Title
Orchard establishment, precocity, and eco-physiological traits of several pomegranate cultivars

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Diurnal Patterns of Photosynthesis and Water Relations for Four Orchard-Grown Pomegranate (*Prunica granatum* L.) Cultivars

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Abstract

Long-term drought, coupled with tighter regulations on limited water resources have caused growers to seek drought tolerant cultivars of common tree crops in California. Yet information on pomegranate physiology is lacking, even though it is grown throughout the world in various climates. The purpose of this research was to determine the effect of time of day and cultivar on pomegranate photosynthesis and water relations, and calculate values for water-use efficiency, defined as photosynthetic carbon gain divided by water lost during transpiration. The study utilized four field-grown cultivars in their fourth year of growth ('Eversweet,' 'Haku Botan,' 'Parfianka,' and 'Wonderful'), in Riverside, California. Variables analyzed included photosynthesis, stomatal conductance, transpiration, instantaneous water-use efficiency, intrinsic water-use efficiency, and pre-dawn and midday water potential. Differences were detected for time of day, with higher rates of assimilation, transpiration, and stomatal conductance in morning. Intrinsic water-use efficiency was higher in the afternoon compared to the morning. There were also differences among cultivars for stomatal conductance and transpiration during the morning but not during the afternoon, with 'Eversweet' having significantly lower rates of stomatal conductance and transpiration than 'Parfianka': other cultivars were intermediate. These results further our understanding of how pomegranate cultivars function on a physiological level during different times of the day, and suggest that efficiency of production can be improved through cultivar selection.

Increasing global temperatures coupled with unpredictable changes in climate threaten food security globally (Altieri and Nicholls, 2017). California has experienced extreme drought conditions for several years, causing fruit growers to face water limitations affecting production and leading to hundreds of millions of dollars in crop revenue losses in 2016 alone (Medellín-Azuara et al., 2016). To lessen the impacts of climate change and increasing temperatures on food security, it is important to utilize diversified cropping systems to reduce vulnerability to extreme climatic events as experienced in California and other regions of the United States (Altieri and Nicholls, 2017). Long term drought in California and other regions of commercial tree fruit production in the United States has caused growers to abandon fruit crops and seek alternatives with less water demand in the short term. Options for mitigating long term drought in California have included crop abandonment, stress irrigation, switching to alternative crops with new plantings (Medellín-Azuara et al., 2016) and utilization of lower quality secondary water sources.

It has been proposed that physiologists and breeders focus on increasing the efficiency of water use in agriculture (Wallace, 2000).

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Improving production efficiency and drought tolerance through cultivar or variety selection has been proposed in tree crops, such as citrus (Savé et al., 1995) *Prunus* species (Rieger and Duemmel, 1992), dates (Djibril et al., 2005), and coffee (DaMatta, 2004). Because tree crops can have a considerable amount of variability in terms of physiological traits, it is useful to study diversity in crop species to determine if there are cultivars that use water more efficiently or are able to be productive in stressful conditions. Because pomegranate (*Punica granatum* L.) is a drought tolerant crop, especially once established (Stover and Mercure, 2007), it is a candidate crop for growers wishing to switch from more water-intensive species, such as avocado, citrus or almond.

Pomegranate is a drought tolerant crop that has been grown in California since the Spanish missionaries arrived from Spain and planted mongrel seeds at missions up and down the coast (Day and Wilkins, 2009; Stover and Mercure, 2007). The pomegranate variety collection located at the United States Department of Agriculture - Agricultural Research Service (USDA-ARS) National Clonal Germplasm Repository, Davis, CA (NCGR) conserves about 200 genotypes of pomegranate sourced from all over the world, many of which have unique phenotypic traits (Stover and Mercure, 2007). Experiments have demonstrated differences in morphology and vegetative growth traits, including differences in relative chlorophyll content, plant vigor, and branching habit, which can be observed during propagation and in the field (Chater et al., 2017). Although available literature on pomegranate physiology is scarce, research has shown that there can be differences among cultivars for many physiological traits of pomegranate in other collections, including transpiration rate, stomatal conductance, water use efficiency, photosynthetic rate and chlorophyll content (Drogoudi et al., 2012). The objectives of this study were 1) to evaluate four unique pomegranate cultivars for physiological field performance in a semi-arid agroecosystem during morning and afternoon hours; and 2) to determine if there are differences among cultivars for physiological traits that would be conducive to commercial crop production in drought conditions.

Materials and Methods

Site conditions. The site was located at the Department of Agricultural Operations in field 5E (33° 58' 9.39" N, 117° 20' 46.93" W) at University of California, Riverside. Riverside is a semi-arid climate with hot, dry summers and cool winters. The mean annual precipitation of the area is 262 mm and mean maximum temperatures are 28.1 and 35.6° C for June and Aug., respectively. Mean minimum temperatures are 12.9 and 18.1° C for June and Aug., respectively. The soil is a sandy loam with good drainage and was previously an established lemon grove. All trees were growing under natural light, outside in field conditions and were irrigated three times per week. All experimental trees were in their third and fourth years of growth and were located on the inside of the grove, with at least one border tree acting as a buffer to reduce the edge effect.

Plant material. An established pomegranate cultivar trial was utilized for this study during years three and four of tree development. The cultivars in the study were 'Eversweet,' 'Haku Botan,' 'Parfianka,' and 'Wonderful' (Table 1). All plants were propagated as dormant hardwood cuttings at the same time in winter of 2012 and sourced from the National Clonal Germplasm Repository, Davis, CA, USA. All trees included were mature and had fruit set typical of trees in commercial production. Trees were grown under conventional commercial management practices and fertilized in spring with urea and sulfate of potash, totaling 31.75 kg N and 34 kg K per year, respectively, over approximately 0.81 ha. The healthiest tree in each of three blocks was selected (among 15 trees total per cultivar in the trial). The trial was planted in a randomized complete block design.

Table 1. Descriptions of the four pomegranate cultivars sourced from the USDA-ARS National Clonal Germplasm Repository used in this study. Variables known include county of origin, countries of commercial production, acidity, flavor, peel color, aril color, and seed hardness.

Cultivar	Country of origin	Countries of commercial production	Acidity	Flavor	Peel color	Aril color	Seed hardness
Eversweet	USA	USA	Very Low	Sweet and yellow	Pink	Pink	Soft
Haku Botan	Japan	Japan, USA	Very High	Sour yellow	White/	White	Hard
Parfianka	Turkmenistan	USA, Australia	High	Sweet-tart	Red	Red	Soft
Wonderful	USA	USA, Chile, Peru, Israel, Mexico, Argentina, South Africa, Uruguay, Turkey, Italy, Spain, Greece	Medium-high	Sweet-tart	Red	Red	Medium hard

'Wonderful' is the industry standard in many countries and was chosen as a control in the experimental cultivar field trial. The other cultivars were selected for their unique phenotypes. 'Eversweet' is a dwarf-like cultivar bred for coastal climates, with pink fruit peel and aril color, and soft seeds. 'Haku Botan' is an ornamental Japanese cultivar that has an upright growth habit with double white flowers and darker green foliage than most other pomegranate cultivars and lacks visible anthocyanin pigments in stem, leaves and fruit. The fruit is very acidic and very light yellow in color. 'Parfianka' is an internationally-renowned cultivar that has a bright red peel and arils with soft seeds and a balanced sweet-tart flavor. The tree is extremely thorny and has a bushy, highly branched growth habit with smaller leaves than other pomegranate cultivars. 'Wonderful' is commercially widely-grown, and in the USA it accounts for approximately 90-95% of production. It is a highly vigorous, thorny tree that has high yield with red fruit and red seeds with moderate seed hardness and a sweet-tart flavor. The growth habit is willowy, with a tendency to sucker at the base of the tree.

Photosynthesis measurements. During fruit development (late June through Aug.), an infrared gas analyzer (6400, Li-Cor, Lincoln, NE, USA) was used to measure maximum rates of net CO_2 assimilation (A), stomatal conductance (g_s), and transpiration (E) during the morning (9:00 - 12:00 hr) and afternoon (15:30 – 17:30 hr). Morning photosynthetically active radiation (PAR) ranged from 1500-1600 μmol $m^{-2}\cdot s^{-1}$ photosynthetic photon flux density (PFD), while afternoon PAR was 1990 μmol $m^{-2}\cdot s^{-1}$ PFD. Morning measurements were pooled for the four cultivars, which occurred on 22, 23 Aug. 2015 and 26 June 2016. Afternoon measurements were taken on 30 June 2016, which was representative of a typical summer afternoon in Riverside (30-34 °C; 32-37% Relative Humidity). Gas exchange characteristics were measured on two leaves per tree and a minimum of three trees per cultivar. All leaves were collected for leaf area, which was quantified on a leaf area meter to normalize photosynthesis data (Li-Cor, Lincoln, NE, USA).

Only the most recently fully-formed, sun-exposed leaves were selected for this study. Cuvette temperatures were allowed to vary with field conditions. Leaves were measured in a chamber that provided 1500 µmol $m^{-2} \cdot s^{-1}$ (PFD). Instantaneous water-use efficiency was calculated as $A \cdot E^{-1}$ and intrinsic water-use efficiency was calculated as $A \cdot g_s^{-1}$.

Stem water potential measurements. Predawn and midday stem water potential measurements were recorded for each data tree. For predawn water potential, non-actively growing shoots were covered with a plastic bag for 10 min before being pruned, placed in a sealed plastic bag and kept in a cooler bag until transferred to an indoor environment for plant moisture stress measurements with a pressure chamber (Model 1000 Pressure Chamber, PMS Instrument Company, Albany, USA). For afternoon stem water potential measurements, canopy-shaded non-actively growing shoots were covered with a plastic bag for 10 min before being pruned, placed in a sealed plastic bag and kept in a cooler until immediately transferred to a cool lit, indoor environment. Stem water potential was immediately measured after being removed from the cooler bag. One stem was measured from three individual trees per cultivar, for a total of three trees, for predawn and midday stem water potential.

Statistical analysis. All variables were analyzed with Analysis of Variance (ANOVA). When ANOVA indicated significant differences, post-hoc comparisons were performed utilizing Tukey's honestly significant difference (HSD) with an experiment-wise type 1 error rate of $\alpha = 0.05$. Relationships between all variables were analyzed using linear regression ($\alpha = 0.05$), with relationships among parameters determined using general regression with Minitab Software, version 16 (Cov-

Table 2. Mean values of maximum rates of net CO_2 assimilation (µmol CO_2 $m^{-2} \cdot s^{-1}$, A), stomatal conductance (mol H_2O $m^{-2} \cdot s^{-1}$, g_s), transpiration (mmol H_2O $m^{-2} \cdot s^{-1}$, E), intrinsic water use efficiency ($A \cdot g_s^{-1}$), and instantaneous water-use efficiency ($A \cdot E^{-1}$) for four pomegranate cultivars grown in Riverside, CA USA. All measurements were made in the morning and afternoon hours during fruit development in summers of 2015 and 2016.

Cultivar	A	g_s	E	$A \cdot g^{-1}$	$A \cdot E^{-1}$
Morning					
Eversweet	13.27 ± 1.18[z]	0.10 ± 0.02b[y]	1.73 ± 0.38b	147.4 ± 24.8	8.25 ± 1.27
Haku Botan	16.49 ± 1.02	0.15 ± 0.02ab	2.41 ± 0.15ab	112.8 ± 4.7	6.85 ± 0.20
Parfianka	19.80 ± 1.57	0.18 ± 0.03a	2.66 ± 0.26a	117.4 ± 13.3	7.52 ± 0.33
Wonderful	19.38 ± 3.71	0.15 ± 0.02ab	2.04 ± 0.17ab	124.1 ± 9.5	9.44 ± 1.66
P-Value	0.289	0.049	0.037	0.540	0.238
Afternoon					
Eversweet	11.98 ± 1.29	0.07 ± 0.02	1.85 ± 0.40	170.0 ± 22.8	6.87 ± 1.03
Haku Botan	10.24 ± 0.78	0.05 ± 0.02	1.29 ± 0.11	208.5 ± 32.4	8.10 ± 1.01
Parfianka	11.78 ± 1.32	0.07 ± 0.03	1.63 ± 0.41	193.4 ± 26.2	7.79 ± 1.15
Wonderful	9.24 ± 1.10	0.04 ± 0.01	1.10 ± 0.17	235.4 ± 6.4	8.34 ± 0.59
P-Value	0.439	0.334	0.446	0.762	0.442
Time of day					
Morning	17.74 ± 1.24a	0.15 ± 0.01a	2.26 ± 0.15a	124.3 ± 7.1b	8.05 ± 0.53
Afternoon	10.81 ± 0.60b	0.06 ± 0.01b	1.47 ± 0.15b	201.8 ± 12.5a	7.78 ± 0.45
P-Value	< 0.001	< 0.001	0.001	< 0.001	0.708

[z] Values expressed as means ± standard error (Morning n = 15, Afternoon n = 12).
[y] Values within columns and variables followed by common letters do not differ significantly by Tukey's HSD test ($P < 0.05$).

entry, UK). Block was coded as a random effect and interaction terms were included in the models. For the purposes of this work, the R^2 value is the proportion of variation in one variable that is explained by the variation in the regressor variable. Regression models were fit to determine differences in slope coefficients and constants (y-intercept) among variables.

Results and Discussion

The pomegranate cultivars were actively photosynthesizing and transpiring during morning and afternoon hours during all days of data collection. There were significant differences among cultivars for morning measurements only (Table 2). 'Eversweet' had significantly lower rates of g_s ($P = 0.049$) and E ($P = 0.037$) than 'Parfianka' during the morning. There were no other differences detected for gas exchange variables among cultivars.

Time of day significantly affected pomegranate leaf physiology (Table 2). Morning rates of A were 64% higher on average than during the afternoon ($P < 0.001$). Similarly, rates of g_s during the morning were 250% higher on average than rates of g_s during the afternoon ($P < 0.001$). Rates of E were 54% higher on average in morning than in afternoon ($P = 0.001$). In contrast, intrinsic water use efficiency was 62% higher in afternoon than in morning ($P < 0.001$). Instantaneous water-use efficiency was similar in morning and afternoon. According to our findings, net CO_2 assimilation and intrinsic water use efficiency were more variable in the afternoon.

Stem water potential was significantly different among cultivars ($P = 0.012$). 'Haku Botan' had higher stem water potential than 'Eversweet' and 'Wonderful.' 'Parfianka' had a higher stem water potential than 'Wonderful' (Fig. 1). There were no differences in stem water potential among cultivars for midday measurements. Although the difference among means in pre-dawn and afternoon were of similar magnitude, variability was much higher in afternoon than during pre-dawn, leading to no significant differences. There was a large difference between time of day for stem water potential ($P < 0.001$). Stem water potential was much less negative in morning than in midday, with average readings of -0.825 and -2.420 MPa, respectively.

There were positive and negative correlations between physiological variables for morning, afternoon and for data pooled for the two times of day. The relationship between A and g_s was positive and linear and significant for morning measurements ($P < 0.001$, $R^2 = 0.7275$), afternoon measurements

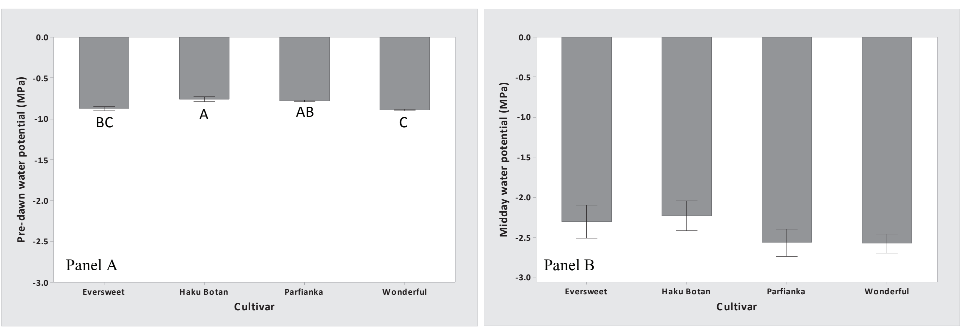

Figure 1. Mean stem water potential (MPa) of four pomegranate cultivars grown in Riverside, CA USA (n = 3 for each cultivar). All stem water potential measurements were made in the pre-dawn (Panel A) or afternoon (Panel B) hours during fruit development in summer of 2015 and 2016. Values followed by common letters do not differ significantly ($P < 0.05$).

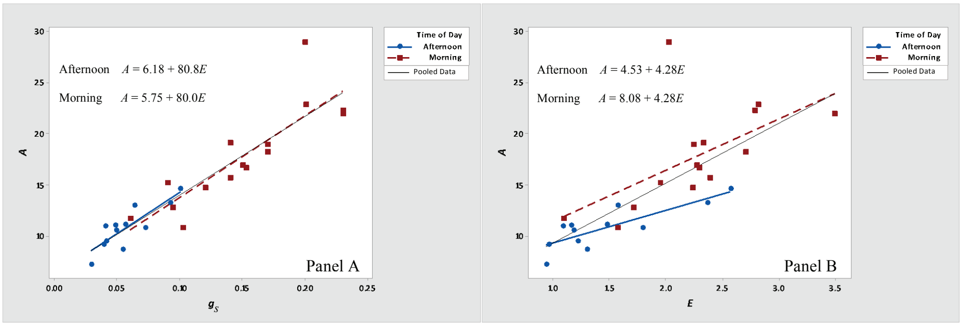

Figure 2. Relationships between maximum rates of net CO_2 assimilation (µmol CO_2 $m^{-2}\cdot s^{-1}$, A), stomatal conductance (mol H_2O $m^{-2}\cdot s^{-1}$, g_s) (Panel A), and net CO2 assimilation (µmol CO_2 $m^{-2}\cdot s^{-1}$, A) and transpiration (mmol H_2O $m^{-2}\cdot s^{-1}$, E) (Panel B). Data represents four pomegranate cultivars grown in Riverside, CA USA (n = 27). All leaf photosynthesis measurements were made in the morning or afternoon hours during fruit development in summer of 2015 and 2016.

($P = 0.001$, $R^2 = 0.7178$) and for pooled data ($P < 0.001$, $R^2 = 0.8533$) (Fig. 2). For A and g_s slopes and intercepts did not differ significantly for time of day. There was also a weak, positive correlation between A and E in the morning ($P = 0.019$, $R^2 = 0.3560$), a stronger relationship in the afternoon ($P = 0.001$, $R^2 = 0.6809$) and a moderately strong relationship for pooled data ($P < 0.001$, $R^2 = 0.5893$), each of which had a weaker relationship than between A and g_s. Intercepts ($P = 0.025$), but not slopes, for the relationship between A and E differed between morning and afternoon. There was a significant interaction between time of day and cultivar for g_s ($P = 0.05$). Eversweet' had similar g_s regardless of time of day, whereas g_s was much higher during the morning for the other cultivars (Fig. 3).

The objectives of this study were to evaluate four pomegranate cultivars for field performance and to determine differences among them for leaf physiological traits. Our findings suggest that all cultivars evaluated in this field study function satisfactorily on an eco-physiological scale for commercial production purposes if the industry standard, 'Wonderful,' is used as the standard. Physiological trait values obtained for 'Wonderful' were much different than those reported for purportedly the same cultivar grown in Greece (Noitsakis et al., 2016). Values were typically of the same order of magnitude, which suggests differences in climate or cultural practices between the two sites may have influenced results because the instrumentation in the two studies are normally well-calibrated against a standard. We found evidence that there are differences among cultivars for physiological traits including stomatal conductance, transpiration and pre-dawn water potential. Values for physiological traits were generally similar in other studies (Hepaksoy et al., 2000; Rodríguez et al., 2012). Strong differences were also detected for time of day, with higher rates of assimilation, transpiration, and stomatal conductance in the morning than afternoon. Intrinsic water-use efficiency was higher in afternoon compared to morning. There were also differences among cultivars for stomatal conductance and transpiration during the morning but not during the afternoon, with 'Eversweet' having significantly lower rates of stomatal conductance and transpiration than 'Parfianka,' and other cultivars were intermediate. Because the larger differences occurred in the afternoon, primarily for g_s and E which describe water loss, afternoon water loss characteristics offer a promising direction for improving water-use efficiency during cultivar selection.

The most interesting finding of this field study is that there are differences among cultivars for important leaf physiological traits, such as E, g_s and water potential. This finding suggests there may be other cultivars in the national germplasm or in other germplasm collections that have even greater production efficiencies than those represented in this study. This finding is important, not only for growers looking for crops and cultivars that use water more efficiently and sustainably, but also for breeders who can use this information for genotype selection. Hepaksoy et al. (2000), studying cultivars 'Lefon,' 'Kadi,' 'Keyiz,' 'Seedless,' 'Siyah,' and 'Koycegiz,' reported that transpiration rate and water use efficiency of pomegranate are correlated with fruit cracking, which means that these cultivars demonstrating differences among these physiological traits should be followed in the field to determine their effects on pomegranate's most destructive physiological disorder, fruit cracking. The next step in this discovery of differences in leaf physiological traits is to investigate why on a genomic or physiological scale some cultivars are more water efficient.

Although literature regarding pomegranate leaf physiology is limited, the results of this study support previous pomegranate cultivar field studies with other germplasm collections, identifying differences among cultivars (Drogoudi et al., 2012). Another interesting finding in this study is that we were able to demonstrate that pomegranates, like other tree fruit crops, fix most carbon in the morning to take advantage of the mild, high light conditions. During the warmer afternoons carbon fixation significantly decreases, which is attributed to stomata closing to reduce water loss in the dry heat of inland Southern California.

Stem water potential values reported in this present study agree with other mid-day

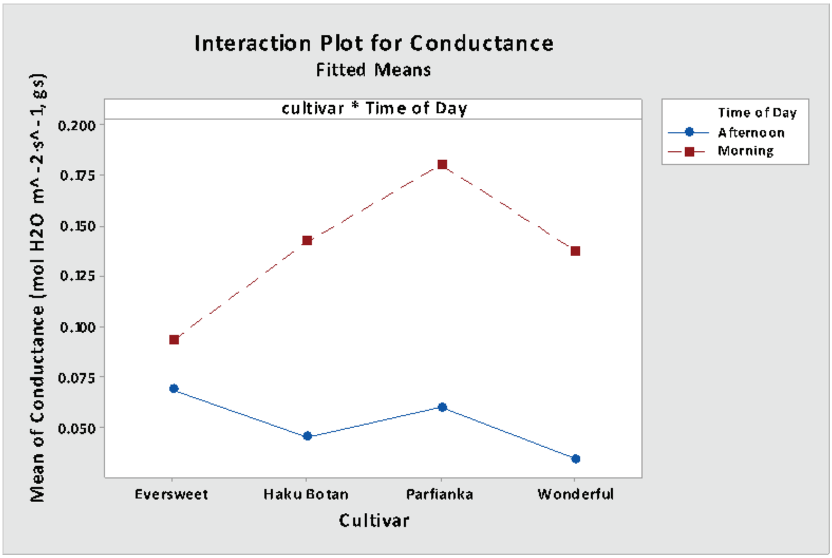

Figure 3. Factorial plot with stomatal conductance (mol H_2O $m^{-2}\cdot s^{-1}$, g_s) as the response variable, visualizing the interaction between time of day and cultivar. The interaction between cultivar and time of day was significant (P-value = 0.05). Data represents four pomegranate cultivars grown in Riverside, CA USA (n = 27) at different times of day (afternoon and morning). All leaf photosynthesis measurements were made in the morning or afternoon hours during fruit development in summer of 2015 and 2016.

values in the literature for pomegranate (Hepaksoy et al., 2000; Rodríguez et al., 2012). These may be the first values for water potential in pre-dawn hours for pomegranate, however there are reports for afternoon water potential. There were significant differences among cultivars for morning, but not afternoon, water potential. These findings indicate there may be differences in water uptake at night as well as differences in water loss at night. This could be a result of differences in root uptake or structure or stomatal number and/or size of stomatal aperture at night compared to other cultivars. Because vapor pressure deficit (VPD) can remain high (ranging from 1.56 to 2.49 kPa) at night in Riverside, CA, it is understandable that there could be differences in these stomata-based factors at night as well (Dawson et al., 2007).

We studied four unique pomegranate cultivars displaying very different phenotypes and found some interesting differences among them in terms of physiological traits and water relations. Despite these differences, the cultivars investigated performed similar to 'Wonderful' in a semi-arid climate, which means they may have potential in commercial orchards. Because we found differences among cultivars for various leaf physiological traits during certain times of day, the next steps would be to investigate these traits in additional cultivars, but to also carry out these physiological and water relations measurements during different times of year as well as different times of day. It would also be important to investigate these cultivars on molecular, morphological or anatomical scales to determine the underlying causes of these differences among cultivars for breeding purposes, specifically for marker assisted selection (MAS).

This investigation was the first of its kind to evaluate diurnal patterns in photosynthesis and water relations in California-grown 'Wonderful' and other pomegranate cultivars available on the market and sold by American nurseries. These results further our understanding of how pomegranate trees function on a physiological level among unique cultivars and during different times of the day in a semi-arid climate, and suggest that efficiency of production can be improved through cultivar selection. We emphasize that the strongest differences among cultivars in leaf gas exchange occurred in the morning, and largely involve water loss traits. More cultivars should be evaluated for their production efficiency using experimental cultivar trials to identify those that are productive under high temperature conditions with less applied irrigation water.

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About The Cover:

'Emma K' black walnut (*Juglans nigra*) is a commonly-grown cultivar for commercial nut production in the Midwestern region of the United States. This cultivar was selected for its large kernel size (> 35% by weight), relatively thin nut shell, and productivity. Grafted trees may start bearing a few nuts in the second year after planting, whereas seedlings do not commonly produce a nut crop until seven years after planting. Black walnuts are mechanically harvested with a tree shaker, collected, hulled, and then dried before cracking. About 13.7 million kg of black walnuts are harvested annually from 15 states, resulting in 1.3 t of marketable kernels. Photo by Michele Warmund, University of Missouri.