

The effects of pre- and post-veraison water stress on growth and physiology of potted Pinot Noir grapevines at varying crop levels

by

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S u m m a r y : The interactions of water stress timing and crop level on growth, gas exchange, water relations and ripening of potted Pinot Noir grapevines were examined. Pre-veraison water stress induced a greater reduction of shoot and berry growth and a more rapid limitation of net photosynthesis (Pn) and stomatal conductance (g_s) as compared to post-veraison stress. At the end of stress, when mid-day and pre-dawn leaf water potential were below -1.1 and -0.6 MPa, the reduction in Pn of stressed vines was more marked in the 2- and 4-cluster plants versus 1-cluster plant. Crop level had almost no significant effects on gas-exchange, growth and ripening and but few interactions with timing of water stress. These responses seem to reflect the high leaf area-to-fruit ratios at each crop level which probably buffered the effects of reduced leaf function induced by water stress.

K e y w o r d s : *Vitis vinifera* L., crop level, water stress, photosynthesis, berry growth, berry ripening.

Introduction

The effects of water stress on vegetative and berry growth, ripening and gas exchange in grapevine have been widely investigated (KRIEDEMANN and SMART 1971; MERIAUX *et al.* 1976; SMART and COOMBE 1983; DÜRING 1988). In general, pre-veraison water stress tends to have greater effects on berry size reduction as compared to post-veraison stress (SMART 1974; HARDIE and CONSIDINE 1976; MATTHEWS and ANDERSON 1988) which, conversely, tends primarily to affect berry ripening (HARDIE and CONSIDINE 1976; HARDIE 1980). However, these effects on berry ripening are not always consistent. Pre- and post-veraison stresses imposed on field-grown Cabernet franc vines did not affect onset of veraison, duration of ripening, juice pH or potassium levels, and little difference was found in °Brix and TA (MATTHEWS and ANDERSON 1989). On the other hand, other findings have shown consistent juice °Brix reduction for post-veraison water stress compared to control and a delay in ripening regardless of stress timing (HARDIE and CONSIDINE 1976).

It has been postulated that the sensitivity of the plant to external stresses (e.g. water stress) may be dependent upon the „source-sink“ balance (FLORE and LAKSO 1990; LAKSO 1990). A widely used indicator of this balance in grapes is the leaf area-to-fruit ratio (LA/F). Inadequate ripening has been commonly associated with LA/F lower than 6-8 cm²/g (MAY *et al.* 1969; KLEWER and OUGH 1970; SHAULIS and SMART 1974), while other studies have shown maximum berry weight, °Brix and coloration at LA/F ranging from 10 to 14 cm²/g (KLEWER and ANTCLIFF 1970; KLEWER and OUGH 1970; KLEWER and WEAVER 1971). Calculation of this index assumes that the leaf area is well exposed to the sun and that the leaves are healthy and fully functional. If the grapevine under non-stress conditions is near the critical leaf area-to-fruit ratio due to high crop load, then the vine would be expected to have more sensitive response thresholds to additional stress due to drought.

The objective of this study was to examine the effects of water stress timing on the growth and physiology of potted Pinot Noir grapevines when varying LA/F ratios were imposed by leaving a series of crop levels on the vine. Potted vines were used in this work since total leaf area can closely approximate the exposed leaf area which should be used in the calculation of the LA/F ratio.

Material and methods

Thirty-six 2- and 3-year-old potted Pinot Noir/Couderc 3309 grapevines were selected for uniformity from a group of 70 vines when shoots were 30 cm long. Within each group the vines were randomly assigned to treatments. Each vine was shoot thinned to 4 fruiting shoots/vine with 1 cluster per shoot. The treatments were timing of water stress (none, pre-veraison and post-veraison) and crop level (1,2 and 4 clusters per vine) in a split-plot design with 4 vine-replicates per treatment combination and with the water treatment as the whole plot. The vines were grown outside in 28 l pots of Cornell Mix A (peat: vermiculite = 1:1 v/v) and were fertilized prior to budbreak with a slow-release fertilizer (Osmocote 14-14-14, Sierra Chemical, Miplitas, CA, USA).

Twelve days after bloom each vine was assigned to a crop level treatment of 1,2 and 4 clusters per vine and thinned accordingly. Seventeen days after bloom, water was withheld from the pre-veraison stress treatment by covering the top of each pot with aluminum foil sealed to the trunk and pot to exclude water. Similar light microclimate in the other treatments was achieved by covering the pots with perforated foil to allow water penetration. Foil was also placed on the side of the pots to minimize radiation-induced heating of the root zone. Nine days thereafter, when growth and photosynthesis had been limited but before induction of leaf abscission, the stressed plants were re-watered and watered for the rest of the season. The post-veraison stress treatment was applied by withholding water in the same way from veraison (64 d after bloom) for 10 d; thereafter the stressed plants were rewatered and watered for the rest of the season.

G r o w t h m e a s u r e m e n t s : One fruiting shoot on each plant was marked for detailed growth measurements. Beginning at bloom, shoot length and the plastochron index (PI) (ERICKSON and MICHELINI 1957), calculated using a reference leaf length of 20 mm, were determined on the 36 marked shoots at intervals of 2-4 d until veraison and 5-8 d post-veraison. Seventeen d after bloom, when the pre-veraison stress began, berry diameters (approximately 7 mm on that date) on 5 marked berries per cluster on the marked shoots (for 20 berries in each of the 9 treatments) were measured with a digital caliper at similar intervals. Since about 10 % of the berries were damaged by disease, birds or mechanical stress at varying times, substitute berries of similar size to the damaged ones were selected to maintain sample berry numbers. Destructive berry sampling for juice °Brix began at the end of the pre-veraison stress period with 1 berry per marked cluster. Post veraison sampling of °Brix was increased to 3 berries/cluster for all clusters to provide proportionate sampling of all crop levels. Prior to and during veraison, effects of the treatments on the timing of veraison were evaluated by force-deformation as measured on an Instron testing instrument (BOURNE 1967; LEE and BOURNE 1980).

At harvest, 89 d after bloom, all shoots were excised and the lengths were measured. The total numbers of nodes and the numbers of mature nodes with periderm were counted. Total leaf areas, fresh weights and dry weights of all leaves remaining at harvest on all plants were estimated from total leaf fresh weights and the fresh weights, dry weights and leaf areas and their relationship on a subsample of about 15 % of the leaves. The numbers of leaves that abscised prior to harvest were recorded. Fruit yields, berry fresh weights (of 5 berries/cluster), juice °Brix, pH, titratable acidity (TA) and K⁺ concentration (by selective electrode) were measured.

Physiological measurements: Photosynthesis (P_n) and stomatal conductance (g_s) of healthy, mature, well exposed mid-shoot leaves in each treatment were estimated at mid-day under light-saturated conditions at intervals throughout the growing season. Measurements were taken 4 and 3 times during the pre- and post-veraison stresses, respectively. Measurements were taken with an ADC LCA-2 field gas analysis system (ADC, Hoddesdon, Herts., U.K.). Typically on the same day, many times concurrently, total leaf water potential (ψ_w) and stem potential (ψ_{st}) from exposed and pre-bagged leaves were estimated with a Scholander pressure bomb (SCHOLANDER *et al.* 1965). Leaf osmotic potentials (ψ_s) on the exposed leaves were estimated by freezing the leaves immediately after total potential measurements, then expressing sap from the thawed leaves for analysis in a microosmometer (μ Osmette, Precision Systems Inc., Nattick, MA, USA). The turgor potentials (ψ_t) were estimated as the difference between osmotic and total water potentials. Pre-dawn water potentials (ψ_{pd}) were determined on pre-bagged leaves early in the morning on vines held overnight in a dark barn to insure the absence of dew and uniformity of darkness during measurement. The gas exchange and water potential readings were taken on 1 leaf/plant.

Soil water status was monitored throughout the season with tensiometers, with 2 tensiometers/crop level in the stressed plants and 3 in the well watered controls. Soil samples were taken at the same time as pre-dawn leaf water potential readings on one date to correlate the soil water content to predawn leaf water potentials.

Statistical analysis of data was performed by PROC GLM of SAS package. Multivariate analysis of variance was carried out on growth and ripening data taken on the same experimental units at several points in time (LITTELL 1989).

Results

Soil water status, gas exchange and leaf water potentials: Tensiometer readings revealed a rapid decrease of soil water potential during the two periods of water stress, the maximum degree of water stress (approximately -0.08 MPa) being reached at the end of each period. Vines stressed at pre-veraison showed a significant reduction in P_n after three days of stress (Fig. 1) at a soil water potential of about -0.05 MPa. The lowest values of P_n , about 70 % reduction from pre-stress rates, were reached at the end of the stress period. Water stress

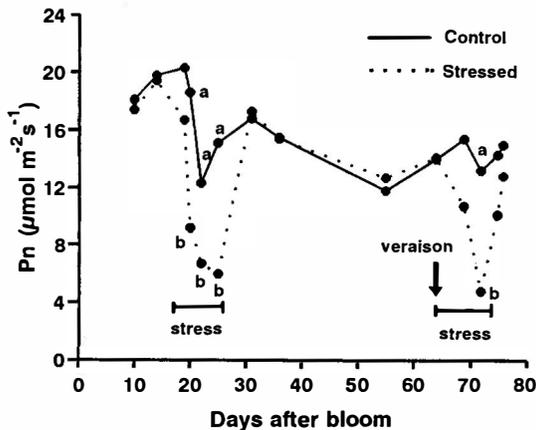


Fig. 1: Seasonal variation of net photosynthesis (P_n) of pre- and post-veraison stressed Pinot Noir grapevines as compared to control. Mean separation within each date by Student-Newman-Keuls test, 5 % level. Lack of separation indicates non-significance.

imposed after veraison, however, induced significant limitation of Pn only after 8 d of stress giving a similar Pn reduction. For both stress periods Pn recovered to levels comparable to control few days after rewatering.

Crop level in this study had no significant impact on photosynthetic rate, except for one date at the beginning of the post-veraison stress. Stomatal conductance showed the same patterns of response to timing of stress and crop level as photosynthesis. A water x crop interaction on Pn and g_s occurred during the pre-veraison stress, reaching significance on day 8 when the reduction in Pn and g_s on stressed vines was greater in the 2- and 4-cluster plants (Fig. 2).

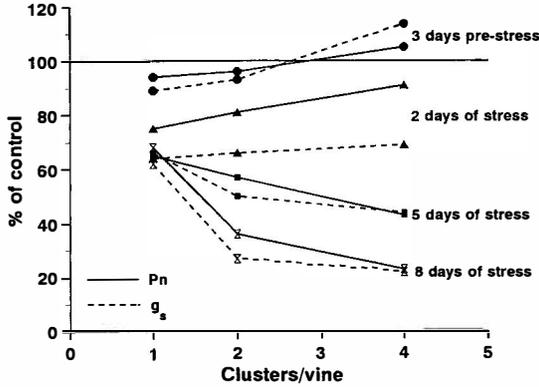


Fig. 2: Net photosynthesis (Pn) and stomatal conductance (g_s) (% of control) of potted Pinot Noir grapevines prior and during the pre-veraison stress period as a function of crop level. Significant water x crop interaction (5 % level) on day 8 of stress for both parameters.

Pre-dawn leaf water potentials 3 d after the beginning of the pre-veraison stress were significantly lower on the stressed vines as compared to the control (Tab. 1). On this date, a linear correlation ($y = 4.85 - 0.724x$, $R^2 = 0.824$) between pre-dawn leaf water potential and soil water content was found. Total leaf water potential progressively decreased on stressed vines and turgor potential showed similar variation since no significant osmotic adjustment occurred (Tab. 1). During the pre-veraison stress period, water relations were not markedly influenced by crop levels.

Variations of leaf water status on vines stressed after veraison generally followed a similar pattern (Tab. 2). Stem and total leaf water potential decreased with increasing stress, and recovery of water potential (Tab. 2) and Pn (Fig. 1) appeared to be complete 2 d after rewatering. Again, crop level had no effect on pre-dawn stem and total leaf water potential. No significant water stress x crop level interactions were found during the 2 periods of stress in relation to leaf water potentials.

Table 1

Pre-dawn stem and leaf water potential (-MPa) during the pre-veraison stress imposed on potted Pinot Noir grapevines

Timing of stress	3 days of stress				5 days of stress			8 days of stress				
	ψ_{pd}	ψ_w	ψ_s	ψ_t	ψ_w	ψ_s	ψ_t	ψ_{pd}	ψ_{st}	ψ_w	ψ_s	ψ_t
Control	.16a	.78	1.35	.57	.79a	1.62	.83a	.16a	.53a	.77a	1.62	.85a
Pre-veraison	.35b	.98	1.48	.50	1.02b	1.65	.63b	.62b	1.07b	1.11b	1.52	.41b
Post-veraison	.20a	.67	1.54	.87	.75a	1.59	.84a	.18a	.54a	.75a	1.66	.91a
Significance ^x	*	ns	ns	ns	**	ns	*	**	**	**	ns	**

^x The pre-veraison stress was imposed 17 days after bloom and vines were rewatered 9 days later.
^x Mean separation within columns by Student-Newman-Keuls test; significant at $p < 0.05$ (*), 0.01 (**) or not significant (ns).

Table 2

Pre-dawn stem and leaf water potential (– MPa) during the post-veraison of potted Pinot Noir grapevines and two days after rewatering

Timing of stress	5 days of stress				8 days of stress			2 days after rewatering		
	ψ_{st}	ψ_w	ψ_s	ψ_t	ψ_{pd}	ψ_{st}	ψ_w	ψ_{pd}	ψ_{st}	ψ_w
Control	.52a	.75a	1.41	.66	.26a	.58a	.82a	.20	.43	.74
Post-veraison	.83b	.99b	1.50	.51	.78b	1.19b	1.31b	.16	.38	.64
Significance ^x	**	**	ns	ns	**	**	**	ns	ns	ns

The post-veraison stress was imposed 64 days after bloom and vines were rewatered 10 days later.

Leaf water potential measurements on vines stressed at pre-veraison were not taken.

^x t-test; significant at $p \leq 0.05$ (*), 0.01 (**), or not significant (ns).

Growth, ripening, and yield: Shoot elongation was significantly reduced during the season only by pre-veraison water stress. This reduction was evident for the rest of the season. Shoot PI showed the same pattern. Final shoot length and PI of vines which experienced post veraison stress did not differ from well watered plants due to the late timing of that water stress. Crop level had no significant influence on shoot elongation and PI.

At harvest, vines stressed after veraison had a significantly higher percentage of defoliated nodes and a lower total leaf area as compared to control. Total leaf area on vines stressed before veraison did not statistically differ from well-watered plants. Both timings of water stress caused a reduction of total shoot length. Total and percentage of nodes with periderm were not statistically affected by timing of water stress. No significant crop level effects or crop level x water stress interactions were found for any of the vegetative parameters measured.

Water stress applied at pre-veraison during the first stage of berry development resulted in a rapid reduction of berry growth expressed as berry diameter (Fig. 3). After rewatering, vines stressed before veraison tended to compensate with 2 d of more rapid berry growth and their berry size did not differ from that of control for the rest of the season. Post-veraison water stress did not result in any significant reduction of berry diameter as compared to that of well-watered vines. Crop level had no influence on berry diameter throughout the period of measurement.

After 7 d of pre-veraison stress the stressed berries were significantly softer than control. Thereafter, yet before veraison, no differences were found; post-veraison stress induced no

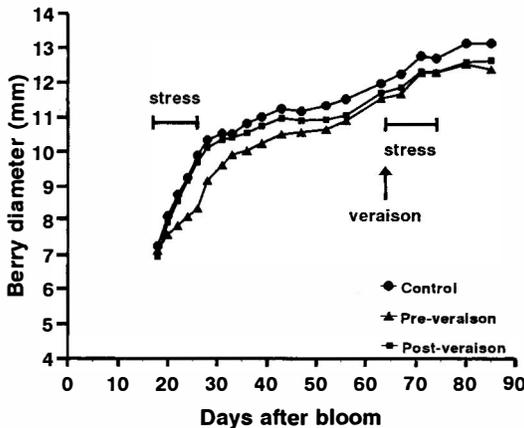


Fig. 3: The effect of pre- and post-veraison water stress on berry diameter of potted Pinot Noir grapevines as compared to control. Significant time x water stress interaction (Wilks' Lambda test, 1 % level). No significant differences in final berry diameter (SNK test, separate analysis).

differences in berry firmness. Juice °Brix and total soluble solids (TSS) were not significantly influenced by timing of water stress or crop level over the season. Must composition was slightly affected by treatments, and only pH was significantly higher on the plants stressed after veraison as compared to control (Tab. 3). Yield increased linearly with crop level, and vines stressed before veraison had a somewhat lower berry fresh weight and yield than in other treatments (Tab. 3). Crop load, as expressed by leaf area-to-yield ratio, decreased linearly with crop, though without reaching limiting values of about 8-10 cm²/g as discussed earlier.

Table 3

Effects of timing of stress and crop level on berry growth, yield and must composition of potted Pinot Noir grapevines at harvest. LA/yield ratios calculated from treatment means.

Factor	Berry weight (g)	Yield (g)	LA/Yield (cm ² /g)	TSS/berry (mg)	Must composition			
					°Brix	TA (g/100ml)	pH	K ⁺ (g/l)
Timing of stress								
Control	1.675	357	36	279	17.1	0.81	3.18a ²⁾	2.467
Pre-veraison	1.390	261	42	232	16.5	0.87	3.26ab	2.900
Post-veraison	1.669	347	27	288	16.3	0.90	3.31b	2.873
Crop level								
1 cluster/vine	1.550	88 ¹⁾	124	269	16.3	0.86	3.30	3.028
2 clusters/vine	1.667	309	37	281	16.6	0.83	3.25	2.654
4 clusters/vine	1.478	552	21	236	16.8	0.90	3.22	2.681

1) Orthogonal polynomial coefficients; Linear (1st), significant at 1% level.

2) Mean separation by Student-Newman-Keuls test, significant at 5% level.

Discussion

Pre- and post-veraison water stresses imposed on Pinot Noir grapevines had the expected effects of temporarily reducing gas exchange, whereas withholding water before veraison resulted in a faster limitation of Pn and g_s and in aggravated effects of water stress with crop at the end of the dry period. This response seems to be related to the higher water use generally recorded in cropping grapevines (LOVEYS and KRIEDEMANN 1974; EIBACH 1981), which may become a major limiting factor under water stress conditions. However, the same effect was not detected after veraison, suggesting that the physiological response to water stress and crop level may also depend on the stage of plant development. The absence of consistent osmotic adjustment under water stress underscores the variability of this adaptive mechanism in vines subjected to water deficit. Considerable osmotic adjustment (-1 MPa) during slow stress was found in Sultana grapevine cuttings (DOWNTON 1983); on the other hand DURING and LOVEYS (1982) found a different degree of osmotic adjustment depending on cultivars and climatic conditions. Also, growing conditions must be taken into account; LAKSO *et al.* (1984) showed little osmotic adjustment on potted apple trees but more than -2.0 MPa of adjustment in nearby field trees.

When the leaf-to-fruit ratios were high, increasing crop did not result in any distinct effect on gas exchange or plant water status. This finding supports the assumption that in general a „sink effect“ on gas exchange is not shown unless the source is strongly limited (FLORE and LAKSO 1990). Reduced leaf area per plant in post-veraison stress was primarily related to the higher pre-harvest defoliation since treatments did not differ in terms of total nodes and total shoot length. Even if total shoot length and final berry size were similar, early water stress was more effective in temporarily limiting shoot and berry growth. These findings agree with others (HARDIE and CONSIDINE 1976; FREEMAN and KLIEWER 1983; LAKSO unpublished data) that show a

high sensitivity of berry growth to soil water deficit during the post-bloom cell division period and, conversely, less sensitivity during the lag phase and the early part of the final growth stage. Response of berry growth to water stress induced at different times during the season in our experiment also supports the assumption of HARDIE and CONSIDINE (1976) that berries exceeding a certain size acquire some resistance to desiccation.

The lack of significant interactions between crop level and water stress regarding the vegetative and fruit development of Pinot Noir grapevines appears to be due to the buffering effect of high leaf area per fruit. Due to very high LA/F ratios (Tab. 3), source limitation probably did not occur as a consequence of reduced leaf function or leaf area induced by transient water stress. In addition, the complete photosynthetic recovery that occurred after each period of stress reduced the long-term effects on growth and berry ripening although stress during the early cell division period caused a marked loss of berry size.

A moderate variation in must composition as related to crop level and water stress at non-limiting leaf area-to-fruit ratios are in agreement with previous work on defoliation showing the existence of a threshold leaf-to-fruit ratio needed to reach maximum values of several maturation and quality parameters (MAY *et al.* 1969; KLEWER and ANTCLIFF 1970; KLEWER and OUGH 1970; KLEWER and WEAVER 1971). This threshold value ranging from 8 to 14 cm² LA/g fresh weight, was not approached in the present Pinot Noir study, even at highest crop level (Tab. 3).

Acknowledgements

The authors would like to thank Dr. R. M. POOL and Dr. M. C. BOURNE for their assistance.

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Received April 13, 1993