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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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×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×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 4×6 m spacing (417 trees ha^{-1}). The soil was clay–loam Typic entisol torrifluvent (Abraham and Martínez, 1996) with a pH of 7.5. Irrigation was performed with one microjet (37 l h^{-1}) 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^3) 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_s) and net photosynthetic rate (P_n) 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
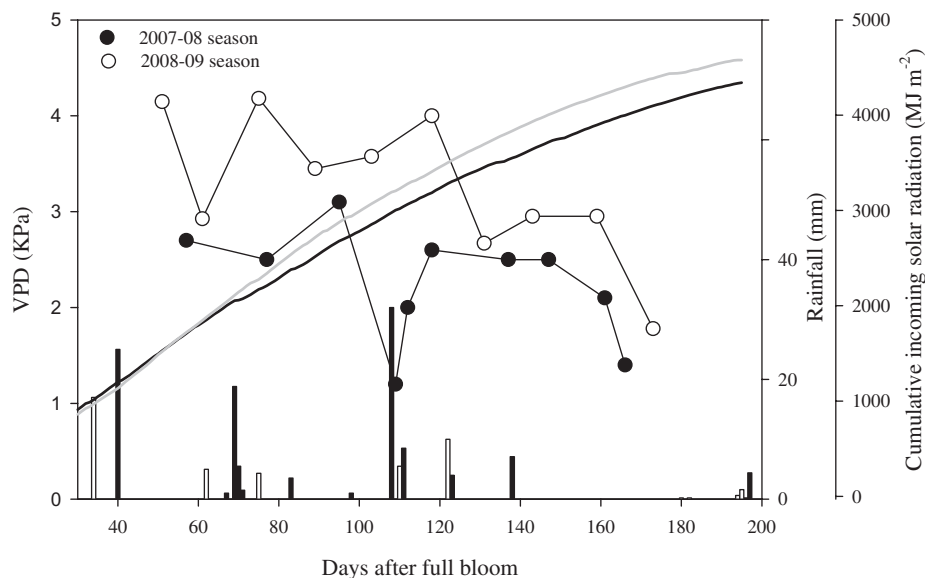
Fig. 1. Rainfall (bars), vapour pressure deficit (VPD; circles), and cumulative incoming solar radiation (line) from flowering to harvest during two growing seasons, 2007–2008 (filled symbols) and 2008–2009 (open symbols) in Lavalle, Mendoza. VPD was measured inside the canopy on the same days as stem 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^3)	S:S (m^3 1000 fruit^{-1})	SWP (MPa)	P_n (μmol m^2 s^{-1})	g_s (mmol m^2 s^{-1})	Fruit fresh weight (g per fruit)	Fruit oil weight (g per fruit)	OC_{DB} (%)
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_{DB}). The least significant difference (LSD) is shown when ANOVA indicated a significant effect ($P < 0.05$).
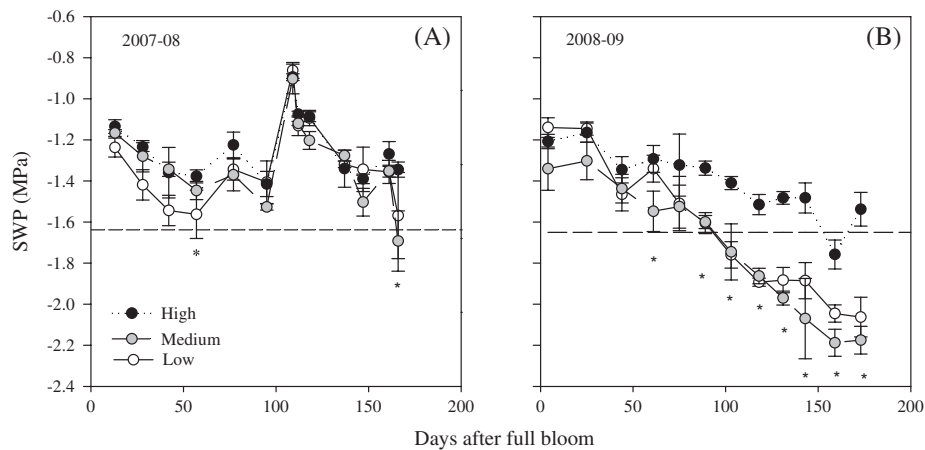NS, non-significant ($P < 0.05$).

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 $g_s > 200$ mmol m^{-2} s^{-1} ($P < 0.001$, Fig. 3D). Below this value, leaf stomatal conductance and SWP were not associated. Stomatal conductance <200 mmol m^{-2} s^{-1} was recorded on three dates, namely 42, 57, and 147 DAFB (Fig. 3A), when the wind speed was >1.5 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±0.05 for the low source:sink ratio was significantly greater than 1 ($P < 0.001$), the slope=1.02±0.04 for the intermediate source:sink ratio was not different from 1 ($P = 0.949$), and the slope=0.76±0.04 for the high source:sink ratio was significantly lower than 1 ($P < 0.001$). A similar ranking in the plasticity of midday
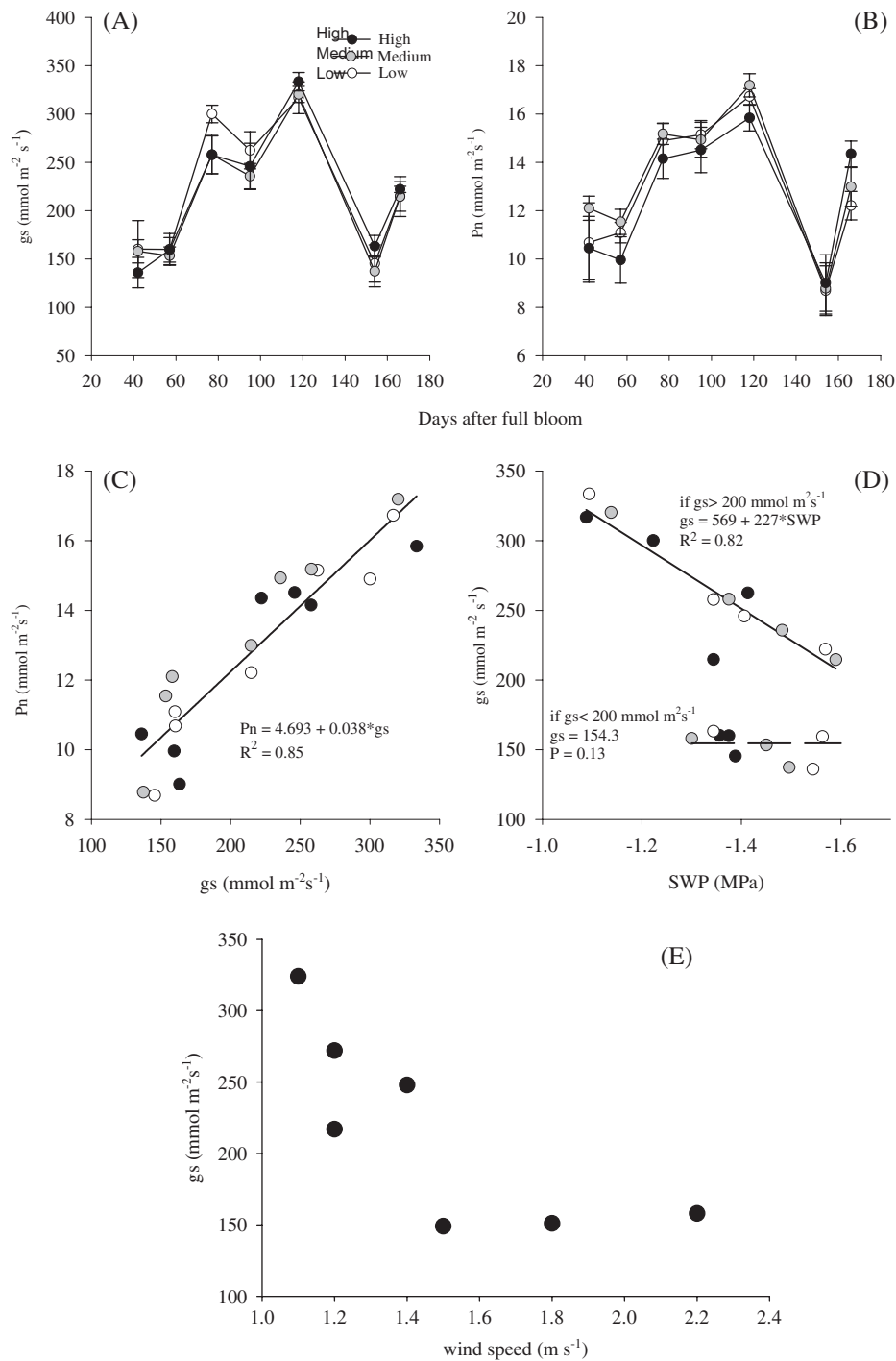
Fig. 3. Seasonal patterns of (A) abaxial stomatal conductance (g_s) and (B) net photosynthetic rate (P_n) in 2007–2008 for high, intermediate, and low source:sink ratios. (C) Relationship between P_n and g_s, and (D) between g_s and midday stem water potential (SWP). Solid lines are regressions fitted 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).
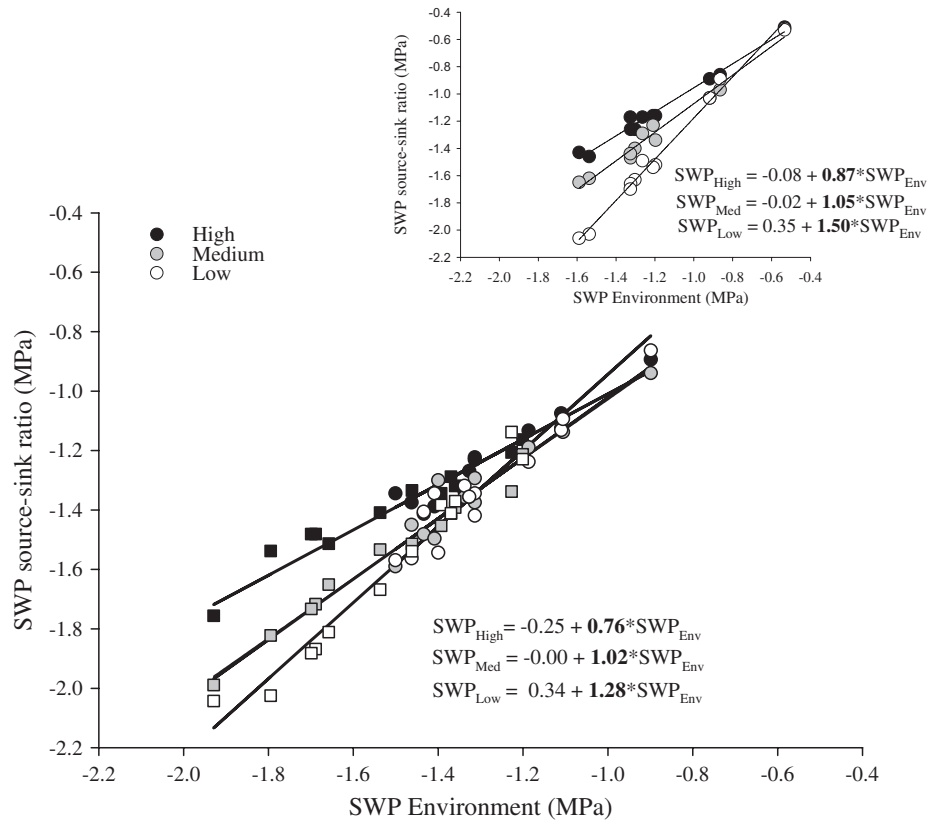
Fig. 4. Norms of reaction of midday stem water potential (SWP) in olive trees with three contrasting source:sink ratios in 2007–2008 (circles) and 2008–2009 (squares). Fitted lines are reduced major axis regressions (Model II) for each source:sink ratio, and slopes (bold) are a measure of plasticity. 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 (Fereres 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 Fereres, 2004).

However, relationships between plant water status and fruit load have been hardly considered in olive (Fereres 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;
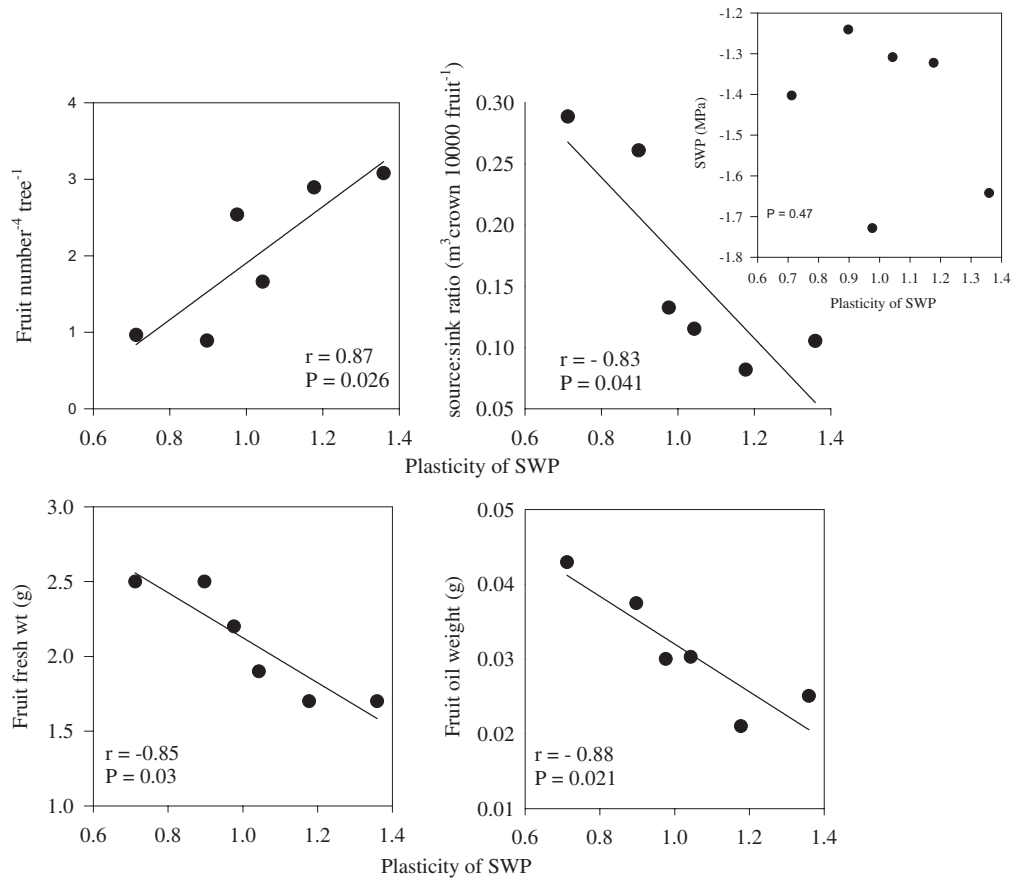
Fig. 5. Correlations between oil yield components and plasticity of midday stem water potential (SWP) in olive trees in response to three contrasting source:sink ratios during two growing seasons. Plasticities are dimensionless.
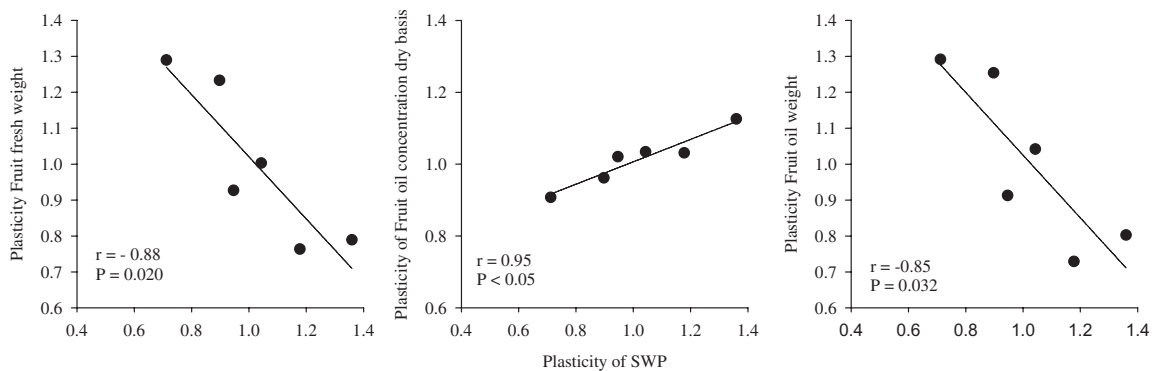

Fig. 6. Correlation between plasticities of oil yield components and plasticity of stem water potential in response to three contrasting source:sink ratios and two growing seasons. Plasticities are dimensionless.

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

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