RELATIVE DROUGHT RESISTANCE AMONG SELECTED SOUTHWESTERN LANDSCAPE PLANTS

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Abstract. A method of determining drought resistance appears to have promise in identifying superior plants for minimal irrigation landscapes. Under conditions of this test, desert willow had greater resistance to drought than either fruitless mulberry or yellow bells. This can be attributed to a greater tolerance rather than a greater avoidance. Drought tolerance of both desert willow and yellow bells was over 1.5 times that of fruitless mulberry. Fruitless mulberry had as great or greater drought avoidance than the xeric species under dry conditions. Based on these results, desert willow and yellow bells are tolerant water spenders that can convert to water savers. Fruitless mulberry is a relatively intolerant water spender that may not convert to a water saver. If this is confirmed in further studies, then the success of mulberry in the arid Southwest may be attributed to an ability to increase water uptake in times of drought.

Landscape water conservation has become increasingly important throughout much of the United States due to local problems in water quantity, quality, or distribution. A common initial response to water shortages in the arid Southwest is to encourage the use of native or adapted xeric plants in place of more traditional 'exotic' landscape plants. This response is often based on a misunderstanding of plant water use and drought resistance, epitomized by the unfortunate nomenclature of 'low water use plants'. Some xeric plants often have high transpiration rates and may use more water per leaf area than mesic plants under nonlimiting conditions (6, 11). Xeric plant communities are also rather inefficient users of water in terms of biomass production (9). Many xeric plants have adapted not to use water efficiently, but to survive drought.

In urban landscapes the ability to survive drought can be more significant than the ability to use water efficiently. There are many situations where the irrigation required to maintain efficient water users, either routinely or during periodic droughts, is neither feasible nor desirable. Selecting plants for use in these cases is complicated by the diverse morphological and physiological adaptations plants have adopted to survive drought. A universal method of estimating plant capacity to survive drought might predict plant performance in these situations.

Levitt (3) proposed a definition and a technique for determining drought resistance. Drought resistance is the absolute environmental water potential resulting in the death of 50 percent of the plants:

$$\text{Resistance} = -\text{ water potential}_{e50}$$

Water potential is a measure of the energy status of water in a system. Free water has a potential of 0 and drier systems have more negative potentials. For example, the water potential of a soil at field capacity and at permanent wilting point is often estimated as -0.03 and -1.5 MPa, respectively. Resistance is difficult to measure directly but may be estimated from drought avoidance and drought tolerance.

Avoidance is the ability to maintain a high internal water potential when at steady state with a low water potential environment. It is measured by the ratio of the environment to plant water potential:

$$\text{Avoidance} = \frac{\text{Water potential}_{e50}}{\text{Water potential}_{p50}}$$

Avoidance should be determined when the plant is at steady state with an environmental water potential that results in 50 percent death, but this is not feasible. Instead, Levitt suggested using predawn water potentials under stress as a measure of relative avoidance.

Tolerance is the ability to survive a low internal water potential. It is measured by determining survival of plant cells allowed to equilibrate in a series of dry environments. The water potential that results in 50 percent death is drought tolerance:

$$\text{Tolerance} = - \text{Water potential}_{p50}$$

Relative drought resistance is the product of relative avoidance times tolerance:

$$\text{Resistance} = \text{Avoidance X Tolerance}$$

The purpose of this study was to evaluate Levitt's technique as a means of identifying superior drought resistance landscape plants for the arid Southwest. Test plants for the evaluation were fruitless mulberry (*Morus alba*), desert willow (*Chilopsis linearis*), and yellow bells (*Tecoma stans*). Fruitless mulberry is a popular mesic landscape tree that does surprisingly well in the area, surviving even with minimal care. Desert willow is a deciduous native tree that grows along desert arroyos. Yellow bells is a deciduous native shrub that grows on dry slopes of low mountains and is related to desert willow. Neither of the latter species displays extreme xeromorphic adaptations. Desert willow is thought to be adapted to desert environments by restricting transpiration and growing in arroyos where subsurface moisture is available longer (1). Based on habitat and general characteristics, I anticipated that desert willow would be more drought resistant than yellow bells which would be more drought resistant than fruitless mulberry.

Materials and Methods

Specimens of desert willow, fruitless mulberry and yellow bells were transplanted from 19 liter (5 gal) plastic containers into individual plots at the Texas A&M Research Center at El Paso. The plots were essentially large bottomless containers constructed by lining the sides of a 1.2 x 1.2 x 1.8 m deep (4 x 4 x 6 ft) hole with corrugated fiberglass panels. Panel seams were sealed with silicone caulk and the native soil, a bluepoint sand (Mixed, Thermic, Typic, Toroipsamments), replaced. The plots were separated by 1.2 m (4 ft) of undisturbed soil. The plants were irrigated weekly to a depth of 60 cm (2 ft) during the first growing season for establishment. During the second and third growing season, plants of each species were irrigated with sufficient water to wet the soil to a depth of 30, 45, or 60 cm (1, 1.5, or 2 ft) at biweekly intervals from March through July. For each species there was three irrigation levels in each of four blocks, or 12 plants. The experimental design was a split plot with species as main plots and irrigation levels as subplots.

Plants were not irrigated during measurement periods that began in August and continued until leaf fall (late November). Predawn plant and atmospheric water potential were measured weekly, the former with a pressure bomb and the latter with an electronic psychrometer. Soil water content of each plot was measured daily at 30, 80, and 130 cm (12, 31.5, and 51 in) with a neutron probe. Drought avoidance was related to atmospheric water potential by multiple linear regression with indicator variables for species and irrigation level (4).

Drought tolerance was measured in September of each year. The atmosphere above a saturated salt solution in a sealed container will have a constant, known humidity depending upon the type of salt and the temperature (10). Atmosphere chambers were developed by placing different saturated salt solutions in resealable plastic containers kept at 20°C (68°F) in a controlled environment chamber. Saturated solutions of potassium chloride (KCl), magnesium sulfate ($MgSO_4 \cdot 7H_2O$), sodium sulfate (Na_2SO_4), sodium sulfite (Na_2SO_3), potassium phosphate (KH_2PO_4), and lead nitrate ($Pb(NO_3)_2$) maintained humidities of 85, 90, 93, 95, 96.5, and 97 percent, equivalent to water potentials of -21.9, -14.2, -9.8, -6.9, -4.8, and -4.1 MPa, respectively. Rafts constructed of plastic mesh glued to a styrofoam ring were placed in each atmosphere chamber. Detached whole leaves from desert willow and yellow bell plants and three 25 mm (1 in) leaf disks from each fruitless mulberry were placed on the rafts for one week to equilibrate. Three 13 mm (0.5 in) disks were then cut from each leaf, or one disk from each mulberry sample, using a cork borer. The disks were immersed in the vital stain Evans Blue (2) for 15 minutes. Fresh mount slides were prepared from the stained edges of each disk and examined under light microscopy. The number of live and dead cells was counted in each of three fields for each slide. Percent cell survival was subjected to an arcsin transformation and the transformed data related to atmospheric water potential by multiple linear regression with indicator variables for species and irrigation level. Detransformed results are reported.

A plant can avoid drought by restricting water loss or by increasing water uptake. The capacity of these plants to modify water loss was investigated by measuring cuticular transpiration. The petiole of detached leaves was placed in deionized water overnight to hydrate in the dark in a controlled environmental chamber at a constant 20°C (68°F). The leaves were removed from the water and weighed at 0, 30, 60, and 90 minutes at they dried in the chamber. The leaves were then oven dried to a constant weight at 95°C (203°F). Water loss on a dry weight basis was related to time by multiple linear regression with indicator variables for species and irrigation level. Area of representative leaves was measured using a television-based system (Decagon Delta-T Area Measurement System). Leaf volume, internal gas volume, density, and thickness were measured following the methods of Raskin (5). These measurements were analyzed in a split plot analysis of variance.

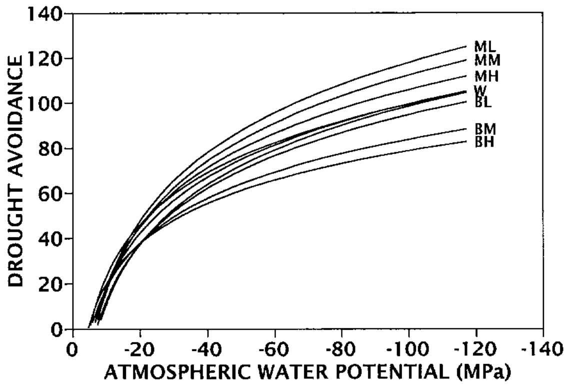

Figure 1. Predicted relative drought avoidance of desert willow (W), fruitless mulberry (M), and yellow bells (B) as influenced by irrigation level (L, M, H = low, moderate, and high irrigation levels, respectively. Lines representing low, moderate, and high irrigation levels for desert willow are present but indistinguishable).

Results

The relationship between drought avoidance and atmospheric water potential was curvilinear (Table 1, Fig. 1). The combined model accounted for only 53 percent of the total variability, but was highly significant ($p<.01$, $n = 468$). Under conditions of low atmospheric demand, between 0 and -30 MPa, the response of the species at different irrigation levels converged. Under drier conditions,

Table 1. Reduced regression equations and predicted relative drought avoidance of desert willow, fruitless mulberry, and yellow bells at -10 and -100 MPa atmospheric water potential.

Species	Irrigation level	Regression equations[z]	Drought avoidance[y] -10MPa	Drought avoidance[y] -100 MPa
Desert willow	Low	Y =-63.8 + 81.7 X abc	18 ± 16	100 ± 12
	Moderate	Y =-52.5 + 76.0 X abc	23 ± 16	99 ± 12
	High	Y =-76.0 + 87.3X abc	11 ± 16	99 ± 12
Fruitless mulberry	Low	Y =-82.5 ± 100.3X c	18 ± 12	118 ± 12
	Moderate	Y =-78.8 ± 95.6 X c	17 ± 12	112 ± 12
	High	Y =-67.7 ± 86.8X bc	19 ± 13	106 ± 12
Yellow bells	Low	Y =-69.0 ± 89.9X abc	13 ± 17	95 ± 13
	Moderate	Y =-47.4 ± 65.7X ab	18 ± 17	84 ± 13
	High	Y =-38.3 ± 58.6X a	20 ± 17	79 ± 14

[z] Y = drought avoidance, X = LOG(-atmospheric water potential). Regression equations followed by the same letter are not significantly different at p=.05 as determined by multiple linear regression with indicator variables for species and irrigation level.
y Predicted drought avoidance ± 95% confidence interval at -10 and -100 MPa atmospheric water potential.

less than -60 MPa, fruitless mulberry had a consistently higher drought avoidance than either desert willow or yellow bells. Irrigation level had little influence on the response of desert willow, at least at less than -60 MPa. Irrigation level appeared to have an effect of the response of fruitless mulberry and yellow bells, but no regressions were significantly different within species. The only significant differences occurred between fruitless mulberry and yellow bells (Table 1).

Table 1 contains the predicted drought avoidance under low (-10 MPa) and high (-100 MPa) atmospheric demand to illustrate the dynamic responses. The higher drought avoidance of fruitless mulberry under dry conditions indicates that these plants maintained a higher internal water potential under stress than did desert willow or yellow bells.

The response of cell survival to dehydrating environments was also curvilinear (Table 2, Fig. 2). The combined model accounted for 83 percent of total variability and was highly significant ($p<.01$, $n=180$). Cell survival for desert willow and yellow bells was consistently higher than that for fruitless mulberry. Irrigation level had no effect within or among species, so the regression equations have been reduced to a single equation per species. Predicted drought tolerance, the plant water potential that results in 50 percent cell survival, is given in Table 2. Desert willow and yellow bells had similar tolerance, and were significantly greater than fruitless mulberry. Cells from these plants were better able to survive dehydration than those from fruitless mulberry.

Table 2. Reduced regression equations and predicted drought tolerance of desert willow, fruitless mulberry, and yellow bells.

Species	Regression equations[z]	Drought tolerance[y] (MPa)
Desert willow	$Y = 198\ X^{-0.73}$ a	-7.7 ± 1.8
Fruitless bulberry	$Y = 131\ X^{-0.68}$ b	-4.8 ± 1.9
Yellow bells	$Y = 188\ X^{-0.74}$ a	-6.9 ± 1.8

z $Y = \sin^{-1}$ (% cell survival/100)$^{1/2}$, X = - atmospheric water potential. Regression equations followed by the same letter are not significantly different at p=.05 as determined by multiple linear regression with indicator variables for species and irrigation level.
y Predicted drought tolerance ± 95% confidence interaval.

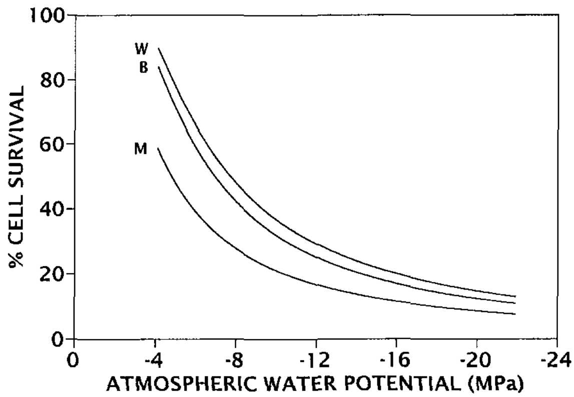

Figure 2. Predicted drought tolerance of desert willow (W), fruitless mulberry (M), and yellow bells (B).

Table 3. Relative drought resistance of desert willow, fruitless mulberry, and yellow bells at -10 and -100 MPa atmospheric water potential.

Species	Irrigation level	Drought resistance (MPa) -10 MPa	-100 MPa
Desert willow	Low	-138	-769
	Moderate	-181	-768
	High	-87	-762
Fruitless mulberry	Low	-85	-566
	Moderate	-81	-539
	High	-92	-508
Yellow bells	Low	-90	-659
	Moderate	-127	-583
	High	-141	-548

Under dry conditions the greater tolerance of desert willow was sufficient to overcome the greater avoidance of fruitless mulberry, resulting in an overall greater resistance (Table 3). The resistance of fruitless mulberry was lower than, but more comparable to that of yellow bells. While fruitless mulberry had a greater ability to either increase water uptake or restrict water loss, desert willow and yellow bells had a greater ability to survive dehydration. The tolerance of dehydration was such that these plants had a greater resistance to drought.

Irrigation level influenced water loss by detached leaves of desert willow and yellow bells but

Table 4. Irrigation level influence on rate of water loss detected leaves of desert willow, fruitless mulberry, and yellow bells.

Irrigation level	Water loss (mg/g dry weight/min) Desert willow	Fruitless mulberry	Yellow bells
Low	1.1a	4.4ab	6.8bc
Moderate	4.0ab	4.7b	9.1c
High	4.4ab	4.9b	13.8d

Mean separation by Waller-Duncan LSD (7,8) at k=100(p=.05).

not fruitless mulberry (Table 4). Leaves of desert willow and yellow bells grown under drought stress were modified to restrict water loss. Fruitless mulberry failed to show this dynamic response. Yellow bell leaves, even those produced under stress, lost water at a higher rate than either of the other plants. Leaves of desert willow grown under stress lost water at a quarter of the rate of those grown with adequate irrigation or of any fruitless mulberry leaf. This study estimated cuticular, not stomatal transpiration. Relative stomatal transpiration rates may be very different from these. Stomata closure, however, is one of the first responses to drought, so cuticular transpiration should be more closely related to drought avoidance by water conservation.

Irrigation level did not influence the measured morphological characteristics of any species. Mulberry leaves were much larger and had a greater volume compared to desert willow and yellow bells, but average leaf thickness was the same for all three species (Table 5). Typically, the xeric species had a greater leaf density but more leaf volume was composed of non-gaseous components in fruitless mulberry.

Discussion

Under conditions of this study, desert willow had a greater resistance to drought than fruitless mulberry or yellow bells. This can be attributed to a greater tolerance rather than a greater avoidance. Drought tolerance of both xeric species was over 1.5 times that of fruitless mulberry. Fruitless mulberry, however, had as great or greater drought avoidance than the xeric species under dry conditions. The only method of maintaining a high internal water potential under these conditions is by either increasing water uptake or restricting water loss. Fruitless mulberry performed one or both functions as well as or better than desert willow and yellow bells.

Cuticular transpiration of mulberry was intermediate but unresponsive to drought stress whereas cuticular transpiration of both desert willow and yellow bells declined with increasing stress. These results suggest that fruitless mulberry had limited ability to restrict water loss and that the greater drought avoidance was likely due to enhanced water uptake. While further studies are required to confirm this supposition, it is consistent with the extensive and intensive root system of this species.

Levitt's method of ascertaining drought resistance appears to have promise for selecting superior plants for minimal irrigation landscapes. In Levitt's terminology, plants that avoid drought by restricting water loss are water savers and those that increase water uptake are water spenders. Some water spenders can convert to water sav-

Table 5. Morphological characteristics of desert willow, fruitless mulberry, and yellow bells leaves.

Species	Area (mm^2)	Volume (mm^3)	Average thickness (mm)	Non-gas density (mg/mm^2)	Non-gas volume (%)
Desert willow	341a	119a	0.34a	1.28b	86.1a
Fruitless mulberry	9275b	2622b	0.29a	0.99a	93.0b
Yellow bells	1122a	291a	0.26a	1.25b	87.1a

Mean separation within columns by Waller-Duncan LSD (7,8) at k=100 (p=.05).

ers. Both types can be tolerant or intolerant. Based on these results, desert willow and yellow bells are tolerant water spenders that can convert to water savers. Fruitless mulberry is a relatively intolerant water spender that may not convert to water saver. If this is confirmed in further studies then the success of mulberry in the arid Southwest may be attributed to an ability to increase water uptake in times of drought. This increased water uptake may occur at the expense of other plants, which would appear to argue against its continued use.

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Résumé. Une méthode pour déterminer la résistance à la sécheresse apparaît être prometteuse pour identifier les plantes supérieures dans les aménagements où l'irrigation doit être réduite au minimum. Sous les paramètres de ce test, le saule du désert possède une plus grande résistance à la sécheresse que le mûrier sans fruit et les «clochettes jaunes». La tolérance à la sécheresse du saule du désert tout comme celle des «clochettes jaunes» était de 1.5 fois supérieure à celle du mûrier sans fruit. Le mûrier sans fruit avait une capacité équivalente ou supérieure aux espèces xériques pour éviter les effets néfastes de la sécheresse sous des conditions sèches. De ces résultats, le saule du désert et les «clochettes jaunes» sont des espèces «dépensières d'eau» tolérantes qui peuvent être converties en espèces «économes d'eau». Le mûrier sans fruits est une espèce «dépensière d'eau» relativement intolérante qui ne pourrait être convertie en «économe d'eau».

Zusammenfassung. Eine Methode zur Bestimmung von Trockenheitsresistenz erscheint erfolgsversprechend zu sein bei der Identifizierung hervoragender Pflanzen für Landschaften mit minimaler Bewässerung. Unter den Bedingungen in diesem Test zeigte die Wüstenweide eine größere Trockenheitsresistenz als die fruchtlose Maulbeere oder Gelbglöckchen. Die Trockenheitsresistenz von Wüstenweide und Gelbglöckchen war anderthalbfach größer als bei der fruchtlosen Maulbeere. Die fruchtlose Maulbeere zeigt eine größe oder größere Vermeidung von Trockenheit als Trockenheitspflanzenarten unter trocknen Bedingungen. Basierend auf diesen Ergebnissen sind Wüstenweide und Gelbglöckchen tolerante Wasserverbraucher, die zu Wassersparern konvertiert werden können. Die fruchtlose Maulbeere ist eine relativ intolerante Wasserverbraucherpflanze, die nicht als Wassereinsparer verwendet werden kann.