

The Influence of *Vitis riparia* Rootstock on Water Relations and Gas Exchange of *Vitis vinifera* cv. Carignane Scion Under Non-Irrigated Conditions

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A two-year study examining the water relations and gas exchange of *Vitis riparia* Michaux, *Vitis vinifera* L. cv. Carignane, and grafted vines comprised of a Carignane scion on *V. riparia* rootstock was conducted in a non-irrigated vineyard at the University of California Kearney Agricultural Center, near Fresno, California. During the two seasons the data was taken (1992 and 1993), soil water content of the trial plot was similar and decreased during the growing season. Pre-dawn leaf water potential (Ψ_{leaf}), pre-dawn leaf osmotic potential (Ψ_{π}), and stem water potential values (Ψ_{stem}) did not differ among the treatments. Net carbon dioxide assimilation (A), stomatal conductance (g_s), and instantaneous water use efficiency (WUE) were influenced by treatment, and behaved similarly comparing the two years. Carignane vines had significantly greater gas exchange values than either *V. riparia* or the grafted vines, but the latter two were similar to one another. These results indicate that under non-irrigated conditions, rootstock can modify gas exchange behavior of the scion cultivar even though vine water status was not altered.

KEY WORDS: *Vitis vinifera*, *V. riparia*, graft, water relations, gas exchange

The prevalence of phylloxera in California has made the use of resistant rootstocks a necessity. It is well-known that rootstocks can affect yield [33], rates of shoot growth [19], mineral nutrition [28] and berry juice composition [17].

How rootstocks influence grapevine physiology and water relations, especially under drought or non-irrigated conditions, is poorly understood. Studies suggest that rootstock influences a grape scion's gas exchange capabilities [12], leaf water potential [13], and water stress recovery time [24]. There are studies that claim that the scion cultivar determines the grafted vines' ability to withstand drought stress [38], but there are also reports that the rootstock cultivar can have a strong influence on vine performance under stress conditions [3].

The objective of this study was to determine how a *V. riparia* rootstock influences gas exchange and water relations of a *V. vinifera* cv. Carignane scion under non-irrigated field conditions in California. Non-grafted vines of *V. riparia* and Carignane were included for comparison. *Vitis riparia* was chosen as the rootstock in this study because it has been shown to be sensitive to water stress [4]. Carignane was selected because of its origins in the semiarid climate of Spain [37], thus being well-adapted to growth in a warm climate such as found in the San Joaquin Valley, California [39].

Materials and Methods

In February 1990, dormant cuttings of *Vitis riparia* (USDA DVIT #1444) were taken from the United States Department of Agriculture National Clonal Germplasm Repository, near Winters, California, and cuttings of *V. vinifera* cv. Carignane (UCD-01) were taken from the University of California, Davis vineyards. The rooted cuttings were planted into 0.95-L milk cartons using a 1:1:2 (sand/compost, vermiculite, and peat moss) soil mix and placed in a greenhouse. In June 1990, the grapevines were transplanted into 3.8-L pots, with coarse sand as the potting medium and tongued, approach grafts were made (Carignane scion on *V. riparia*). The successfully grafted vines along with the *V. riparia* and Carignane potted vines were moved into a shaded lath-house for the remainder of the 1990 season. These three vine types were assigned the following treatment numbers: *V. riparia* vines - Treatment 1; Carignane vines - Treatment 2; and the grafted vines - Treatment 3.

The potted vines were moved to the University of California Kearney Agricultural Center during their first dormant period (Winter 1990-1991). Treatments 1 and 2 used in this study were part of a larger study investigating drought tolerance of 17 different *Vitis* species [26]. Vines of all 17 species and Treatment 3 were planted March 1991 in a 0.40-hectare vineyard utilizing a completely randomized block design on a 2.44 × 3.66 m spacing. Each treatment consisted of five individual vines. The soil was a Hanford fine sandy loam with a hardpan at a depth of 1.5 m. Standard pest control measures were used throughout the study. A single wire trellis, atop a stake at each vine (1.0 m above the soil surface) was employed to support shoots of the vines as the season progressed. Clusters were removed from all vines each year prior to anthesis.

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Vines were pruned to 8 to 12 buds per vine during the winters of 1991-92, 1992-93, and 1993-94.

During the 1991 growing season, the vineyard was furrow irrigated weekly. Vines were not irrigated at any time during the next two growing seasons. Data collection occurred during the summers of 1992 and 1993. All measurements for gas exchange, water potential and its components were collected from three replicate grapevines using two leaves per vine. Fully exposed leaves were taken between the seventh and fourteenth node counting from the base of the shoot for midday readings. Net CO₂ assimilation rate and stomatal conductance (to water vapor) were measured with a portable infrared gas analyzer (Analytical Development Company, Ltd. #DL2-12744, Hoddeson, England). Leaf and stem water potentials were measured with a pressure chamber (PMS Instrument Company, Corvallis, OR) as described by McCutchan and Shackel [23]. Leaf samples, for osmotic potential, were taken at predawn, quick frozen on dry ice, followed by storage at -80°C. For analysis, the leaf samples were thawed, brought to 37°C, and osmotic potentials read on a vapor pressure osmometer (Wescor 5500, Wescor, Inc. Logan UT).

Soil water content in the vineyard was monitored using a neutron probe (Troxler depth moisture gauge, model #3320). There were five access tube sites, two tubes per site, placed 0.5 m from the vine's trunk, both parallel and perpendicular to the row direction. Two of the five sites were located at an individual vine of Treatments 1 and 2. Readings were taken at increments of 0.3 m, starting 0.3 m beneath the soil surface down to 1.5 m. In 1992, measurements were taken the

entire season (Day of Year 118 to 240), while in 1993 measurements were taken sporadically throughout the season. Temperature, rainfall, and evaporative demand data were obtained from a California Irrigation Management Information System weather station located 300 m from the experimental vineyard.

Statistical analyses of stem water potential, stomatal conductance, net CO₂ assimilation and instantaneous water use efficiency included only the late season (DOY 185 – 255) data both years, collected on comparable days (a total of 5 separate measurement dates each year). Analyses of variance (ANOVA) was performed using a split-plot design, with the day of year as the "split". Least squares means are the combined data points from both years, five measurement dates and three replicates.

Results

Precipitation from the first of April until the last measurement date in 1992 totaled three mm (the rain fell on 12 April, DOY 102). There were three precipitation events during the same period in 1993; 2, 3, and 5 mm of rain fell on 17 April, 25 May, and 4 June, respectively. Maximum daily temperature for the months of July and August (DOY 181 to 243) in 1992 were 33.8°C and 35.8°C, respectively, and in 1993 were 33.4°C and 33.5°C, respectively. Potential ET (ET_p) ranged from 6 to 6.7 mm per day during the months of July and August both years.

The soil water content in the experimental vineyard decreased during both growing seasons (Fig. 1). The soil water content of the vineyard in 1993 was similar to that in 1992.

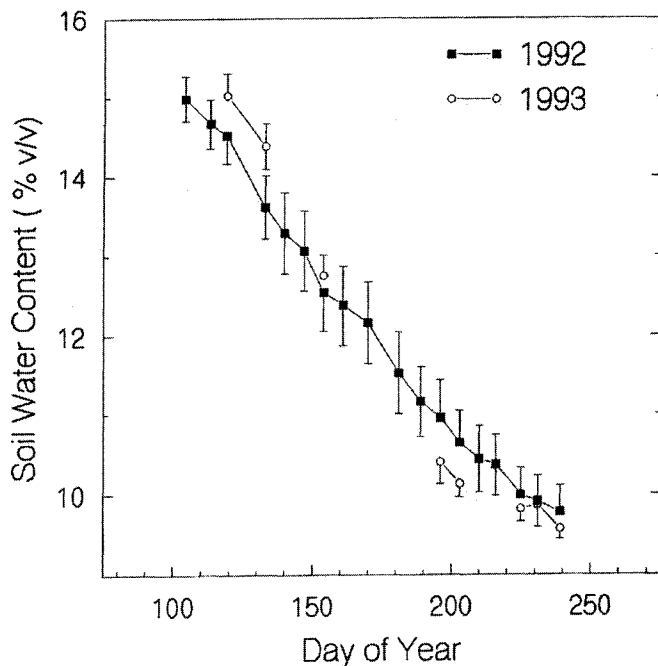


Fig. 1. Soil water content of the experimental plot during the course of two growing seasons. Values are the means of 10 access tube sites with five readings taken from 0.3 to 1.5 m deep. Bars represent ± 1 SE.

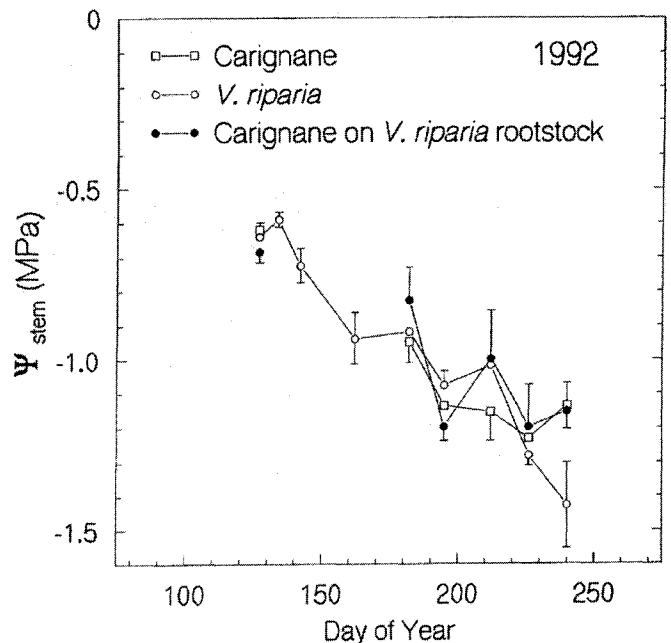


Fig. 2. Midday stem water potential values of the three treatments measured in 1992. Values represent the means of three vines. Bars represent ± 1 SE.

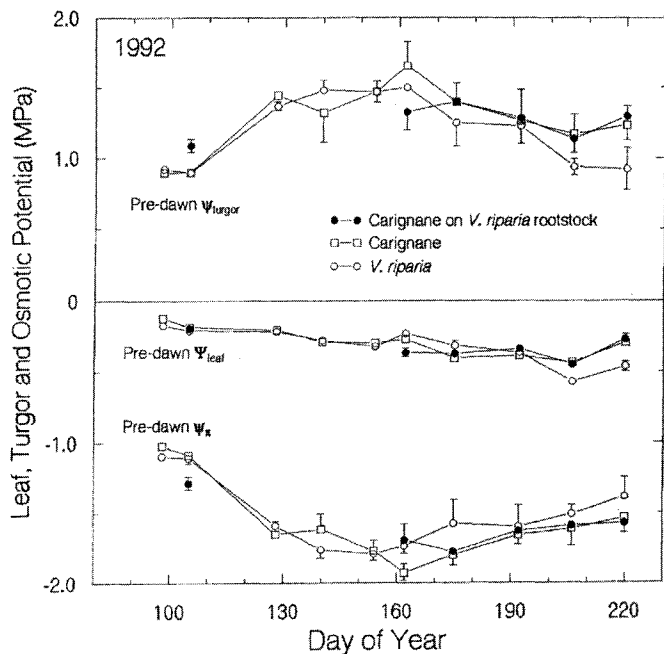


Fig. 3. The 1992 growing season pre-dawn leaf (Ψ_{leaf}), turgor (Ψ_{turgor}) and osmotic (Ψ_{π}) potentials of leaves from vines in the three treatments. Other information as found in Figure 2.

Midday stem water potential (Ψ_{stem}) of all grapevines decreased over time in 1992 (Fig. 2), as did midday leaf water potential (data not given). There were no significant differences among treatments, or between years. However, Ψ_{stem} values differed significantly as a function of the day of the year that the measurements were taken ($p < 0.0001$).

There was a gradual decrease in pre-dawn leaf water potential values (Ψ_{leaf}) during the 1992 growing season, with all three treatments having similar values

(Fig. 3). The lowest values of pre-dawn Ψ_{leaf} were -0.60, -0.43, and -0.44 for treatments 1, 2, and 3, respectively. The three treatments' pre-dawn leaf osmotic potential (Ψ_{π}) and turgor potential also had similar patterns over the season. Pre-dawn Ψ_{π} decreased for all treatments until day of year 160, then increased until the end of the season. Turgor potential initially increased and then decreased from day of year 160 until the last measurement date. There were no significant differences among treatments in late season means of pre-dawn Ψ_{leaf} , Ψ_{π} , and midday Ψ_{leaf} . The lowest values for midday Ψ_{leaf} were -1.44, -1.48 and -1.46 for Treatments 1, 2, and 3, respectively.

Early in the 1992 season, stomatal conductance of all three treatments was high ($\sim 500 \text{ mmol m}^{-2} \text{ s}^{-1}$), then decreased sharply (Fig. 4A). After the third measurement date and continuing until the end of the season, the own-rooted Carignane vines had significantly greater stomatal conductance values than either of the other two treatments; *V. riparia* and the grafted vines had comparable stomatal conductance values. Data collection in 1993 again demonstrated differences among treatments late in the season with results similar to those in 1992 (Fig. 4B). There were significant differences among treatments ($p < 0.0075$), but no differences between years (data not shown). The day of year on which measurements were taken was a significant source of variation ($p < 0.0001$). Late season (DOY 185–255) mean stomatal conductance of the Carignane vines was significantly higher than those of *V. riparia* and the grafted vines (Table 1).

The seasonal pattern of net CO_2 assimilation (A) in 1992 was similar to that of stomatal conductance. Net CO_2 assimilation rates were high ($\sim 16 \mu\text{mol m}^{-2} \text{ s}^{-1}$) early on, and decreased as the season progressed with significant differences among treatments (Fig. 5A).

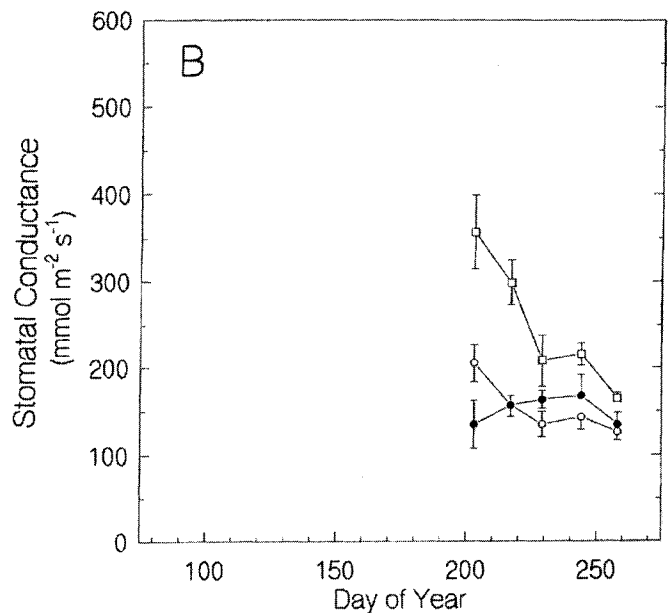
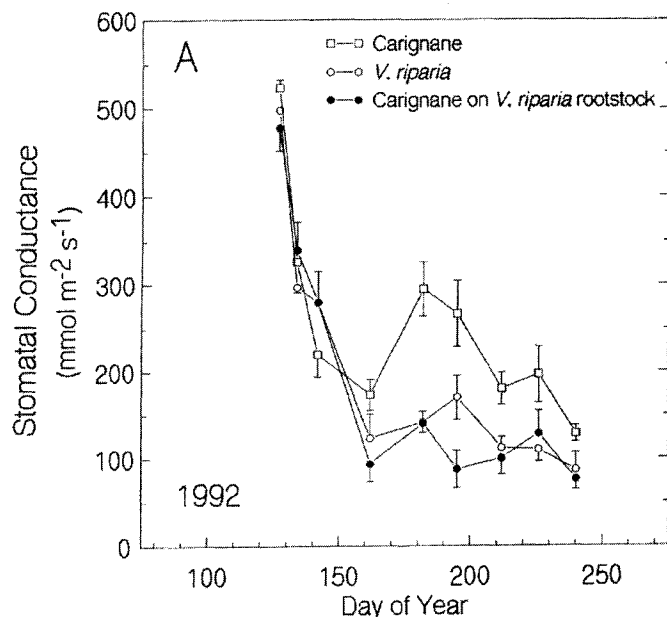


Fig. 4. Stomatal conductance of the three treatments measured during the 1992 growing season (A) and the latter part of the 1993 growing season (B). Other information as found in Figure 2.

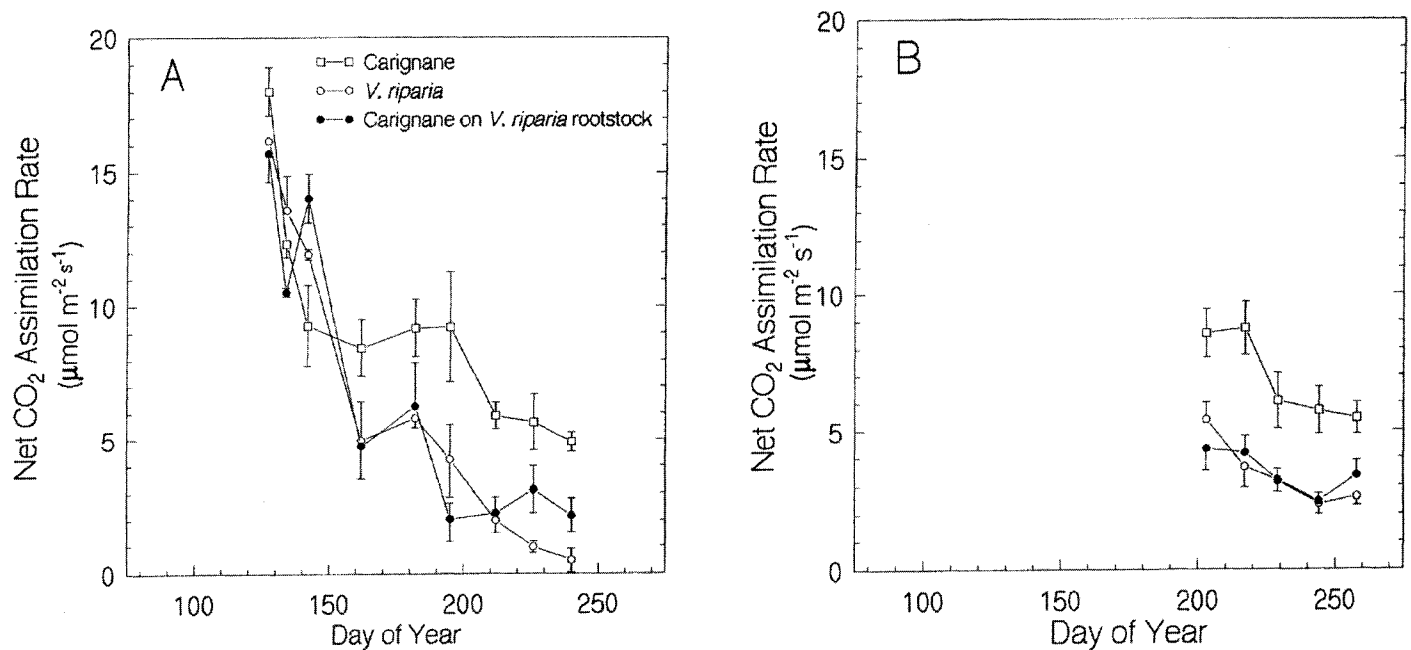


Fig. 5. Net CO₂ assimilation rates of the three treatments during the 1992 growing season (A) and the latter part of the 1993 growing season (B). Other information as found in Figure 2.

Carignane vines maintained the highest A throughout the latter part of the season. This pattern was repeated in 1993 (Fig. 5B). There were significant differences among treatments ($p < 0.0001$) but not between years. Carignane vines had the highest A, while there were no significant differences between *V. riparia* vines and the grafted vines (Table 1).

Instantaneous water use efficiency (WUE) is the ratio of net CO₂ assimilation to H₂O transpired, *i.e.*, μmol CO₂/mmol H₂O [9]. There were significant differences among the treatments ($p < 0.0016$) and between years ($p < 0.0078$). The seasonal means demonstrated that Carignane vines had significantly higher WUE than either *V. riparia* or the grafted vines (Table 1).

Pooling data from both years, a regression analysis of net CO₂ assimilation rate as a linear function of stomatal conductance resulted in significant regressions for each of the treatments (data not shown). As g_s decreased, A also decreased. However, contrast analysis of the slopes of these three regressions resulted in no significant differences among treatments.

Table 1. Comparison of Least Squares Means (1992 and 1993, days of year 185-255, 5 measurement dates each year, 3 replicates per date). Treatment 1 is *V. riparia*, Treatment 2 is Carignane, and Treatment 3 is the grafted vine unit. Means were separated using Tukey's adjustment for multiple comparisons. Different letters following the means denote a significant difference at $p < 0.05$.

Treatment	Stomatal conductance (mmol m ⁻² s ⁻¹)	Net CO ₂ assimilation (μmol m ⁻² s ⁻¹)	Water use efficiency (μmol CO ₂ / mmol H ₂ O)
1	136.3 b	2.80 b	0.458 b
2	229.5 a	6.07 a	0.683 a
3	137.3 b	3.31 b	0.550 b

There were no significant differences in pruning weights among the three treatments at the end of either growing season (data not given). Treatment 1 had the highest pruning weights while those of Treatment 3 had the lowest.

Discussion

The data presented in this paper demonstrated that there was a gradual decrease in soil water content throughout both growing seasons, and this was reflected in all measures of vine water status and gas exchange. The lowest values of predawn, stem and midday Ψ_{leaf} were -0.60, -1.43, and -1.48 MPa, respectively. The lowest predawn values measured during this experiment are much less negative than those reported in several potted vine studies [27,32] and field studies [31,35] examining water stress in grapevines. However, the values are similar to those reported in several other field studies for non-irrigated vines [5,38]. The minimum Ψ_{stem} values for the three treatments in this study are similar to the minimum diurnal value measured on *V. labruscana* [21]. Lastly, the lowest values of midday Ψ_{leaf} measured at the end of the growing season are comparable to those measured at this location on Thompson Seedless grapevines [2,15,35] and in many of the studies cited above.

When data from both years was pooled, stem water potential was not influenced by treatment. Natali *et al.* [24] and Williams and Smith [36] reported that rootstock did not affect midday leaf water potential (as opposed to midday stem water potential) of the common *V. vinifera* scion used in their experiments. However, rootstock significantly affected leaf water potential of grafted *V. vinifera* cv. Ruby Seedless vines [13]. It was found that rootstock also affected stem water

potential of apple trees [25]. They reported that an apple cultivar on dwarfing rootstock types had lower Ψ_{stem} values than the same cultivar grafted onto a vigorous rootstock. In addition, rootstock cultivar determined the Ψ_{leaf} of grafted beans (*Phaseolus vulgaris* on *P. acutifolius*, and vice versa) under drought conditions [29]. The results from this study would indicate that rootstock did not affect the scion's water status. In a field situation, the ability of the rootstock to explore more of the soil profile may assist in the extraction of additional water which would affect vine water status. In this study, the shallow depth of the soil profile (due to a hardpan at approximately 1.5 m) would limit rooting depth and thus the availability of water. Since vegetative growth of the treatments was similar and potential rooting depth the same, there was only a finite amount of water for each vine. The fact that there were no significant differences among treatments in vine water status values should not be surprising.

It has been reported that grapevines can osmoregulate [11]. Grimes and Williams [15] concluded that water stressed vines' Ψ_{π} declined 0.38 MPa compared to that of no or slightly water stressed vines, a value similar to that reported by Schultz and Matthews [32]. Rodriguez *et al.* [27] demonstrated an active osmotic adjustment of approximately 0.45 to 0.5 MPa in potted vines that were water stressed.

Early in the growing season, small changes in predawn Ψ_{leaf} were accompanied by large decreases in Ψ_{π} for all three treatments. Such a response has been purported to indicate that osmotic adjustment has taken place (5). However, there were no significant differences among the treatments with regards to Ψ_{π} at comparable predawn Ψ_{leaf} in this study indicating all three treatments responded similarly. It is interesting to note that the osmotic potential of all three treatments increased from day of year 160 until measurements were terminated at the end of the growing season in 1992 (Fig. 3). Such a response may indicate that as the season progressed, the ability of the vines to osmoregulate diminished. Schultz [31] reported that the osmotic potentials (measured at full turgor) of water stressed Grenache and Syrah vines were higher than those of the control (irrigated) vines. It was hypothesized that lowered carbon assimilation together with night temperatures favoring increased respiratory carbon losses would reduce the active solutes (principally sugars) found in the leaves. Such may have occurred in the present study, resulting in an increase in the osmotic potential as the growing season progressed.

Stomatal conductances of Carignane vines were significantly greater than those of *V. riparia* and the grafted vines, whereas the grafted vines' g_s values were similar to *V. riparia*. This data agrees with the report of Williams and Smith [36] in that the rootstock affected g_s of a common *V. vinifera* scion. Grapevine cultivars Orion and Gf. Ga-54-14 grafted onto 5BB rootstock showed increased g_s compared to the same ungrafted cultivars [12], but g_s of the 5BB rootstock was

not measured. A study on drought-stressed grafted apple trees reported that the rootstock determined g_s of the scion [16]. The results of Düring and Guilivo *et al.* agree with those found in this study, in that the grafted grapevines exhibited stomatal behavior similar to that of the rootstock.

Carignane had the highest A late into the season. A of the grafted vines and *V. riparia* were similar to each other, but significantly lower than Carignane. Williams and Smith [36] reported that rootstock did not affect the photosynthetic rate of a *V. vinifera* scion; however, Düring [12] did show that several cultivars' rates of photosynthesis were increased when grafted to 5BB rootstock. Rootstock was shown to affect the photosynthetic rate of apple [30].

Instantaneous WUE, as measured in this study has been shown to be correlated with integrated time scale measures of WUE (leaf carbon isotope discrimination, D) [9]. Carignane had a higher mean late season WUE than either *V. riparia* or the grafted vines; *Vitis riparia* and Carignane grafted onto *V. riparia* had similar WUE values.

There have been numerous reports indicating that, under dry soil conditions, gas exchange is controlled by a chemical signal that originates in the roots and is sent via the transpiration stream to the shoots [7,8,34]. It has been suggested that abscisic acid (ABA) is that signal [14,18]. Abscisic acid has been shown to decrease stomatal conductance of grapevines [10]. There are reports that water-stressed grapevines have higher levels of leaf ABA, ultimately affecting gas exchange [20,22]. Another study examining *V. vinifera* vines showed that afternoon stomatal conductance was highly correlated with ABA concentration in the xylem sap [6]. ABA, sent as a root signal may be a more sensitive indicator of water stress than leaf water potential, and thus would control stomatal conductance before a drop in Ψ_{leaf} [8]. This would effectively uncouple Ψ_{leaf} from Ψ_{soil} . If stomatal conductance can be controlled by a root signal, then Ψ_{leaf} would not necessarily continue to become more negative. Perhaps this finding would explain why the Ψ_{stem} values among the treatments in this study were not different, whereas the gas exchange values among treatments differed significantly. The high correlation between A and g_s found in this study would indicate that any reduction in g_s would decrease the carbon assimilation of the vine. Future work on whether ABA levels in the transpiration stream vary among *Vitis* species under varying levels of drought stress is needed. It has been demonstrated that ABA in leaves will differ for different *V. vinifera* cultivars [1].

The apparent uncoupling of Ψ_{leaf} from Ψ_{soil} may also be explained by the different rooting habits of *V. riparia* and *V. vinifera* cv. Carignane in this study. Root distributions of both species were mapped from trenches dug both parallel and perpendicular to the row direction (n = 3 for each direction) in 1993 down to the hardpan. Approximately 65% of *V. riparia*'s roots were found in the upper 0.5 m of soil (the remaining 0.5

to 1.5 m deep) while only 45% of Carignane's roots were in the upper 0.5 m [26]. Measurements of soil water content indicated that the upper portion of the rooting profile (0 to 0.5 m deep) dried out much more rapidly and was lower than the 0.5 to 1.5 m depth at the end of the season. Thus the exposure of a greater proportion of *V. riparia*'s roots to rapidly drying soil could also have stimulated that species to produce a greater amount of ABA when compared to Carignane. Unfortunately, roots were not mapped for the grafted vine treatment but one could probably assume that the rooting habit of the grafted vine would be similar to that of *V. riparia*.

The results of this study indicate that under non-irrigated or drought conditions, *V. riparia* influenced the gas exchange of the scion cultivar grafted onto it. However, the rootstock did not significantly affect vine water status (*i.e.*, Ψ_{stem} , predawn Ψ_{leaf} , Ψ_{π} , or Ψ_{turgor}) under the conditions of this study. As California viticulture gradually moves onto more marginal (drier) land with less available water and as human population pressures make agricultural water more costly, farming with less water may become more common. Rootstock choices for farming under these constraints become even more critical.

Conclusions

This study was conducted to determine how two *Vitis* species and a grafted vine of the two (Carignane on *V. riparia*) responded to a gradual decrease in soil water content under environmental conditions in the San Joaquin Valley. All measures of vine water status did not differ among treatments. This was probably the result of the limited amount of water available in the soil profile, due to a hardpan at a depth of 1.5 m in the experimental vineyard. Therefore, any morphological adaptation of the root system of either species that might favor drought tolerance, such as the ability of the vine's roots to explore the soil to greater depths, would not be expressed. However, the rootstock of the grapevines significantly influenced gas exchange. Stomatal conductance, photosynthetic rates, and instantaneous water use efficiency of the grafted vines were similar to those of the rootstock vines and different from those of the scion cultivar vines. One drought tolerance mechanism found in this study was a greater WUE for the *V. vinifera* cultivar used.

Literature Cited

1. Albuquerque-Regina, M. Réponses des cépages de *Vitis vinifera* L. aux variations de l'environnement: Effets de la contrainte hydrique sur la photosynthèse, la photorespiration et la teneur en acide abscissique des feuilles. These: Doctorat de l'Université de Bordeaux II, 212 pp. (1993).
2. Araujo, F., L. E. Williams, and M. A. Matthews. A comparative study of young 'Thompson Seedless' grapevines (*Vitis vinifera* L.) under drip and furrow irrigation. II. Growth, water use efficiency and nitrogen partitioning. *Sci. Hortic.* 60:251-265 (1995).
3. Candolfi-Vasconcelos, M. C., W. Koblet, *et al.* Influence of defoliation, rootstock, training system, and leaf position on gas exchange of Pinot noir grapevines. *Am. J. Enol. Vitic.* 45:173-180 (1994).
4. Carboneau, A. The early selection of grapevine rootstocks for resistance to drought conditions. *Am. J. Enol. Vitic.* 36:195-198 (1985).
5. Chaves, M. M., and M. L. Rodrigues. Photosynthesis and water relations of grapevines growing in Portugal - response to environmental factors. *In: NATO ASI Series Vol. G15, Plant Response to Water Stress.* J. D. Tenhunen *et al.* (Eds.). Springer-Verlag, Berlin, Heidelberg (1987).
6. Corriea, M. J., J. S. Pereira, *et al.* ABA xylem concentrations determine maximum daily leaf conductance of field-grown *Vitis vinifera* L. plants. *Plant Cell Environ.* 18:511-521 (1995).
7. Davies, W. J., F. Tardieu, and C.L. Trejo. How do chemical signals work in plants that grow in drying soil? *Plant Physiol.* 104:309-314 (1994).
8. Davies, W. J., and J. Zhang. Root signals and the regulation of growth and development of plants in drying soil. *Ann. Rev. Plant Physiol. Plant Molec. Biol.* 42:55-76 (1991).
9. Donovan, L. A., and J. R. Ehleringer. Carbon isotope discrimination, water use efficiency, growth, and mortality in a natural shrub population. *Oecologia* 100:347-354 (1994).
10. Downton, W. J. S., B. R. Loveys, and W. J. R. Grant. Stomatal closure fully accounts for the inhibition of photosynthesis by abscisic acid. *New Phytol.* 108: 263-266 (1988).
11. Düring, H. Evidence for osmotic adjustment to drought in grapevines (*Vitis vinifera* L.). *Vitis* 23:1-10 (1984).
12. Düring, H. Photosynthesis of ungrafted and grafted grapevines: Effects of rootstock genotype and plant age. *Am. J. Enol. Vitic.* 45:297-299 (1994).
13. Ezzahouani, A., and L. E. Williams. The influence of rootstock on leaf water potential, yield, and berry composition of Ruby Seedless grapevines. *Am. J. Enol. Vitic.* 6:559-563 (1995).
14. Gibson, A., K. T. Hubick, and E. P. Bachelard. Effects of abscisic acid on morphological and physiological responses to water stress in *Eucalyptus camaldulensis* seedlings. *Austral. J. Plant Physiol.* 18:153-163 (1991).
15. Grimes, D. W., and L. E. Williams. Irrigation effects on plant water relations and productivity of Thompson Seedless grapevines. *Crop Sci.* 30:255-260 (1990).
16. Guillivo, C., G. Ponchia, *et al.* Effect of rootstock on water balance of Golden Delicious apple. *Acta Hortic.* 171:399-404 (1985).
17. Hale, C. R., and C. J. Brien. Influence of Salt Creek rootstock on composition and quality of Shiraz grapes and wine. *Vitis* 17:139-146 (1978).
18. Khalil, A. A., and J. Grace. Does xylem sap ABA control the stomatal behavior of water-stressed sycamore (*Acer pseudoplatanus* L.) seedlings? *J. Exp. Bot.* 44:1127-1134 (1993).
19. Lefort, P. L., and N. Legisle. Quantitative stock-scion relationships in vine preliminary investigations by the analysis of reciprocal graftings. *Vitis* 16:149-161 (1977).
20. Liu, W. T., R. Pool, *et al.* Changes in photosynthesis, stomatal resistance and abscisic acid of *Vitis labruscana* through drought and irrigation cycles. *Am. J. Enol. Vitic.* 19:239-246 (1978).
21. Liu, W. T., W. Wenkert, *et al.* Soil-plant water relations in a New York vineyard: Resistances to water movement. *J. Am. Soc. Hortic. Sci.* 103:226-230 (1978).
22. Loveys, B. R., and H. Düring. Diurnal changes in water relations and abscisic acid in field grown *Vitis vinifera* cultivars. II. Abscisic acid changes under semi-arid conditions. *New Phytol.* 97:37-47 (1984).
23. McCutchan, H., and K. A. Shackel. Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). *J. Am. Soc. Hortic. Sci.* 117:607-611 (1992).
24. Natali, S., C. Xiloyannis, and M. Castagneto. Effect of soil water content on leaf water potential and stomatal resistance of grapevine (*Vitis vinifera*) grafted on different rootstocks. *Acta Hortic.* 171:331-340 (1985).
25. Oliën, W. C., and A. N. Lakso. Effect of rootstock on apple (*Malus domestica*) tree water relations. *Physiol. Plant.* 67:421-430 (1986).
26. Padgett-Johnson, M. Vine water relations, gas exchange, growth and root distribution of several *Vitis* species under irrigated and non-

irrigated conditions. Thesis, Univ. California, Davis, 420 pp. (1999).

27. Rodriguez, M. L., M. M. Chaves, *et al.* Osmotic adjustment in water stressed grapevine leaves in relation to carbon assimilation. *Austral. J. Plant Physiol.* 20:309-321 (1993).

28. Rühl, E. H. Effect of potassium supply on cation uptake and distribution in grafted *Vitis champinii* and *Vitis berlandieri* x *Vitis rupestris* rootstocks. *Austral. J. Exp. Agric.* 31:687-691 (1991).

29. Sanders, P. L., and A. H. Markhart III. Interspecific grafts demonstrate root system control of leaf water status in water-stressed *Phaseolus*. *J. Exp. Bot.* 43:1563-1567 (1992).

30. Schechter, I., D. C. Elfving, and J. T. A. Proctor. Canopy development, photosynthesis and vegetative growth as affected by apple rootstocks. *Fruit Va. J.* 45:229-237 (1991).

31. Schultz, H. R. Water relations and photosynthetic responses of two grapevine cultivars of different geographical origin during water stress. *Proceedings: Workshop Strategies to Optimize Wine Grape Quality. Acta Hort.* 427:251-266 (1996).

32. Schultz, H. R., and M. A. Matthews. Growth, osmotic adjustment and cell-wall mechanics of expanding grape leaves during water deficits. *Crop Sci.* 33:287-294 (1993).

33. Striegler, R. K., and G. S. Howell. The influence of rootstock on the cold hardiness of Seyval grapevines. *Vitis* 30:1-10 (1991).

34. Tardieu, F., and W. J. Davies. Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants. *Plant Cell Environ.* 16:341-349 (1993).

35. Williams, L. E., N. K. Dokoozlian, and R. Wample. Grape. *In: Handbook of Environmental Physiology of Fruit Crops. Vol. I. Temperate Crops.* B. Shaffer and P. C. Anderson (Eds.) pp 86-133. CRC Press, Boca Raton (1994).

36. Williams, L. E., and R. J. Smith. The effect of rootstock partitioning of dry weight, nitrogen and potassium, and root distribution of Cabernet Sauvignon grapevines. *Am. J. Enol. Vitic.* 42:118-122 (1991).

37. Winkel, T., and S. Rambal. Stomatal conductance of some grapevines growing in the field under a Mediterranean environment. *Agric. For. Meteorol.* 51:107-121 (1991).

38. Winkel, T., and S. Rambal. Influence of water stress on grapevines growing in the field: from leaf to whole-plant response. *Austral. J. Plant Physiol.* 20:143-157 (1993).

39. Winkler, A. J., J. A. Cook, *et al.* *General Viticulture.* University of California Press, Berkeley, CA (1974).