Contents lists available at ScienceDirect





Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Belowground dynamics in two olive varieties as affected by saline irrigation



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ARTICLE INFO

Article history: Received 11 June 2012 Received in revised form 22 August 2013 Accepted 23 August 2013

Keywords: Olea europaea Root growth Root longevity Root morphology Salt stress Soil respiration

ABSTRACT

Olive is a major tree crop found naturally in the Mediterranean basin, Asia and Africa, considered to be moderately salt-tolerant. Because most studies focus on aboveground parameters, detailed information regarding root-system functioning under salinity is scarce. We examined the belowground traits of two mature olive varieties (salt-tolerant Barnea and salt-sensitive Leccino) after 13 years of saline irrigation (EC 4.2 dS m⁻¹) to better understand the causes underlying their diverging salt tolerance.

Stem growth of Barnea variety was less impaired by salinity compared to Leccino trees. Fine-root regrowth was reduced in both varieties under salinity. Compared to growth under freshwater irrigation, the impairment was 10% higher for salt-stressed Leccino roots. However, Leccino trees may partially compensate smaller root systems under salinity by an increased specific root area. Median fine root lifespan was reduced by 12 days in Barnea variety under salinity but still remained higher than in Leccino trees under both irrigation treatments. Soil respiration around Leccino trees was twice as high as in the vicinity of Barnea trees.

Root regrowth of the salt-tolerant Barnea variety was less constrained by salinity than Leccino's. Data on root longevity and soil respiration indicated that Leccino trees transfer more C belowground to rebuild and maintain their root system under both control and saline conditions. Subsequently, fewer C is available for aboveground growth, likely resulting in the previously reported lower stem growth and yield in Leccino trees.

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1. Introduction

In recent years, fertile farm land has been increasingly turned non-arable (Dehaan and Taylor, 2002). One cause for the increase in non-arable land is secondary soil salinization in (semi-)arid areas, triggered by high evaporative demand and faulty fertilization and irrigation practices (Munns, 2002; Rengasamy et al., 2003), as well as the use of saline irrigation water (Beltran, 1999). Today, more than 7% of the world's land area and up to 50% of irrigated agricultural areas are salt-affected (Pitman and Läuchli, 2004).

Levels of salt tolerance differ significantly among species, varieties and ontogenetic stages, as reflected by changes in biomass production and survival rate. However, high soil salinity results in a general reduction in yield of most crops (Maas and Hoffman, 1977; Tanji, 1990), via both challenging osmotic potentials and direct ionic effects, causing "physiological drought", malnutrition, and toxicity by excess salt ions (Ashraf and Harris, 2004; Rewald et al., 2012b).

Olive (*Olea europaea* L.) trees are cultivated for fruit and oil production especially under Mediterranean climate conditions (Chartzoulakis, 2005; Gucci et al., 1997; Tattini et al., 1992). While olive trees are quite salt-tolerant in general, typically tolerating soil salinities between 3 and 6 dS m⁻¹ (FAO, 1985), there is a large variation in salt tolerance between varieties (Chartzoulakis, 2005; Tattini et al., 1992, 1994).

Salt exclusion, salt compartmentation, osmoregulation and conservative water use are mechanisms that are considered to increase the salt tolerance of plants in general and olives in particular. However, adaptation to salinity is determined by the integration of several mechanisms' effects at the molecular, cellular, tissue and organ levels (Chartzoulakis, 2005; Munns and Tester, 2008; Shannon, 1997; Tattini, 1994; Tattini et al., 1992; Zekri and Parsons, 1992). Previous research on salt-tolerance mechanisms has generally focused on aboveground organs (Demiral and Türkan, 2005; Junghans et al., 2006), under the assumption that decreasing growth/yield is primarily related to a reduction in photochemical efficiency (Centritto et al., 2003; Flexas et al., 2006), and that shoots are generally more sensitive to salinity than roots (Munns and Termaat, 1986).

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^{0304-4238/\$ -} see front matter © 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.scienta.2013.08.032

Nevertheless, roots are the first organ to be affected by excess salinity (Córdoba et al., 2001); they exhibit enormous plasticity in response to different environmental parameters, such as excess ions (Deak and Malamy, 2005; Rewald et al., 2012a), and other important processes of plant salt tolerance are located in the roots (Flowers, 2004; Greenway and Munns, 1980; Kozlowski, 1997). Furthermore, fine roots (i.e. ephemeral roots of small diameter) are major components of the plant carbon (C) metabolism. Fine-root turnover, i.e. the inverse of root longevity, has been estimated to account for as much as 33% of global net primary production (NPP; Jackson et al., 1997). In trees, NPP_{root} may be >50% of NPP_{total}, with fine roots comprising a substantial part of the total belowground NPP. Thus, the construction and maintenance (respiration) of a sufficiently sized and functional root system under salt stress, e.g. to sustain water uptake (Rewald et al., 2011a), might generate additional C costs (Buwalda, 1993; Rewald et al., 2012b). In addition to impaired photosynthesis, this will cause a significant burden on plants' C budget, resulting in reduced growth/yield. However, despite the plausibility of the claim that differences among root systems may (partly) influence salt tolerance, root performance under salt stress has rarely been addressed (Munns, 2002; Vadez et al., 2007), especially in mature trees (Cimato et al., 2010; Perica et al., 2008; Tabatabaei, 2006).

In this paper, we present the results of a study of two varieties of mature olive trees with different levels of salt tolerance subjected to long-term salinity. The study examined whether (i) salinity influences fine-root regrowth and morphology and (ii) fine-root longevity and soil respiration with implications for C allocation, and (iii) whether root traits differ between olive varieties.

2. Materials and methods

2.1. Study site

The study site was the Ramat Negev Experimental Station $(34^{\circ}41'03'' \text{ N}, 31^{\circ}05'00'' \text{ W})$, located about 35 km southwest of the city of Beer-Sheva, Israel. The mean annual rainfall in the region is 102 mm spread over 4 months (November–February). Maximal air temperature reaches about 34.9 °C from July to August, and mean minimal temperature is close to 5.4 °C (January). Annual class 'A' pan evaporation is 2294 mm. The relative humidity during the summer months varies from 20 to 30%. The soil is light loess (sandy loam) in a uniform profile, consisting of 51.4% silt, 8.8% clay and 39.8% sand. The soil water content at field capacity is approximately 24 vol.% (Oron et al., 1999).

2.2. Plant material

The olive (*Olea europaea* L.) varieties Barnea and Leccino were planted as rooted cuttings in 1997. Trees were arranged in rows; the distance between individual trees in a row was 4 m, with a distance of 6 m between rows. Each variety was planted in blocks of five individuals per irrigation treatment, thus, research was conducted on 20 trees in total (see Section 2.3). Barnea is a salt-tolerant olive variety originating from native olive trees grown in the western Negev Desert, Israel (Wiesman et al., 2004). Leccino is considered to be a salt-sensitive variety originating from Tuscany, Italy (Tattini, 1994; Tattini et al., 1992). We chose two differently salt-tolerant varieties to identify possibly divergent belowground traits under long-term salinity.

2.3. Irrigation treatment

The olive trees were surface drip-irrigated with 50 cm distance between drip emitters; the irrigation rates was 656 mm per year to reach soil water content levels close to field capacity (Wiesman et al., 2004). Irrigation was based on multiyear local pan evaporation data and was rechecked and corrected on a daily basis. During the first 3 years after planting, trees were irrigated following any rainfall event to prevent excess salinization of the upper root zone (Hanson and May, 2011). From the year 2000, supplements of 100 mm fresh water were added to the soil twice a year to leach excess salt (Wiesman et al., 2004). During the experiment from January 2010 to August 2011, irrigation was continued but soil leaching was stopped because a layer of plastic mulch had been installed on the soil surface to reduce evaporation and consequently, salt accumulation. Since 1997, five trees each of Barnea and Leccino varieties were irrigated with fresh water [control; electrical conductivity (EC) $1.2 \, \text{dS} \, \text{m}^{-1}$] and five trees of both varieties were irrigated with saline water (moderate salinity; EC 4.2 dS m^{-1}). The saline irrigation water came from local wells (EC approx. 7.5 dS m^{-1}) and was diluted with fresh water to reach the target EC. The rate of NPK fertilization was determined based on the results of annual leaf nutrient analysis performed by the Negev Regional Agricultural Research Center.

2.4. Basal area increment

The stem circumference of five trees per variety and treatment was measured (30 cm above the ground) with a tape measure between June 2010 and June 2011. Results for stem growth are presented as basal area increment (BAI) during the measurement period (cm² yr⁻¹; percent of control).

2.5. Root regrowth potential

Fine-root growth into ingrowth cores is frequently used as a simple method to estimate fine-root production (Meinen et al., 2009). However, because of root-system damage during installation, we used the ingrowth cores to estimate root regrowth potential under different levels of saline irrigation. In mid-November 2010, 40 ingrowth cores (35 cm depth, 10 cm in diameter) were dug within a 20-cm distance of the drip-line emitters (to ensure similar soil moisture conditions; see Rewald et al., 2011a); 10 ingrowth cores were established per variety and treatment. The cores were refilled with root-free, sieved sand from the vicinity. In mid-February 2011, the cores were harvested and the roots were carefully rinsed. Debris and dead roots were discarded (Rewald et al., 2011b). Twelve root branches per ingrowth core were subsampled and scanned to analyze the specific root area [SRA, in cm² per g dry weight (DW)]; root surface areas determined with the PC program WinRhizo 2005c Pro (Regent Instruments, Canada) were divided by DW (65 °C, 48 h). Similarly, the total root biomass per ingrowth core was dried, weighed to a precision of ± 0.02 g using an analytical scale (AJ 6200, Vibra, Japan), and the fine-root density $(g DW L^{-1})$ per core was calculated.

2.6. Root longevity

The minirhizotron technique was used to determine the longevity of fine roots (Rewald and Ephrath, 2013). In early January 2010, five acrylic minirhizotron tubes per variety and treatment were installed vertically at a distance of 1 m from the tree bole and 20 cm from the drip line. The distances to tree boles and drip lines were chosen to provide similar root-biomass densities and soil-moisture levels (Rewald et al., 2011a). Starting in May 2010, roots were photographed once every 2 weeks until May 2011 using a minirhizotron camera (Bartz Technology Corporation, USA). Along the length of the tube, 15–17 coherent pictures (1.8 cm × 1.5 cm) were taken, down to approx. 30 cm soil depth. The median root lifespans of Barnea and Leccino trees under saline treatment were calculated based on the biweekly observation of ~2000 roots

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