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 ($\Psi_p$), predawn leaf osmotic potential ($\Psi_l$), midday leaf ($\Psi_m$), and stem water potential ($\Psi_{stem}$), stomatal conductance ($g_s$), net CO$_2$ 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 $\Psi$ 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 which were native to California 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. lineecumii, 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 CO$_2$ assimilation rates ($A$) and more negative leaf water potential ($\Psi$) (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 ($\Psi_{stem}$) become more negative the more xeric adapted Prunus species exhibited higher water use efficiency (WUE) than those of mesic origin (Rieger and Durenmel, 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 ($\Psi_T$) 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, we selected for 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 placed 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, nonacidic, thermic Typic Xerorthent) with a hardpan at 1.2 m. Standard pest control measures were used throughout the
Table 1. Vitis species used in the study, description of their native habitats and ranges in North America or elsewhere and references.

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

1I = 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.

2Vitis champinii is a natural hybrid of V. candicans x V. rupestris (Galet, 1979).

3Vitis doaniana is a natural hybrid of V. candicans x 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 increments beginning 0.3 m below the soil surface. An individual access tube site was located in both irrigation treatments near

The differences 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,) data were collected with a portable infrared

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

Predawn leaf water potential (Ψpd) and midday leaf (Ψm) and stem (Ψs) 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 (Ψs) were taken at predawn and quick-frozen on dry ice followed by storage at −80 °C. For analysis of Ψs, 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 separ-
rations were determined using Duncan’s multiple range test (DMRT). Additionally, predawn Ψ₀ of each species, within each irrigation treatment, was analyzed as function of Ψ₀ 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 Ψₐ data. Gas exchange performance indicators were the nonirrigated vines’ A, g, and WUE. Vine water status parameters used were the Ψ difference in Ψ₁ and Ψ₀, and the percent Ψ₀ – midday Ψₐ gradient portion of the total Ψ₀ – Ψ₁ gradient (Chone et al., 2001). The predicted osmotic potential of each species in the NI treatment, at a Ψ₀ 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 Ψ₀ 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 while the greatest reduction in A compared to its irrigated counterpart was assigned number 1, with the lowest, number 17. The species with the lowest reduction was assigned a number (1 to 17) in each category. For example the species in the nonirrigated treatment with the exception of Ψₐ and Ψ₀ indicated that the slopes differed significantly among species within each irrigation treatment (data not given). The predicted predawn Ψₐ (based on the above referenced ANCOVA) at a Ψ₀ of −0.205 MPa was greatest for V. treleasei and lowest for V. monticola and V. riparia. The predicted values of predawn Ψₐ were similar to the seasonal least squares means of each species in both irrigation treatments (data not given).

Midday Ψₐ of nonirrigated V. californica on the last measurement date was significantly different from 15 of the other species (Table 3). The lowest value for Ψₐ on that date was −1.46 MPa for V. monticola and V. riparia. Vitis species with a midday Ψ₁ more negative than −1.65 MPa (V. cinerea, V. champinii, V. monticola and V. riparia) were significantly different from V. californica with a midday Ψ₁ of −1.33 MPa. Vitis champinii had the lowest midday Ψ₁ (−1.75 MPa) on the last date.

The difference between midday Ψ₁ and Ψₐ of nonirrigated V. californica on the last measurement date was significantly greater for V. champinii and V. californica than 11 other Vitis species, i.e., those with Ψ₁ − Ψₐ values <0.24 MPa (Table 3). There were no significant differences in this parameter among species in the irrigation portion of the study. The Ψ₀ − Ψₐ portion of the Ψ₀ − Ψ₁ 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 (gₛ), 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 = Ψₛ, predawn leaf osmotic potential = Ψ₀, midday leaf water potential = Ψ₁, and midday stem water potential = Ψₐ.

| Parameter measured | I | Species | I × S | DOY | DOY × I × S |
|--------------------|---|---------|------|-----|-------------|
| Ψ₀                 | ***| ***     | **   | *** | ***         |
| Ψₛ                 | ***| ***     | NS   | NS  | NS          |
| Ψ₁                 | ***| ***     | NS   | NS  | **          |
| Ψₐ                 | ***| NS      | NS   | NS  |             |
| Ψₐ                 | ***| NS      | NS   | NS  |             |
| Ψₛ                 | ***| NS      | NS   | NS  |             |
| A                  | ***| NS      | NS   | NS  |             |
| E                  | ***| NS      | NS   | NS  |             |
| WUE                | ***| NS      | NS   | NS  |             |
| PWt 1992           | ***| NS      | NA   | NA  |             |
| PWt 1993           | ***| NS      | NA   | NA  |             |

***Nonsignificant or significant at P < 0.05, 0.01, or 0.001, respectively.
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 _Vitis champinii_ was significantly greater than 11 other _Vitis_ species, i.e., those with H₂O values less than 170 mmol-m⁻²-s⁻¹. _Vitis californica_ had the highest gₚ among species in the irrigated treatment. Lastly, there were significant differences in intrinsic WUE of species in the nonirrigated treatment with _V. rupestris_ having the highest and _V. californica_ and _V. candidicans_ 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. berklandieri_ had the lowest pruning weights regardless of treatment. The species with the greatest percent reduction in pruning weights, comparing irrigated to 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.

Table 3. Predawn (Ψ₀), midday (Ψₚ), and midday stem (Ψₛₚₚ) water potentials of the nonirrigated (NI) species on the last measurement date. The difference between Ψ₀ and Ψₛₚₚ and the percent of the predawn to midday stem ((Ψ₀ – Ψₛₚₚ) / Ψₛₚₚ) gradient of the total predawn to midday leaf (Ψ₀ – Ψₚ) gradient on the last measurement date for both the irrigated (I) and nonirrigated vines and the predicted predawn Ψₚ was not analyzed.

| _Vitis_ species | Ψ₀ | Ψₛₚₚ | Ψₚ | Ψ₀ – Ψₛₚₚ | (Ψ₀ – Ψₛₚₚ) / Ψₛₚₚ | Predicted predawn Ψₚ |
|-----------------|-----|------|-----|------------|---------------------|---------------------|
| _arizonica_     | -0.45 c | -1.14 b | -1.48 b | 0.34 abc  | 0.40 | -1.33 -1.44 |
| _berlandieri_   | -0.33 ab | -0.88 a | -1.25 ab | 0.37 a   | 0.42 | -1.27 -1.41 |
| _californica_   | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _candidicans_   | -0.33 ab | -0.88 a | -1.25 ab | 0.37 a   | 0.42 | -1.27 -1.41 |
| _champinii_     | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _cinerea_       | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _cordofolia_    | -0.33 ab | -0.88 a | -1.25 ab | 0.37 a   | 0.42 | -1.27 -1.41 |
| _doaniana_      | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _girdiana_      | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _lincecumii_    | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _longii_        | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _monticola_     | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _riparia_       | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _rupestris_     | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _solonis_       | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _treleasei_     | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |
| _vinifera_      | -0.33 abc | -0.18 b | -1.39 abc | 0.20 ef  | 0.29 | -1.26 -1.16 |

Fig. 1. Three measures of vine water status (Ψ₀, predawn, midday Ψₛₚₚ, stem, and midday Ψₚ, 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 ± 1SE.

Fig. 2. Net CO₂ 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.

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nonirrigated, were *V. riparia*, *V. monticola* and *V. lincecumii*, 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. lincecumii* 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.

### Table 4. Net CO$_2$ assimilation rate (A), stomatal conductance (g$_s$) and intrinsic water use efficiency (WUE, A/g$_s$ x 10$^3$) (NI treatment only) of 17 *Vitis* species on the last measurement date.$^*\text{ Other information as found in Table 3. There were no significant differences among means in the A, NI column.}$

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

$^*$A and g$_s$ are expressed as mmol m$^{-2}$ s$^{-1}$ CO$_2$ and mmol m$^{-2}$ s$^{-1}$ H$_2$O, 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.

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

**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...
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, on the last date, V. cinerea, and V. lincecumii, also had the greatest reductions in g, 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,) was used as the basis for classification. Such a basis would presumably be a measure of growth and gas exchange. ‘Riparia 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 V, 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 V, 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. candidas, 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 Ψl will decrease as soil water deficits develop and it has been reported that under water stress, drought-tolerant plants will maintain higher Ψl’s than drought-sensitive ones (Kirkham, 1990). However, in our study we used the differences in Ψl and Ψs 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 Ψl and one of the lowest values of Ψl and Ψs on the last measurement date was V. champinii. Its values were similar to V. riparia. However, V. champinii had the highest A, g, and pruning weights, unlike V. riparia. It was recently reported that the difference between Ψs and Ψl was linearly correlated with leaf transpiration (Chone et al., 2001). Such a relationship was also found in this study (r^2 = 0.64, data not given). Thus, V. champinii with low values of Ψl and Ψs had the highest Ψl and Ψl, and that was reflective of its gas exchange measurements and its Ψl – Ψl was similar to the irrigated cohort’s value. Thus, using only

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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.

| Vitis Species | NI | NI/ | NI | NI/ | NI | NI/ | NI | NI/ | NI | NI/ | NI | NI/ | Mean score |
|---------------|----|-----|----|-----|----|-----|----|-----|----|-----|----|-----|------------|
| champinii     | 1  | 9   | 1  | 2   | 12 | 8   | 2  | 4   | 3  | 1   | 1  | 1   | 50 a       |
| doaniana      | 12 | 2   | 1  | 5   | 10 | 2   | 11 | 3   | 6  | 3   | 4   | 80 ab      |
| longii        | 2  | 2   | 11 | 5   | 3  | 15  | 15 | 9   | 7  | 5   | 4   | 79 abc     |
| girdiana      | 9  | 5   | 7  | 6   | 10 | 14  | 16 | 5   | 8  | 5   | 4   | 94 abc     |
| arizonica     | 7  | 14  | 6  | 11  | 10 | 8   | 13 | 3   | 1  | 4   | 3   | 93 abc     |
| californica   | 10 | 16  | 3  | 10  | 16 | 3   | 9  | 1   | 2  | 2   | 11  | 14 99 abc  |
| vinifera      | 4  | 6   | 12 | 12  | 4  | 4   | 5  | 8   | 9  | 9   | 14  | 10 105 bcd |
| cordifolia    | 3  | 4   | 9  | 4   | 5  | 6   | 12 | 7   | 13 | 10  | 14  | 12 111 bcd |
| treleasi      | 6  | 7   | 13 | 14  | 2  | 17  | 11 | 13  | 5  | 10  | 7   | 9  | 1   115 bcd |
| monticola     | 8  | 11  | 5  | 8   | 13 | 1   | 1  | 16  | 10 | 15  | 11  | 16 125 bde |
| rupestris     | 5  | 8   | 15 | 15  | 15 | 7   | 15 | 16  | 16 | 17  | 5   | 6   131 bde |
| candidas      | 14 | 17  | 4  | 7   | 17 | 12  | 4  | 12  | 8  | 4   | 13  | 138 cde    |
| solonis       | 12 | 10  | 14 | 9   | 6  | 13  | 17 | 14  | 11 | 13  | 6   | 2   138 cde |
| riparia       | 11 | 12  | 10 | 13  | 8  | 1   | 6  | 11  | 15 | 15  | 17  | 139 cde    |
| berlandieri   | 15 | 3   | 7  | 3   | 11 | 14  | 17 | 14  | 17 | 16  | 16  | 8   155 de  |
| lincecumii    | 15 | 15  | 16 | 16  | 9  | 16  | 13 | 10  | 6  | 12  | 10  | 15 158 de  |
| cineria       | 17 | 13  | 17 | 17  | 7  | 8   | 16 | 16  | 6  | 13  | 17  | 12 165 e    |

NI = not irrigated, I = irrigated, A = net CO₂ assimilation rate, g = stomatal conductance, A/g = intrinsic water use efficiency, Ψs = predicted predawn osmotic potential at a Ψl of −0.205 MPa, Grad = ((Ψl – Ψs)/(Ψl – Ψl)) × 100, ∆Ψ = Ψs – Ψl, PWt = pruning weight.
absolute values of $\Psi$ 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 $\Psi_{so} - \Psi_{stem}$ and $\Psi_{stem} - \Psi_{f}$ gradient proportions were reflective of the hydraulic conductance of the soil–stem pathway in grapevines. In our study, the proportion of $\Psi_{so} - \Psi_{stem}$ gradient to the total $\Psi_{so} - \Psi_{f}$ 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 $\approx0.3$ 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 $\Psi_{l}$ for the next 30 min. It was assumed that leaves having the more negative $\Psi_{l}$ were not osmoregulating while the opposite was true for leaves with less negative $\Psi_{l}$. It was concluded that *V. riparia* and *V. rupestris* were drought sensitive, as they had the most negative $\Psi_{l}$ values, whereas, V. monticola, V. berlandieri and V. cinerea were drought tolerant because they had the least negative $\Psi_{l}$ 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 $\Psi_{s}$ 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 (Carboneau, 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. lineccumii, *V. riparia* and *V. solonis*. These species generally had low rates of A, gs, 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 (Carboneau, 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 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 Carboneau (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. lineccumii, 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 Carboneau (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 × 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. cандicans 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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