Crop load affects maximum daily trunk shrinkage of plum trees

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Summary We studied the effects of low fruit load (3–4 fruits cm⁻² of trunk cross-sectional area (TCSA)), and high fruit load (6–7 fruits cm⁻² TCSA) on maximum daily trunk shrinkage (MDS) and trunk growth rates (TGR) over two seasons in plum (Prunus salicina Lindell) trees receiving full irrigation or deficit irrigation. Seasonal changes in MDS and TGR were compared with those in midday stem water potential (Ψₑ) and leaf stomatal conductance (gₛ). Crop load increased gₛ in fully irrigated trees approaching harvest. Although crop load did not affect plant water status in either watering regime, there were considerable differences in both MDS and TGR as a function of crop load. Compared with high-cropping trees, MDS was 34% higher and TGR was 48% lower in low-cropping trees. The differential responses of MDS and Ψₑ to crop load were a consequence of an increased assimilate demand, or by reducing water uptake as a result of restricted root growth (Williamson and Coston 1989). In some cases, high crop load has been found to increase tree water use (Mpelasoka et al. 2001), stomatal conductance (DeJong 1986) and leaf photosynthesis (Gucci et al. 1994), and to reduce stem or leaf water potential (Blanco et al. 1995, Marsal et al. 2003). In other studies, low

Introduction Precise determination of plant water status is important for planning irrigation scheduling protocols (Naor 2006). Stem water potential (Ψₑ) has been widely used in fruit trees as a water stress indicator (Garnier and Berger 1985, McCutchan and Shackel 1992). Recently, research has focused on evaluating trunk diameter measurements as a plant water status indicator, because they can be more easily automated at the field scale than Ψₑ measurements (Goldhamer and Fereres 2001). Two indices derived from trunk diameter measurements that have been commonly used as water stress indicators are trunk growth rate (TGR) and maximum daily trunk shrinkage (MDS).

Keywords: reference equations, stem water potential, trunk growth.

Trunk growth is a developmental trait affected by plant water stress, and provides an indirect measurement of plant water status. The daily shrinking and swelling of tissues is a well-known phenomenon (Kozlowski 1967). Daily changes in trunk diameter mainly depend on the degree of plant tissue hydration (Simonneau et al. 1993), with the phloem and cambium tissues being responsible for more than 90% of daily trunk diameter fluctuations (Irvine and Grace 1997). Xylem water potential is the driving force of stem shrinkage during the day (Klepper et al. 1971).

Several studies have determined the sensitivity of MDS and TGR to water availability (Goldhamer and Fereres 2001, Ortuño et al. 2004). Because evaporative demand has a large influence on MDS (Goldhamer and Fereres 2001), reference equations that can predict day-to-day variations in MDS of well-irrigated trees as a function of various environmental variables have been developed (Fereres and Goldhamer 2003, Intrigliolo and Castel 2006a). This information has been used to develop and successfully test protocols to schedule irrigation based on MDS for almond trees (Goldhamer and Fereres 2004).

Recently, we observed that the relationship between MDS and plant water status changes during the season and that MDS is dependent on organ size at the point of measurement (Intrigliolo and Castel 2006b). In addition, because of the high variability in MDS measurements, we found that the ability of both MDS and TGR to predict fruit size responses to deficit irrigation was limited (Intrigliolo and Castel 2006b). In alternate-bearing olive trees, Moriana and Fereres (2004) compared seasonal variation in MDS between one “off year” and one “on year” and found higher MDS for a given evaporative demand in the on year compared with the off year. To our knowledge, however, there are no comprehensive studies of the possible effects of crop load on MDS.

Crop load can affect tree water relations either by increasing transpiration rates (Hansen 1971, Chalmers et al. 1983) as a consequence of an increased assimilate demand, or by reducing water uptake as a result of restricted root growth (Williamson and Coston 1989). In some cases, high crop load has been found to increase tree water use (Mpelasoka et al. 2001), stomatal conductance (DeJong 1986) and leaf photosynthesis (Gucci et al. 1994), and to reduce stem or leaf water potential (Blanco et al. 1995, Marsal et al. 2003). In other studies, how-
ever, the effect of crop load on tree water status was not noticeable (Naor et al. 1999) or was evident only under deficit irrigation conditions (Naor 2004). Crop load may affect MDS not only by increasing transpiration rates, but also by directly affecting trunk growth through increased competition for photoassimilates between the fruit and other developing organs (Flore and Layne 1997). Several studies (Marsal et al. 2002, Intrigliolo and Castel 2006a) have shown that the relationship between MDS and \( \Psi_s \) is affected by the presence or absence of fruit, indicating that crop load might directly influence this relationship, but this hypothesis remains to be tested.

In stone fruit trees, fruit thinning is a frequent cultural practice. Thus, the study of the effects of crop load on MDS has interest from both a physiological and a practical point of view. We determined the usefulness of MDS as an indicator of tree water status for irrigation management and tested the hypothesis that crop load influences the relationship between MDS and \( \Psi_s \). Our specific objectives were: (1) to compare seasonal changes in MDS and \( \Psi_s \) in fully irrigated and deficit irrigated trees differing in crop load; (2) to determine the influence of climatic factors on MDS as a function of crop load in fully irrigated plants; and (3) to examine the influence of crop load on the relationship between MDS and \( \Psi_s \).

Materials and methods

Experimental plot and climatic conditions

The experiment was performed over two consecutive years (2004–2005), in a commercial Japanese plum orchard (Prunus salicina, ‘Black Gold’ grafted on ‘Mariana GF81’ rootstock) at Líria, Valencia, Spain, (40°45′ N, 0°38′ W, elevation 300 m). The soil is a sandy loam with many stones (32% w/w), and an effective depth of 80 cm. The irrigation water has a mean EC of 1.1 dS m–1 and a mean Cl – concentration of 0.40 and 0.43 in 2004 and 2005, respectively. Agricultural practices followed were those common for the area. Fruit were manually thinned between the end of April and the beginning of May.

Climatic data were recorded at an automated weather station near the orchard and mean daily air vapor pressure deficit (VPD) and daily reference evapotranspiration (ET\(_d\)) were calculated according to Allen et al. (1998). During the irrigation season, (March–October), annual precipitation and ET\(_d\) were, respectively, 275 mm and 866 mm in 2004 and 154 and 952 mm in 2005.

Treatments

The experimental plot had six treatments and three replicates in a randomized complete block design; however, only two and four treatments in 2004 and 2005, respectively, were instrumented with sensors and used for the present study. Each experimental plot comprised three adjacent rows of eight trees per row, but only the two center rows of the central row were measured. Trees were drip irrigated with six emitters per tree, each delivering 3.85 l h\(^{-1}\), that were located in a double irrigation line parallel to each tree row. The effect of crop load on tree water relations was tested in the fully irrigated trees only in 2004, and in both deficit and fully irrigated trees in 2005. Crop loads tested were: low (L commercial), 3.5–4.5 fruits cm\(^{-2}\) of trunk cross-sectional area (TCSA)), and high (H, 6.5–7.5 fruits cm\(^{-2}\) of TCSA). Crop load treatments were established during fruit thinning. In 2004, a full irrigation treatment (100) of 100% of crop evapotranspiration (ET\(_c\)) was applied to the low- (100-L) and high-cropping (100-H) trees. In 2005, a full irrigation treatment (100) and a deficit irrigation treatment (DI) were applied to give four treatments: 100-L, 100-H, DI-L and DI-H. The DI treatment was applied during May (phase II of fruit growth) at 25% of ET\(_c\) and during post-harvest at 50% of ET\(_c\). The same experimental plots used in 2004 were used in 2005. Mean crop load and crop yield values for the trees used for the water relations studies are reported in Table 1.

In addition to the trees in the 100-L, 100-H, DI-L and DI-H treatments, eight additional trees, three in 2004 and five in 2005 were included to increase the range of crop load. These additional trees were located in the same experimental plot in a guard row of a 100-L plot. Their crop loads were 2.7, 8.3 and 10.4 cm\(^{-2}\) of TCSA; and 0.8, 1.2, 2.5, 5.34, 7.3 and 7.9 cm\(^{-2}\) of TCSA, for trees selected in 2004 and 2005, respectively. These additional trees received full irrigation, except in June when irrigation was withheld for 20 days.

Crop evapotranspiration was estimated as the product of ET\(_d\) and crop coefficient (\( K_c \)). The reference evapotranspiration was calculated from the Penman-Monteith equation (Allen et al. 1998) and \( K_c \) values were adjusted for tree size following Fereres and Goldhamer (1990). Mean seasonal \( K_c \) values were 0.40 and 0.43 in 2004 and 2005, respectively.

Trunk diameter variations

Trunk diameter was measured continuously with linear variable differential transformers (LVDT, Schlumberger Mod. DF-2.5, West Sussex, U.K.) on six representative trees per treatment. A sensor was fixed to the main trunk of each tree by a metal frame of Invar (a metal alloy with a minimal thermal expansion) located about 20 cm from the ground on the north side. Other details on sensor characteristics, calibration and

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data recording were as described by Intrigliolo and Castel (2004). From these sensor measurements we calculated: (1) maximum daily shrinkage (MDS), obtained as the difference between the maximum diameter reached early in the morning and the minimum reached normally during the afternoon; and (2) trunk growth rate (TGR), determined as the mean increment in maximum diameter in 10-day periods.

**Stem water potential and stomatal conductance**

Midday stem water potential (Ψ<sub>s</sub>) was measured with a pressure chamber, following procedures described by Turner (1981). Determinations were performed on two leaves per tree of two trees per treatment that also had an LVDT sensor installed. On each occasion, Ψ<sub>s</sub> was measured in the additional trees. Mature shaded leaves from the north face near the trunk were enclosed in plastic bags covered with foil at least 2 h before the measurements, which were made between 1200 and 1300 h solar time. Determinations were made about twice a week from May to harvest and every 15 days during the rest of the season.

Stomatal conductance (g<sub>s</sub>) was determined around solar midday, in the same trees used for Ψ<sub>s</sub> measurements, on five fully expanded sun-facing leaves per tree. In 2004, measurements were made with a dynamic diffusion porometer (AP4, Delta-T Devices, Cambridge, U.K.), and in 2005 determinations were made with a portable IRGA system (Model ADC LC Pro+, The Analytical Development Co. Ltd., Hoddesdon, U.K.). Determinations of g<sub>s</sub> were made at weekly intervals from May to harvest.

**Reference equations**

Data from fully irrigated trees were pooled over years and used to explore the effects of VPD, ETo and mean daily air temperature (T<sub>air</sub>) on the relationship between MDS and Ψ<sub>s</sub> in low- and high-cropping trees. Data used to derive the reference equations were collected from the beginning of May, when trees had developed up to 70% of their total leaf area and the final fruit load was established, until harvest. Some of the MDS data from 2004 for the low-cropping trees used in our study have already been reported by Intrigliolo and Castel (2006a), who developed reference equations for the same trees as a function of the phenological period.

**Influence of crop load on the relationship between MDS and midday stem water potential**

The effect of crop load on the relationship between MDS and Ψ<sub>s</sub> was studied in trees from all the irrigation treatments and the additional trees. The MDS:Ψ<sub>s</sub> ratio was calculated for all days on which Ψ<sub>s</sub> was measured. Mean seasonal MDS:Ψ<sub>s</sub> was then calculated and plotted against tree crop load expressed as number of fruit per tree per unit of TCSA. The number of fruits per tree was obtained at harvest using a commercial grading machine (Fomesa SA, Spain).

**Statistical analysis**

Simple linear regression analysis was carried out to explore relationships between variables. Significance values of the correlation coefficient at 5% or higher are reported. In all cases where the relationship appeared to depart from linearity, statistical tests with nonlinear equations were performed. Nonlinear equations are shown only when they significantly improve the goodness of fit.

**Results**

**Seasonal changes in water stress indicators**

During both years (2004 and 2005), crop load had no significant effect on g<sub>s</sub> in the well-irrigated trees until day of the year (DOY) 170, one month before harvest; thereafter, 100-H trees had higher g<sub>s</sub> (P < 0.05) than 100-L trees (Figures 1A and 2A). Conversely, Ψ<sub>s</sub> in well-irrigated trees was not significantly (P > 0.1) affected by crop load in any year (Figures 1B and 2B). Averaged over the fruit thinning to harvest period, Ψ<sub>s</sub> in the high-cropping, fully irrigated trees was only 8 and 2% lower than in the low-cropping fully irrigated trees, in 2004 and 2005, respectively.
Before fruit thinning, MDS values of trees in both crop load treatments were similar, but during the period from fruit thinning to harvest there were differences in MDS as function of tree crop load (Figures 1C and 2C). Crop load had a greater effect on MDS than on $\Psi_s$. Thus, in most instances, from DOY 140 to DOY 172, 100-H trees had higher MDS than 100-L trees ($P < 0.05$). Averaged over the period from fruit thinning to harvest, MDS of the high-cropping, fully irrigated trees was 28 and 40% higher in 2004 and 2005, respectively, than in the low-cropping fully irrigated trees. After harvest, similar MDS values were observed in the 100-L and 100-H trees (Figures 1C and 2C).

Trunk growth as a function of crop load varied between study years (Figures 1D and 2D). In Year 2004, TGR tended to be lower in the high-cropping trees, but differences between crop loads were not significant ($P > 0.05$). Averaged over the fruit thinning to harvest period, TGR of the 100-H trees was 28.7 $\mu$m day$^{-1}$, which was not significantly lower ($P > 0.05$) than TGR of the 100-L trees (37.2 $\mu$m day$^{-1}$). However, in Year 2005, TGR was significantly reduced by high crop load from DOY 125 to DOY 185 ($P < 0.05$). Averaged over the 2005 fruit growth period, TGR in the 100-H trees was 14.6 $\mu$m day$^{-1}$ compared with 31.6 $\mu$m day$^{-1}$ in the 100-L trees.

In the deficit irrigated trees, the reduction in available water caused $\Psi_s$ and $g_s$ to decrease. When irrigation was returned to full supply before harvest, trees in the deficit irrigated treatments recovered to similar water status to trees in the fully irrigated treatment (Figures 2 and 3). In the deficit irrigated trees, differences in $g_s$ between crop loads were significant ($P < 0.05$) only on DOY 145, 153 and 180, whereas crop load had no effect on $\Psi_s$ throughout the season.

As observed in the fully irrigated trees, there were large differences in MDS between DI-H and DI-L trees (Figure 3). The effect of crop load on MDS of DI trees was significant ($P < 0.05$) from DOY 130 to DOY 170 of 2005. In DI trees, high crop load significantly reduced TGR from DOY 125 to DOY 185 ($P < 0.05$). After harvest, TGR and MDS of the DI-H trees returned to values similar to those of DI-L trees (Figure 3).

Influence of crop load on the relationship of MDS with environmental variables

In fully irrigated trees, higher MDS values for a given $ETo$, and VPD were observed in the high-cropping trees compared with the low-cropping trees (Figure 4). Thus, for the pooled data...
over both years for the fruit growth period only, the slopes of
the regression equations of MDS versus ET₀ and VPD were
higher (P < 0.05, P < 0.01, respectively) for the high-cropping
trees than for the low-cropping trees. However, for the linear
regression equations of MDS versus Tₘₐₓ, differences in slopes
were not statistically significant (P < 0.05). Independently of
crop load, MDS was better related to ET₀ with an exponential
relationship than with a linear relationship.

Influence of crop load on the relationship between MDS and
midday stem water potential

Although the slope of the MDS–Ψₛ relationship was not sig-
nificantly affected by crop load (P > 0.05), for a given Ψₛ, there
was a trend of larger MDS with heavy crop load (Figure 5). More-
over, the MDS:Ψₛ ratio of each tree was negatively re-
lated to its crop load (P < 0.01) (Figure 6). As crop load in-
creased, there was a reduction in the MDS:Ψₛ ratio, indicating
that a higher MDS for a given Ψₛ with increasing tree crop
load.

Discussion

We demonstrated that crop load has a direct effect on MDS
that is unrelated to its possible effects on lowering plant water
status. Although crop load did not affect plant water status in
either the fully irrigated or deficit irrigated trees, crop load had
significant effects on MDS and TGR. For instance, pooling
data for the fully irrigated trees over both years revealed that
high crop load increased MDS by 34% and decreased TGR by
48%.

Although crop load slightly increased stomatal conductance
it had no effect on stem water potential, probably because the
reduction in leaf area observed in the high-cropping trees (re-
sults not shown) counteracted the increase in stomatal conduc-
tance. The finding that crop load had no effect on stem water
potential suggests that xylem water potential at the point
where stem shrinkage was measured was also unaffected by
tree crop load. Thus, the effect of crop load on MDS is unlikely
to be associated with the effect of increasing transpiration rate
on xylem water potential, but is likely a consequence of the ef-
effect of crop load on the relationship between Ψₛ and MDS.

Overall results in Figures 5 and 6 indicate that not only the
presence or absence of fruit as previously reported (Marsal et
al. 2002, Intrigliolo and Castel 2006a), but also fruit load, in-
fluences the MDS–Ψₛ relationship. The physiology underly-
ning the effect of crop load on the MDS–Ψₛ relationship is
probably related, in part, to the observed decrease in trunk
growth rate in the high-cropping trees. Trunk growth and trunk

Figure 4. Relationships of maximum daily shrinkage (MDS) of the
fully irrigated trees having low crop load (solid lines) and high crop
load (dotted lines) with (A) mean daily air temperature (Tₘₐₓ), (B)
daily reference evapotranspiration (ET₀), and (C) mean daily air va-
por pressure deficit (VPD). Values are means of six linear variable
transformer sensors. Significance: ***, P < 0.001.

Figure 5. Relationships between maximum daily shrinkage (MDS)
and midday stem water potential (Ψₛ) separated by crop load. Values
are means of determinations with six sensors and four leaves. Signifi-
cance: ***, P < 0.001.
shrinkage represent opposing processes, leading McBurney and Costigan (1984) to suggest a higher trunk shrinkage for a given \(\Psi_s\) when trunk growth is low. However, we found that differences in trunk growth rates between the high- and low-cropping trees explained only 30% of the difference in MDS observed with crop load. Differences in trunk growth between 100-H and 100-L trees reached a maximum of about 40 \(\mu m\) day\(^{-1}\), whereas differences in MDS were in many cases greater than 60 \(\mu m\), indicating the likely involvement of factors distinct from growth.

It has been shown that the magnitude of stem shrinkage for a given xylem water potential may be affected by differences in osmotic pressure between the bark and the xylem (Cochard et al. 2001). In fruit trees, there is evidence that high crop load reduces the sugar concentration of woody tissues (Ryugo et al. 1977, Buwalda and Lenz 1992), thereby presumably increasing the osmotic potential of phloem tissues. This should lead to a larger water potential gradient between the bark and the xylem, and, in turn, to larger trunk contractions for a given stem water potential in trees with a high crop load. Recent studies (Sevanto et al. 2003, Daudet et al. 2005) have implicated plant carbon status as a factor affecting stem contraction. Thus, when assessing plant water status from MDS measurements, it should be considered that a given MDS value might correspond with different values of plant water status depending on crop load. In the range of crop loads we evaluated (1 to 11 fruit \(cm^{-2} \) TCSA), MDS increased 15.2 \(\mu m\) per unit increment of crop load and of \(\Psi_s\) (MPa). The equation in Figure 6 could be used to extrapolate \(\Psi_s\), based on empirical relationships with MDS of plum trees with different crop loads.

In well-irrigated trees, the effects of environmental conditions on day-to-day variations in MDS were dependent on crop load (Figure 4). This finding implies that the reference equation previously established by Goldhamer and Fereres (2004) cannot be applied universally to MDS measurement for determining irrigation schedules. Instead, specific reference equations that adjust for tree crop load should be used, because failure to take crop load into consideration will result in errors in the estimation of MDS for a given evaporative demand. Moriana and Fereres (2004) showed that the slope of the relationship between MDS and VPD increased by 29% in an “on year” compared with an “off year” in alternate-bearing olive trees. Differences in trunk growth were low and started to increase only after fruit thinning. Toward harvest, fruit dry matter accumulation rate is maximal (Grossman and DeJong 1995) and trunk growth stopped because fruits, especially during stage III of their development, are strong sinks and have priority for assimilates (Flore and Layne 1997). The inhibitory effect of fruits on trunk growth rates is indicated by the sudden increase in trunk growth after fruit harvest. Moreover, during the last phase of rapid fruit growth, particularly in June, trunk growth also decreased. Toward harvest, fruit dry matter accumulation rate is maximal (Grossman and DeJong 1995) and trunk growth stopped because fruits, especially during stage III of their development, are strong sinks and have priority for assimilates (Flore and Layne 1997). The inhibitory effect of fruits on trunk growth rates is indicated by the sudden increase in trunk growth after fruit harvest. These observations highlight the strong effects of crop load on TGR, which is why TGR cannot serve as an independent measure of plant water status in fruit trees crops.

Overall, our results highlight the importance of considering crop load when attempting to use MDS or TGR as a water stress indicator. This is particularly important for stone fruit trees, where crop load may vary greatly according to market conditions, and crop load regulation might be used as a strategy to mitigate the negative effects of deficit irrigation on fruit.
size (López et al. 2006). Our results together with previous findings (Intrigliolo and Castel 2006a) indicate that MDS is influenced by factors besides plant water status that can have important influences on the MDS–Ψ stressed plant water status for irrigation scheduling in plum. Irrig. Sci. 23:93–102.


References


