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Impact of fruiting on gas exchange, water fluxes and frond development in irrigated date palms

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ABSTRACT

The cultivation of date palms in Israel's Arava Valley, which is characterized by a high evaporative demand, is widespread and exclusively depends on high-frequency irrigation. Fruit sets are usually thinned early in their development to produce large, high-quality dates. However, no effort has yet been made to comprehensively examine fruit load effects on date palm water use, CO_2 fluxes and growth. The objective of this study was to investigate the effects of fruit load on these factors. Twelve date palms, six with fruit removed ("without fruit") and six untreated ("with fruit"), were irrigated with equal amounts of water at sufficient levels for maintaining optimal soil water conditions. Sap flow and frond elongation were continuously measured. Gas exchange parameters (i.e., stomatal conductance and CO_2 assimilation rate) and fruit growth (i.e., fruit size, mass, and sugar content) were monitored periodically. No significant differences were found in gas exchange, water consumption and frond elongation between the two treatments several weeks after the onset of the fruit load differentiation. However, a pronounced increase in stomatal conductance and CO_2 assimilation rates in palms with fruit compared to those without fruit was identified during the sugar accumulation and post-harvest periods. Continuously increasing water consumption in palms with fruit was also observed during these periods, probably as a result of the progressive recovery of depleted carbohydrate and water storage in the tree. In addition, the frond elongation rate of palms with fruit was remarkably lower than those without fruit until the end of the harvest. It is concluded that crop load has a pronounced effect on physiological behaviors and water use of the cultivated date palm. Therefore, irrigation management must consider fruit load to achieve optimal yield.

1. Introduction

The increasing consumption of date palm fruit worldwide has enhanced the demand for large, high-quality dates that possess high nutritional and commercial value (Al-Khayri et al., 2015; Chao and Krueger, 2007). Around 40% of Israel's date yield is exported, mainly to Europe. The cultivation of date palms is widespread in Israel's Arava Valley and is expanding, exclusively depending on irrigation application (Cohen and Glasner, 2015). The Arava Valley is characterized as a hyper-arid region with an annual average class A pan evaporation of 3200 mm while the yearly precipitation is only 25 mm (Tripler et al., 2011). The amounts of irrigated water in date palm orchards are usually determined by multiplying the reference evapotranspiration (ET_0) by an empirical crop factor ranging from 0.5 to 1, regardless of fruit load (Cohen and Glasner, 2015; Sperling, 2013). Nevertheless, water resources for date palm irrigation are limited and mainly come from brackish groundwater (Tripler et al., 2011; Wiesman, 2009). In order to maximize crop quality and yield, large amounts of water need to be applied to compensate for evapotranspiration and also for soil leaching, as annual water application for a commercial mature plantation reaches 2500 mm (Tripler et al., 2011). Moreover, agricultural water quota restriction is expected to be aggravated to some extent, with continuous expansion of palm orchards in this region.

As a monocot species, date palm is not able to renew its vascular bundles with secondary growth in the trunk (Zimmermann and Tomlinson, 1972). Primary vascular bundles containing both phloem and xylem serve for entire growth, which goes on for up to several decades, rendering the tree susceptible to hydraulic disruption (Sperling et al., 2012; Sperry, 1986). Therefore, keeping the tree hydrated helps prevent vessel cavitation that could be destructive. In

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order to overcome water uptake difficulty, the tree uses its trunk as an important water reservoir. The palm trunk was found capable of holding up to 1 m^3 of water, supplying 25% of daily transpiration estimated by trunk sap flow measurement (Sperling et al., 2015). The heat dissipation method of estimating tree sap flow has been already well developed (Clearwater et al., 1999; Granier, 1985; Renninger et al., 2010; Sperling et al., 2012). The heat dissipation sensor designed specifically for date palm trees consists of one heated probe at a constant power and a non-heated one, measuring temperature differences (Sperling et al., 2012). This sensor is long enough to reach the stem's inner core in which stable and massive flow occurs (Sellami and Sifaoui, 2003; Sperling et al., 2012). Palm sap flow was found to quickly increase in the morning with a peak at around midday, then gradually decrease in the afternoon and attain stable low values throughout the nighttime hours, regardless of the sensor height along the trunk (Sellami and Sifaoui, 2003; Sperling et al., 2012). Additionally, sap flow in the early night in the upper part of the tree was found to be slower than in the lower part, allowing a nighttime recharge of the internal water storage (Sellami and Sifaoui, 2003; Sperling et al., 2015). This allows the continuance of stomatal opening and physiological activities under the high daytime evaporative demand.

Fruit thinning is the main practice of regulating fruit size and quality in fruiters (Dennis, 2000; Link, 2000). In Israel's Arava Valley, fruit thinning is conducted commonly by reducing the fruit load intensity after fruit set in order to harvest high-quality dates (Cohen and Glasner, 2015). Fruit load can be managed by controlling the bunch number on a tree, the spikelet number on each bunch and the fruitlet number on each spikelet. Usually half of the fruit on a date palm is removed after fruit set by Arava growers. Nevertheless, high fruit loads may increase palm water consumption due to higher assimilation demand and increased stomatal opening (Golan, 2014). On the other hand, high fruit load may also exert water stress on trees, e.g., mandarin (Yonemoto et al., 2004), resulting in reduced water consumption.

Fruit presence alters tree gas exchange parameters, i.e., stomatal conductance and CO_2 assimilation rate (Flore and Lakso, 1989). High fruit load leads to high photosynthetic demand for fruit development (Wünsche and Ferguson, 2005). Photosynthesis in trees with a high fruit load is enhanced in order to meet the carbohydrate requirements, as a result of higher stomatal conductance for more CO_2 absorption (Gucci et al., 1991; Schaffer et al., 1987; Syvertsen et al., 2003; Wünsche et al., 2005). This process is naturally accompanied by water loss for transpiration. A much higher transpiration rate (by roughly 30%) was found in a fruit-loaded olive tree in comparison with low- and non-yielding trees, thus increasing water consumption (Bustan et al., 2016). In addition, lower water potential either in the leaf or the stem of trees, e.g., peach (Marsal and Girona, 1997) and olive (Martín-Vertedor et al., 2011), with a high fruit load was reported due to high stomatal conductance in the daytime. Furthermore, vegetative growth in apple trees was constrained and reduced by a high fruit load during the growing season (Forshey and Elfving, 1989). However, non-significant effects of fruit load on photosynthesis, stomatal conductance and transpiration were documented in olive (Proietti, 2000), pear (Naor, 2001) and peach (Mahhou et al., 2005) trees.

Trees synthesize carbohydrates in leaves by photosynthesis, for growth (both vegetative and reproductive) and maintenance requirements (Amthor, 1984). Leaves not only serve as a carbohydrate source for photosynthetic assimilation, but also act as a carbohydrate sink because of their assimilate consumption for growth and maintenance, e.g., leaf area expansion (Gifford and Evans, 1981). Leaf-synthesized carbohydrates, primarily in the form of sucrose, move from mesophyll cells into the phloem, and are further allocated into other organs, i.e., the stem, branches, roots and fruit (Foyer, 2001). These assimilate-acceptance organs are classified in the carbohydrate sink (Kozlowski, 1992). Within crop organs, allocated carbohydrates are partitioned for different purposes, i.e., growth, maintenance and storage (Ho, 1988). The ability of a sink organ to attract carbohydrate allocations from the source by competing with other organs is termed its sink strength, which is determined by its physical and physiological capabilities (Herbers and Sonnewald, 1998; Marcelis, 1996). In addition, environmental conditions also alter the sink strength to some extent for crop adaptation (Génard et al., 2008). Fruit presence in a tree generally increases the sink strength for attracting greater carbohydrate allocations from leaves in order to ensure normal fruit development (Ho, 1988). Consequently, a high fruit load increases the assimilate demand and impels leaves to enhance photosynthetic assimilation, leading to higher stomatal conductance and a lower vegetative growth rate (Génard et al., 2008). However, the fruit sink strength, e.g., peach, fluctuates, depends on the fruit growth stages, and is much stronger during the sugar accumulation period (Berman and Dejong, 2003).

No effort has yet been made to comprehensively investigate fruit load effects on date palm water use, CO_2 fluxes and growth, despite irrigation water quota restrictions in Israel's Arava Valley. We hypothesized that a fruit load increase would lead to higher assimilate fixation, a lower rate of vegetative growth and a higher water consumption rate in date palms during fruit growth and maturation periods. The objectives of the present study were: (i) to explore fruit load effects on date palm water consumption during different stages of the fruit growth season, and (ii) to characterize the relations between water use, photosynthetic activity and assimilate fates in the tree.

2. Materials and methods

2.1. The experimental site and trees

The experiment was conducted at the Yair Experimental Station (30°46′45.3″N 35°14′31.1″E) situated in Israel's Central Arava Valley, 130 m below sea level. The central Arava Valley is characterized by an average annual precipitation of 30 mm and mean daily maximum and minimum temperatures of 40.1 °C (July) and 9.2 °C (January), respectively. Twelve fully grown date palm trees (*Phoenix dactylifera* L., cv. Medjool) were chosen for the experiment. They were 8 years old and 5 m high, with a trunk diameter of 0.6 m. They were irrigated (four drippers per tree, 25 L h^{-1} drippers, Netafim, Israel) with equal amounts of water at sufficient levels for maintaining optimal soil water conditions. The electrical conductivity (EC) of the irrigation water (which contains fertilizer) was measured once a week and was 2.4 ± 0.11 dS m^{-1} throughout the experiment. These trees were previously trimmed in order to have the same number of 54 leaves prior to the experiment. On DOY (day of year) 120, fruit was completely removed from six trees ("without fruit"), whereas the remaining six trees were not treated ("with fruit").

2.2. Meteorological data

Meteorological data, including air temperature, relative humidity, solar radiation and wind speed, were obtained from the Hazeva meteorological station (30°46′43.3″N 35°14′20.0″E). The reference evapotranspiration was calculated according to the Penman-Monteith equation as specified by the FAO protocol (Allen et al., 1998):

$$ET_0 = \frac{0.408\Delta(R_n - G) + \gamma\frac{900}{T+273}U_2(e_s - e_a)}{\Delta + \gamma(1 + 0.34U_2)} \quad (1)$$

where Δ (kPa $°C^{-1}$) is the vapor pressure curve slope, R_n (W m^{-2}) is the net radiation (derived from the solar radiation), G (W m^{-2}) is the soil heat flux, γ (kPa $°C^{-1}$) is the psychrometric constant, U_2 (m s^{-1}) is the wind speed at 2 m height, $e_s - e_a$ is the vapor pressure deficit (VPD, kPa), and T (°C) is the air temperature at 2 m height.

2.3. Periodic measurements

Ten pieces of fruit from five fruit bunches were sampled from each