

Comparison of drought resistance among *Prunus* species from divergent habitats

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Summary

Root and shoot characteristics related to drought resistance were compared among cultivated peach (*Prunus persica* (L.) Batsch.), *P. andersonii* (Nevada Desert almond), *P. besseyi* (western sand cherry), *P. maritima* (beach plum), *P. subcordata* (Sierra or Pacific plum), and *P. tomentosa* (Nanking cherry). In all species, shoot characteristics were more closely associated with drought adaptation than root characteristics. The most xeric species, *P. andersonii*, had the lowest specific leaf area, smallest leaves, highest stomatal conductance (before stress), highest rate of carbon assimilation (A), high root length/leaf area and root weight/leaf area ratios, and the highest leaf nitrogen content on an area basis. Root hydraulic conductivity was similar for all species, indicating a lack of importance of this parameter for drought resistance. During a 5–7 day drought, water use efficiency (WUE) increased as shoot water potentials (Ψ) declined to -3.0 to -4.0 MPa for the xeric *P. andersonii* and *P. subcordata*, whereas after an initial increase, WUE decreased with declining Ψ in the -1.5 to -3.0 MPa range for the more mesic *P. maritima*, *P. persica* and *P. tomentosa* as a result of non-stomatal limitations to A . Carbon assimilation rate decreased linearly with Ψ during drought in all species, but the Ψ at which A reached zero was not associated with drought adaptation. We conclude that the variation in leaf characteristics among *Prunus* species could be exploited to improve the drought resistance of commercial cultivars.

Introduction

The genus *Prunus* contains many economically important fruit tree species, including peach, nectarine, almond, apricot, plum, sweet and sour cherry, and several species of minor importance as scions or rootstocks. Drought stress severely limits successful cultivation of these fruits in arid climates and in areas with shallow soils. In large-fruited species like peach, both yield and quality are negatively affected by drought stress, particularly during the 4–6 week period before harvest, when the fruits increase rapidly in weight and diameter (Chalmers and Wilson 1978). Because irrigation may become more expensive as a result of water shortages and competition between agricultural and domestic water needs, methods for improving drought stress resistance of *Prunus* species are of interest.

Mechanisms of drought resistance in plants have been documented extensively in agronomic crops, but to a lesser extent in tree crops. Some mechanisms of drought resistance are associated with shoot characteristics, e.g., small leaves with high leaf weight/leaf area ratios, heavy cutinization or reflective pigmentation and drought-induced leaf fall. Other mechanisms of drought resistance are associated with roots, e.g., high hydraulic conductivity, high root length density and a deeply rooting habit. Mechanisms such as osmotic adjustment and changes in root/shoot ratio may involve

the whole plant. Despite extensive research, the relative importance of each mechanism in conferring drought resistance is uncertain.

Characterization of the various drought resistance mechanisms in *Prunus* may reveal whether drought resistance can be increased by using rootstocks with drought resistant characteristics, or by changing the structure or physiology of the canopies of scion cultivars. We compared several drought resistance characteristics in six *Prunus* species from divergent habitats. Because many *Prunus* species are graft-compatible and can be interbred, the development of a single tolerant genotype may impact the cultivation of several species.

Materials and methods

Plant material and growth conditions

Five *Prunus* species from habitats differing in drought frequency and severity were compared to the cultivated peach, which performs poorly when drought stressed compared to other fruit crops (Table 1). Of the species examined, *P. andersonii* inhabits the most xeric environment (Nevada), followed by *P. besseyi*. *Prunus maritima* receives moderate to high rainfall in its native range, but grows on shallow, sandy soils and sand dunes and has been reported to tolerate drought (Farmer 1964). *Prunus subcordata* grows along streams and lakes, but can inhabit xeric niches such as rock slides at high elevations (Roberts and Hammers 1951). *Prunus tomentosa* is native to northern China, Korea, and Japan where adequate rainfall and relatively short growing seasons occur (Kask 1989). All of these species except *P. andersonii* have been exploited horticulturally as minor fruit crops or rootstocks.

In January 1990, stratified seed of all species was sown in flats containing a 10/3/7 (v/v) mixture of peat, vermiculite and perlite in a heated greenhouse. Following germination, seedlings were transplanted to 15-cm pots containing sand and fertilized weekly with soluble N,P,K fertilizer (20/8.6/12 plus micronutrients). Because

Table 1. Names and native ranges of *Prunus* species used for drought resistance measurements.

| Species | Common name | Native range |
|----------------------|------------------------|---|
| <i>P. andersonii</i> | Nevada Desert almond | Southwestern United States (xeric) |
| <i>P. besseyi</i> | Western sand cherry | Manitoba/Kansas, west to Utah (semi-arid grasslands) |
| <i>P. maritima</i> | Beach plum | Coastal areas Virginia–Nova Scotia (mesic sandy soils) |
| <i>P. persica</i> | Peach | China (mesic temperate/subtropical) |
| <i>P. subcordata</i> | Sierra or Pacific plum | S. Cascade–N. Sierra ranges 300–2000 m elevation (mesic/xeric) |
| <i>P. tomentosa</i> | Nanking cherry | N. China, Korea, Japan (mesic cold climates) |

seedling and mature leaf characteristics vary (Rieger 1992), and comparisons of other species to the mature form of peach was desired, peach seedlings were chip budded with "Redhaven" scions on June 9, 1990. All plants except *P. maritima* were stored in a cooler at 7 °C from July 9 until October 17, 1990 to satisfy chilling requirements. *Prunus maritima* plants were allowed to grow for another 3 months to attain the size of other species, because germination and growth were slow in this species. All plants were grown for 2.5–3 months after removal from the cooler, and 5–7 representative plants of each species were then selected for all measurements. All plants were trained to have a side shoot attached at the base of the main stem to facilitate root hydraulic conductivity and plant water potential measurements. Greenhouse day/night temperatures were 20–30/15–20 °C, and light transmission was $\approx 80\%$ during the growth period preceding measurements.

Gas exchange and root hydraulic conductivity

Each plant canopy was enclosed in a 42-liter gas exchange chamber for measurement of carbon dioxide assimilation (A) and transpiration (E) (Rieger and Motisi 1990). Assimilation was calculated as the flow rate of CO_2 enriched air ($[\text{CO}_2] \approx 2700 \mu\text{l l}^{-1}$) into the chamber multiplied by the difference in CO_2 concentration between the air source and chamber. Chamber air was pumped through a tube of desiccant in a closed loop outside the chamber to maintain a vapor pressure gradient (VPG) of 2.0 ± 0.1 kPa, and transpiration rate was obtained by weight change of the tube per unit time, plus a correction for water vapor displaced from the chamber by the CO_2 enriched air. Stomatal conductance (g) was calculated as $E/\text{VPG} - g_{\text{bl}}$, where g_{bl} is the leaf boundary layer conductance, estimated from wet filter paper replicas of leaves. Boundary layer conductances ranged from 780 to 2010 $\text{mmol m}^{-2} \text{s}^{-1}$ for the widest and narrowest leaves, respectively. Water use efficiency (WUE) was calculated as A/E . Saturating irradiance ($> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) for $> 90\%$ of the leaves was obtained with three 400-W metal halide lamps arranged in a 120° arc about the chamber, yielding A values within 1 SE of those obtained with single-leaf systems for peach (Flore and Lakso 1989). Temperature was 27 ± 1.5 °C and CO_2 concentration was $350 \pm 5 \mu\text{l l}^{-1}$ for all measurements.

Simultaneously with initial gas exchange measurements, root hydraulic conductivity (L_p) was estimated from the slope of the relationship of E ($\text{g H}_2\text{O m}^{-1} \text{h}^{-1}$) to the water potential gradient across the root system ($\Delta\Psi$) (Rieger and Motisi 1990). The soil was maintained at saturation during measurement and its Ψ was assumed to equal 0; therefore $\Delta\Psi$ was estimated as the xylem pressure potential (pressure chamber method) of non-transpiring leaves attached to a shoot at the base of the main stem. The y-intercept of this relationship is defined as the offset, which can be interpreted as the minimum $\Delta\Psi$ required to permit flow across roots (Passioura and Munns 1984). Linear regressions were developed from paired measurements of E and $\Delta\Psi$ made at two or three different VPGs for each plant.

Following determination of L_p , the soil was allowed to dry for a 5–7 days, during which time periodic measurements of A and Ψ were made to obtain a relationship between these variables for each species. The Ψ of the non-transpiring leaves was

0.1 to 0.3 MPa higher than that of the leaves in the canopy at high soil water content, but within 0.1 MPa of canopy leaves when soil was dry. Plants were maintained in the laboratory under metal halide lamps with a 12-h photoperiod and an irradiance of $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the dry-down period.

Growth characteristics and dry weight partitioning

Plants were destructively sampled following gas exchange measurements to determine leaf area, root length, and leaf, stem and root dry weights. Leaf area was measured with a LI-3000 leaf area meter (Li-Cor, Lincoln, NE). Root length was estimated by the line intersect method of Tennant (1975) using a 3×3 cm grid. Roots were divided into two classes based on diameter; fibrous roots had diameters ≤ 1 mm, and large roots had diameters > 1 mm. Length and weight of large roots were measured separately from those of fibrous roots. Dry weights of leaves, roots, and stems were determined after drying at 80°C for at least 1 week.

Leaf nitrogen content was determined by Kjeldahl digestion and colorimetric quantitation with an autoanalyzer apparatus, calibrated with standard ammonium sulfate solutions.

Results and discussion

Growth and dry weight partitioning

Leaf characteristics generally reflected the drought adaptation of each species. Specific leaf area (SLA) was lowest for *P. andersonii*, from the most xeric environment, and highest for *P. tomentosa*, from a mild, mesic environment (Table 2). However, SLA was lower for the more mesic *P. maritima* than for the more xeric *P. besseyi*. Low SLA for *P. maritima* may be a reflection of the thick cuticle, which confers resistance to salt spray in its native habitat, and is not necessarily a drought adaptation. Individual leaves of *P. besseyi* and *P. andersonii* were smaller than leaves of the more mesic species (data not shown). Similar relationships between leaf size and drought adaptation have been found in ecotypes of *Cercis canadensis* from varying habitats (Donselman and Flint 1982, Abrams 1988). The fraction of biomass allocated to leaves ranged from 15 to 19% and was similar for all species, suggesting that the proportion of biomass devoted to carbon acquisition is relatively constant within *Prunus* species (data not shown).

Root system characteristics alone were less closely associated with drought adaptation than leaf characteristics (Table 2). The root/shoot weight ratio was poorly associated with drought adaptation because *P. andersonii* had a lower root/shoot weight ratio than the more mesic species. However, when root length and weight were normalized per unit leaf area, *P. andersonii* had the highest ratios of root length and root weight per unit leaf area, as expected for a desert species. Moreover, *P. tomentosa* had a relatively low amount of root length and root weight per leaf area, in addition to having among the most mesophytic leaf characteristics. Ranney et al. (1991) also found higher root/leaf area ratios for the more drought-tolerant *Prunus*

Table 2. Growth characteristics and dry weight partitioning of *Prunus* species

| Species | Leaf area (m ² × 10 ²) | SLA ¹ (m ² g ⁻¹) | Root length (m) | Root weight (g) | Fibrous root fraction | Root/ shoot ratio | RL ² /LA ³ (m ⁻¹ × 10 ⁻³) | RW ⁴ /LA (g m ⁻² × 10 ³) |
|----------------------|--|---|--------------------|--------------------|--------------------------|-------------------------|---|---|
| <i>P. andersonii</i> | 5.25d ⁵ | 0.14d | 150bc | 8.9d | 0.54a | 0.61c | 3.0a | 9.5 a |
| <i>P. besseyi</i> | 8.75bc | 0.25b | 227a | 11.4cd | 0.44b | 1.46b | 2.7ab | 5.8 b |
| <i>P. maritima</i> | 10.37b | 0.19c | 192ab | 17.1a | 0.38bc | 1.35b | 1.9b | 6.2 b |
| <i>P. persica</i> | 10.51b | 0.23bc | 224a | 14.8ab | 0.38bc | 1.35b | 2.2ab | 5.4 b |
| <i>P. subcordata</i> | 6.51cd | 0.21bc | 141c | 12.8bc | 0.42b | 2.00a | 2.2ab | 9.1 a |
| <i>P. tomentosa</i> | 14.83a | 0.33a | 142c | 14.4abc | 0.31c | 1.24b | 1.0c | 3.2 b |

¹ SLA = Specific leaf area.

² RL = Root length.

³ LA = Leaf area.

⁴ RW = Root weight.

⁵ Means followed by the same letters are not significantly different; separation by Duncan's multiple range test, 5% level.

cerasus "Meteor" than for the less drought-tolerant *Prunus avium* × *pseudocerasus* "Colt."

The fraction of root biomass in fibrous roots (≤ 1 mm), which presumably have the greatest absorptive capacity in the root system, was highest for *P. andersonii* and lowest for *P. tomentosa*. Thus, although *P. andersonii* partitioned less than half of its total biomass to the root system, it developed the most favorable relationship between absorptive and evaporative surface area of all the species. The high root/shoot weight ratio and low fibrous root weight fraction of *P. subcordata* may be associated with a tendency of this species to produce shallow, horizontal roots for adventitious shoot production rather than a reflection of its drought adaptation.

Gas exchange

Under well-watered conditions, carbon assimilation rate and leaf conductance were greatest for *P. andersonii*, the most xeric species (Table 3). Carbon assimilation rates of *P. andersonii* were 2-fold higher than those of the cultivated *P. persica*, and 3-fold higher than those of *P. tomentosa*, both more mesic species. However, lower *A* in *P. tomentosa* was balanced by higher leaf area per plant, such that total CO₂ acquisition per plant was similar for this species and *P. andersonii*.

Greater *A* for *P. andersonii* was at least partially accounted for by higher *g* and intercellular CO₂ (*C_i*) compared with the other species. Abrams et al. (1990) reported that *Fraxinus pennsylvanica* seedlings of South Dakota (semi-arid) origin had higher *A* and *g* than seedlings from New York (mesic) under both water-stressed and non-stressed conditions. Differences in nitrogen content per unit leaf area among species (Table 3) may also have contributed to differences in *A*, because much of the leaf N is located inside the chloroplasts (Evans 1989). Both higher N and higher SLA for *P. andersonii* indicate greater amounts of photosynthetic "apparatus" (i.e., chlorophyll, carboxylation enzymes, chloroplasts, mesophyll cells) per unit leaf area, giving rise to greater carbon assimilation rates on a leaf area basis, but similar assimilation rates when expressed on a leaf nitrogen basis. This is supported by similar nitrogen use efficiencies (NUE = *A* per leaf N content) for all species except *P. persica* (Table 3). Thus, with the exception of *P. persica*, the ability to fix CO₂ per unit of photosynthetic resources may be similar among species differing widely in drought adaptation. Low NUE for *P. persica* may have resulted from selection of the "Redhaven" cultivar for high yield and fruit size under conditions of high nitrogen fertility.

All species exhibited linear decreases in *A* with decreasing shoot Ψ as soil dried over a 5–7 day period (Figure 1). Similar linear responses of *A* to Ψ have been reported for peach seedlings (Tan and Buttery 1982) orange (Germana and Sardo 1990), olive (Jorba et al. 1984), and apple (Lankes 1984). Carbon assimilation rates of *P. besseyi* and *P. maritima* declined to zero at higher Ψ than those of *P. andersonii*, *P. subcordata* and *P. tomentosa* (Table 3). The cultivated *P. persica* was similar to all species except *P. tomentosa* in its ability to maintain positive *A* as Ψ declined. Thus, the parameter Ψ at *A* = 0 did not appear to reflect drought adaptation very well, because the mesophytic *P. tomentosa* and xeric *P. andersonii* were similar in this

Table 3. Non-stressed leaf gas exchange, nitrogen content, nitrogen use efficiency (NUE = $A/\text{leaf N}$), and water potential at zero carbon assimilation (Ψ at $A = 0$) following short-term drought of *Prunus* species.

| Species | A ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | g ($\text{mmol m}^{-2} \text{s}^{-1}$) | WUE ($\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) ($\times 10^3$) | C_i ($\mu\text{l l}^{-1}$) | Ψ at $A = 0$ (MPa) | Leaf N (mmol m^{-2}) | NUE (s^{-1}) ($\times 10^3$) |
|----------------------|---|---|--|-----------------------------------|----------------------------|------------------------------------|---|
| <i>P. andersonii</i> | 21.4a ¹ | 447a | 3.39c | 268a | -3.24ab | 18.6a | 1.14a |
| <i>P. besseyi</i> | 12.2b | 193b | 4.17b | 244b | -2.22c | 12.0b | 1.04ab |
| <i>P. maritima</i> | 9.8bc | 127b | 4.80a | 225b | -2.46c | 10.0b | 1.00ab |
| <i>P. persica</i> | 10.7bc | 169b | 4.11b | 238b | -2.87bc | 11.6b | 0.91b |
| <i>P. subcordata</i> | 12.8b | 187b | 4.18b | 240b | -3.17ab | 10.9b | 1.17a |
| <i>P. tormentosa</i> | 7.0c | 103b | 4.12b | 241b | -3.54a | 6.5c | 1.08ab |

¹ Means followed by the same letters are not significantly different; separation by Duncan's multiple range test, 5% level.

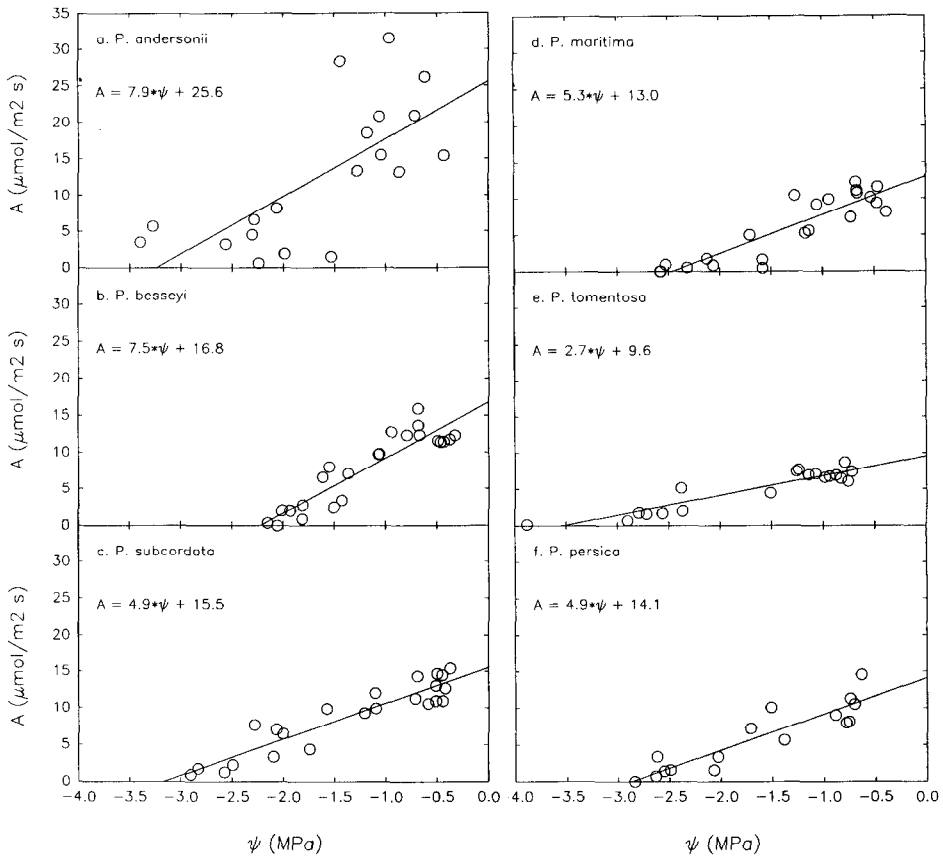


Figure 1. Carbon dioxide assimilation (A) as a linear function of stem water potential (Ψ) during a 5–7 day drought for six *Prunus* species. Slopes and intercepts of all regressions were significantly different from zero ($P < 0.05$); estimates of x -intercept or the Ψ at $A = 0$ are compared statistically in Table 3. Relationships were developed from 5–7 replicates for each species.

respect, and the somewhat xeric *P. besseyi* reached an A of zero at -2.2 MPa. In a related study, McGee et al. (1981) also found small differences in Ψ at $A = 0$ (≈ 0.2 MPa) among floodplain and sand dune ecotypes of *Populus deltoides* despite differences in growth and morphology during drought. In *Fraxinus pennsylvanica*, there was a poor relationship between drought adaptation and Ψ at $A = 0$ across five genotypes, although the most xeric genotype reached $A = 0$ at a Ψ of ≈ 0.8 MPa lower than most mesic genotype (Abrams et al. 1990). Lack of association between this parameter and drought adaptation may be associated with changes in the relationship between A and Ψ with leaf age. Substantial changes in relationships between A and Ψ occurred in apple leaves as the season progressed from May through September (Lakso 1979). Although leaves of all *Prunus* species were 2.5 to 3 months old when measurements were made, there may have been differences in physiological age due to variation in growing season length among the species from different habitats.

Water use efficiency differed among the species, but not in a manner consistent with drought adaptation (Table 3). Water use efficiency was more closely related to g and A than drought adaptation across species, as WUE was lowest for *P. andersonii* (high g and A) and highest for *P. maritima* (low g and A). Similarly, WUE was greatest and g and A lowest for *Vaccinium darrowii* compared to *V. corymbosum*, which had low WUE but high g and A (Flore et al. 1985). Low WUE at high g may be a consequence of diminishing increases in A and linear increases in E per incremental increase in g at constant VPG (Lakso 1985). In other words, an increase in stomatal aperture when g is already high yields little in terms of CO_2 gain, but accelerates water loss. High WUE may not be a wise selection criterion for improvement of drought stress tolerance in *Prunus*.

Within a species, WUE increased with declining Ψ as soil dried (Figure 2), but

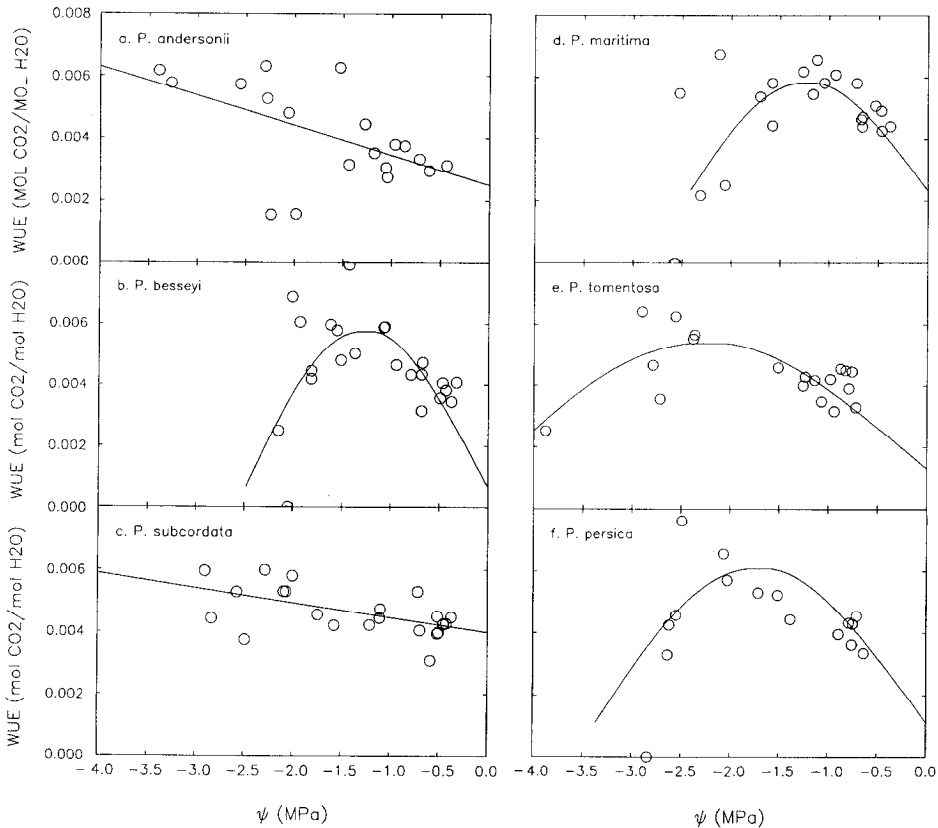


Figure 2. Water use efficiency (WUE) as a function of stem water potential (Ψ) during a 5–7 day drought for six *Prunus* species. For *P. andersonii* (a) and *P. subcordata* (c), linear regressions were significant ($P < 0.05$) and quadratic regressions were nonsignificant; for *P. besseyi* (b), *P. tomentosa* (e), and *P. persica* (f), linear regressions were nonsignificant and quadratic regression were significant. For *P. maritima* (d), both linear and quadratic regressions were significant, but there was significant r^2 improvement of the quadratic over the linear model. Relationships were developed from 5–7 replicates for each species.

then decreased with Ψ as stress became more severe for *P. besseyi*, *P. maritima*, *P. tomentosa* and *P. persica*. For *P. andersonii* and *P. subcordata*, however, WUE increased linearly as stress intensified and reached a maximum at the lowest values of Ψ and g . Species showing a linear response of WUE to Ψ (*P. andersonii* and *P. subcordata*) also had significant positive correlations between C_i and Ψ , indicating a progressive stomatal limitation of A as stress intensified. The other four species showed a hyperbolic response of WUE to Ψ and no significant correlation between C_i and Ψ , but had high C_i at the lowest values of g , suggesting that non-stomatal factors were affected by drought stress within the range of Ψ values examined. Alternatively, non-uniform closure of stomata among leaves or within a single leaf (stomatal patchiness) could have resulted in high values of C_i at low water potentials (Laik 1983).

Root hydraulic conductivity

Root hydraulic conductivity did not differ among species (Table 4). All species exhibited great variation among replicates ($cv > 50\%$) despite relatively low variation in morphological and physiological characteristics among replicates. However, significant differences in the minimum $\Delta\Psi$ required to initiate flow through roots (offset) were observed, although there was no apparent relationship between offset and drought adaptation. Differences in the offset would account for the small differences in shoot Ψ among species at similar rates of water uptake (data not shown). Similarity of L_p across divergent species of *Prunus* suggests a lack of importance of this parameter in conferring drought resistance.

Conclusions

Shoot characteristics were better correlated with drought adaptation than root characteristics in the species studied. For example, great differences in leaf morphology and gas exchange occurred between the desert species *P. andersonii* and the other species, whereas root length and hydraulic conductivity were similar for *P. andersonii* and the more mesic species. Of the root parameters measured, only the

Table 4. Root hydraulic conductivity (L_p) and minimum Ψ gradient required for flow through roots (offset) of *Prunus* species.

| Species | L_p ($\text{g m}^{-1} \text{h}^{-1} \text{MPa}$) | Offset (MPa) |
|----------------------|---|-----------------|
| <i>P. andersonii</i> | 0.345a ¹ | -0.36bc |
| <i>P. besseyi</i> | 0.318a | -0.28ab |
| <i>P. maritima</i> | 0.252a | -0.29ab |
| <i>P. persica</i> | 0.238a | -0.45cd |
| <i>P. subcordata</i> | 0.260a | -0.20a |
| <i>P. tomentosa</i> | 0.386a | -0.52d |

¹ Means followed by the same letters are not significantly different; separation by Duncan's multiple range test, 5% level.

fraction of root biomass in fibrous roots was correlated with drought resistance. The whole-plant parameter root weight/leaf area was also associated with drought resistance.

Perhaps the most inconsistent response was obtained for *P. besseyi*, which was expected to show greater drought resistance than more mesic species because it is native to semi-arid grasslands of the North American great plains. One possible explanation for the inconsistent response of *P. besseyi* is that seed was obtained from an eastern nursery (Massachusetts), so that seedlings used in this study may not have been representative of the ecotypes native to semi-arid habitats. Intraspecific variation in drought resistance has been reported in other tree species when seed is collected from diverse habitats (McGee et al. 1981, Parker and Pallardy 1985, Bongarten and Teskey 1986, Abrams et al. 1990).

The ability to produce deep root systems and acquire water at depth in soils was not assessed in this study. Greater drought resistance of herbaceous crops has been attributed to greater rooting depth of tolerant genotypes (Lorens et al. 1987, Sponchiado et al. 1989). Osmotic adjustment is another important drought stress parameter that was not investigated here. However, rapid development of drought stress, as occurred in this study, may preclude osmotic adjustment (Jones et al. 1985).

Great variation in shoot characteristics among *Prunus* species suggests that genetic improvement of drought resistance of stone fruits may be accomplished by incorporating xerophytic leaf characteristics into scion cultivars. However, this approach may result in initial reductions in yield and quality, and may require extensive backcrossing to produce suitable commercial cultivars (Parsons 1979). Therefore, it is important that xerophytic leaf characteristics are accompanied by high rates of carbon assimilation, as with *P. andersonii*, so that yield is not reduced in proportion to water use. Altering drought resistance through changing root hydraulic conductivity, which was successful in wheat (Richards and Passioura 1989), may not be possible due to an apparent lack of variation of L_p in *Prunus*. The use of drought-tolerant species as rootstocks cannot be ruled out, however, because variation in the ability to acquire water at depth in soil was not assessed.

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