Night-time sap flow is parabolically linked to midday water potential for field grown almond trees.

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ABSTRACT

To quantify night-time (S_n) and diurnal (S_d) tree water uptake, two sets of sap flow sensors (heat-pulse compensated) were installed per tree in the North-East and South-West sides of the trunk in three trees per treatment. There were two treatments: i) control, irrigated with 100% ET_c (T_{100}) and ii) deficit, irrigated at 60% ET_c (T_{60}) with daily irrigations at the peak atmospheric demand (Dec – Jan). Normalised S_n by trees was in the range of 15 to 25% throughout the season, compared to normalised S_d , for T_{100} and T_{60} respectively. Furthermore S_n was parabolically correlated to plant water status from the previous day, measured as midday stem water potential (Ψ_s). We also found strong correlations between S_n and nocturnal VPD for T_{100} and T_{60} , indicating that nocturnal transpiration (E_n) was significant for both treatments. Differences in S_n were observed for the NE and SW sensors for T_{60} , being significantly less for the NE side (sunny side) compared to the SW side (more shaded). No differences were observed for T_{100} regarding probe positioning.

Keywords: Night-time sap flow, midday stem water potential, night-time VPD, soil moisture.

INTRODUCTION

Due to climate change predictions regarding reductions in rain events for most regions in Australia, there is a growing interest in the Australian Almond industry in increasing water use efficiency (WUE), especially in semi-arid regions, such as Berri (South Australia). One of the strategies considered to increase WUE is reducing water applied through regulated deficit irrigation (RDI), to achieve better stomata control through hormonal signals (mainly abscisic acid (ABA)) from roots to shoots. The hormonal effects of RDI in stomatal control and WUE have been widely studied for grapevines (Collins et al., 2009; Loveys et al., 2000; McCarthy et al., 2002; Rodrigues et al., 2008; Romero et al., 2012) and almonds (FuBeder et al., 1992; Wartinger et al., 1990). However, little attention has been given to nocturnal water uptake, and how much of this water corresponds to night-time transpiration (E_n).

It has been shown that the proportion of nocturnal sap flow to diurnal sap flow (S_n/S_d) can reach values up to 30 to 60% for arid and semi-arid regions in a range of ecosystems (Snyder et al., 2003). Furthermore, night-time water uptake does not always correspond to rehydration, and more often a significant part of S_n has been ascribed to E_n in a range of different species (Caird et al., 2007; Rogiers et al., 2009; Zeppel et al., 2010). Since E_n is not associated with photosynthesis, it contributes toward decreased water use efficiency (WUE), which has a significant implication for the whole-tree water budget (Zeppel et al., 2010). When E_n accounts for a high fraction of the S_n/S_d

1 proportion, S_n is commonly highly correlated to nocturnal vapour pressure
2 deficit (VPD) (Benyon, 1999; Fisher et al., 2007; Zeppel et al., 2010).
3 Therefore, it is expected that E_n would increase in a climate change scenario,
4 which predicts that nocturnal temperatures will increase at a higher rate
5 compared to diurnal temperatures (Brunetti et al., 2000; Easterling et al.,
6 1997).

7 Since higher E_n rates are expected with more soil moisture availability and
8 higher night-time VPD, it will be difficult for plants to equilibrate their water
9 status with that of the soil at night. For irrigation purposes, pre-dawn leaf
10 water potential (Ψ_{PD}) has been commonly used to estimate plant water status
11 under equilibrium conditions (Liang and Zhang, 1999; Remorini and Massai,
12 2003; Sousa et al., 2006). However, studies have already shown that this
13 equilibrium between Ψ_{PD} and soil water potential does not necessarily occur
14 at night in a range of trees and shrubs (Bucci et al., 2005; Bucci et al., 2004;
15 Donovan et al., 1999; Donovan et al., 2001; Sellin, 1999), and this lack of
16 equilibrium has been associated with E_n (Kavanagh et al., 2007). Therefore, it
17 is important to characterise the proportion of S_n/S_d through accurate
18 quantification of these parameters to improve our understanding of the factors
19 affecting E_n , and to obtain techniques to minimise this process.

20 Nocturnal water uptake and transpiration has been studied in a range of
21 different species over the last 10 years (Caird et al., 2007), mostly trees
22 (Kavanagh et al., 2007; Moore et al., 2008; Phillips et al., 2010; Wang et al.,
23 2008; Zeppel et al., 2010), kiwifruit (Green et al., 1989) and grapevines
24 (Flexas et al., 2002b; Rogiers et al., 2009). Until now, there has not been
25 much literature available on night-time water uptake for Almond trees. This

1 study had as a general aim to contribute to the understanding of the dynamics
2 of S_n associated with plant water stress and atmospheric demand for irrigated
3 almond trees grown in field conditions. Specific aims of this study were to
4 compare S_n and tree water stress, measured as midday stem water potential
5 (Ψ_s) from the previous day and to explore the night-time capacity of almond
6 trees to recover from water stress endured the previous day.

7

8 **MATERIALS AND METHODS**

9 *Field conditions and experimental details*

10 The experiment was conducted on 11-year-old almond trees [*Prunus dulcis*
11 (Mill.) Webb] at a commercial orchard (Clark Taylor farms) located in Berri,
12 South Australia (34°20'S and 140°35'E) during the 2009 – 2010 season. The
13 experimental site received an annual rainfall of 312mm in 87 rain days for the
14 season (July 2009 to June 2010). Temperature ranged from -1.3°C in July to
15 44.3°C in January, with a maximum surface soil temperature of 49°C. There
16 were two and six days with day-time temperature exceeding 40°C in
17 December and January respectively. Weather conditions during summer
18 (December, January and February) are presented in Table 1. The soil is
19 classified as Sandy, uniform up to a depth of 150cm with a mean soil particle
20 distribution of 89% sand, 2% silt, 9% clay, and a bulk density of 1.61 g cm⁻³.
21 The almond orchard was planted in 1998 with the rows oriented roughly
22 north–south. Trees were spaced 6.7m between rows and 6.1m within rows.
23 The almond variety Nonpareil (50%), was considered for the experiment,
24 these were inter-planted with Carmel (33%) in alternate rows and Ne Plus
25 Ultra (17%) in every sixth row, both as pollinators. All trees were grafted on to

1 Nemaguard rootstock. Trees selected for the study had a trunk circumference
2 of 90 to 100 cm at 30 cm from the ground, with a bark thickness of 5 to 8 mm.

3

4 *Irrigation and experimental design*

5 The orchard was drip irrigated. Each row of trees had two laterals, one on
6 either side at 1 m offset from the tree trunk. The laterals had 4 L h⁻¹ pressure
7 compensated button drippers spaced at 1 m interval. The laterals were buried
8 at 10cm below ground level and water was delivered to the ground surface via
9 a small tube attached to the outlet of each dripper. Each tree had
10 approximately 12 drippers in total. Irrigation events occurred daily,
11 commencing at 8 am with alternate on and off pulse cycles. The average flow
12 rate of each dripper was 3.87 L h⁻¹.

13 Water for irrigation was pumped directly from the River Murray, with a
14 separate water meter installed for each treatment to measure the volume of
15 water applied. A Class-A evaporation pan was used to measure daily
16 evaporation (E_{pan}) at the experimental site. Daily irrigation requirements (mm)
17 were based on different crop factors according to the almonds' phenological
18 stage. The crop factor (K_c) corresponding to this period from 11th December
19 2010 until the 1st of February 2010 was $K_c = 1.0$. After this date a change of
20 K_c to 0.8 was implemented. This K_c change coincided with the final growth
21 stage leading to harvesting. Further K_c changes were applied from the 12th of
22 March ($K_c = 0.7$), 19th of March ($K_c = 0.6$) and 26th of March ($K_c = 0.5$). The
23 crop factor (K_c) was multiplied by E_{pan} to obtain crop evapotranspiration (ET_c).
24 Rainfall was considered to be effective only when the total daily rainfall
25 exceeded 12 mm.

1 The experiment consisted of five treatments with combinations of different
2 fertilizer and water levels. Treatments were laid out in a randomised block
3 design with three replications each. Treatment T₁₀₀ with 100% ET_c irrigation
4 and treatment T₆₀ with 60 % ET_c irrigation were selected for sap flow studies.
5 Both these treatments received the same levels of fertilizers viz., 320:54:600
6 (N:P:K) kg ha⁻¹ with the same fertilizer distribution pattern through the year,
7 applied via fertigation.

8

9 *Sap flow measurements*

10 Three trees within each treatment were selected for sap flow measurements.
11 Two sets of sensor probes were installed in each tree. The first probe for each
12 tree was positioned on the North-East (NE) side of the tree and the second
13 sensor on the South–West (SW) at around 50 cm above the ground surface.
14 Sap flow measurements were performed using the heat pulse method as
15 outlined (Green et al., 2003). The heat pulse velocity system used was based
16 on the compensation method, with two temperature probes placed
17 asymmetrically on either side (10 mm above and 5mm below) of the heater.
18 The sensors and heater probes used for the study were purchased from
19 TRANSFLO NZ LTD (Palmerston North, New Zealand)(Green, 1998).
20 Stainless steel probes of 50mm length and 1.8mm thickness with four
21 thermocouples at 5, 15, 25 and 40mm were used.
22 The sensors and heater probes were differentially wired to an AM25T
23 multiplexer (Campbell Scientific Inc., Utah, USA). Heat pulses were
24 automatically generated every 30 minutes using a CR1000 Campbell
25 Scientific data logger (Campbell Scientific Inc., Utha, USA). Heat pulse

1 velocity was calculated according to the manufacturer specifications (Green,
2 1998). A correction factor for a 2.4mm wound width was used for calculations.
3 The wood and sap fractions were 0.5 and 0.4 respectively. Volumetric sap flux
4 was integrated over the sapwood area; taking into consideration the tree
5 circumference, bark thickness and heartwood radius.

6 Night-time sap flow (S_n) was considered between 7 PM and 5 AM the next
7 day (10 hours from sun-set to sun-rise). Sap flow for the period morning until
8 midday (S_{md}) was considered from 5 AM until 3 PM (10 hours from sun-rise to
9 end of measurements). Total day-time sap flow (S_d) was considered
10 considering a 23.5 hour period (from 12:00 AM until 11:30PM).

11 Leaf area index (LAI) was obtained the 1st of February 2010 using digital
12 cover photography from trees in which sap flow probes were installed. Images
13 were obtained just below the tree and in between of trees to calculate an
14 averaged LAI (with a total of three images per tree). The digital images were
15 analysed following the methodology proposed by Fuentes et al. (2008).

16

17 *Meteorological data*

18 Meteorological data for calculation of vapour pressure deficit (VPD) was
19 obtained from the South Australian Murray-Darling Basin Natural Resource
20 Management Board website (<http://www.aws-samdbnrm.sa.gov.au>). Data was
21 collected from Bookpurnong (34°21'S; 140°36'E), the nearest meteorological
22 station to the site,, located 200 m away from the trial site. .

23

24

1 *Soil moisture, soil physical and chemical properties*

2 Six Enviroscan® soil moisture probes (Sentek Pty. Ltd., Stepney, SA,
3 Australia) where installed at 20 cm intervals laterally out from the drippers at
4 distances between 0 and 100 cm. Each probe had five sensors at 20, 40, 60,
5 80 and 120 cm depths. All probes were wired to a RT6® data logger, and soil
6 moisture data was recorded every hour.

7 Soil samples were obtained at similar depths to the soil moisture sensors (30,
8 60, 90, 150 cm), before installation of sap flow sensors. Soil textural
9 properties were analysed separately for per cent of clay, silt and sand
10 according to the procedure outlined by Day (1965). Salinity levels (dsm^{-1}) and
11 organic matter (%) were determined using soil samples and laboratory
12 analysis (Rayment and Higginson, 1992) (Table 2).

13

14 *Pre-dawn soil water potential calculations ($\Psi_{PD\text{soil}}$)*

15 Pre-dawn soil water potential was calculated from soil moisture data obtained
16 from the three probes (0, 20 and 40 cm) closest to the drippers. The
17 conversion from volumetric soil moisture (θ_s) to tension [$\Psi_{PD\text{soil}}$ (MPa)] was
18 made using the hydrological solutions approach (Saxton and Rawls, 2006;
19 Saxton and Willey, 2004). The derived conversion equations were obtained
20 using the SPAW hydrologic model (Saxton and Rawls, 2006; Saxton and
21 Willey, 2004) and soil physical and chemical properties for each soil layer
22 obtained from Table 2.

23

24

1 *Leaf (Ψ_L) and Stem (Ψ_S) water potential measurements*

2 Midday observations on leaf water and stem water potentials were carried out
3 in parallel for the two treatments using Plant Water Status Console Apparatus,
4 *Model 3000* (Soil Moisture Equipment Corporation Santa Barbara, CA, USA).
5 Measurements were expressed in mega Pascals (MPa). Measurements were
6 made on a weekly basis from the 1st of December 2009 until the 10th of
7 February 2010. In total there were eight measurement dates for water
8 potential (Table 3). The time of measurements was between 12:00 noon and
9 3:00 pm, which was regarded as “midday”. Leaves for Ψ_S were enclosed in a
10 plastic bag coated with aluminium foil for a minimum of 10-15 minutes prior to
11 measurement (Fulton et al., 2001).

12 Leaf water potential measurements (Ψ_L) were carried out on three fully
13 expanded leaves per tree replicated three times for each treatment. The
14 leaves selected were positioned in the top, middle and lower sections of tree
15 canopies from the sunny side. All Ψ_L measurements were performed within 30
16 s from leaf removal and expressed in MPa. Stem water potential (Ψ_S)
17 measurements were carried out on one fully expanded leaf per tree replicated
18 three times for each treatment.

19

20 *Zero-flow models*

21 A simple zero-flow model was proposed for each irrigation treatment. These
22 zero-flow models were obtained by solving the equations obtained from the
23 parabolic relationships comparing S_n and S_{md} with midday Ψ_S . The two
24 solutions for each model (roots) were obtained using the “solver” function from
25 MATLAB® R2011b (The Mathworks Inc., Natick, MA, USA).

1 *Data analysis*

2 To compare midday Ψ_S with S_n and S_{md} ; S_n with night-time VPD; midday Ψ_S
3 with Ψ_L ; and S_n/S_d proportion across treatments, general linear and curvilinear
4 models were fitted to the data using MATLAB® R2011b (The Mathworks Inc.,
5 Natick, MA, USA) and the Curve Fitting Toolbox™. To evaluate the strength
6 of relationships the standard error of estimates (SEE) and the root mean
7 squared error (RMSE) were calculated. To explore whether specific
8 treatments were uncoupled from the different relationships, a residual analysis
9 with statistical significance was assessed using SigmaPlot® (Cranes software
10 international Ltd, Bangalore. India) (Mayo et al., 2009; Monzon et al., 2006;
11 Sadras and Moran, 2012; Tang et al., 2011).

12 Maximum, minimum and actual values of S_n and S_d per irrigation treatment
13 were used to obtain the normalised ratio ($N(S_n/S_d)$) of sap flows using the
14 following relationship:

15

16
$$\text{Equation 1}$$

17

18 where, $NS_{(n,d)}$ is the normalised value of S_n or S_d ; $Si_{(n,d)}$ is the actual value of
19 S_n or S_d ; S_{min} = the minimum flow of S_n or S_d ; S_{max} = the maximum flow of the
20 dataset.

21

22

1 RESULTS

3 *Night-time dynamics of S_n compared to available water and S_d*

4 The dynamics of S_n was strongly influenced by the amount of water supplied
5 by irrigation and rain events for both treatments (T_{100} and T_{60}). Figure 1a
6 shows total night-time water uptake by trees with their corresponding water
7 inputs as irrigation and rain. The correlation between S_n and water supply was
8 closer during the early season period, which corresponded from the beginning
9 of the study (24th November 2009) until the 2nd of February 2010. After this
10 period, S_n was lower in both irrigation treatments, right up to the end of the
11 experimental period (24th March 2010) (regarded as late season period).

12 Figure 1b shows the S_n trends compared to Ψ_{PDsoil} (MPa) calculated at 5 am
13 from soil moisture measurements. There was an apparent inverse relationship
14 between S_n and Ψ_{PDsoil} , which was more evident in T_{60} , especially for the early
15 season period (until the 2nd of February 2010). From the 2nd of February to the
16 4th of March 2010, this relationship was maintained even though there was
17 more water available in the soil through rain and irrigation. From the 4th of
18 March until the end of the season the soil was close to field capacity. Non
19 water-stressed conditions are marked with a horizontal dashed line passing
20 through -0.5 MPa for Ψ_{PDsoil} (Romero et al., 2004).

21 Values of S_n were consistently higher for T_{100} compared to T_{60} throughout the
22 whole season, with the exception of the first and last week of the period
23 shown in Figure 1a and 1b. The average seasonal reduction of S_n for T_{60}
24 compared to T_{100} was 21%, with a maximum of 39% and a minimum of 3%.

1 Table 4 shows the total water applied (TWA) for the whole season (including
2 irrigation and rain). Only 45% of the TWA was accounted for as diurnal sap
3 flow (S_d) for T_{100} and 55% for. From this total sap flow, 20% corresponded to
4 S_n for both treatments.

5 The normalised proportion comparing both irrigation treatments is shown in
6 Figure 2, minimum and maximum values of this relationship corresponded to
7 between 15 - 25% respectively from the S_n/S_d relationship throughout the
8 entire study period (early season and late season) for both treatments.

9 Specifically, these S_n/S_d percentages corresponded to minimum flows of
10 around $S_n = 8 \text{ L tree}^{-1} \text{ night}^{-1}$ and $S_d = 52 \text{ L tree}^{-1} \text{ day}^{-1}$ and maximum flows of
11 $S_n = 55 \text{ L tree}^{-1} \text{ night}^{-1}$ and $S_d = 218 \text{ L tree}^{-1} \text{ day}^{-1}$ for both treatments in
12 average. In general, as shown in Fig. 2, the $N(S_n/S_d)$ proportion was similar
13 for T_{100} compared to T_{60} as demonstrated by a high and statistically significant
14 correlation ($R^2 = 0.71$; $SEE = 0.054$; $RMSE = 0.017$; $P < 0.05$) with slope
15 close to unity ($b = 0.86$).

16

17 *Relationship between S_n and midday Ψ_s*

18 Significant parabolic relationships were found when comparing S_n with midday
19 Ψ_s measured the previous day for both treatments (Figure 3a; Table 5) for the
20 measurement days (Table 3). These relationships were found for the early
21 season period described, which ended the 2nd of February 2012. Two sections
22 were identified for each parabolic relationship: i) the first section corresponded
23 to Ψ_s values from close to zero down to the peak of S_n for each parabola
24 (Table 5); ii) the second section corresponded to values of Ψ_s to the left of
25 peak S_n . Data from T_{100} fell entirely within the first section described above. A

1 semi-parabola was found for T_{100} and a more complete parabola was found
2 for T_{60} (Table 5). Statistical analysis of residuals showed that the treatments
3 were uncoupled from each other for the Ψ_S versus S_n relationship ($P <$
4 0.0006) (Figure 3a). Results of the Ψ_S versus S_n relationship for different
5 probe locations and treatments are shown in Figure 3b. Statistical analysis
6 showed that the residuals for $T_{100}NE$, $T_{100}SW$ and $T_{60}SW$ were not statistically
7 different for the first section of the parabola. By contrast, residuals from $T_{60}NE$
8 were statistically different from both T_{100} probe locations and the $T_{60}SW$ ($P <$
9 0.0001). Data from $T_{60}NE$ corresponded to a reduction of up to 31% from
10 maximum values found in $T_{60}SW$ and T_{100} (Table 5).

12 *Relationship between S_n and night-time VPD*

13 Statistically significant linear correlations ($P < 0.05$) were observed when
14 comparing S_n with night-time VPD (Table 6). The correlations were different
15 during the two periods identified in Figure 1a. Hence, Figure 4a shows the S_n
16 vs night time VPD relationship from the early season period. Figure 4b shows
17 the S_n vs night time VPD relationship for the late season period. There was
18 consistently higher S_n in T_{100} compared to T_{60} for the same night-time VPD
19 conditions during the early season period (Figure 4a), assessed by analysis of
20 residuals ($P < 0.001$). There was less difference between T_{100} and T_{60} in the
21 late season period (Figure 4b), however the S_n vs VPD relationships of both
22 treatments were also statistically significant and uncoupled, as assessed by
23 analysis of residuals ($P < 0.001$).

1 *Relationship between S_{md} and midday Ψ_S*

2 Significant parabolic relationships were obtained when comparing S_{md} with
3 midday Ψ_S for both treatments (Figure 5 ; Table 5), which were similar to the
4 results of S_n and Ψ_S for measurement dates (Table 3). Again, two sections
5 were identified for each parabolic relationship. Data from T_{100} and T_{60} fell only
6 in the first section and peak of a semi-parabola (Table 5).

7 Statistical analysis showed that the residuals for $T_{100}NE$ and $T_{100}SW$ were not
8 statistically different (Figure 5, inset a). By contrast, residuals from $T_{60}NE$
9 were statistically different from $T_{60}SW$ ($P < 0.001$) (Figure 5, inset b). The
10 calculated curve for $T_{60}NE$ corresponded to a reduction of 26% from
11 maximum values of $T_{60}SW$, and a 40% reduction from T_{100} (Table 5).

12

13 **DISCUSSION**

14 *Night-time water uptake (S_n) responds to soil water availability*

15 As demonstrated in Figure 1a, S_n closely follows water input throughout the
16 study period for both treatments. Therefore, it can be said that S_n is a
17 sensitive representation of tree water uptake at night-time, and that this will
18 depend on the water availability within the soil surrounding the root-system,
19 supplied mainly by irrigation and rain. The two main periods identified within
20 the study season corresponded to the early season, characterised by more
21 variable S_n and water availability due to irrigation, rain and active diurnal and
22 nocturnal water uptake. This period corresponds to the phenological stage of
23 pit hardening and nut development followed by hull splitting in almond trees in
24 the region. Two other factors might have contributed to reductions in S_n for
25 both treatments: i) a heavy rain event and strong winds on the 2nd of February

1 2010 (Figure 1a), which coincided with the onset of leaf senescence, and ii)
2 incidence of leaf rust (*Tranzschelia discolor*) in that season following the
3 rain. The combined effect of phenological stage of trees and the latter effects
4 could explain the apparent non-responsiveness of S_n to higher water
5 availability by irrigation and rain for the late season period. Higher soil
6 moisture (close to field capacity) and low water uptake by trees from both
7 treatments demonstrates that there were over irrigations in the late season
8 period. Therefore, the use of Kc for this period did not accurately reflect plant
9 water use.

10 Furthermore, S_n trends inversely responded to Ψ_{PDsoil} for the early season
11 period, as shown in Figure 1b. Therefore, S_n is directly correlated to soil water
12 availability, which is consistent with data presented in Fig 3a for the first
13 section of the parabolic curve. Higher S_n values for both treatments were
14 associated with more negative Ψ_{PDsoil} and *vice versa* and were associated to
15 higher Ψ_s values at midday. The Ψ_{PDsoil} for T100 showed that trees on this
16 irrigation treatment were maintained without water stress after irrigation
17 events ($\Psi_{PDsoil} > -0.5$) (Romero et al., 2004). By contrast, T₆₀ was maintained
18 below this threshold for the early season period.

19

20

1 *Similar proportions of S_n over S_d found for T_{100} and T_{60}*

2 The normalised S_n/S_d proportion for both treatments corresponded to 15 to
3 25% (Figure 2), which falls in the lower range reported for trees in semi-arid
4 regions (Snyder et al., 2003). A recent work found values of 6-8% on average
5 for the season, with maximum values of 19% for a woodland area located in
6 Richmond NSW (Temperate climate), which was ascribed mainly to E_n
7 (Zeppel et al., 2010).

8

9 *Night-time parabolic relationship between S_n and midday Ψ_S*

10 Semi-parabolic relationships found for T_{100} (Figure 3a) can be explained by
11 the lack of stress in this treatment ($0 < \Psi_S < -1.2$ MPa) in all measurement
12 dates (Table 3), which corresponded to the early season period analysed.
13 Therefore, there is not sufficient data for T_{100} to characterise the S_n behaviour
14 for lower Ψ_S values. However, in preliminary data obtained in different
15 grapevine varieties under initial no water-stress situations, followed by
16 progressively greater water stress (Fuentes et al, unpublished) a complete
17 parabolic relationship was found.

18 From the full parabolic relationship found in T_{60} , two stages were identified.
19 The first section was characterised by higher Ψ_S values (closer to zero), which
20 corresponded to high water availability in the soil for both treatments for the
21 corresponding measurement days (Table 3; Figure 1b), and low atmospheric
22 demand at night-time for these dates (data not shown). Once that soil
23 moisture started to deplete, S_n increased up to a maximum (peak) value,
24 which corresponded to mild water stress values of Ψ_S for almond trees
25 (Nortes et al., 2005; Shackel, 1995). This S_n water flux may be associated

1 with increased E_n and rehydration at night-time. The second stage of the
 2 parabolic curve was characterised by Ψ_s values in the range associated with
 3 moderate to severe water stress in trees (Nortes et al., 2005; Shackel, 1995).
 4 The S_n versus Ψ_s relationship was uncoupled for T_{100} and T_{60} , as can be seen
 5 in Figure 3a, and through residual analysis. However, the main contributor to
 6 this decoupling between irrigation treatments is the NE (sunny side) of the T_{60}
 7 treatment (Figure 3b). For stage 1 of the parabolic curves, there were no
 8 statistically significant differences between T_{100} and $T_{60}SW$. This evidence
 9 supports the idea that the NE side of trees were submitted to higher stress
 10 compared to the SW side, the latter behaving at night-time as the T_{100}
 11 treatment during stage 1 of the parabolic curves. Furthermore, it is a clear
 12 indication that single sap flow probes installed on large trees are not sufficient
 13 to assess accurately whole tree water uptake for both daytime (Figure 5b) and
 14 night-time (Figure 3b) flows, specially under mild to moderate water stress
 15 conditions.
 16 The relationship between S_n and Ψ_s for higher Ψ_s values (first part of
 17 parabola) might reflect the sensitivity of nocturnal stomatal conductance
 18 (g_{night}) to decreased soil water availability for stage 1 of the parabolic
 19 relationship, which is expected to be more evident during day-time, as shown
 20 in Figure 5a and 5b, where T_{60} reduced daily maximum transpiration rate
 21 down to 32% of that recorded in T_{100} . Similar results were found for
 22 grapevines cv. Shiraz in Australia (Collins et al., 2009) and seven grapevine
 23 varieties in Mallorca (Spain) (Escalona et al., 2012). Figure 5b shows that
 24 significant differences were also found for day-time data between $T_{60}SW$ and
 25 $T_{60}NE$, following the same pattern as night-time data for the measurement

1 days (Table 3).

2 Split root system experiments in tomato plants have demonstrated that under
3 reduced water supply, ABA was also produced in leaves (Dodd, 2007; Dodd
4 et al., 2008a; Dodd et al., 2008b). Furthermore, it is expected that the sunny
5 side (NE) of trees under high VPD conditions will have a higher leaf synthesis
6 of ABA (Davies et al., 2002; Wilkinson and Davies, 2002; Zhang and Zhang,
7 1994). Therefore, reduced water application and high sun exposure to a
8 reduced leaf area index (from LAI in $T_{100} = 2.24^a$ to LAI in $T_{60} = 1.89^b$; $P <$
9 0.05) for T_{60} NE side of trees could explain reduced S_{md} and S_n for T_{60}
10 compared to T_{100} . According to these results, is possible that T_{100} will be more
11 affected by disequilibrium between pre dawn water potential and soil water
12 content due to higher S_n , which may be associated to higher E_{night} compared
13 to T_{60} .

14

1 *Night-time atmospheric demand (VPD) as main driver of S_n*

2 Nocturnal sap flow (S_n) has been shown to contribute towards both nocturnal
3 rehydration and E_n (Snyder et al., 2003; Zeppel et al., 2010). Even though in
4 this study we cannot possibly discriminate between night-time rehydration and
5 E_n from S_n data, high correlations found between S_n and night-time VPD
6 (Figure 4a and 4b) for the early season period analysed suggest that E_n could
7 be the main component of this balance. This higher proportion of E_n and high
8 correlations with VPD has been previously showed for other tree species
9 (Daley and Phillips, 2006; Kavanagh et al., 2007; Oren et al., 1999; Phillips et
10 al., 2010; Zeppel et al., 2010), kiwifruits (Green et al., 1989) and grapevines
11 (Fuentes et al., unpublished). A third component to account for in the S_n
12 balance is cuticular transpiration (C_n). However, it has been demonstrated
13 that this component is minimal compared to E_n and rehydration for trees
14 (Zeppel et al., 2010) and grapevines (Flexas et al., 2002a).

15 According to Figure 1a, S_n for both treatments increased as water availability
16 within the rootzone increased. Since there were high and significant
17 correlations between S_n and VPD at night-time, it can be said that the same
18 dynamics are expected for E_n . This is supported by observations of other tree
19 species (Donovan et al., 2003; Zeppel et al., 2010)

20

21 *Night-time recovery capacity of trees from water stress endured the previous*
22 *day*

23 Pre-dawn water potential (Ψ_{PD}) has been commonly used in almond trees to
24 assess tree water status (Stevens et al., 2012). This has been based on the
25 assumption that at night-time (pre-dawn) the Ψ_{PD} will equilibrate with that of

1 the soil at zero-flow. However, there is evidence that this equilibrium is not
 2 met at night-time for a number of species, especially when trickle irrigation is
 3 used, which increases heterogeneity of wetting patterns within the rootzone
 4 (Bucci et al., 2005; Bucci et al., 2004; Donovan et al., 1999; Donovan et al.,
 5 2003; Donovan et al., 2001; Egea et al., 2011; Kavanagh et al., 2007; Sellin,
 6 1999; Zeppel et al., 2010). By suggesting that an important proportion of S_n
 7 corresponds to E_n , it is clear that the above assumption is not valid for our
 8 study in almond trees. Furthermore, the proportion of S_n/S_d demonstrated a
 9 wide range, reaching values up to 25%, with an associated maximum value of
 10 $S_d = 62.4 \text{ L tree}^{-1} \text{ day}^{-1}$ and $S_d = 48.5 \text{ L tree}^{-1} \text{ day}^{-1}$ for T_{100} and T_{60}
 11 respectively, indicating for the latter case that more likely there is
 12 disequilibrium of Ψ_{PD} is large in these situations. These large S_n/S_d
 13 proportions may be used to more accurately estimate root surface water
 14 potentials and whole-tree hydraulic conductance (Zeppel et al., 2010). This
 15 disequilibrium also can be expected in the first stage, closer to the peak of the
 16 parabolic relationships between S_n and Ψ_{PD} according to data presented from
 17 the early season stage, which suggest that higher S_n , associated with higher
 18 E_{night} is the main driver for higher S_n/S_d . Furthermore, the second stage found
 19 in the parabolic relationships between S_n and Ψ_{PD} is associated to lower
 20 capacity of trees to recover from stresses endured the day before, especially
 21 in T_{60} . The difficulties in recovery in stage 2 are also associated with reduced
 22 water availability in the soil, reduced tree hydraulic conductivity and shorter
 23 time period for recovery at night-time (summer period with shorter nights).

CONCLUSIONS

Our study found that the proportion S_n/S_d can reach values up to 25% for different irrigation treatments, and that E_n might account for a large proportion of S_n throughout the period of study. Differences in sap flow on different sides of the tree (exposed to sun and shade) are more evident in reduced water application treatments compared to control treatments. This effect needs to be taken into account when measuring S_d and S_n using sap flow probes, by installing at least two sets of probes per tree.

Two stages were apparent in the parabolic relationship between S_n and midday Ψ_s . The results obtained in this study helped to support the hypothesis that stage 1 is characterised by the predominance of E_n over rehydration due to more soil moisture availability and in stage 2 E_n could be reduced due to reduced soil moisture available and less capacity to recover by the plant. Further research is required to separate the components of plant water uptake (rehydration, E_n and E_c) to assess whether rehydration is maintained under mild to moderate water stress. This study supports the idea of developing this method further as a potential monitoring tool of the recovery capacity of plants from water stress.

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TABLES

Table 1: Monthly average weather conditions at the experimental site during the early season period separated by day and night.

Month	Temperature (°C)		Relative humidity (%)		Wind speed (m s ⁻¹)		Rainfall (mm)
	Day	Night	Day	Night	Day	Night	Total
December 2009	26	19	37	54	3.06	1.94	25
January 2010	28	21	31	48	2.78	2.22	10
February 2010	28	22	41	56	2.50	1.94	21

Table 2: Soil texture, organic matter and salinity at different depths for the experimental site.

Treatment	Soil depth (cm)	Soil texture		Organic Matter (%) Wt	Salinity dS m ⁻¹
		Sand (%)	Clay (%)		
T ₁₀₀	30	90.2	9.8	0.50	2.02
	60	89.2	6.31	0.53	1.79
	90	87.2	6.10	0.17	1.26
	150	28.1	57.0	0.15	0.73
T ₆₀	30	92.1	5.9	0.69	2.41
	60	88.4	9.7	0.37	2.30
	90	90.2	9.8	0.16	1.50
	150	88.3	11.7	0.16	1.23

Table 3: Measurement dates for leaf (Ψ_L) and stem (Ψ_S) water potentials performed in both treatments (T_{100} and T_{60}), showing average values obtained for each date corresponding to the early season.

Date	Day of the year (DOI)	$T_{100} (\Psi_S; \Psi_L)$ MPa	$T_{60} (\Psi_S; \Psi_L)$ MPa
1/12/2009	335	-0.94; -1.42	-1.04; -1.73
9/12/2009	343	-0.62; -1.06	-0.74; 1.26
22/12/2009	356	-1.13; -1.88	-1.38; 2.15
29/12/2009	363	-1.25; -2.10	-2.00; -2.21
6/01/2010	6	-1.11; -1.59	-1.21; -1.89
13/01/2010	13	-0.76; -1.38	-0.81; -1.17
20/01/2010	20	-1.17; -1.96	-1.61; -2.19
27/01/2010	27	-0.82; -1.52	-0.97; -1.55

Table 4: Comparison between total water applied for the whole studied season (TWA, includes irrigation and rain), irrigation only (I), diurnal sap flow (S_d), night-time sap flow (S_n) and water use efficiency (WUE) calculated by dividing total yield per treatment (data not shown) by total water applied.

Treatment	TWA ML ha⁻¹	I ML ha⁻¹	S_d ML ha⁻¹	S_n ML ha⁻¹	WUE kg ML⁻¹
T ₁₀₀	10.97	9.53	4.98	1.00	293
T ₆₀	7.26	5.82	4.02	0.80	374

Table 5: Statistical analysis of correlations and equations obtained for the relationships between S_n (L tree⁻¹ night⁻¹); S_{md} (L tree⁻¹) and Ψ_s (MPa) for irrigation treatments and sap flow sensors orientation for the early season period.

Treatment	Quadratic Equation ($S_n =$) Quadratic Equation ($S_{md} =$)	SEE	R ²	RMSE	Peak (Ψ_s ; S_n) (Ψ_s ; S_{md})	Zero-flow night Zero-flow day (MPa)
T ₁₀₀	$-34.9 * \Psi_s^2 - 93.05 * \Psi_s - 21.67$	27.3	0.90 [*]	2.61	-1.34; 40.33	-2.65 ^{ns} ; -0.26 ^{**}
	$-135.3 * \Psi_s^2 + 307.62 * \Psi_s - 52.14$	39.1	0.96 [*]	4.42	-1.14; 122.7	-2.09 ^{ns} ; -0.22 ^{**}
T ₆₀	$-24.53 * \Psi_s^2 - 72.52 * \Psi_s - 20.3$	29.2	0.85 [*]	2.70	-1.48; 33.30	-2.64 [*] ; -0.31 ^{**}
	$-30.4 * \Psi_s^2 + 103.29 * \Psi_s + 0.46$	170	0.82 [*]	5.83	-1.70; 88.20	-3.95 ^{ns} ; -0.37 ^{**}
T ₁₀₀ NE	$-30.9 * \Psi_s^2 - 83.76 * \Psi_s - 16.97$	42.7	0.84 [*]	3.27	-1.34; 39.78	-2.50 ^{ns} ; -0.22 ^{**}
	$-191.4 * \Psi_s^2 + 413.6 * \Psi_s - 94$	15.8	0.98 [*]	2.81	-1.08; 129.4	-1.90 ^{ns} ; -0.26 ^{**}
T ₁₀₀ SW	$-38.95 * \Psi_s^2 - 102.4 * \Psi_s - 26.4$	34.3	0.89 [*]	2.90	-1.32; 40.90	-2.34 ^{ns} ; -0.29 ^{**}
	$-135.3 * \Psi_s^2 + 307.62 * \Psi_s - 52.1$	39.13	0.96 [*]	4.42	-1.14; 122.8	-2.09 [*] ; -0.18 ^{**}
T ₆₀ NE	$-20.3 * \Psi_s^2 - 59.39 * \Psi_s - 15.68$	34.3	0.89 [*]	2.90	-1.46; 27.67	-2.63 [*] ; -0.29 ^{**}
	$-14.9 * \Psi_s^2 + 52.17 * \Psi_s + 28.5$	63.5	0.80 [*]	3.25	-1.76; 74.16	-3.98 ^{ns} ; -0.48 ^{**}
T ₆₀ SW	$-28.7 * \Psi_s^2 - 85.70 * \Psi_s - 24.96$	41.6	0.85 [*]	3.23	-1.50; 38.95	-2.66 [*] ; -0.33 ^{**}
	$-22.7 * \Psi_s^2 + 83.8 * \Psi_s + 22.45$	7.22	0.80 [*]	1.10	-1.89; 99.79	-3.94 [*] ; -0.25 ^{**}

* Correlations are statistically significant at $P < 0.05$

** Zero-flow values were within 95% confidence bounds

^{ns} non-significant.

Table 6: Statistical analysis of correlations and equations obtained for the relationship between S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) and night-time VPD (kPa) for the irrigation treatments during two periods; December-January (early season) and February-March (late season).

Period	Treatment	Equation ($S_n =$)	SEE	R^2	RMSE
1	T_{100}	$14.22 * \text{VPD} + 20.93$	600	0.89^*	3.22
	T_{60}	$10.39 * \text{VPD} + 15.80$	381	0.87^*	2.56
2	T_{100}	$10.11 * \text{VPD} + 7.41$	1130	0.68^*	2.82
	T_{60}	$6.22 * \text{VPD} + 7.81$	417	0.69^*	1.71

*Correlations are statistically significant at $P < 0.05$;

Table 7: Statistical analysis of correlations and equations obtained for the relationships between S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) and Ψ_s (MPa) for irrigation treatments, and sap flow sensor orientation for T_{60} . Linear equations from non water-stressed Ψ_s (MPa) values were used to obtain the diurnal and nocturnal behaviour in non-stressed situations for the early season.

Treatment	Linear Equation night ($S_n =$)	SEE	R^2	RMSE
	Linear Equation day ($S_{md} =$)			
T_{100}	$-27.33 * \Psi_s^2 + 7.65$	38.7	0.86*	2.78
	$57.5 * \Psi_s^2 + 56.2$	208	0.78*	8.33
T_{60}	$-21.40 * \Psi_s + 5.10$	38.5	0.78*	3.58
	$23.62 * \Psi_s + 49.98$	52.2	0.88*	2.95
$T_{60} \text{ NE}$	$-11.8 * \Psi_s + 9.1$	25.5	0.71*	2.91
	$16.4 * \Psi_s + 48.5$	88.5	0.67*	3.84
$T_{60} \text{ SW}$	$-25.95 * \Psi_s + 4.70$	53.9	0.78*	4.24
	$30.8 * \Psi_s + 51.4$	36.9	0.95*	2.48

*Correlations are statistically significant at $P < 0.05$.

FIGURES

Figure 1: (a) Night-time dynamics of S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) for T_{100} (black filled circles) and T_{60} (open circles) in response to water application (rain and irrigation in $m^3 \text{ tree}^{-1} \text{ day}^{-1}$) for an almond tree plantation (season 2009-10). Arrows indicate rain events; the length of the arrow is proportional to effective rain in $L \text{ tree}^{-1}$ associated with the S_n scale. (b) Night-time dynamics of S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) for T_{100} (black filled circles) and T_{60} (open circles) in relation to $\Psi_{PD\text{soil}}$ (MPa).

Figure 2: Relationship between the normalised S_n/S_d proportion ($N S_n/S_d$) for T_{100} compared to T_{60} for the early season (black filled circles) and late season (grey filled circles).

Figure 3: (a) Parabolic relationships between midday Ψ_s (MPa) and S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) for T_{100} (black filled circles) and T_{60} (grey filled circles) for measurement days throughout the early season. Residual analysis was performed to assess decoupling of treatments. (b) Parabolic relationships between midday Ψ_s (MPa) and S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) by positioning of the probes within T_{100} and T_{60} . Residual analysis was performed to assess decoupling of treatments and location of probes.

Figure 4: Relationship between night-time VPD (kPa) and S_n ($L \text{ tree}^{-1} \text{ night}^{-1}$) for T_{100} (black circles) and T_{60} (grey filled circles) for the early season period

(a); and the late season period (b). Residual analysis was performed to assess decoupling of treatments.

Figure 5: Parabolic relationships found between sap flow data measured from 5 AM until 2 PM (S_{md} in $L\ tree^{-1}$) and midday Ψ_s (MPa) for $T_{100}NE$; $T_{100}SW$ (black filled symbols) and $T_{60}NE$; $T_{60}SW$ (grey filled circles). Residual analysis was performed to assess decoupling of treatments (insets a and b).

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Fig. 1a

Fig 1b

Fig. 2

Fig. 3a

Fig. 3b

Fig 4a

Fig 4b

Fig 5

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