Abstract. Native American tribes have been cultivating peaches \emph{Prunus persica (L.) Batsch} since their introduction to North America in the 1600s. In the American Southwest, peach orchards derived from centuries of seed selections have been maintained in relative isolation from commercial cultivars. These Native American peach selections may be better adapted to the arid climate of the Intermountain West. We compared physiological robustness during water stress of seedling peaches from a 60-year-old orchard maintained by Navajo farmers in southwestern Utah to the commercial peach rootstock Lovell. Six replicate trees of each rootstock were subjected to eight cycles of controlled drought on an automated lysimeter system, which monitored transpiration rate continuously. Trees were selected for uniform size and transpiration rate at the start of the study. During the drought cycles, individual trees were watered when their transpiration rate decreased to less than 250 g of water per day, ~20% of their well-watered daily transpiration rate. After the first cycle of drought, the transpiration rate of the Navajo trees was greater than the Lovell trees, so they depleted their root-zone water more rapidly and experienced greater water stress. Despite greater stress, the Navajo selection had greater leaf area and dry weight at harvest. Because the root system was confined, these results indicate that the Navajo selection may have greater resilience when experiencing drought, independent of the depth and distribution of the root system. However, this study was not able to determine whether physiological resilience during drought was a result of canopy or root characteristics. Field studies are needed to determine whether root distribution or depth also contribute to drought tolerance in the Navajo selection.

Irrigated agricultural crops account for 70% of water consumption in the United States, and can be as high as 90% in some western states (Schaible and Allfrey, 2017). Agricultural water scarcity is expected to increase as a result of increased population growth and climate change (Strzepek and Boehlert, 2010). Tree fruits such as peaches, apples, cherries, and apricots are high-value crops with some of the greatest water requirements (Fereres and Evans, 2006). In commercial orchard production, a fruited scion is nearly always grafted onto a rootstock cultivar. Breeding and selection of rootstock cultivars frequently targets tree size and precocity, pest and disease resistance, and adaptability to different soils. Less effort has been devoted to the selection of rootstocks that might confer tolerance to drought (Ernst et al., 2012). Selection of rootstocks adapted to drought would benefit arid fruit-growing regions. Native American populations in southwestern North America, including the Navajo, Hopi, and Zuni tribes, have been cultivating peaches for more than 400 years (Benavides, 1996). Native American cultivation practices differ dramatically from European production. Rather than relying on grafting to combine desirable stock and scions, seeds of desirable trees are collected and planted directly to form new orchards (Jett, 1977). Orchards receive no formal irrigation after initial establishment and often receive as little as 280 mm of annual precipitation (Singletary et al., 2014). Orchards were commonly planted below canyon rims, which historically receive precipitation runoff from mesa cliffs, as demonstrated by Navajo, Hopi, and Zuni historic orchard sites (Ferguson, 1996; Jett, 1979; Singletary et al., 2014). The seed selection of peaches from orchards in these remote locations over hundreds of years resulted in landrace-type populations that may have greater drought tolerance than commercial rootstock cultivars. Using these as rootstocks could improve the drought tolerance of modern orchards, requiring less irrigation. Weighing lysimeters provide a reliable method of applying drought stress because the transpiration rate of an entire tree can be determined over short intervals, summed over a day and integrated over the study (Ben-Gal et al., 2010). Studies with lysimeters require that the plants be grown in a limited root zone, which eliminates the variable of root distribution and facilitates studies of physiological adaptation to stress. Several studies have compared rootstocks in containers in a greenhouse environment. A study of drought effects on apple rootstocks in a greenhouse withheld water and used single-leaf measurements of water potential and stomatal conductance to assess the magnitude of water stress (Tworkoski et al., 2016). This was a valuable study, but there are significant challenges in extrapolating from short-term measurements on single leaves to whole plants (Jones, 2004).
A common technique in drought-stress container studies is to maintain a constant frequency of watering but reduce the volume of water applied. This leads to less negative water potential at the top of the container than the bottom because the hydraulic conductivity of soil declines exponentially with decreasing water content. This problem is even more significant in coarse-texture media (Hillel, 1998). Atkinson et al. (1999) studied drought in apple rootstocks in 14-L containers with a compost media; Chahal et al. (2018) imposed water stress for Amaranthus in 9-L containers with a silt loam soil. Both studies reduced the volume of water applied without changing the frequency of watering. Chahal et al. (2018) measured water potential or volumetric content carefully, but only in the top 30% of the container. Differences in root-zone water potential between the top and bottom of the container make it difficult to know the magnitude of water stress of the plant. Changing the frequency of watering, rather than the volume of water, provides a better method of regulating water stress because it allows uniform wetting of the root zone.

Both Tworkoski et al. (2016) and Atkinson et al. (1999) used potting soil as a medium, which is well aerated but is a poor substrate for drought studies because it has a rapid decrease in water potential over a narrow range of volumetric water content (Bunt, 1988; Handrek and Black, 2005). Weighing lysimeters facilitate the use of soil because overwatering and waterlogging can be avoided. The use of soil allows for a gradual decrease in water potential that better approximates field conditions. Lysimeters not only indicate volumetric water content of the entire container, they provide a real-time measurement of water stress via the hourly transpiration rate.

Our objective was to use weighing lysimeters for precision water stress to compare resilience during drought of a Navajo peach selection to the commercial seed-propagated rootstock cultivar Lovell.

Materials and Methods

Seeds from a Navajo peach landrace population were collected from an orchard near Navajo Mountain, UT, that has been maintained by native Navajo residents for at least 60 years. Peaches from the Navajo population are predominately white freestone, but can have yellow flesh. Irrigation is occasional, and thinning is not practiced, potentially contributing to a reduced fruit size vs. that of commercial varieties. The trees are shrublike as a result of no pruning practices. The seed selection was a sub-sample of all peach trees within the orchard. Efforts for further characterization of these

**Fig. 2.** Cumulative transpiration for Navajo (black line) and Lovell (red line; color in online version only) peach selections. Data were normalized to the first day of the trial. Cumulative transpiration rates were used to trigger irrigation and provide an indication of the size of the trees. When the cumulative transpiration of an individual tree fell to less than 250 g per day, irrigation was triggered, returning the soil to field capacity. Error bars indicate se.

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*P* < 0.05, **P** < 0.01, and ***P*** < 0.001.
populations are ongoing. The peach cultivar Lovell was used as a control standard because it is a widely used seed-propagated rootstock. Lovell rootstock seeds were provided by a commercial source (Sierra Gold Nurseries, Yuba City, CA). Both selections were planted in 4-L containers filled with an 80% peat/20% perlite media and were grown for 2 months with supplemental lighting in the Utah State University Research greenhouses. Plants were watered with a complete nutrient solution at 100 ppm N fertilization (Peters Excel 21N–2.2P–16.6K; Everris, Dublin, OH). When the root system reached the bottom of the containers, six trees from each seed source were selected for uniformity and were transplanted into 22-L containers with a 90% silty clay loam/10% peat mixture. Soils were a Battle Creek silty clay loam series obtained from an agricultural field located in Cove, UT (lat. 41°57′48″N, long. 111°48′26″W). Silty clay loam was used to achieve a longer, more gradual release of water in the container. Because of the addition of peat and careful soil placement in the container, the bulk density in the containers was $\approx 1.2$ kg·m$^{-3}$. The soil mixture had an initial electrical conductivity (EC) of 1.97 mS·cm$^{-1}$ and was irrigated with water that had an EC of $\approx 0.35$ mS·cm$^{-1}$, so salt stress was judged to be minimal. To ensure ample nutrients, the soil was amended with 8 g·L$^{-1}$ controlled-release fertilizer (Polyon 16N–2.6P–9.1K, 5- to 6-month release; Pursell Industries, Syla-cauga, AL). After 30 d of growth the trees were established in the larger containers. Each tree was visually equal in size at the start of the trial. Before the start of the first trial, Navajo trees had an average transpiration rate that was 4.3% greater than Lovell (593 vs. 565 g·d$^{-1}$). During this pretrial period, differences were not statistically significant and the uniform transpiration rate indicated the relative uniformity of the trees. Peak transpiration rates, generally observed 2 to 3 d after the last irrigation event, increased to $\approx 1000$ g·d$^{-1}$ at the start of the trial.

Each container and its tree was then placed on a load cell platform in a 12-container weighing lysimeter system (Fig. 1). This greenhouse lysimeter system has been described in detail by Chard et al. (2016). Each container had two 2-L·h$^{-1}$ drip emitters at the surface, which were used to add water slowly until leaching was observed from drain tubes at the bottom. Before filling, porous ceramic cylinders (1.5-cm diameter × 6.5-cm length; effective pore size, $\approx 1.7$ μm) were installed at the bottom of each container by drilling a hole through the side wall and fixing the cups in place. After irrigation, when leaching was observed to stop, a vacuum (–0.05 MPa) was connected to the porous ceramic cylinders and run overnight. This removed $\approx 250$ mL additional water from each container. The container surface was then covered with 5 cm perlite to minimize surface evaporation. The combined weight of each tree and container was then determined ($\approx 22–27$ kg/tree) and programmed into the measurement and control software as the near-field-capacity baseline weight.

Transpiration rates were determined every 30 min from the change in container weight, summed daily, and a cumulative transpiration total was calculated at midnight. Trees were irrigated when the daily cumulative transpiration decreased to less than a programmed threshold of 250 g/tree·d. This change represented an approximate 80% decline in daily transpiration from maximum, or peak, daily transpiration totals after irrigation. This threshold was selected because it was associated with visual wilting of the leaves. The transpiration rate of each tree was measured independently and irrigated automatically using a data logger-based controller. After each drought cycle, containers were drip-irrigated back up to the near-field-capacity baseline weight. To allow daily measurements of transpiration, plants were irrigated only at night. Irrigation cycled on for 15 s each minute to minimize ponding and allow for slow percolation of water into the soil. This slow irrigation (up to 6 h) preserved the soil structure and air-filled porosity during the trial. Each tree was subjected to four dry-down and irrigation cycles, followed by a 2-week well-watered recovery period, and then four additional dry-down and irrigation cycles, for a total of eight drought and six recovery events.

Internal circulation fans in the greenhouse minimized variation in temperature and humidity. During the first trial, the average day/night temperature was 28.9/20.3 °C and was 27.8/18.2 °C in the second trial. The vapor pressure deficit averaged 3.2 kPa for the first trial and 2.5 kPa for the second trial. The CO$_2$ concentration was constant (200 ppm) for both trials. Supplemental lighting was provided by four, 1000-W high-pressure sodium fixtures arranged to provide a uniform photosynthetic photon flux density at the canopy surface. Trees were arranged in a complete randomized design to minimize any potential differences in lighting intensity. The integrated daily photon flux density (measured with multiple replicate full-spectrum quantum sensors, model SQ-500; Apogee Instruments, Logan, UT) averaged 45.5 mol·m$^{-2}$·d$^{-1}$ for the first trial and 41.6 mol·m$^{-2}$·d$^{-1}$ for the second trial. These values are about 85% of full summer sunlight under regional field conditions.

![Fig. 3. Daily transpiration rate during maximum drought stress as a percentage of the maximum daily well-watered transpiration rate. There were four drought cycles in each trial. Each load cell was controlled independently. When cumulative transpiration fell to less than 250 g per day, irrigation was triggered. Because the Navajo trees grew more rapidly during the trial, they had a greater transpiration rate and thus were subject to greater stress, as indicated by the lower percentage of the maximum daily transpiration rate at the time of irrigation. Error bars indicate se. The differences in drought stress between selections was statistically significant in trial 1 ($P = 0.02$) but not in trial 2.](image-url)
Trees were harvested destructively at the end of the second trial. Trunk diameter at 3 cm above the soil surface was measured and the cross-sectional area was calculated. Chlorophyll was measured on 10 recently developed, fully expanded leaves per tree using a hand-held chlorophyll meter (model MC-100; Apogee Instruments). Leaves were removed and counted, and the area was measured (model LI-3100C area meter; LI-COR, Lincoln, NE). Leaf and wood tissue dry weight were measured after drying for 3 d at 80 °C. Root balls were removed from their containers and shaken to remove bulk soil, weighed, evaluated visually, and photographed.

The six replicate trees were arranged in a completely randomized design, with seed sources treated as fixed effects. Cumulative transpiration and number of dry-down days were analyzed using two-way repeated measures multivariate analysis of variance (ANOVA). All other variables were analyzed using two-way ANOVA. Trees dried down to threshold transpiration rates over a variable number of days, which resulted in irrigation frequency differing for each tree. Cumulative transpiration was normalized in the graphs so that the start of each drought cycle began with the first day after an irrigation event for all trees. The total number of dry-down days was averaged and the graph was normalized to reflect that average. All data were analyzed using R statistical software (R Foundation for Statistical Computing, Vienna, Austria).

**Results and Discussion**

The time between irrigation intervals was shorter for the larger trees, but individual trees were watered when transpiration decreased to less than 250 g/tree/d. In practice, transpiration rates always declined below this threshold, with minimum daily transpiration rates averaging 220 g/tree/day for the first trial and 205 g/tree/d for the second trial. Comparing these minimum values to peak daily transpiration rates observed after the last irrigation event (initially around 1000 g/tree/d), the minimum transpiration rates represent 22.5% of peak daily transpiration for the first trial and 16% for the second trial. As trees approached lower threshold transpiration rates, there was visible wilting of the leaves throughout the canopy; during the subsequent recovery periods, leaf necrosis and abscission were observed in all trees. Girona et al. (2002) used a similar reduction to 20% of maximum tree evapotranspiration and reported ≈80% reduction in stem water potential by the end of the dry-down period.

Osmotic adjustment of *Prunus* species has been reported to occur after prolonged, gradual dry-downs, most commonly observed under field conditions or carefully controlled greenhouse studies (Arndt et al., 2000; Jiménez et al., 2013). Through this mechanism, leaf turgor can be maintained under stress, although species vary greatly in their capacity for osmotic adjustment (Abrams, 1994). Mellisho et al. (2011) reported that *Prunus persica* (L.) Batsch cv. Floradostar grafted to the *P. persica* × *Prunus amygdalus* GF-677 rootstock did not have sufficient osmotic adjustment to overcome the turgor loss point in leaves. Their study used eight cyclic periods of 7 to 9 d of withholding irrigation and it is uncertain whether osmotic adjustment occurred in either rootstock or to

| Cultivar | Trunk and stem dry wt (g) | Trunk diam (cm) | Total leaf area (m²) | Leaf dry wt (g) | No. of leaves/tree | Root ball wt (g) |
|----------|--------------------------|-----------------|----------------------|----------------|-------------------|------------------|
| Navajo   | 106                      | 1.57            | 1.27                 | 95.8           | 847               | 1,625            |
| Lovell   | 97                       | 1.55            | 0.98                 | 79.1           | 568               | 1,197            |
| Ratio    | 1.10                     | 1.01            | 1.29                 | 1.21           | 1.49              | 1.36             |
| Significance | NS                    | NS              | 0.05                 | 0.05           | 0.01              | NS               |

NS = not significant.

**Fig. 4.** Navajo and Lovell peach trees at harvest. The increased leaf area and leaf number are visually apparent in the photo. Navajo trees tended to have more horizontal branching than Lovell. Although the Navajo root ball weight was 36% greater than the Lovell, the difference was not statistically significant.
what extent it may have contributed to resilience.

Despite drought stress, in our study both genotypes recovered to their predrought peak transpiration rates within 3 d of rewatering (Fig. 2). For the entire first trial and the last two drought events of the second trial, Navajo had greater peak transpiration rates. As a result, the Navajo selection experienced greater drought stress as a percentage of peak daily transpiration in the first trial ($P = 0.02$). The Navajo selection also tended to have greater drought stress in the second trial, but the difference was not statistically significant (Fig. 3).

At harvest, the Navajo selection had a 16% greater leaf dry weight per tree ($P = 0.05$), a 32% greater number of leaves ($P = 0.01$), and a 30% greater leaf area ($P = 0.05$) (Table 1). Because the trees were of equal size at the start of the trials, these differences reflect increased growth of the Navajo selection during the trial, despite slightly greater drought stress. Transpiration rate is highly correlated with CO$_2$ uptake, photosynthesis, and growth of trees (Adams et al., 2018; Bréda and Granier, 1996; Obojes et al., 2018; Welander and Ottosson, 2000), so reduced transpiration rates are a good indicator of reduced whole-tree photosynthesis and dry weight gain. Higher measurements of leaf biomass at harvest confirm that the differences in transpiration rate during the trial were associated with growth differences. Rieger and Duemmel (1992) reported that shoot characteristics in six cultivated peach species correlated more with drought adaptation than root characteristics. In our study, there was no significant difference between specific leaf area of the Navajo and Lovell rootstocks (13.3 and 12.4 $m^2$kg$^{-1}$, respectively), which suggests that leaf contribution to resilience during water stress may be minimal. However, because these were ungrafted rootstocks, adaptation of the shoot may have contributed to the resilience of the tree to water stress. Further studies with each rootstock grafted to a common scion could help differentiate rootstock from scion cultivars adapted to arid environments.

### Conclusions

This study indicates that the Navajo selection is physiologically more robust under drought conditions than Lovell rootstock when root volume is held constant. Commercial peach rootstocks in the field can differ in root distribution (Black et al., 2010). Additional work is needed to determine how root distribution compares between the Navajo selection and commercial rootstocks, as well as how the differences observed here translate into differences in field-based drought response. The historic peach landraces developed by traditional Native American farmers in the American desert Southwest may provide useful traits to commercial breeders in the development of rootstocks and scion cultivars adapted to arid environments.

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