089.4 | * | 1342.9 | 1409.0 | * | 1788.3 | 1845.5 | * | 2139.1 | 1750.0 | * | 2213.0 | 2109.9 | | 2190.3 |
| **Total shoot leaf area (cm$^2$)** | 3168.7 | * | 3499.9 | 3791.4 | * | 4194.3 | 4059.9 | * | 4550.1 | 3989.6 | * | 4493.9 | 4403.7 | ns | 4640.5 |
| **Total primary leaves (n°)** | 18.2 | ns | 18.2 | 20.1 | ns | 21.9 | 21.8 | ns | 23.6 | 20.6 | ns | 24.2 | 25.5 | ns | 30.7 |
| **Total lateral leaves (n°)** | 23.7 | ns | 25.2 | 29.7 | ns | 36.8 | 33.4 | ns | 46.6 | 42.3 | ns | 48.5 | 47.9 | ns | 52.5 |

Table 2.  Reproductive parameters as affected by shoot orientation.

| Measurement stage | Berry set | | | Pea size | | | Veraison | | | Post ve raison | | | Ripeness | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | down | | up | down | | up | down | | up | down | | up | down | | up |
| **Bunch lenght (cm)** | 16.8 | ns | 16.6 | 17.6 | ns | 17.4 | 17.3 | ns | 17.0 | 16.7 | ns | 17.3 | 16.3 | ns | 16.6 |
| **Bunch volume (cm $^3$)** | 15.17 | ns | 19.72 | 101.65 | ns | 107.72 | 198.75 | ns | 197.24 | 217.0 | ns | 223.0 | 200.3 | ns | 201.8 |
| **N°berries/bunch** | | | | | | | | | | | | | 151.7 | | 151.7 |
| **Bunch mass (g)** | 17.6 | ns | 19.8 | 99.3 | ns | 105.1 | 205.9 | ns | 203.8 | 232.9 | * | 247.2 | 209.7 | ns | 211.6 |
| **Berry mass (g)** | 0.1 | ns | 0.1 | 0.6 | ns | 0.6 | 1.3 | ns | 1.3 | 1.5 | ns | 1.6 | 1.3 | ns | 1.3 |
| **Rachis mass (g)** | 4.0 | ns | 4.6 | 7.3 | ns | 8.0 | 8.7 | ns | 9.6 | 6.8 | ns | 7.4 | 6.4 | ns | 6.8 |
| **Tot leaf area/bunch mass (cm$^2$)/g** | 93.5 | | 92.2 | 19.9 | | 20.8 | 10.3 | | 11.6 | 8.9 | | 9.5 | 10.9 | | 11.4 |

Table 3. Physiological parameters as affected by shoot orientation.

| Measurement stage | Berry set | | | Pea size | | | Veraison | | | Post veraison | | | Ripeness | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | down | up | | down | up | | down | up | | down | up | | down | up | |
| **Apical Photo (µMOL/m ²/s)** | 6.6 | 7.1 | ns | 10.0 | 10.6 | * | 10.4 | 10.9 | ns | 5.9 | 7.2 | ns | 4.1 | 6.8 | * |
| **Basal Photo (µMOL/m²/s)** | 8.5 | 9.7 | ns | 5.0 | 6.6 | * | 5.2 | 5.3 | ns | 3.1 | 4.8 | * | 2.3 | 3.3 | * |
| **Apical ψ ( KPa)** | -782.8 | -748.7 | ns | -663.7 | -700.0 | ns | -935.0 | -908.5 | * | -1114.8 | -1041.3 | * | -976.2 | -953.7 | ns |
| **Basal ψ ( KPa)** | -771.8 | -775.6 | ns | -612.5 | -648.5 | * | -950.0 | -853.5 | ns | -1198.3 | -1124.8 | ns | -1173.7 | -997.5 | ns |
| **Apical STEM ( KPa)** | -607.5 | -603.1 | ns | -528.7 | -518.5 | ns | -711.2 | -734.0 | ns | -1026.5 | -973.1 | ns | -875.0 | -863.7 | ns |
| **Basal STEM ( KPa)** | -522.5 | -543.5 | ns | -454.7 | -454.7 | ns | -668.5 | -662.5 | ns | -974.8 | -880.0 | ns | -925.0 | -885.0 | ns |
| **Apical Trans (µMOL/m ²/s)** | 2.9 | 4.6 | ns | 3.8 | 3.9 | * | 4.5 | 4.3 | ns | 5.7 | 5.1 | ns | 2.8 | 2.9 | ns |
| **Basal Trans(µMOL/m ²/s)** | 3.3 | 6.7 | ns | 2.9 | 3.1 | ns | 3.0 | 3.0 | ns | 3.5 | 4,6 | * | 1.5 | 1.9 | ns |
| **Apical Stom Cond (mMOL/m ²/s)** | 103.5 | 107.0 | ns | 173.9 | 175.1 | ns | 139.1 | 167.2 | ns | 159.1 | 129.7 | ns | 88.0 | 103.5 | ns |
| **Basal Stom Cond (mMOL/m ²/s)** | 131.2 | 152.05 | * | 122.5 | 133.3 | ns | 100.9 | 143.0 | ns | 77.3 | 108.1 | * | 40.8 | 65.1 | ns |

**Fig. 1a - Soil water 2002/03**

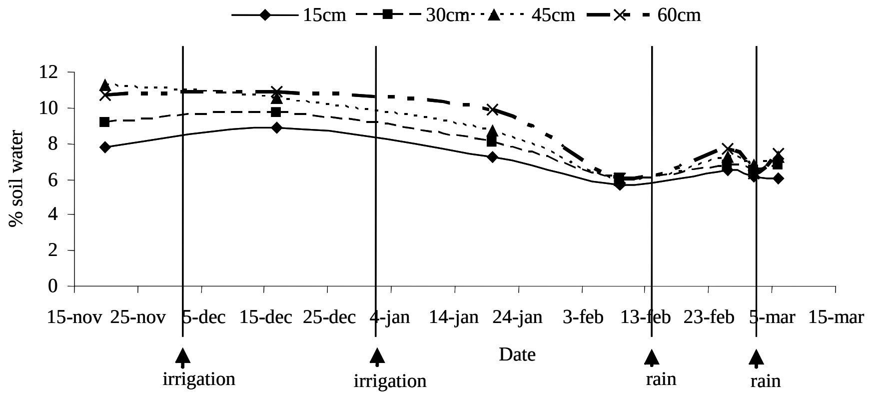

**Fig. 1b - Soil water 2003/04**

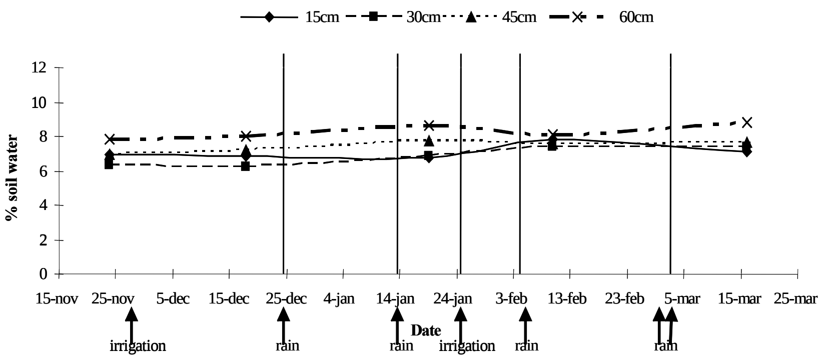

Fig.4 - % water in the skins

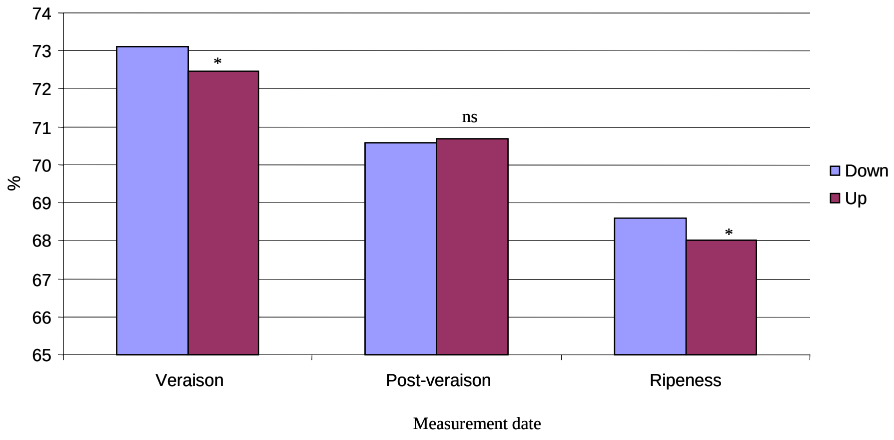

Fig.2 - Mean of number nodes of lateral shoots *versus* node position of the main shoot

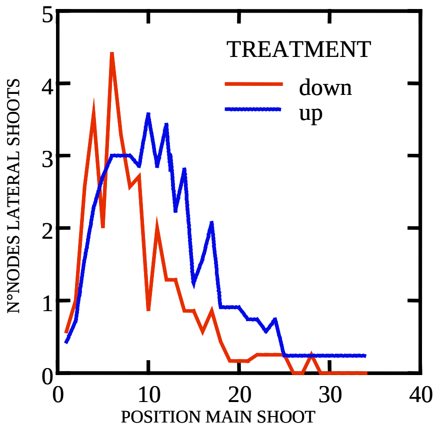

Fig.5 - Absorbance

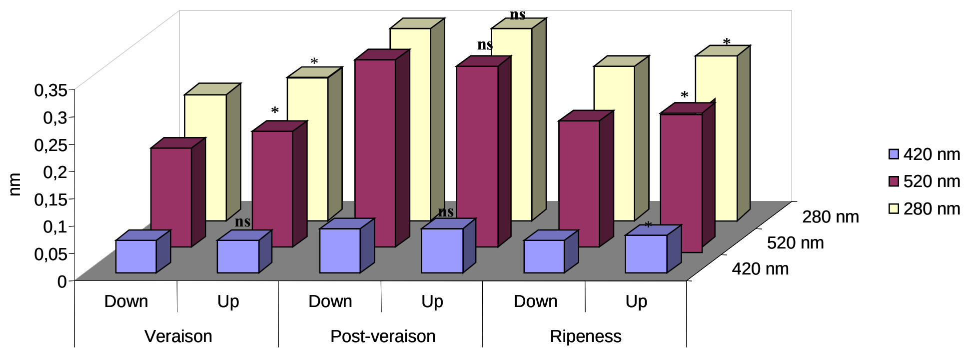

Fig.3 - Light interception above the cordon

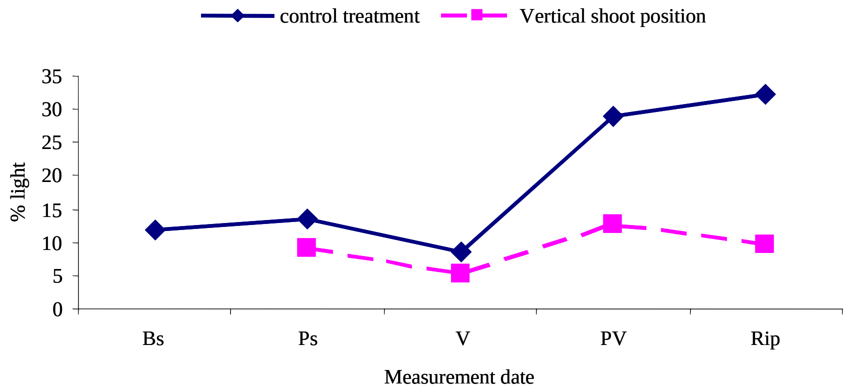

**Fig.6 - Sugars and acids content**