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Evaluation of leaf carbon isotopes and functional traits in avocado reveals water-use efficient cultivars

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ABSTRACT

Plant water-use efficiency (*WUE*) describes the ratio of carbon gain to water loss during photosynthesis. It has been shown that *WUE* varies among crop genotypes, and crops with high *WUE* can increase agricultural production in the face of finite water supply. We used measures of leaf carbon isotopic composition to compare *WUE* among 24 cultivars of *Persea americana* Mill (avocado) to determine genotypic variability in *WUE,* identify potentially efficient cultivars, and to better understand how breeding for yield and fruit quality has affected *WUE*. To validate carbon isotope measurements, we also measured leaf photosynthetic gas exchange of water and carbon, and leaf and stem functional traits of cultivars with the highest and lowest carbon isotope composition to quantify actual *WUE* ranges during photosynthesis. Our results indicate large variation in *WUE* among cultivars and coordination among functional traits that structure trade-offs in water loss and carbon gain. Identifying cultivars of subtropical tree crops that are efficient in terms of water use is critical for maintaining a high level of food production under limited water supply. Plant functional traits, including carbon isotopes, appear to be an effective tool for identifying species or genotypes with particular carbon and water economies in managed ecosystems.

1. Introduction

Functional traits have now been used extensively in ecological studies as easy-to-measure proxies for more complex processes (Cornelissen, 1999; Westoby, 1998). The study of functional traits arose from earlier efforts to place numerous species into fewer and more tangible functional groups (Grime, 1977, 1974; Smith et al., 1997), or to place species along axes of ecological strategy variation (Reich et al., 1997; Westoby, 1998; Westoby et al., 2002). Functional traits have mostly been used to advance plant biology through simplified representations of complex processes and their use in managed systems is increasing in importance for identifying differences among species, genotypes or documenting responses to environmental change (Gleason et al., 2016; Vitoria et al., 2016; Wood et al., 2015). This trend coincides with the expansion of managed and human impacted terrestrial ecosystems across the globe. For example, at large scales, functional traits have important linkages to ecosystem and landscape processes, such as water and carbon exchange between vegetated surfaces and the atmosphere (Ainsworth and Long, 2005; Baldocchi et al., 2004), or nutrient absorption and cycling by crop plants (Chapin, 1980; Wendling et al., 2016). As climate change proceeds and the growing range of crops changes (Challinor et al., 2015; Kenny and Harrison, 1992; Lobell et al., 2006), functional traits may offer a way forward to organizing crop species along axes of trait variation that also reflect habitat suitability. Functional traits may also be applied to crop cultivars to select for particular traits that promote efficiency of resource use (Farquhar and Richards, 1984; Lauteri et al., 1997; Zhang et al., 2009). All of these applications benefit from emphasizing the main strengths of trait approaches, which center on quantifiable traits that are continuous and comparable across plant species or genotypes (Westoby, 1998).

In agriculture, functional traits that relate to water consumption are increasingly important because water is a major limiting resource for agriculture. In many parts of the world, the water resources available for agriculture are declining in availability or quality, or increasing in expense due to droughts, floods, or political disagreements (Fu et al., 2013; Lenihan et al., 2003; Mendelsohn and Dinar, 2003; Rosegrant et al., 2009). Thus, there is great interest in identifying cultivars with high water-use efficiency, which is normally expressed as yield or productivity divided by water consumed in the process (Cernusak et al., 2007). At the leaf scale, photosynthetic water-use efficiency is

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expressed as photosynthetic rate, divided by stomatal conductance (Richards et al., 2002). A proxy for long-term time-integrated plant water-use efficiency can be obtained by the measurement of bulk leaf carbon isotope composition ($\delta^{13}C$). This relationship exists because conditions that cause the plant to reduce stomatal aperture cause an increase in water-use efficiency and also a reduction of CO_2 concentration at the site of carboxylation, forcing Rubisco to assimilate more $^{13}CO_2$ (Farquhar et al., 1982; Farquhar and Richards, 1984). Thus, a significantly larger $\delta^{13}C$ value is interpreted as greater water-use efficiency (Cernusak et al., 2013). Furthermore, water supply to leaves by stems creates coordination of leaf traits with stem traits, such as wood density (Santiago et al., 2004). Plants often achieve low-density wood through construction of large xylem vessels, which tend to have high water transport capacity and can sustain high rates of transpiration at the leaf level, but also tend to be more vulnerable to drought-induced xylem cavitation (Gleason et al., 2016; Pockman and Sperry, 2000; Wheeler et al., 2005). Therefore, further information about the regulation of leaf carbon and water economy can be obtained by considering water relations, and certain stem traits, along the transpiration pathway.

Stable isotope analysis of carbon has been used extensively as a key functional trait in agricultural and forestry systems to provide information on long-term time-integrated water-use efficiency (Brendel et al., 2002; Brugnoli et al., 1988; Farquhar and Richards, 1984; Lauteri et al., 1997; Monclus et al., 2005). This has allowed researchers to identify water-use efficient crop cultivars (Brugnoli et al., 1988; Farquhar and Richards, 1984; Hubick et al., 1986), investigate relationships between *WUE* and productivity (Marguerit et al., 2014; Martin and Thorstenson, 1988; Monclus et al., 2005), and link genotypic and phenotypic responses to water deficit by experimentally mapping quantitative trait loci (Brendel et al., 2008, 2002; Brugnoli et al., 1988; Hausmann et al., 2005; Marguerit et al., 2014). Such studies that provide a long-term integrated signal for *WUE* are important because they differ from short-term traits associated with photosynthetic carbon assimilation. In agroecosystems, information on both short- and long-term traits associated with carbon assimilation and water-use efficiency, as well as knowledge of the relationships among them, is critical for crop selection and crop breeding. Thus studies on crop cultivar $\delta^{13}C$ have contributed to identification of water-use efficient varieties of wheat, peanut, tomato, barley, cowpea, coffee and rice (Farquhar and Richards, 1984; Hall et al., 1990; Hubick et al., 1986; Hubick and Farquhar, 1989; Martin and Thorstenson, 1988; Meinzer et al., 1990; Zhao et al., 2004). The combined analysis of $\delta^{13}C$ with leaf and stem functional traits has emerged as a useful tool to identify water-use efficient crop genotypes.

We investigated the use of leaf $\delta^{13}C$ in combination with leaf functional traits in *Persea americana* (avocado), a meso-American tree species with a global yield of 5,028,756 kg from 547,849 ha across 70 countries in 2014 (FAO, 2017). Like many crops, avocado cultivars have been selected for yield or fruit quality but not for being water-use efficient or having other physiological traits that allow survival and production under scare resources. There is a growing interest in water-use efficient avocado cultivars because of reduced water quality and availability. For example, the most recent California drought lasted four years and was the driest three-year record in California history (Department of Water Resources, 2015), putting half of the state in a category of exceptional drought (US Drought Monitor, 2015). This situation increased water supply costs and reduced water quality for food producers throughout California. Cultivation of citrus, avocado and other subtropical tree crops have been especially impacted (Campbell, 2011; Spann, 2014). With further scarcity of water resources predicted, crop varieties or cultivars that are especially efficient in water use may play an increasing role in securing food production in the future. Although there are seven avocado cultivars grown commercially in California, about 95% of California avocado production is based on a single cultivar, *Hass*. This study aims to identify water-use efficient avocado cultivars using an integrated trait analysis of leaf carbon isotope composition and leaf and stem functional traits across 24 cultivars. Our main objectives were to: 1) analyze the variation in $\delta^{13}C$ among avocado cultivars; 2) use measurements of instantaneous water-use efficiency to determine what physiological factors are related to $\delta^{13}C$ in avocado leaves; 3) evaluate relationships between physiological and proxy traits; 4) describe relationships among leaf and stem traits.

2. Materials and methods

2.1. Study site and plant material

The study was conducted in the University of California South Coast Research and Extension Center (REC), Irvine, California, United States (33°41′18″N, 117°43′20″W), at an elevation of 124 m. The site has a mean annual precipitation of 165 mm with 56% of rainfall occurring from November to February and an average daily temperature range of 29–17 °C in July and 18–7 °C in January over the past three years (CIMIS, 2016). Sample collection and measurements were conducted between June and September 2016 on 24 cultivars of *P. americana* (avocado) that are part of the Avocado Breeding Program of the University of California and the California Avocado Commission. Irrigation rates are determined using an irrigation scheduling calculator (Hofshi and Hofshi, 2007), that is based on the Irvine 75 CIMIS station (CIMIS, 2016). Fertilizer is applied twice per year with a granular application of 21:7:14 NPK in April and a liquid application of 17:0:0 NPK in November. Trees were not pruned. The trees came from two experimental plots, an established 40-year old plot and a newer 5-year old plot. The plots are located in an open flat (0–2° slope) area and share the same deep, moderately sloped, alluvial fan soil. All trees were randomly planted at 6 m row spacing and 4.5 m tree spacing. The 5-year old trees were grafted onto *Dusa* rootstocks and the 40-year old trees were grafted onto *Thomas* rootstocks, except *Floccosa*, which was not grafted, and there were five additional cultivars with unknown rootstocks (Table 1). All trees were physiologically mature during sample collection and measurements.

Table 1
Scion and rootstock cultivar and number of individuals sampled for avocado study trees at South Coast Research and Extension Center, Irvine, California, USA.

Scion	Rootstock	Sample size
UC05-1	Dusa	6
UC99-1	Dusa	6
UC99-2	Dusa	6
UC99-3	Dusa	6
UC99-4	Dusa	3
UC00-1	Dusa	6
UC00-2	Dusa	6
Flavia	Dusa	6
Eugenin	Dusa	6
AO.48	Dusa	6
UCBL	Dusa	6
Carmen	Dusa	6
Fairchild	Thomas	3
Floccosa	Floccosa	2
Gem	Dusa	6
Hass	Dusa	6
LT01	Thomas	6
Mother Hass	Dusa	6
XX3	Dusa	6
Walden	Unknown	3
Nahlat	Unknown	2
Maoz	Unknown	2
Thomas	Unknown	6
Simmons	Unknown	2