

## RESEARCH PAPER

# Effects of the source:sink ratio on the phenotypic plasticity of stem water potential in olive (*Olea europaea* L.)

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Received 15 December 2010; Revised 15 December 2010; Accepted 28 January 2011

## Abstract

The aims of this work were to quantify (i) the effect of the source:sink ratio on stem water potential (SWP) and (ii) the phenotypic plasticity of SWP and its relationship to oil yield components in olive. Trees with a 3-fold variation in the source:sink ratio (crown volume/fruit number per tree) were monitored in 2007–2008 and 2008–2009 in a fully irrigated orchard in Mendoza, Argentina. The combination of rainfall, irrigation, and evaporative demand led to a steady SWP largely above  $-1.65$  MPa in 2007–2008 and a marked seasonal decline from  $-1.13$  MPa to  $-2.04$  MPa in trees with a medium and low source:sink ratio in 2008–2009. Plasticity was quantified as the slope of the norm of reaction for each trait. Across seasons, trees with a high source:sink ratio had a higher SWP than their counterparts with a medium and low source:sink ratio. Plasticity of SWP was highest in olives with a low source:sink ratio (slope=1.28) and lowest for trees with a high source:sink ratio (slope=0.76). The average SWP for each source:sink ratio and season was unrelated to both the source:sink ratio and yield components. On the other hand, the plasticity of SWP was positively associated with fruit number and negatively associated with the source:sink ratio, fruit weight, and fruit oil weight. The plasticity of the SWP was unrelated to SWP *per se*. It is concluded that understanding the effect of the source:sink ratio on plant water relations would benefit from a dual perspective considering the trait *per se* and its plasticity. A dual approach would also allow for more robust plant-based indicators for irrigation.

**Key words:** Environment, fruit load, fruit fresh weight, norm of reaction, oil fruit concentration, plant water status indicators.

## Introduction

In Argentina, the olive industry has expanded greatly during the past 15 years to reach >100 000 ha (SAGPyA, 2010). More than 95% of olive plantations are in arid and semi-arid environments between 28°S and 40°S and a range of annual rainfall from 100 mm to 400 mm. Irrigation throughout the growing season is essential to profitable yield and quality, but studies on olive irrigation capturing the local soil and weather conditions are scarce (Rousseaux *et al.*, 2008; Puertas, 2009). In a broader context, water availability for agricultural use is decreasing worldwide (Connor, 2005; Fereres and Evans, 2006), including the arid and semi-arid regions of Argentina.

Monitoring plant water status and understanding its responses to water supply is essential for the scheduling and design of irrigation strategies (Allen *et al.*, 1998). Owing

to its sensitivity to water supply, midday stem water potential (SWP) is a reliable indicator of plant water status in both deciduous and olive trees (Goldhamer *et al.*, 1999; Moriana *et al.*, 2003; Intrigliolo and Castel, 2004; Naor *et al.*, 2006). In deciduous trees, low source:sink ratios often associated with high fruit load may enhance stomatal conductance, the photosynthetic rate, and the transpiration rate (Gucci *et al.*, 1994; Berman and DeJong, 1996; Wünsche *et al.*, 2000; Mpelasoka *et al.*, 2001; Sadras *et al.*, 2008). Nevertheless, reported effects of fruit load on SWP are contradictory. For example, Bussakorn *et al.* (2001) in apple, Marsal and Girona (1997) in peach, and Naor *et al.* (2001) in nectarine found that high fruit load caused a decline in SWP of both well-watered and water-stressed trees. In other studies, the decline in SWP with increasing

fruit load was found for trees grown under water deficit, but not for their well-watered counterparts (Berman and DeJong, 1996; Naor *et al.*, 2008; Marsal *et al.*, 2010). Other authors found no relationships between fruit load and plant water status irrespective of water supply (Mahhou *et al.*, 2005; Intrigliolo and Castel, 2007; Conejero *et al.*, 2010).

The relationships between fruit load and SWP have rarely been studied in olive (Gucci *et al.*, 2007). Owing to the alternate bearing typical of olive trees, where high and low fruit loads alternate in successive seasons (Lavee, 2006), the association between fruit load and SWP is physiologically interesting and important for irrigation management. The lack of consistent associations between SWP and fruit load needs to be interpreted in terms of genotypic, environmental, and genotype $\times$ environment sources of variation.

Norms of reaction are functions that relate phenotype and environment (Woltereck, 1909), and phenotypic plasticity is the slope of these functions (DeWitt and Scheiner, 2004). Norms of reaction and plasticity are of interest to breeders as they deal with genotype $\times$ environment interaction and to physiologists, ecologists, and evolutionary biologists interested in plant and crop adaptation to dynamic environments, particularly in the context of global change (DeWitt and Scheiner, 2004; Pigliucci, 2005; Sadras *et al.*, 2009; Nicotra and Davidson, 2010). Here it is proposed that the analysis of the effect of the source:sink ratio on plant water status from the perspective of phenotypic plasticity can partially remove environmental influences and contribute to understanding the mechanisms related to the adaptation of the olive tree to environmental changes. This approach may also help to make a better use of plant-based indicators for irrigation management, which is fundamental for an efficient and sustainable use of water (Ortuño *et al.*, 2009; Conejero *et al.*, 2010).

Bradshaw (1965) advanced the notion of a hierarchy of plasticities, whereby high plasticity of a trait (e.g. seed number) is associated with low plasticity of a related trait (e.g. seed size). In contrast to these negative correlations, recent studies have revealed positive associations between plasticities of yield and phenological development (Sadras *et al.*, 2009). Bradshaw (1965) also proposed that plasticity is a trait on its own, with its own genetic control independent of the trait *per se*, and Reymond *et al.* (2003) conclusively demonstrated that this is the case for leaf expansion. Associations between plasticities of selected traits are therefore of biological interest.

The aims of this work were therefore to quantify (i) the effect of the source:sink ratio on midday SWP of olive trees and (ii) the phenotypic plasticity of SWP and its relationship to oil yield components and their plasticities.

## Materials and methods

### *Experimental conditions, plant material, and treatments*

The experiment was carried out during the 2007–2008 and 2008–2009 seasons in an intensive olive (cv. Arbequina) orchard in Lavalle (32°43' S, 68°36' W, 920 m.a.s.l.), Mendoza, Argentina.

The region has an average annual temperature of 15.8 °C, a frost-free period between October and March, and an average annual rainfall of 165 mm, concentrated during summer. The orchard was planted in 1997, with 4 $\times$ 6 m spacing (417 trees ha<sup>-1</sup>). The soil was clay-loam Typic entisol torrifuvent (Abraham and Martínez, 1996) with a pH of 7.5. Irrigation was performed with one microjet (37 l h<sup>-1</sup>) per plant to restore 100% of the estimated crop evapotranspiration (ETc) during the whole season (Pizarro, 1996) and crop coefficient Kc=0.68 (Girona *et al.*, 2002). Reference evapotranspiration was estimated as the average from two meteorological stations located between 10 km and 15 km from the experimental site. Vapour pressure deficit (VPD) was measured simultaneously with SWP in a meteorological micro-station placed inside one tree.

Three treatments, namely low, medium, and high fruit load, were established in a randomized complete block design, with four replicates. During the 2007–2008 season the fruit load was defined in two steps. First, 200 trees were inspected and classified in the three nominal categories of fruit load during the flowering stage in mid-November. From this set, four plants with similar crown volume determined with a spherical cap equation (Del Río *et al.*, 2005) were selected for each category. Secondly, the assignment of plants to load levels was confirmed through direct estimation of fruit number at harvest. The source:sink ratio was calculated as the ratio between crown volume (m<sup>3</sup>) and actual fruit number per tree. The same trees were evaluated in the second growing season.

### *Measurements*

Midday SWP was measured at 2 week intervals using a Scholander-type pressure chamber (BioControl, Buenos Aires, Argentina) in two replicates per tree following the procedure outlined by McCutchan and Shackel (1992). Mature leaves near the trunk were enclosed in a small plastic bag covered with aluminium foil at least 2 h before measurements. The leaves were excised with a sharp blade and immediately placed with the bag inside the chamber. The measurements were carried out on clear days between 11:30 h and 12:30 h solar time.

To complement the measurements of SWP, gas exchange was measured in 2007–2008. Stomatal conductance (g<sub>s</sub>) and net photosynthetic rate (P<sub>n</sub>) were measured during mid-morning (10:00–11:00 h) with a portable infrared gas analysis system (CIRAS 2, PP Systems, Hitchin, UK). Measurements were taken in four mature, sun-exposed leaves per tree at 42, 57, 77, 95, 118, 154, and 166 days after full bloom (DAFB).

From early December, 25, 20, and 15 fruits were extracted fortnightly from high, medium, and low fruit load trees, respectively, to quantify the evolution in oil fruit weight, fruit fresh weight, and fruit oil concentration; sampling and measurement procedures are explained in Trentacoste *et al.* (2010). In both seasons, trees were manually harvested on May 27 (191 DAFB) to determine yield and yield components.

### *Phenotypic plasticity*

A common method to quantify phenotypic plasticity involves models of phenotype versus environment, where the parameters of the functions are taken as a measure of plasticity. This approach has been successfully applied to all sorts of organisms, traits, and environments (DeWitt and Scheiner, 2004). Where the key environmental drivers are known and can be measured, phenotype versus environment models are robust (e.g. Reymond *et al.*, 2003). A shortcut when many environmental drivers interact in complex ways is to use the average value of the trait across phenotypes (Finlay and Wilkinson, 1963; Calò *et al.*, 1975; Greenberg *et al.*, 1992; Lacaze *et al.*, 2009; Sadras *et al.*, 2009). This approach has limitations derived from the partial lack of independence between variables, and a series of methods have been developed to overcome these limitations (Gauch, 1988; Bidinger *et al.*, 1996;

DeLacy *et al.*, 1996). Owing to data availability and the aims of this study, however, a simple phenotype versus environment model was used which was originally developed for grain yield (Finlay and Wilkinson, 1963), but with broader applications as shown in studies of phenotypic plasticity of phenological development of wheat, sunflower, and grapevine (Calò *et al.*, 1975; Sadras *et al.*, 2009) and grain size and grain protein content in barley (Lacaze *et al.*, 2009). Briefly, linear regressions were fitted between the particular trait for each source:sink ratio and the environmental mean. For example, for each date of measurement, the trait (e.g. SWP) averaged across the source:sink ratio was taken as the 'environmental mean' and regressions were performed for the averaged value of this trait for each source:sink ratio and the 'environmental mean'.

The slope ( $b$ ), calculated with Model II (reduced major axis) regression to account for error in both  $x$  and  $y$  (Niklas, 1994) was taken as a measure of phenotypic plasticity. In the present case,  $b=1.0$  indicates that the source:sink ratio does not have any significant impact on the phenotypic plasticity of the considered trait;  $b$  significantly greater than 1.0 indicates above average phenotypic plasticity (i.e. the source:sink ratio increased the phenotypic plasticity of the trait); and  $b$  significantly lower than 1.0 indicates below average phenotypic plasticity (i.e. the source:sink ratio decreased the phenotypic plasticity of the considered trait). For all regressions, the null hypothesis, slope=1, was tested with IRENE software (Fila *et al.*, 2003), and the effects of the source:sink ratio on slopes was tested using dummy variables and related  $t$ -test (Draper and Smith, 1998).

## Results

### Growing conditions

The average daily air temperature was similar in both growing seasons (20.2 °C versus 20.4 °C). Total seasonal rainfall was 112 mm in 2007–2008 compared with 44 mm in 2008–2009 (Fig. 1). VPD and incoming solar radiation were lower in 2007–2008 than in 2008–2009 (Fig. 1). Across source:sink ratios, SWP was higher in 2007–2008 than in 2008–2009 (Table 1). This seasonal difference was partially

associated with higher rainfall in 2007–2008 (Fig. 1) and highlights the considerable water deficit developed in 2008–2009 despite the irrigation target (100% ETC).

### Fruit load, crown volume, and source:sink ratio

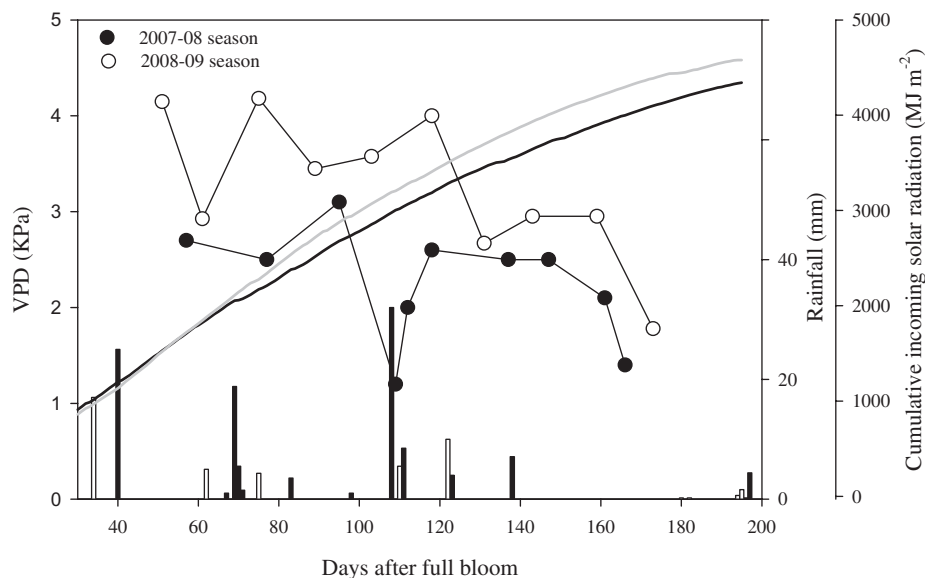
In both seasons, selection of trees with a similar crown volume and achievement of target fruit loads led to a 3-fold variation in source:sink ratio (Table 1). There was a strong, negative correlation between fruit load in 2007–2008 and fruit load in 2008–2009 ( $r = -0.78$ ,  $P = 0.0025$ ), reinforcing the notion that variation in the source:sink ratio in this study was primarily driven by the typical alternate bearing pattern of olive trees rather than other sources of variation such as soil heterogeneity. A summary of oil yield components, previously reported by Trentacoste *et al.* (2010), is presented in Table 1.

### Effect of source:sink ratio on stem water potential

Averaged across two seasons, trees with a high source:sink ratio had a significantly higher SWP than their counterparts with a medium and a low source:sink ratio (Table 1).

In 2007–2008, seasonal dynamics revealed (i) a steady SWP largely above the  $-1.65$  MPa stress threshold determined in olive by Moriana *et al.* (2002); and (ii) small source:sink effects on SWP (Fig. 2A). In 2008–2009, the SWP of trees with a medium and a low source:sink ratio showed a marked seasonal decline from  $-1.13$  MPa to  $-2.04$  MPa (Fig. 2B). The seasonal trend was also evident, but the rate of decline was much smaller in trees with a high source:sink ratio (Fig. 2B). Moreover, in both seasons, the significant differences between treatments appeared when the environmental SWP was below  $-1.4$  MPa (Fig. 2).

Consistent with the lack of effect of the source:sink ratio on SWP in 2007–2008, the source:sink ratio did not affect

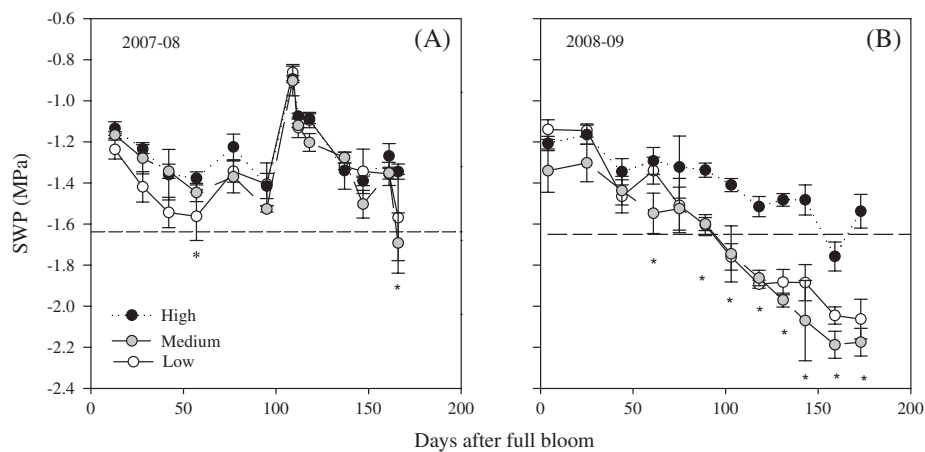


**Fig. 1.** Rainfall (bars), vapour pressure deficit (VPD; circles), and cumulative incoming solar radiation (line) from flowering to harvest during two growing seasons, 2007–2008 (filled symbols) and 2008–2009 (open symbols) in Lavalle, Mendoza. VPD was measured inside the canopy on the same days as stem water potential measurements.

**Table 1.** Fruit number, crown volume, source:sink ratio (S:S), midday stem water potential (SWP), net photosynthesis ( $P_n$ ), and stomatal conductance ( $g_s$ ) during fruit growth of olive trees with three contrasting fruit loads, similar crown volume, and hence a contrasting source:sink ratio

Season and treatments	Fruit number (fruits/tree)	Crown volume (m <sup>3</sup> )	S:S (m <sup>3</sup> 1000 fruit <sup>-1</sup> )	SWP (MPa)	$P_n$ ( $\mu\text{mol m}^2 \text{s}^{-1}$ )	$g_s$ ( $\text{mmol m}^2 \text{s}^{-1}$ )	Fruit fresh weight (g per fruit)	Fruit oil weight (g per fruit)	OC <sub>DB</sub> (%)
2007–2008									
Low	28 138	22.97	0.80	-1.32	12.8	224.9	1.7	0.21	47
Medium	16 606	19.33	1.15	-1.31	13.2	215.5	2.2	0.30	45
High	08 891	21.91	2.61	-1.24	13.6	216.8	2.5	0.37	48
2008–2009									
Low	30 793	32.33	1.05	-1.64			1.7	0.25	52
Medium	25 381	32.58	1.33	-1.73			1.9	0.30	52
High	09 645	26.28	2.89	-1.40			2.5	0.43	51
LSD(0.05)									
Source:sink	4974.4	NS	0.654	0.121	NS	NS	0.119	0.004	NS
Season	NS	3.95	NS	0.099	—	—	NS	NS	3.21
Interaction	NS	NS	NS	NS	—	—	NS	NS	NS

Additional oil yield components are also shown: fruit fresh weight, fruit oil weight, and oil concentration on a dry weight basis (OC<sub>DB</sub>). The least significant difference (LSD) is shown when ANOVA indicated a significant effect ( $P < 0.05$ ). NS, non-significant ( $P < 0.05$ ).



**Fig. 2.** Seasonal patterns of midday stem water potential (SWP) in response to high, intermediate, and low source:sink ratios in 2007–2008 (A) and 2008–2009 (B). The dashed line indicates the threshold of water stress ( $-1.65$  MPa) determined by Moriana *et al.* (2002) from relationships between midday leaf conductance and vapour pressure deficit. Asterisks indicate a significant difference between source:sink ratio treatments ( $P < 0.05$ ).

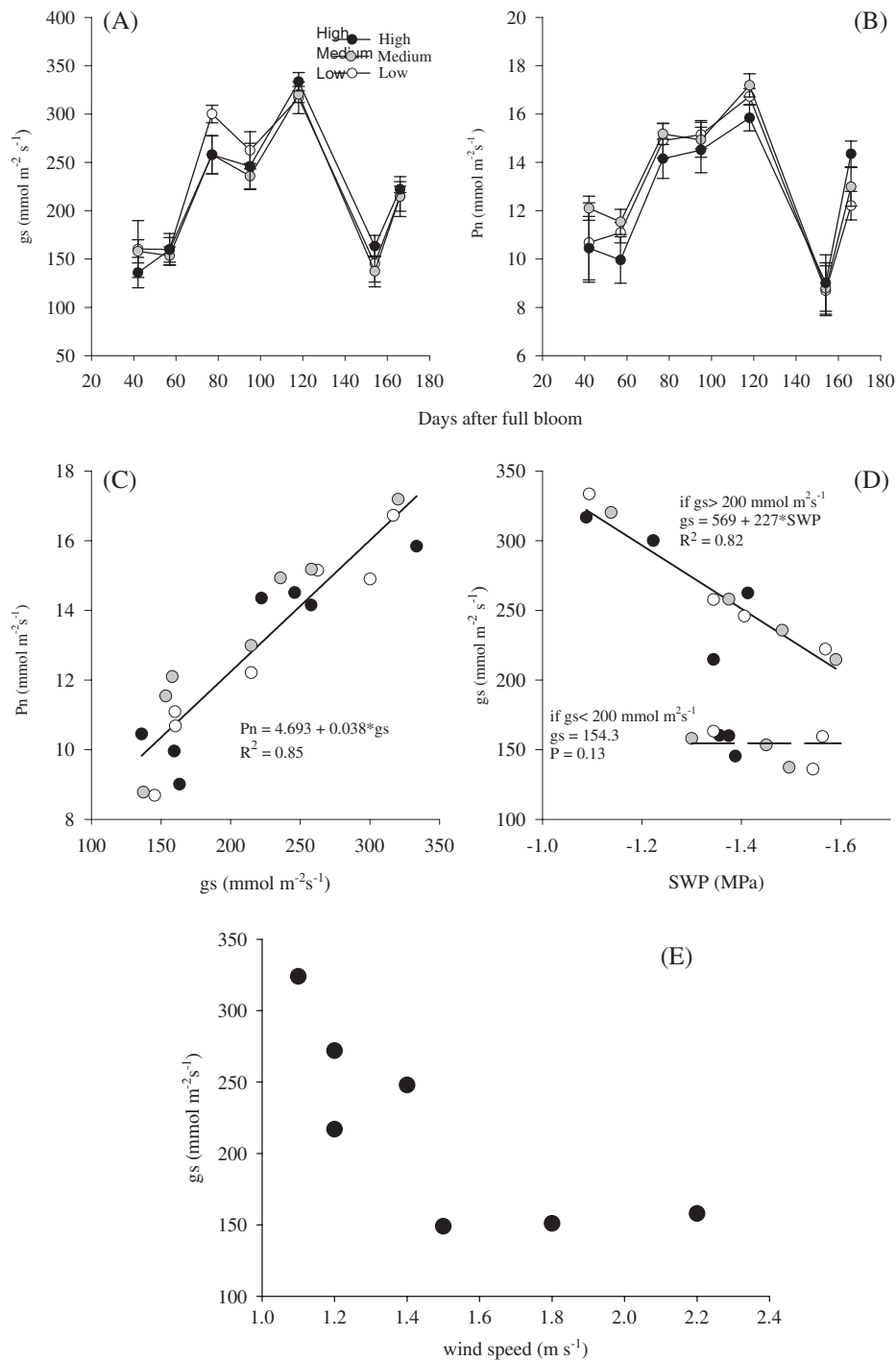
stomatal conductance or net photosynthesis (Table 1, Fig. 3A, B). For the pooled data, stomatal conductance accounted for 85% of the variation in net photosynthesis ( $P < 0.001$ , Fig. 3C). Stomatal conductance was associated with SWP for  $g_s > 200 \text{ mmol m}^{-2} \text{ s}^{-1}$  ( $P < 0.001$ , Fig. 3D). Below this value, leaf stomatal conductance and SWP were not associated. Stomatal conductance  $< 200 \text{ mmol m}^{-2} \text{ s}^{-1}$  was recorded on three dates, namely 42, 57, and 147 DAFB (Fig. 3A), when the wind speed was  $> 1.5 \text{ m s}^{-1}$  (Fig. 3E).

#### Phenotypic plasticity of stem water potential

Figure 4A shows the reaction norms of SWP for the data pooled across seasons. In more restrictive water environ-

ments, namely environmental stem water potential less than  $-1.4$  MPa, a low source:sink ratio corresponded to the lowest SWP and a high source:sink ratio to the highest. Convergence of reaction norms highlighted the lack of effect of the source:sink ratio on SWP in more favourable environments, namely environmental SWP more than  $-1.4$  MPa.

This pattern is captured quantitatively in the coefficients of plasticity: the slope =  $1.28 \pm 0.05$  for the low source:sink ratio was significantly greater than 1 ( $P < 0.001$ ), the slope =  $1.02 \pm 0.04$  for the intermediate source:sink ratio was not different from 1 ( $P = 0.949$ ), and the slope =  $0.76 \pm 0.04$  for the high source:sink ratio was significantly lower than 1 ( $P < 0.001$ ). A similar ranking in the plasticity of midday



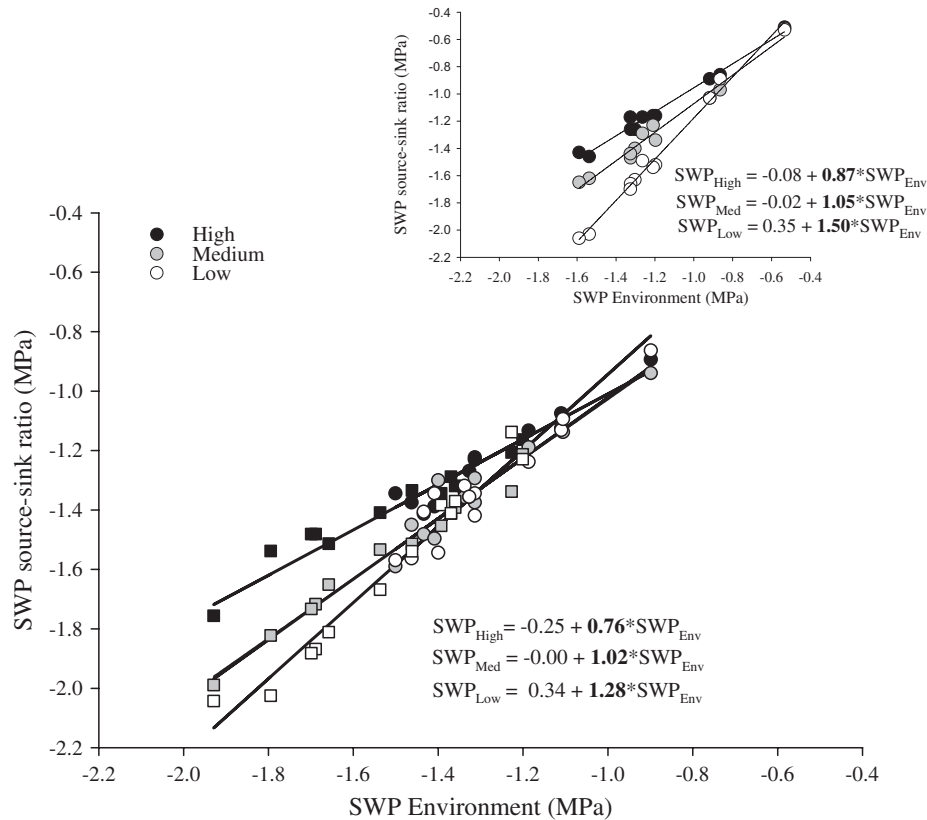
**Fig. 3.** Seasonal patterns of (A) abaxial stomatal conductance ( $g_s$ ) and (B) net photosynthetic rate ( $P_n$ ) in 2007–2008 for high, intermediate, and low source:sink ratios. (C) Relationship between  $P_n$  and  $g_s$ , and (D) between  $g_s$  and midday stem water potential (SWP). Solid lines are regressions fitted to the pooled data and dashed lines indicate trends when regressions were not significant. (E) Relationships between  $g_s$  and wind speed.

SWP was identified for individual seasons, with significant variation in plasticity in response to the source:sink ratio in 2007–2008 ( $P=0.003$ ) and 2008–2009 ( $P < 0.001$ ).

#### *Relationships between plasticities of different traits*

Average midday SWP for each source:sink ratio and season was unrelated to the source:sink ratio or oil yield compo-

nents (data not shown). The plasticity of the SWP was unrelated to SWP *per se*, but was positively associated with fruit number and negatively with the source:sink ratio, fruit fresh weight, and fruit oil weight (Fig. 5). The plasticity of the SWP was positively associated with the plasticity of fruit oil concentration and negatively with both plasticity of fruit fresh weight and plasticity of fruit oil weight (Fig. 6).



**Fig. 4.** Norms of reaction of midday stem water potential (SWP) in olive trees with three contrasting source:sink ratios in 2007–2008 (circles) and 2008–2009 (squares). Fitted lines are reduced major axis regressions (Model II) for each source:sink ratio, and slopes (bold) are a measure of plasticity. The regressions were fitted for each date of measurement, the SWP averaged across source:sink ratio was taken as the ‘environmental mean’, and regressions were performed for the averaged value of SWP for each source:sink ratio and the ‘environmental mean’. For comparison, the inset shows data for deficit-irrigated pear trees in response to three contrasting source:sink ratios (derived using data from Fig. 1A in Marsal *et al.*, 2010).

## Discussion

### *Relationship between stem water potential and source:sink ratio*

Motivated by production and environmental drivers, substantial research effort has been invested in improving water management in olive orchards worldwide (Feres and Castel, 1981; Villalobos *et al.*, 2000; Palomo *et al.*, 2002; Orgaz *et al.*, 2006; Allen and Pereira, 2009; Rousseaux *et al.*, 2009; Martínez-Cob and Faci, 2010). Many studies focused on the advantages and drawbacks of plant-based indicators for irrigation management (Moriana *et al.*, 2003; Moriana and Feres, 2004).

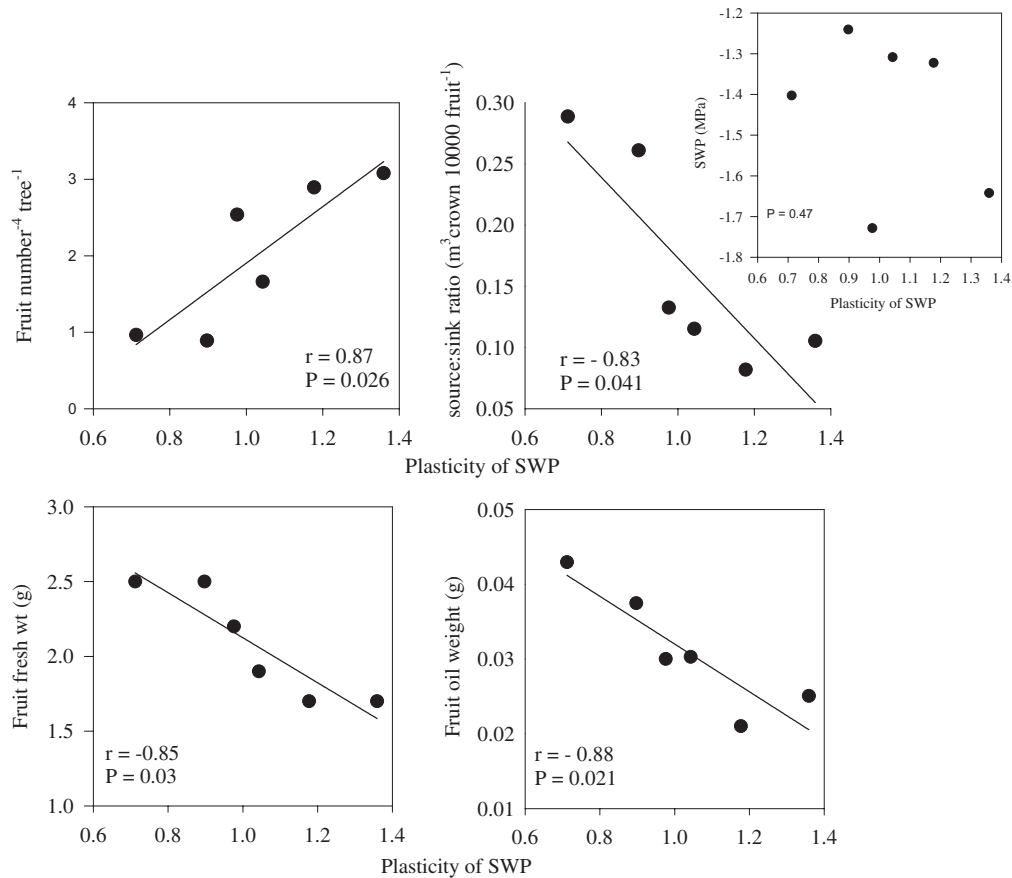
However, relationships between plant water status and fruit load have been hardly considered in olive (Feres and Soriano, 2007). Under the present experimental conditions, an increase in SWP associated with a high source:sink ratio was only evident when the environmental SWP declined below  $-1.4$  MPa. This approximate threshold compares with the  $-1.65$  MPa proposed by Moriana *et al.* (2002). These authors focused on the effect of VPD on midday SWP and stomatal conductance in olive, where maximum stomatal conductance was recorded when the midday SWP exceeded  $-1.65$  MPa.

There are short- and longer-term mechanisms by which a high source:sink ratio coupled with water limitations may lead to an improvement in plant water status. In the short term, feedback inhibition of photosynthesis and stomatal closure may increase SWP, and in the longer term increased allocation of plant resources to roots may also improve plant water status (Gucci *et al.*, 1991; Lopez *et al.*, 2008; Marsal *et al.*, 2008).

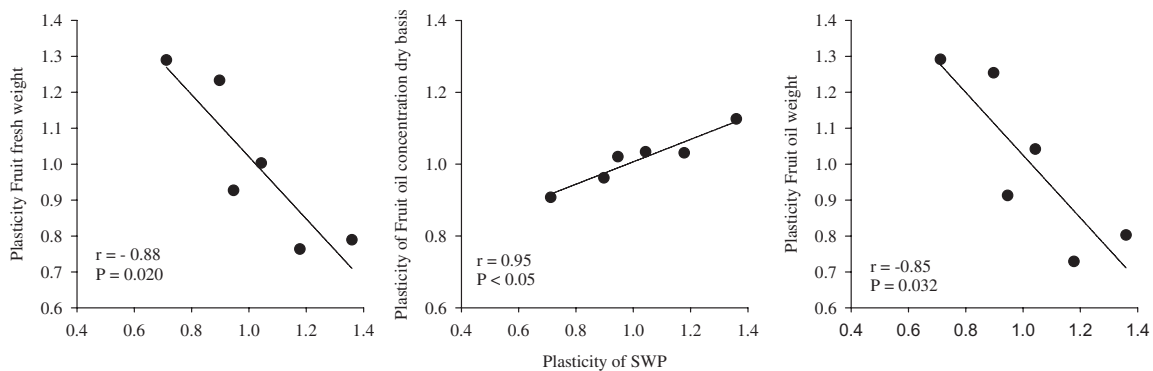
### *Phenotypic plasticity of stem water potential*

Midday SWP was highly responsive to the source:sink ratio, with plasticity coefficients between 0.76 and 1.28. The effect of the source:sink ratio on SWP was highly dependent to soil water moisture and seasonal conditions. In contrast, there was a robust relationship between plasticity of SWP and the source:sink ratio. Analysis of the data of Marsal *et al.* (2010) for pear trees growing with three source:sink levels also revealed a similar pattern of plasticity in response to source:sink ratios (inset Fig. 4). Furthermore, phenotypic plasticity of SWP showed significant correlations with key oil yield traits *per se* and their plasticity (Figs 5, 6).

SWP *per se* and plasticity of SWP were not associated, suggesting some degree of independence in the genetic control of both traits (Bradshaw, 1965; Sadras *et al.*, 2009;



**Fig. 5.** Correlations between oil yield components and plasticity of midday stem water potential (SWP) in olive trees in response to three contrasting source:sink ratios during two growing seasons. Plasticities are dimensionless.



**Fig. 6.** Correlation between plasticities of oil yield components and plasticity of stem water potential in response to three contrasting source:sink ratios and two growing seasons. Plasticities are dimensionless.

Auld *et al.*, 2010). From a breeding perspective, Nicotra and Davidson (2010) suggested that selection criteria should consider adaptive plasticity, particularly in relation to adaptation to climate changes. The present study suggests that this may also apply to olive, a species that has only recently been submitted to formal plant breeding.

It is concluded that olive trees with a high source:sink ratio had a significantly higher SWP than their counterparts with a medium and a low source:sink ratio. However, this effect was contingent on soil water availability and environ-

mental conditions between growing seasons. In contrast, the plasticity of SWP had a more robust pattern of response to the source:sink ratio across environmental conditions. Understanding the effect of the source:sink ratio on plant water relations would benefit from a dual perspective considering the trait *per se*, for example SWP, and its plasticity. This dual approach would also allow for more robust plant-based indicators for irrigation, particularly in species with alternate bearing or where factors such as foliar pests or chemical thinning alter the source:sink ratios.

## Acknowledgements

We thank B. Terraza, O. Gómez, and P. Molina (INTA-EEA Junín, Argentina) for their help with the field work. This paper is dedicated to the memory of Pedro Puertas, father of CMP.

## References

- Abraham EM, Martínez FR.** 1996. Inventario de recursos para la planificación y gestión de la región andina argentina. [www.crycit.edu/ladito/catalogo/cdandes.htm](http://www.crycit.edu/ladito/catalogo/cdandes.htm).
- Allen P, Pereira L, Raes D, Smith M.** 1998. *Crop evapotranspiration: guidelines for computing crop water requirements*. FAO Irrigation and Drainage Paper No. 56. Rome: FAO.
- Allen RG, Pereira LS.** 2009. Estimating crop coefficients from fraction of ground cover and height. *Irrigation Science* **28**, 17–34.
- Auld JR, Agrawal AA, Relyea RA.** 2010. Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proceedings of the Royal Society B: Biological Sciences* **277**, 503–511.
- Berman ME, DeJong TM.** 1996. Water stress and crop load effects on fruit fresh and dry weights in peach (*Prunus persica*). *Tree Physiology* **16**, 859–864.
- Bidinger FR, Hammer GL, Muchow RC.** 1996. The physiological basis of genotype × environment interaction in crop adaptation. In: Cooper M, Hammer GL, eds. *Plant adaptation and crop improvement*. CAB International, Cambridge, 329–347.
- Bradshaw AD.** 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**, 115–155.
- Bussakorn S, Mpelasoka BS, Behboudian MH, Mills T.** 2001. Water relations, photosynthesis, growth, yield and fruit size of ‘Braeburn’ apple: responses to deficit irrigation and crop load. *Journal of Horticultural Science and Biotechnology* **76**, 150–156.
- Calò A, Costacurta A, Lorenzoni C.** 1975. Stabilità ambientale di alcune caratteristiche fenologiche in varietà di *Vitis vinifera*. *Rivista di Viticoltura e di Enologia de Conegliano* **11–12**, 3–33.
- Conejero W, Ortuño MF, Mellisho CD, Torrecillas A.** 2010. Influence of crop load on maximum daily shrinkage reference equations for irrigation scheduling of early maturing peach trees. *Agricultural Water Management* **97**, 333–338.
- Connor DJ.** 2005. Adaptation of olive (*Olea europaea* L.) to water-limited environments. *Australian Journal of Agricultural Research* **56**, 1181–1189.
- Del Río C, Caballero JM, García-Fernández MD.** 2005. Vigor. In: Rallo L, Barranco D, Caballero JM, Del Río C, Martín A, Tous J, Trujillo I, eds. *Varietades de olivo en España*. Madrid; Spain: Junta de Andalucía, MAPA and Mundi-Prensa, 249–250.
- DeLacy IH, Basford KE, Cooper M, Bull JK, McLaren CG.** 1996. Analysis of multi-environment trials—An historical perspective. In: Cooper M, Hammer GL, eds. *Plant adaptation and crop improvement*. CAB International, Wallingford, UK, 39–124.
- DeWitt TJ, Scheiner SM.** 2004. Phenotypic variation from single genotypes. In: DeWitt TJ, Scheiner, eds. *Phenotypic plasticity. Functional and conceptual approaches*. New York: Oxford University Press, 1–19.
- Draper NR, Smith H.** 1998. *Applied regression analysis*, 3rd edn. New York: J. Wiley and Sons.
- Fereres E, Castel JR.** 1981. *Drip irrigation management*. Division of Agricultural Science, University of California (Publication Leaflet 21259).
- Fereres E, Evans RG.** 2006. Irrigation of fruit trees and vines: an introduction. *Irrigation Science* **24**, 55–57.
- Fereres E, Soriano MA.** 2007. Deficit irrigation for reducing agricultural water use. *Journal of Experimental Botany* **58**, 147–159.
- Fila G, Bellocchi G, Acutis M, Donatelli M.** 2003. IRENE: software to evaluate model performance. *European Journal of Agronomy* **18**, 369–372.
- Finlay KW, Wilkinson GN.** 1963. The analysis of adaptation in a plant breeding programme. *Australian Journal of Agricultural Research* **14**, 742–754.
- Gauch HGJ.** 1988. Model selection and validation for yield trials with interaction. *Biometrics* **44**, 705–715.
- Girona J, Luna M, Arbonés A, Mata M, Rufat J, Marsal J.** 2002. Young olive trees responses (*Olea europaea* L. cv. Arbequina) to different water supplies. Water function determination. *Acta Horticulturae* **586**, 277–280.
- Goldhamer DA, Fereres E, Mata M, Girona J, Cohen M.** 1999. Sensitivity of continuous and discrete plant and soil water status monitoring in peach trees subjected to deficit irrigation. *Journal of the American Society for Horticultural Science* **124**, 437–444.
- Greenberg DC, Williams JH, Ndunguru BJ.** 1992. Differences in yield determining processes of groundnut (*Arachis hypogaea* L.) genotypes in varied drought environments. *Annals of Applied Biology* **120**, 557–566.
- Gucci R, Corelli Grappadelli L, Tustin S, Ravaglia G.** 1994. The effect of defruiting at different stages of fruit development on leaf photosynthesis of ‘Golden Delicious’ apple. *Tree Physiology* **15**, 35–40.
- Gucci R, Lodolini E, Rapoport HF.** 2007. Productivity of olive trees with different water status and crop load. *Journal of Horticultural Science and Biotechnology* **82**, 648–656.
- Gucci R, Xiloyannis C, Flore JA.** 1991. Gas-exchange parameters, water relations and carbohydrate partitioning in leaves of field-grown *Prunus domestica* following fruit removal. *Physiologia Plantarum* **83**, 497–505.
- Intrigliolo DS, Castel JR.** 2004. Continuous measurement of plant and soil water status for irrigation scheduling in plum. *Irrigation Science* **23**, 93–102.
- Intrigliolo DS, Castel JR.** 2007. Crop load affects maximum daily trunk shrinkage of plum trees. *Tree Physiology* **27**, 89–96.
- Lacaze X, Hayes PM, Korol A.** 2009. Genetics of phenotypic plasticity: QTL analysis in barley. *Hordeum vulgare*. *Heredity* **102**, 183–173.
- Lavee S.** 2006. Biennial bearing in olive (*Olea europaea* L.). *Olea* **25**, 5–13.
- Lopez G, Arbonés A, Mata M, Paris C, Girona J, Marsal J.** 2008. Root growth following defruiting improves peach tree water status. *Journal of Horticultural Science and Biotechnology* **83**, 804–808.



- Mahhou A, DeJong TM, Cao T, Shackel KS.** 2005. Water stress and crop load effects on vegetative and fruit growth of 'Elegant Lady' peach [*Prunus persicae* (L) Batch] trees. *Fruits* **60**, 55–68.
- Marsal J, Behboudian MH, Mata M, Basile B, del Campo J, Girona J, Lopez G.** 2010. Fruit thinning in 'Conference' pear grown under deficit irrigation to optimize yield and to improve tree water status. *Journal of Horticultural Science and Biotechnology* **85**, 120–130.
- Marsal J, Girona J.** 1997. Relationship between leaf water potential and gas exchange activity at different phenological stages and fruit loads in peach trees. *Journal of the American Society for Horticultural Science* **122**, 415–421.
- Marsal J, Mata M, Arbonés A, del Campo J, Girona J, Lopez G.** 2008. Factors involved in alleviating water stress by partial crop removal in pear trees. *Tree Physiology* **28**, 1375–1382.
- Martínez-Cob A, Faci JM.** 2010. Evapotranspiration of an hedge-pruned olive orchard in a semiarid area of NE Spain. *Agricultural Water Management* **97**, 410–418.
- McCutchan H, Shackel KA.** 1992. Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). *Journal of the American Society for Horticultural Science* **117**, 607–611.
- Moriana A, Fereres E.** 2004. Establishing reference values of trunk diameter fluctuations and stem water potential for irrigation scheduling of olive trees. *Acta Horticulturae* **664**, 407–412.
- Moriana A, Orgaz F, Pastor M, Fereres E.** 2003. Yield responses of a mature olive orchard to water deficits. *Journal of the American Society for Horticultural Science* **128**, 425–431.
- Moriana A, Villalobos FJ, Fereres E.** 2002. Stomatal and photosynthetic responses of olive (*Olea europaea* L.) leaves to water deficit. *Plant, Cell and Environment* **25**, 395–405.
- Mpelasoka BS, Behboudian MH, Green SR.** 2001. Water use, yield and fruit quality of lysimeter-grown apple trees: responses to deficit irrigation and crop load. *Irrigation Science* **20**, 107–113.
- Naor A, Gal Y, Peres M.** 2006. The inherent variability of water stress indicators in apple, nectarine and pear orchards, and the validity of a leaf-selection procedure for water potential measurements. *Irrigation Science* **24**, 129–135.
- Naor A, Hupert H, Greenblat Y, Peres M, Kaufman A, Klein I.** 2001. The response of nectarine fruit size and midday stem water potential to irrigation level in stage III and crop load. *Journal of the American Society for Horticultural Science* **126**, 140–143.
- Naor A, Naschitz S, Peres M.** 2008. Responses of apple fruit size to tree water status and crop load. *Tree Physiology* **28**, 1255–1261.
- Nicotra AB, Davidson A.** 2010. Adaptive phenotypic plasticity and plant water use. *Functional Plant Biology* **37**, 117–127.
- Niklas KJ.** 1994. *Plant allometry: the scaling of form and process*. Chicago, IL: University of Chicago Press.
- Orgaz F, Testi L, Villalobos FJ, Fereres E.** 2006. Water requirements of olive orchards—II: determination of crop coefficients for irrigation scheduling. *Irrigation Science* **24**, 77–84.
- Ortuño MF, Brito JJ, García-Orellana Y, Conejero W, Torrecillas A.** 2009. Maximum daily trunk shrinkage and stem water potential referent equations for irrigation scheduling of lemon trees. *Irrigation Science* **27**, 121–127.
- Palomo MJ, Moreno F, Fernández JE, Díaz-Espejo A, Girón IF.** 2002. Determining water consumption in olive orchards using the water balance approach. *Agricultural Water Management* **55**, 15–35.
- Pigliucci M.** 2005. Evolution of phenotypic plasticity: where are we going now? *Trends in Ecology and Evolution* **20**, 481–486.
- Pizarro F.** 1996. *Riegos localizados de alta frecuencia. Goteo, microaspersión y exudación*. Madrid: Spain: Mundi-Prensa.
- Puertas C.** 2009. Efecto del riego deficitario controlado sobre el rendimiento y calidad de aceite en olivo (*Olea europaea* L.) cv. *Arbequina* MSc thesis, Universidad Nacional de Cuyo.
- Reymond M, Muller B, Leonardo A, Charcosset A, Tardieu F.** 2003. Combining quantitative trait loci analysis and ecophysiological model to analyze the genetic variability of the responses of maize leaf growth to temperature and water deficit. *Plant Physiology* **131**, 664–675.
- Rousseaux MC, Benedetti JP, Searles PS.** 2008. Leaf-level responses of olive trees (*Olea europaea*) to the suspension of irrigation during the winter in an arid region of Argentina. *Scientia Horticulturae* **115**, 135–141.
- Rousseaux MC, Figuerola PI, Correa-Tedesco G, Searles PS.** 2009. Seasonal variation in sap flow and soil evaporation in an olive (*Olea europaea* L.) grove under two irrigation regimes in an arid region of Argentina. *Agricultural Water Management* **96**, 1037–1044.
- Sadras VO, Collins M, Soar CJ.** 2008. Modelling variety-dependent dynamics of soluble solids and water in berries of *Vitis vinifera*. *Australian Journal of Grape and Wine Research* **14**, 250–259.
- Sadras VO, Reynolds MP, de la Vega AJ, Petrie PR, Robinson R.** 2009. Phenotypic plasticity of yield and phenology in wheat, sunflower and grapevine. *Field Crops Research* **110**, 242–250.
- SAGPyA.** 2010. Secretaría de Agricultura, Ganadería, Pesca y Alimentos, Cadenas Alimentarias: Producción Olivícola. [www.alimentosargentinos.gov.ar/olivicola/](http://www.alimentosargentinos.gov.ar/olivicola/).
- Trentacoste ER, Puertas CM, Sadras VO.** 2010. Effect of fruit load on oil yield components and dynamics of fruit growth and oil accumulation in olive (*Olea europaea* L.). *European Journal of Agronomy* **32**, 249–254.
- Villalobos FJ, Orgaz F, Testi L, Fereres E.** 2000. Measurement and modeling of evapotranspiration of olive (*Olea europaea* L.) orchards. *European Journal of Agronomy* **13**, 155–163.
- Woltreck R.** 1909. Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. *Verhandlungen der Deutschen Zoologischen Gesellschaft* **19**, 110–172.
- Wünsche JN, Palmer JW, Greer DH.** 2000. Effects of crop load on fruiting and gas-exchange characteristics of 'Braeburn'/M.26 apple trees at full canopy. *Journal of the American Society for Horticultural Science* **125**, 93–99.