

Vine Water Relations, Gas Exchange, and Vegetative Growth of Seventeen *Vitis* Species Grown under Irrigated and Nonirrigated Conditions in California

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ADDITIONAL INDEX WORDS. grapevines, water potential, photosynthesis, stomatal conductance, drought tolerance

ABSTRACT. A comparison was made among 16 native North American *Vitis* species and *Vitis vinifera* L. ('Carignane') grown in the San Joaquin Valley of California with or without irrigation over 2 years. Predawn water potential (Ψ_{PD}), predawn leaf osmotic potential (Ψ_{π}), midday leaf (Ψ_L), and stem water potential (Ψ_{stem}), stomatal conductance (g_s), net CO₂ assimilation rate (A), and intrinsic water use efficiency (WUE) were measured on five dates during the growing season the first year of the study and pruning weights were evaluated both years. Net gas exchange and water potential components taken on the last measurement date in 1992 and pruning weights of the nonirrigated species were less (or more negative for Ψ components) than those of the irrigated vines. The 17 *Vitis* species were ranked according to their relative drought tolerance based upon their performance without irrigation and when compared to their irrigated cohort. The *Vitis* species considered most drought tolerant were *V. californica*, *V. champinii*, *V. doaniana*, *V. longii*, *V. girdiana*, and *V. arizonica*. Those six species generally had high values of A, g_s , and pruning weights and more favorable vine water status at the end of the study than the other species when grown without irrigation. The drought-induced reductions in the measured parameters also were less for those species when compared to their irrigated cohorts. The least drought tolerant species were, *V. berlandieri*, *V. cinerea*, *V. linceseumii*, *V. riparia*, and *V. solonis*. The drought-tolerant rankings were generally associated with the species' native habitat and probable soil water availability.

Plants subjected to severe water deficits show decreases in stomatal conductance (g_s), net CO₂ assimilation rates (A) and more negative leaf water potential (Ψ) (Jones, 1992). The drought responses of agronomic and perennial crops can include reduced A, g_s , transpiration rates and osmotic adjustment (Chartzoulakis et al., 1993; Martin and Ruiz-Torres, 1992; McCree and Richardson, 1987; Stoneman et al., 1994; Wong et al., 1985). As stem water potential values (Ψ_{stem}) become more negative the more xeric adapted *Prunus* species exhibited higher water use efficiency (WUE) than those of mesic origin (Rieger and Duemmel, 1992). The responses of grapevines (*Vitis* spp.) to drought can include reductions of A, g_s , reduced stomatal frequency, increased root density, and reduction of leaf area and leaf number (Smart and Coombe, 1983).

Differences among *V. vinifera* cultivars in response to water deficits have also been documented. Drought stressed 'Trollinger' grapevines responded to water deficits by reducing A (Düring, 1988), while 'Riesling' vines osmotically adjusted resulting in a higher turgor potential (Ψ_T) than 'Sylvaner' vines (Düring and Loveys, 1982). Additionally, 'Riesling' and 'Sylvaner' grapevines had differing degrees of osmotic adjustment and changes in WUE when subjected to water stress (Düring, 1984; 1987). Grimes and Williams (1990) found that 'Thompson Seedless' vines osmotically adjusted ≈ 0.4 MPa when deficit irrigated while Düring (1984) found an osmotic adjustment of 0.7 MPa. In another drought response study 'Carignane' had greater maximum g_s and higher stomatal

sensitivity to changes in air humidity than did 'Shiraz' or 'Merlot' grapevines (Winkel and Rambal, 1990).

There has been relatively little work done on the effects of soil water deficits on other *Vitis* species. The objective of this study was to rank the relative drought tolerance of 17 *Vitis* species under irrigated and nonirrigated conditions in the San Joaquin Valley of California. This was accomplished by measuring leaf water relations, gas exchange and vine growth and then comparing each species within the nonirrigated portion of the vineyard with one another and with their irrigated cohort. In addition to several North American species, which are used either as commercial rootstocks or parents of other grape rootstocks, this study included several *Vitis* species indigenous to the arid southwestern United States. It was expected that the diverse, native habitats of the 17 species would have selected for a wide range drought tolerance characteristics that may be of use in future rootstock breeding programs.

Materials and Methods

Dormant cuttings of the *Vitis* species listed in Table 1 were taken from vines growing in the United States Department of Agriculture National Clonal Germplasm Repository, Davis, Calif. holdings, in February 1990. Rooted cuttings were initially planted into 0.95 L milk cartons using a 1 sand : 1 compost-vermiculite : 2 peatmoss soil mix. The vines were transplanted into 3.8-L pots of coarse sand, and moved to a lath house for the remainder of the 1990 growing season. The dormant vines were transported to the University of California, Kearney Agricultural Center, near Fresno, California, during the 1990-91 winter. Five individual vine replicates per species were planted in March 1991 in a 0.4 ha vineyard using a completely randomized block design. A buffer vine was planted on either side of each data vine down the row. Vine and row spacings were 2.44 and 3.66 m, respectively. A single wire trellis (1.0 m above the soil surface) was used. The soil was a Hanford fine sandy loam (coarse-loamy, mixed, nonacid, thermic Typic Xerorthent) with a hardpan at 1.2 m. Standard pest control measures were used throughout the

Received for publication 30 Nov. 2001. Accepted for publication 12 Nov. 2002. We thank N.K. Dokoozlian, M.A. Matthews, K.A. Shackel, and J. Syvertsen for their helpful advice and review of this manuscript. We also thank M. Watnik for statistical advice.

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Table 1. *Vitis* species used in the study, description of their native habitats and ranges in North America or elsewhere and references.

<i>Vitis</i> species	Habitat	Range	Reference ^z
<i>arizonica</i> (Englemann)	Canyons, rocky canyon walls	Ariz., N.M., Trans-Pecos of Texas	1, 5, 6
<i>berlandieri</i> (Planchon)	Limestone soils, moist sites	Texas to Mexico	1, 8
<i>californica</i> (Bentham)	Stream banks	California's coastal mountain range, central valley, Sierra foothills, and southern Ore.	9
<i>candicans</i> (Englemann)	All situations, edge of woods, sandy slopes, disturbed ground, coastal oak woods	East and south central Texas	1, 4, 11
<i>champinii</i> ^y (Planchon)	Dry, chalky, limestone soils	Throughout Texas	8
<i>cinerea</i> (Englemann)	Low woodlands and alluvial soil along streams	Southeast U.S.: Texas to N.C and S.C., Ariz., Mo., Kans., Ill.	3, 12, 13
<i>cordifolia</i> (Michaux)	Along streams and moist wooded areas	Texas to Kans. and southeastern U.S.	2
<i>doaniana</i> ^x (Munson)	Woods, stream bottoms, rocky slopes or alkaline soils	Texas panhandle/east of Pecos River and N.M.	1, 6, 8
<i>girdiana</i> (Munson)	Canyon bottoms and along streams	Coastal to inland Calif. (including Mojave Desert)	9
<i>linceumii</i> (Buckley)	Woods and thickets, upland wooded soils, riverbeds	Texas to Kans.	1, 3, 11
<i>longii</i> (Prince)	Sandy soils, dry hillsides, dunes, rocky slopes	Kans. and Texas panhandle	1, 3
<i>monticola</i> (Buckley)	Rocky hills, limestone hills, canyons, ridges	N.M. and Texas	1, 6
<i>riparia</i> (Michaux)	Streambanks, low woodlands, alluvial soils	Eastern, central, and northern U.S.	3, 10, 13
<i>rupestris</i> (Scheele)	Sand and gravel bars	Once widely scattered from Tenn. to Texas	1
<i>solonis</i> (Hort. Berol.)	Open woods and rocky canyon slopes	Texas	1
<i>treleasei</i> (Munson)	Glabrous form of <i>V. arizonica</i>	Occurs on northern extent of <i>V. arizonica</i> 's range	1
<i>vinifera</i> L. 'Carignane'	Indigenous to Eurasia		7

¹ = Correll and Johnson, 1970, 2 = Galet, 1979, 3 = Gates, 1940, 4 = Jones, 1975, 5 = Kearney and Peebles, 1951, 6 = Martin and Hutchins, 1980, 7 = Mullins et al., 1992, 8 = Munson, 1909, 9 = Munz and Keck, 1959, 10 = Ownbey and Morley, 1991, 11 = Reeves and Bain, 1947, 12 = Smith, 1978, 13 = Steyermark, 1978.

^y*Vitis champinii* is a natural hybrid of *V. candicans* × *V. rupestris* (Galet, 1979).

^x*Vitis doaniana* is a natural hybrid of *V. candicans* × *V. longii* (M.A. Walker, unpublished data).

study. Vines were head-trained and dormant pruned to 8 to 12 buds. Clusters present on the vines were removed at anthesis each year.

All vines were furrow irrigated each week during the 1991 growing season. Two irrigation treatments of either weekly furrow irrigations (I) or a nonirrigated (NI) drought stress treatment were imposed at the beginning of the 1992 growing season and continued during 1993. Soil water content in the field was monitored with a neutron probe (Troxler depth moisture gauge, model 3320) using 10 access tubes per treatment, and read at five successive 0.3 m increments beginning 0.3 m below the soil surface. An individual access tube site was located in both irrigation treatments near individual vines of *V. arizonica*, *V. champinii*, *V. riparia*, *V. rupestris* and *V. vinifera* 'Carignane'. Each site consisted of two access tubes, one within the row (0.5 m from the vine) and one between rows (0.5 m from the vine). Environmental conditions at this location were obtained from a weather station operated by the California Irrigation Management Information System ≈0.5 km from the vineyard.

Pruning weights were taken during the dormant period (from five replicate vines) in 1992 and 1993. All reported measurements of gas exchange, water potential and water potential components were collected from three replicate grapevines, two leaves per vine, during the 1992-growing season. At midday (one hour on either side of solar noon), fully exposed leaves were selected for gas exchange measurements between the 7th and 14th node counting from the base of the shoot. Net CO₂ assimilation rate (A) and stomatal conductance to water vapor (g_s) data were collected with a portable infrared

gas analyzer, LCA-2, using the broad leaf cuvette (Analytical Development Company, Ltd., Hoddeson, England). Leaf intrinsic water use efficiency (WUE) was calculated dividing A by g_s.

Predawn leaf water potential (Ψ_{PD}) and midday leaf (Ψ_L) and stem (Ψ_{stem}) water potentials were measured on the same day as photosynthesis measurements with a pressure chamber (PMS Instrument Company, Corvallis, Ore.), according to the procedures of McCutchan and Shackel (1992). Measurements were made on leaves similar to those used for gas exchange. Leaf samples for osmotic potential (Ψ_{π}) were taken at predawn and quick-frozen on dry ice followed by storage at -80 °C. For analysis of Ψ_{π} , the leaf samples were thawed at 37 °C and osmotic potentials read on a vapor pressure osmometer (Wescor 5500; Wescor, Inc. Logan Utah).

Water relations and gas exchange measurements were taken on several dates spanning the growing season, so data were analyzed as a split plot (through time with day of year being the split). All measurements for each of the 17 species were collected on five paired days of year (DOY): 118 and 119, 140 and 141, 182 and 183, 204 and 205, 232 and 233 as 2 d were necessary to measure all replicates since we imposed a 2-h limit for readings at midday to minimize diurnal effects. These paired dates were considered as a single day for analysis. Least squares means for data analyzed on a seasonal basis are combined values from the five measurement dates using three replications. Means for gas exchange and Ψ parameters collected on the last measurement date are data from three individual vine replicates (two measurements per vine). Data were analyzed via analysis of variance (ANOVA) and mean sepa-

rations were determined using Duncan's multiple range test (DMRT). Additionally, predawn Ψ_{π} of each species, within each irrigation treatment, was analyzed as function of Ψ_{PD} throughout the growing season and an ANCOVA was used to test for differences among the slopes.

Drought performance indicators used to rank the species were pruning weights of the nonirrigated vines (averaged across the two years) and their percent reduction compared to the irrigated treatment. Since day of year had a significant effect on all water relations and gas exchange parameters measured, only measurements taken on the last date were used to assess the relative drought tolerance of the species in the nonirrigated treatment with the exception of Ψ_{π} data. Gas exchange performance indicators were the nonirrigated vines' A , g_s , and WUE. Vine water status parameters used were the Ψ difference in Ψ_1 and Ψ_{stem} and the percent Ψ_{PD} - midday Ψ_{stem} gradient portion of the total Ψ_{PD} - midday Ψ_1 gradient (Chone et al., 2001). The predicted osmotic potential of each species in the NI treatment, at a Ψ_{PD} of -0.205 MPa (using the results from the ANCOVA mentioned in the previous paragraph) was calculated and used as a relative indicator of the species' ability to accumulate solutes. The -0.205 MPa Ψ_{PD} value was chosen as it was the overall seasonal mean of all species in both irrigation treatments. The gas exchange and Ψ characteristics of the species in the NI treatment were also compared to those of the irrigated treatment. Each species was assigned a number (1 to 17) in each category. For example the species with the highest A was assigned number 1, while the species with the lowest, number 17. The species with the lowest reduction in A compared to its irrigated counterpart was assigned number 1, while the greatest reduction in A (NI vs. I) the highest number (17). Values in the rankings table were tested for skewness and kurtosis and the results indicated that the data were normally distributed. In addition, Bartlett's test of the species' rankings in each category indicated that their variances were homogeneous. Subsequently, a one-way, completely randomized ANOVA was conducted on the 13 drought performance values and species' means separated using DMRT.

Results

Precipitation from 1 Apr. until the last measurement date in 1992 totaled 3 mm, whereas the total for the same time period in 1993 was 10 mm. Soil water content was significantly lower in the nonirrigated plots than in the irrigated plots both years (data not given). Based upon neutron probe readings, the amount of water depleted in the soil profile of the NI treatment amounted to 0.74 and 0.94 m³ of water in 1992 and 1993, respectively. Applied water and depletion of water in the soil profile of the irrigated treatment amounted to greater than 1.8 m³ per vine both years.

All days in which midday Ψ and gas exchange were measured were cloud free. Ambient temperature during each two-hour measurement period ranged from 23 to 29 °C and vapor pressure deficit (VPD) ranged from 1.5 to 2.5 kPa on the first four dates. Solar radiation, ambient temperature and VPD on the last measurement date(s) (19 and 20 Aug.) averaged 826 W·m⁻², 34.5 °C and 3.2 kPa, respectively, for the 2-h measurement period.

Irrigation treatment had a significant effect on most of the measured parameters when averaged across dates (Table 2). There was a significant irrigation treatment by species interaction on all measures of vine water status taken predawn, stomatal conductance, and pruning weights in 1993. As the season progressed, measurement date had a significant effect on most of the measured parameters throughout the season.

Averaged across all species and irrigation treatments, measurements of vine water status (Ψ_{PD} and midday Ψ_1 and Ψ_{stem}) decreased as the season progressed, with the exception of the irrigated vines' Ψ_{PD} (Fig. 1). Net CO₂ assimilation rate decreased almost linearly from DOY 135 until the last measurement date for the nonirrigated species while that for the irrigated treatment tended to level off from DOY 141 to the last measurement date (Fig. 2). Similar results were found for g_s (data not given).

Under nonirrigated conditions, the species with the least negative Ψ_{PD} on the last measurement date were *V. berlandieri*, *V. doaniana*, *V. treleasei*, and *V. vinifera* and they were significantly higher than *V. arizonica*, *V. champinii* and *V. riparia* (Table 3). Predawn Ψ_{π} generally decreased through the first half of the growing season for the vines in the NI treatment but it tended to increase throughout the remainder of the season for many of the species in that treatment (see Padgett-Johnson et al., 2000, for an example). An ANCOVA of the relationship between predawn Ψ_{π} and Ψ_{PD} indicated that the slopes differed significantly among species within each irrigation treatment (data not given). The predicted predawn Ψ_{π} (based on the above referenced ANCOVA) at a Ψ_{PD} of -0.205 MPa was greatest for *V. treleasei* and lowest for *V. monticola* and *V. riparia*. The predicted values of predawn Ψ_{π} were similar to the seasonal least squares means of each species in both irrigation treatments (data not given).

Midday Ψ_{stem} of nonirrigated *V. californica* on the last measurement date was significantly different from 15 of the other species (Table 3). The lowest value for Ψ_{stem} on that date was -1.46 MPa for *V. monticola* and *V. riparia*. *Vitis* species with a midday Ψ_1 more negative than -1.65 MPa (*V. cinerea*, *V. champinii*, *V. monticola* and *V. riparia*) were significantly different from *V. californica* with a midday Ψ_1 of -1.33 MPa. *Vitis champinii* had the lowest midday Ψ_1 (-1.75 MPa) on the last date.

The difference between midday Ψ_1 and Ψ_{stem} on the last measurement date was significantly greater for *V. champinii* and *V. californica* than 11 other *Vitis* species, i.e., those with $\Psi_1 - \Psi_{stem}$ values <0.24 MPa (Table 3). There were no significant differences in this parameter among species in the irrigated portion of the study. The $\Psi_{PD} - \Psi_{stem}$ portion of the $\Psi_{PD} - \Psi_1$ gradients of *V. arizonica*, *V. californica*, *V. champinii* and *V. doaniana* (values <70) under

Table 2. Analysis of variance of irrigation (I) treatment, species, irrigation (I) × species (S) interaction, day of year (DOY) and I × S × DOY interaction on different vine water status measurements, net CO₂ assimilation rate (A), stomatal conductance (g_s), transpiration (E), intrinsic water use efficiency (WUE), and pruning weight (PWt) of 17 *Vitis* species. All data were collected during the 1992 growing season except the pruning weights of 1993; predawn leaf water potential = Ψ_{PD} , predawn leaf osmotic potential = Ψ_{π} , midday leaf water potential = Ψ_1 , and midday stem water potential = Ψ_{stem} .

Parameter measured	I	Species	I × S	DOY	DOY × I × S
Ψ_{PD}	***	***	**	***	***
Ψ_{π}	***	***	***	***	NS
Ψ_1	***	***	NS	***	NS
Ψ_{stem}	***	***	NS	***	**
g_s	***	***	***	***	NS
A	***	***	NS	***	*
E	***	***	NS	NS	NS
WUE	*	***	NS	***	NS
PWt 1992	***	***	NS	NA	NA
PWt 1993	***	***	***	NA	NA

NS, *, **, *** Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

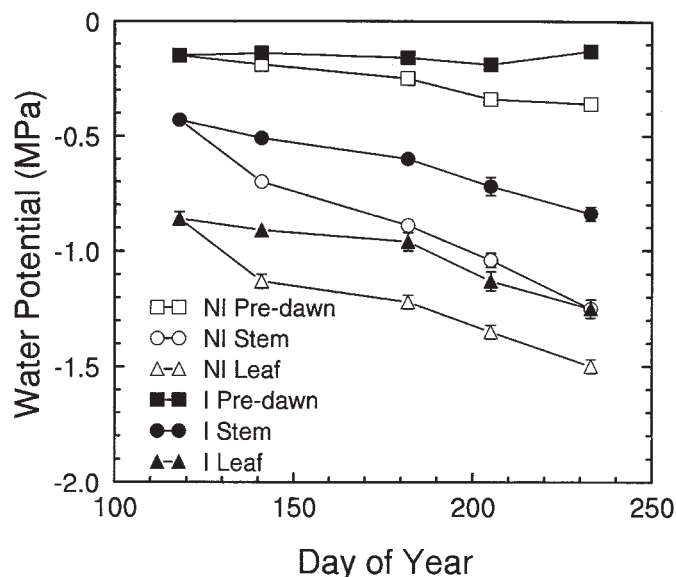


Fig. 1. Three measures of vine water status [Ψ_{PD} (predawn), midday Ψ_{stem} (stem), and midday Ψ_l (leaf)] for all species in the nonirrigated (NI) and irrigated (I) treatments on five different dates during the 1992 growing season. Each individual point is the mean of all 17 *Vitis* species used in the study. Bars, larger than the symbol, represent $\pm 1SE$

nonirrigated conditions were significantly different from 9 other species (values >83). There were also significant differences among species in the irrigated portion of the trial.

There were no significant differences in A on the last measurement date among species in the nonirrigated treatment; however, there were significant differences among the species in the irrigated treatment (Table 4). Stomatal conductance of nonirrigated *V. champinii* was significantly greater than 11 other *Vitis* species, i.e., those with H_2O values less than $170 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. *Vitis californica* had the highest g_s among species in the irrigated treatment. Lastly,

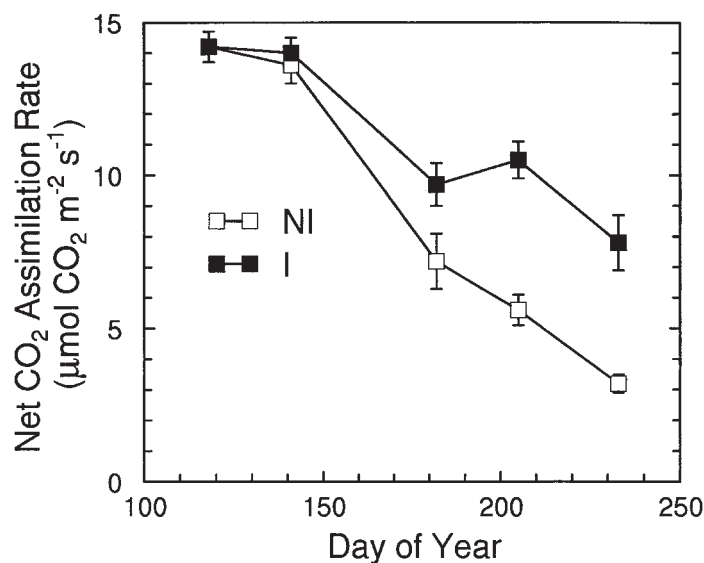


Fig. 2. Net CO_2 assimilation rate for all species in the nonirrigated and irrigated treatments on five different dates during the 1992 growing season. Other information as found in Fig. 1.

there were significant differences in intrinsic WUE of species in the nonirrigated treatment with *V. rupestris* having the highest and *V. californica* and *V. candicans* having the lowest (Table 4).

There were significant differences in pruning weights between irrigation treatments species in 1992 and 1993 (Table 2) and among species in the nonirrigated treatment both years (Table 5). *Vitis champinii* had the highest mean pruning weight for both irrigation treatments, followed by *V. girdiana*, *V. doaniana* and *V. longii* (Table 5). *Vitis cinerea* and *V. berlandieri* had the lowest pruning weights regardless of treatment. The species with the greatest percent reduction in pruning weights, comparing irrigated to

Table 3. Predawn leaf (Ψ_{PD}), midday leaf (Ψ_l) and midday stem (Ψ_{stem}) water potentials of the nonirrigated (NI) species on the last measurement date. The difference between Ψ_l and Ψ_{stem} and the percent of the predawn to midday stem ($(\Psi_{PD} - \Psi_{stem}) / (\Psi_{PD} - \Psi_l)$) gradient of the total predawn to midday leaf ($\Psi_{PD} - \Psi_l$) gradient on the last measurement date for both the irrigated (I) and nonirrigated vines and the predicted predawn Ψ_{π} at a Ψ_{PD} of -0.205 MPa are also given. Water potential values are expressed in MPa. Means followed by a different letter are significantly different at $P < 0.05$. Means were not significantly different in the irrigated (I), $\Psi_l - \Psi_{stem}$ column. The predicted predawn Ψ_{π} was not analyzed.

<i>Vitis</i> species	Ψ_{PD}	Ψ_{stem}		$\Psi_l - \Psi_{stem}$		$[(\Psi_{PD} - \Psi_{stem}) / (\Psi_{PD} - \Psi_l)] \times 100$		Predicted predawn Ψ_{π}	
		NI	I	NI	I	NI	I	NI	I
<i>arizonica</i>	-0.45 e	-1.14 b	-1.48 bcd	0.34 abc	0.40	66.3 ef	65.0 abcd	-1.33	-1.44
<i>berlandieri</i>	-0.31 ab	-1.36 b	-1.52 bcd	0.16 d	0.41	86.9 a	63.6 bcd	-1.27	-1.41
<i>californica</i>	-0.33 abc	-0.88 a	-1.25 ab	0.37 a	0.42	59.8 f	56.0 de	-1.45	-1.45
<i>candicans</i>	-0.33 abc	-1.19 b	-1.39 abc	0.20 ef	0.29	81.1 abc	73.6 a	-1.26	-1.16
<i>champinii</i>	-0.44 de	-1.34 b	-1.75 d	0.41 a	0.42	68.9 def	64.4 bcd	-1.33	-1.18
<i>cinerea</i>	-0.41 cde	-1.37 b	-1.68 cd	0.31 abcde	0.58	75.6 bcde	53.5 e	-1.37	-1.32
<i>cordifolia</i>	-0.34 abc	-1.12 b	-1.34 abc	0.22 cdef	0.43	78.0 abcd	59.5 cde	-1.39	-1.50
<i>doaniana</i>	-0.30 ab	-1.00 ab	-1.35 abc	0.35 ab	0.47	66.0 ef	53.5 e	-1.32	-1.32
<i>girdiana</i>	-0.41 cde	-1.22 b	-1.54 bcd	0.32 abcd	0.39	71.7 cde	60.1 cde	-1.20	-1.45
<i>lincecumii</i>	-0.36 bcd	-1.27 b	-1.48 bcd	0.21 def	0.36	80.5 abc	69.4 ab	-1.08	-0.98
<i>longii</i>	-0.36 bcd	-1.36 b	-1.60 bcd	0.24 bedef	0.32	80.4 abc	71.5 ab	-1.14	-1.29
<i>monticola</i>	-0.40 cde	-1.46 b	-1.65 cd	0.19 ef	0.35	84.8 ab	69.5 ab	-1.55	-1.28
<i>riparia</i>	-0.46 e	-1.46 b	-1.70 cd	0.24 cdef	0.51	80.8 abc	57.9 cde	-1.55	-1.48
<i>rupestris</i>	-0.33 abc	-1.33 b	-1.51 bcd	0.18 f	0.47	84.7 ab	60.0 cde	-1.41	-1.37
<i>solonis</i>	-0.34 abc	-1.27 b	-1.47 cd	0.20 ef	0.37	82.4 abc	66.5 abc	-1.22	-1.51
<i>treleasei</i>	-0.27 a	-1.24 b	-1.46 cd	0.22 def	0.31	81.8 abc	73.6 a	-0.96	-0.99
<i>vinifera</i>	-0.30 ab	-1.10 b	-1.33 abc	0.23 cdef	0.37	78.1 abcd	65.5 abc	-1.43	-1.33

nonirrigated, were *V. riparia*, *V. monticola* and *V. lincedumii*, while *V. treleasei* was reduced the least.

The drought performance indicator means of *V. doaniana*, *V. longii*, *V. girdiana*, *V. arizonica* and *V. californica* were not significantly different from *V. champinii* (species with the lowest overall score) (Table 6). *Vitis berlandieri*, *V. lincedumii* and *V. cinerea* had lower scores than *V. riparia*, which was considered as the standard nondrought tolerant species. Based upon total points and their mean separations, species with a score of 100 points and below were considered highly drought tolerant while those with a score of 138 and greater, least drought tolerant. The remaining six species were classified as intermediate.

Discussion

Modern viticulture is dependent on the use of rootstocks resistant to Phylloxera (*Daktulosphaira vitifolia* FITCH) and other soilborne pests (Mullins et al., 1992). Most commercially available rootstocks today are either native North American *Vitis* species or the result of crosses between them. Due to the diversity of these species' native habitats (Table 1), differences in the ability to tolerate soil water deficits were expected. Multiple criteria (measurements of water status, gas exchange and growth characteristics) were used in this study to assess the drought tolerance of 16 North American *Vitis* species and *V. vinifera*. Since the vines were grown in the field

Table 4. Net CO₂ assimilation rate (A), stomatal conductance (g_s) and intrinsic water use efficiency (WUE, A/g_s × 10³) (NI treatment only) of 17 *Vitis* species on the last measurement date.² Other information as found in Table 3. There were no significant differences among means in the A, NI column.

<i>Vitis</i> species	A		g _s		WUE
	NI	I	NI	I	NI
<i>arizonica</i>	3.27	12.3 abc	172 abc	493 ab	19.8 bcd
<i>belandieri</i>	1.90	2.98 h	145 bc	268 b	13.6 cd
<i>californica</i>	2.98	11.9 abc	193 ab	550 a	12.2 d
<i>candicans</i>	2.68	13.4 ab	190 ab	473 abc	12.1 d
<i>champinii</i>	5.02	14.1 a	263 a	438 abcd	18.9 bcd
<i>cinerea</i>	1.28	4.57 fgh	65 c	348 bcd	25.4 abcd
<i>cordifolia</i>	4.53	7.63 def	140 bc	330 bcd	30.5 abcd
<i>doaniana</i>	2.70	3.6 gh	195 ab	310 cd	13.2 cd
<i>girdiana</i>	3.00	5.53 efgh	145 bc	360 bcd	19.8 bcd
<i>lincedumii</i>	1.90	7.27 defg	92 bc	448 abc	20.6 bcd
<i>longii</i>	4.62	6.93 defg	132 bc	318 bcd	33.1 ab
<i>monticola</i>	3.03	8.90 cde	182 ab	455 abc	17.7 bcd
<i>riparia</i>	2.97	10.1 bcd	138 bc	450 abc	22.2 bcd
<i>rupestris</i>	4.13	11.0 abcd	97 bc	420 abcd	42.4 a
<i>solonis</i>	2.70	7.83 def	105 bc	298 cd	25.4 abcd
<i>treleasei</i>	3.80	8.55 cdef	110 bc	387 abcd	33.4 ab
<i>vinifera</i>	4.17	8.77 cde	128 bc	398 abcd	31.6 abc

²A and g_s are expressed as mmol·m⁻²·s⁻¹ CO₂ and mmol·m⁻²·s⁻¹ H₂O, respectively.

Table 5. Pruning weights (Pwt) from the 1992 and 1993 growing seasons for the NI treatment and mean Pwt for both years of the NI and I treatments for 17 *Vitis* species. Mean Pwt of the NI treatment are also expressed as a percent of the irrigated treatment (% of I). Other information as found in Table 3. There was no statistical analysis of the mean pruning weight values for the NI and I treatments.

<i>Vitis</i> species	Pwt (kg/vine)				
	NI 1992	NI 1993	NI Mean	I Mean	NI (% of I)
<i>arizonica</i>	1.59 bc	1.98 bc	1.78	4.34	41
<i>berlandieri</i>	0.56 c	0.69 c	0.63	1.55	41
<i>californica</i>	1.02 bc	1.09 c	1.06	3.24	33
<i>candicans</i>	1.11 bc	2.37 bc	1.74	4.51	39
<i>champinii</i>	4.95 a	6.08a	5.52	12.2	45
<i>cinerea</i>	0.36 c	0.78 c	0.57	1.50	38
<i>cordifolia</i>	0.71 bc	1.36 c	1.04	2.74	38
<i>doaniana</i>	2.51 b	2.57 bc	2.54	5.74	44
<i>girdiana</i>	2.1 bc	3.45 b	2.78	5.77	48
<i>lincedumii</i>	0.60 bc	0.73 c	0.66	2.38	28
<i>longii</i>	2.02 bc	1.88 bc	1.95	4.61	42
<i>monticola</i>	1.05 bc	1.33 c	1.19	4.42	27
<i>riparia</i>	0.65 bc	1.30 c	0.98	4.04	24
<i>rupestris</i>	1.43 bc	2.37 bc	1.90	4.42	43
<i>solonis</i>	1.72 bc	1.97 bc	1.84	3.78	49
<i>treleasei</i>	1.16 bc	1.72 bc	1.44	2.30	63
<i>vinifera</i>	0.77 bc	0.92 c	0.84	2.11	40

Table 6. Relative drought tolerance of 17 *Vitis* species based upon their total score. See Materials and Methods section for explanation of how each species was rated in each category. Mean score (not given) separation determined using Duncan's multiple range test. Different letters in the mean score column indicates species means are significantly different at $P < 0.05$.²

<i>Vitis</i> Species	NI A	NI/I A	NI g _s	NI/I g _s	NI A/g _s	NI Ψ _π	NI/I Ψ _π	NI Grad	NI/I Grad	NI ΔΨ	NI/I ΔΨ	NI PWt	NI/I PWt	Total	Mean score
<i>champinii</i>	1	9	1	2	12	8	2	4	3	1	1	1	4	50	a
<i>doaniana</i>	12	1	2	1	15	10	10	2	11	3	6	3	4	80	ab
<i>longii</i>	2	2	11	5	3	15	15	9	7	7	5	4	7	92	abc
<i>girdiana</i>	9	5	7	6	10	14	16	5	8	5	4	2	3	94	abc
<i>arizonica</i>	7	14	6	11	10	8	13	3	1	4	3	7	8	95	abc
<i>californica</i>	10	16	3	10	16	3	9	1	2	2	2	11	14	99	abc
<i>vinifera</i>	4	6	12	12	4	4	5	8	8	9	9	14	10	105	bcd
<i>cordifolia</i>	3	4	9	4	5	6	12	7	13	10	14	12	12	111	bcde
<i>treleasei</i>	6	7	13	14	2	17	11	13	5	10	7	9	1	115	bcde
<i>monticola</i>	8	11	5	8	13	1	1	16	10	15	11	10	16	125	bcde
<i>rupestris</i>	5	8	15	15	1	5	7	15	16	16	17	5	6	131	bcde
<i>candicans</i>	14	17	4	7	17	12	4	12	4	13	8	8	11	131	bcde
<i>solonis</i>	12	10	14	9	6	13	17	14	11	13	11	6	2	138	cde
<i>riparia</i>	11	12	10	13	8	1	6	11	15	7	15	13	17	139	cde
<i>berlandieri</i>	15	3	7	3	14	11	14	17	14	17	16	16	8	155	de
<i>lincecumii</i>	15	15	16	16	9	16	3	10	6	12	10	15	15	158	de
<i>cinerea</i>	17	13	17	17	6	7	8	16	16	6	13	17	12	165	e

²NI = not irrigated, I = irrigated, A = net CO₂ assimilation rate, g_s = stomatal conductance, A/g_s = intrinsic water use efficiency, Ψ_π = predicted predawn osmotic potential at a Ψ_{PD} of -0.205 MPa, Grad = ((Ψ_{PD} - Ψ_{stem})/(Ψ_{PD} - Ψ_I)) × 100, ΔΨ = Ψ_{stem} - Ψ_I, PWt = pruning weight.

without applied water, a gradual depletion of the soil water content occurred as the season progressed and thus changes in vine physiology and/or morphology in response to water stress would also have taken place gradually. It should be pointed out that, generalizations regarding results from this study are the result of an individual species' above and below ground response to water deficits. In a commercial vineyard situation, the grafted scion would have its own response to water deficits. It has been demonstrated, though, that the rootstock can affect the physiology of the scion under soil water deficit conditions (Padgett-Johnson et al., 2000).

A reduction in stomatal conductance to limit water vapor loss via transpiration is one drought avoidance mechanism (Kirkham, 1990; Passioura, 1994). Under nonirrigated conditions in this study, all species exhibited this behavior. However, the two species with the lowest g_s on the last date, *V. cinerea*, and *V. lincecumii*, also had the greatest reductions in g_s compared to their irrigated counterparts and ranked as least drought tolerant. A study on greenhouse-grown, one year-old 'Cabernet Sauvignon' grafted onto different rootstocks to investigate drought tolerance was conducted in France (Carbonneau, 1985). The ratio of leaf area to the reciprocal of stomatal conductance (1/g_s) was used as the basis for classification. Such a basis would presumably be a measure of growth and gas exchange. 'Rupestris du Lot' (*V. rupestris*) and 'Riparia Gloire' (*V. riparia*) were classified as susceptible to drought. The rootstock selections 7383 and 7405 (open pollinated *V. berlandieri*) were classified as resistant and less resistant to drought, respectively. When the pruning weight to seasonal mean 1/g_s ratios were calculated for species in the nonirrigated treatment of this study, *V. riparia*, *V. lincecumii*, *V. berlandieri* and *V. cinerea* ranked 14th, 15th, 16th, and 17th, respectively (out of the 17 species), while *V. rupestris* ranked 8th. The four lowest ranked species based on this criterion were also rated least drought tolerant in our study. *Vitis rupestris* would be classified as intermediate for drought tolerance using this criterion. Using the pruning weight to mean seasonal 1/g_s ratio, the top five species in this study were *V. champinii*, *V. doaniana*, *V.*

girdiana, *V. longii* and *V. arizonica* (highest to lowest, respectively), all of which we ranked as most drought tolerant. Therefore, the means of classifying the drought tolerance of vines used by Carbonneau (1985) for the species in this study agreed favorably (the exception being *V. rupestris*) with our multiple criteria classification. However, our drought tolerance classification of one of the three species used in both studies (*V. berlandieri*) did differ from Carbonneau's ranking.

Another drought avoidance mechanism would be the development of a very deep, extensive root system (Jones, 1992). However, in our study a hardpan was present at a depth of 1.2 m, which restricted the exploration of roots to greater depths (Padgett-Johnson, 1999). Therefore, the ability of a species to avoid drought using this mechanism was not expressed in our study. Padgett-Johnson (1999) also found that the distribution of roots within the soil profile did not differ significantly among seven species (*V. arizonica*, *V. berlandieri*, *V. candicans*, *V. champinii*, *V. riparia*, *V. rupestris* and *V. vinifera*) that were examined in the nonirrigated portion of the vineyard. This would indicate these species had equal access to available water in the soil profile.

A plant's Ψ will decrease as soil water deficits develop and it has been reported that under water stress, drought-tolerant plants will maintain higher Ψs than drought-sensitive ones (Kirkham, 1990). However, in our study we used the differences in Ψ_{PD}, Ψ_I, and Ψ_{stem} to assess the water status of the vines for use in ranking a species' drought tolerance. This was due in part to the fact that the species having the lowest midday Ψ_I and one of the lowest values of Ψ_{PD} and Ψ_{stem} on the last measurement date was *V. champinii*. Its values were similar to *V. riparia*. However, *V. champinii* had the highest A, g_s and pruning weights, unlike *V. riparia*. It was recently reported that the difference between Ψ_{stem} and Ψ_I was linearly correlated with leaf transpiration (Chone et al., 2001). Such a relationship was also found in this study (r² = 0.64, data not given). Thus, *V. champinii* with low values of Ψ_{PD}, Ψ_I, and Ψ_{stem} had the highest ΔΨ_{stem} - Ψ_I and that was reflective of its gas exchange measurements and its ΔΨ_{stem} - Ψ_I was similar to the irrigated cohort's value. Thus, using only

absolute values of Ψ to rank a species may result in conclusions that are not consistent with actual performance.

Another factor influencing water uptake by plants is hydraulic conductance to water flow and differences among plant species have been demonstrated (Turner, 1986). Chone et al. (2001) proposed that the $\Psi_{PD} - \Psi_{stem}$ and $\Psi_{PD} - \Psi_I$ gradient proportions were reflective of the hydraulic conductance of the soil–stem pathway in grapevines. In our study, the proportion of the $\Psi_{PD} - \Psi_{stem}$ gradient to the total $\Psi_{PD} - \Psi_I$ gradient was lowest for *V. arizonica*, *V. californica* and *V. champinii* and their values were close to those of their irrigated cohorts. The assumption would be that hydraulic conductance of those nonirrigated species was high. The species with the lowest purported hydraulic conductance were all rated least drought tolerant. *Vitis rupestris*, has been reported to have narrow xylem vessels (Rives, 1925), which may possibly restrict the flow of water. However, one may have expected the irrigated *V. rupestris* also to have a low conductance, compared to the other species, but it didn't. It has been demonstrated that even moderate water stress can reduce vessel size and xylem hydraulic conductance of grape (Lovisolo and Schubert, 1998). The narrow vessels reported by Rives (1925) for *V. rupestris* may have been due to the fact the vines had been stressed when the measurements were taken.

Osmoregulation by plants is considered a drought tolerance mechanism (Kirkham, 1990; Passioura, 1994). Grapevines have been shown to osmoregulate ≈ 0.3 to 0.5 MPa in response to soil water deficits (Grimes and Williams, 1990; Schultz and Matthews, 1993; Rodrigues et al., 1993). Düring and Scienza (1980) examined drought tolerance in several *Vitis* species by excising leaves and then measuring Ψ_I for the next 30 min. It was assumed that leaves having the more negative Ψ_I were not osmoregulating while the opposite was true for leaves with less negative Ψ_I . It was concluded that *V. riparia* and *V. rupestris* were drought sensitive, as they had the most negative Ψ_I values, whereas, *V. monticola*, *V. berlandieri* and *V. cinerea* were drought tolerant because they had the least negative Ψ_I values. We classified three of the five species used in Düring and Scienza's study (*V. berlandieri*, *V. cinerea*, and *V. riparia*) in our least drought tolerant category while the remaining two, *V. monticola* and *V. rupestris*, were ranked intermediate. Therefore, our rankings differed from those species used in Düring and Scienza's study. While we did not explicitly measure osmoregulation (such as done in the studies on grapevines mentioned above) it would appear that the accumulation of solutes (or more negative values of Ψ_{π} measured in this study, Table 3) did not impart any significant ability of *V. riparia* or *V. monticola* to tolerate drought.

A third category of drought tolerant adaptations/mechanisms, are those associated with efficiency (Kirkham, 1990; Passioura, 1994). A greater WUE under drought conditions may result in continued productivity (Passioura, 1994). *Vitis rupestris* had the highest intrinsic WUE, whereas, *V. doaniana*, *V. californica* and *V. candicans* had the lowest (Table 4). If one were to calculate WUE as the ratio of biomass produced to the amount of water used in this study a different conclusion would be drawn. *Vitis champinii* and to a lesser extent *V. girdiana*, *V. doaniana* and *V. longii* (i.e., those species with the highest pruning weights under nonirrigated conditions, Table 5) would have had the greatest WUE. Soil water depletion at the five access tube sites in the nonirrigated portion of the vineyard were similar, indicating that the five vines at each location probably used the same amount of water as those with lower pruning weights. Therefore, intrinsic WUE (a single measurement of gas exchange on a particular day) did not provide an accurate assessment of the long-term production of biomass as a function of water used.

All *Vitis* species in this study exhibited some level of drought tolerance, not just avoidance as suggested by Smart and Coombe (1983). The interaction and coordination of these adaptations and mechanisms may provide a better means of describing a given species' ability to tolerate drought, if ultimately used as a commercial rootstock. Using multiple criteria to categorize drought tolerance in *Vitis* may be better than assessing the extent of drought tolerance in which only a single mechanism is measured (Carbonneau, 1985; Düring and Scienza, 1980).

The species ranked as most drought tolerant, were *V. arizonica*, *V. californica*, *V. champinii*, *V. doaniana*, *V. girdiana* and *V. longii*. Since the native habitats of *V. arizonica* and *V. californica* and *V. girdiana* are associated with canyons in the arid southwestern United States and stream banks in California, respectively (Table 1), the availability of mid- to late-season rainfall would probably be minimal. *Vitis champinii* and *V. longii* are found on dry, chalky, limestone soils or sandy soils and dry hillsides. The descriptions of the above two species' native habitats indicate that drought tolerance is a necessary attribute in these arid locations. *Vitis doaniana*, also ranked as highly drought tolerant, can be found in woods and stream bottoms, areas in which water deficits may be uncommon. Although this appears to contradict the idea of selection for drought tolerance, one parent of *V. doaniana* is *V. longii* (Table 1) and *V. doaniana* may have inherited some of *V. longii*'s drought tolerant characteristics.

The species determined to be the least drought tolerant in this study were *V. berlandieri*, *V. cinerea*, *V. linccumii*, *V. riparia* and *V. solonis*. These species generally had low rates of A, g, and less favorable vine water statuses, low pruning weights under nonirrigated conditions and a greater reduction of those parameters when compared to the irrigated controls. *Vitis riparia* rootstock is usually not considered drought tolerant based upon vine water relations (Carbonneau, 1985; Düring and Scienza, 1980) and yield performance under dry-land conditions (Galet, 1979; Southey, 1992). In addition, its mesic habitat and range would also indicate that strong drought avoidance or tolerance mechanisms are not necessary. The native habitats of the other four *Vitis* species, also ranked as least drought tolerant are similar to that of *V. riparia* (Table 1).

All species ranked intermediate in terms of drought tolerance generally had mean performance scores that were not significantly different from five of the six species ranked as most drought tolerant. One of the intermediate drought tolerant species, *V. treleasei*, is a glabrous form of *V. arizonica*. It is unknown why there were differences among the two as their native habitats overlap.

Conclusions

The drought tolerance rankings of species in this study compared favorably with several other studies in which *Vitis* species were included. It has been concluded by Carbonneau (1985), Delas, (1992), Düring and Scienza (1980), Galet (1979) and Pongracz (1983) that 'Riparia Gloire' (*V. riparia*) is not drought tolerant, as was shown here. We also concluded that *V. berlandieri*, *V. cinerea*, *V. linccumii*, and *V. solonis*, which responded similarly to *V. riparia* in many respects, are not drought tolerant. In this study *V. rupestris* was classified as intermediate to drought tolerant species, which differs from its rankings by Carbonneau (1985) and Southey (1992). 'Dog Ridge' and 'Ramsey' are two commercial rootstock cultivars derived from *V. champinii*; the species we concluded as having the highest drought tolerance in our study. Both of these rootstocks impart vigorous vegetative growth to their grafted scions (Pongracz, 1983) as would be expected from our results. However,

'Dog Ridge' and 'Ramsey' have been classified as being moderately susceptible and susceptible, respectively, to drought under South African conditions (Southey, 1992). Winkler et al. (1974) recommended 'Dog Ridge' for use on light textured soils (i.e., those with less water holding capacity). Fregoni (1977) has concluded that there is no definite relationship between excess vigor and drought tolerance of rootstocks. The differences in the conclusions noted above by Southey (1992) and Fregoni (1977) and our conclusions regarding *V. champinii* warrant further studies on the drought tolerance of this species when used as a grafted rootstock with an accompanying fruit producing scion. In such a case, actual fruit production in vineyards with less available water would be the major criterion with which to assess drought tolerance (Jones, 1992).

The classifications of drought tolerance for the 17 *Vitis* species used in this study may assist in breeding drought tolerant rootstocks. It is interesting to note that the commercial rootstocks typically classified as being highly drought tolerant (i.e., '110 Richter', '140 Ruggeri' and '1103 Paulsen') are *V. berlandieri* x *V. rupestris* hybrids. In this study, *V. berlandieri* was classified as least drought tolerant while *V. rupestris* was classified as intermediate. It would appear that these two species' hybrids either increase or maintain the scion's (commonly a *V. vinifera* cultivar) fruit production in a commercial situation, a factor not considered in this study. *Vitis champinii*, which we classified as the most drought tolerant, is a natural hybrid of *V. candicans* and *V. rupestris*, both of which were not considered to be highly drought tolerant in this study. In addition, the rootstocks derived from *V. champinii* are often discouraged for use in commercial vineyards due to their invigorating effect on the scion's vegetative growth, especially in situations where soil water is readily available, which may negatively impact fruit quality. Lastly, a wide range of characteristics, including pest resistance and ease of propagation, in addition to drought tolerance are considered when selecting species for use in breeding.

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