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Stem water potential, stomatal conductance and yield in irrigated apple trees

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Abstract: Plant-based indicators of water status, such as midday stem water potential (Ψ_{stem}) and leaf stomatal conductance (g_s), are used to optimise irrigation scheduling in horticultural crops because they integrate the effect of soil and climatic conditions and the internal physiological constraints. The use of these indicators relies on experimentally acquired thresholds that relate the value of the indicator to negative effects on yield. In five irrigation treatments, we monitored yield, fruit size and the courses of Ψ_{stem} and g_s throughout four consecutive growing seasons. We found that Ψ_{stem} was more sensitive to irrigation treatment than g_s. Both indicators increased with available soil water content (ASWC) and decreased with evaporative demands of the atmosphere (ET_C). On a seasonal basis, crop load had a stronger impact on g_s than Ψ_{stem}. In summary, our study explored the effect of environmental conditions and crop load on plant-based indicators of tree water status and can be useful for establishing thresholds for irrigation scheduling in apple tree orchards.

Keywords: drought; water dynamic; fruit trees; gas exchange; deficit; abiotic stress

In many arid and semi-arid regions, the sustainable yield of horticultural crops largely depends on irrigation water. Yet, irrigation is becoming an important agricultural practice even in temperate regions due to ongoing climate change (Cancela et al. 2006). Irrigation scheduling has been traditionally based on the estimation of orchard water balance from measured climatic conditions and estimated crop coefficients (Allen et al. 1998, Allen and Pereira 2009) or on soil moisture-based criteria (Campbell et al. 1982, Hanson et al. 2000). However, these approaches have limitations as they do not account for the spatial and temporal heterogeneity which is common under field conditions. For instance, soil moisture measured by point sensors does not capture well the complex soil water dynamics within the tree's rooting zone (Dodd 2007, Bauerle et al. 2008). In addition, there are inherent physiological differences in water use between crop species and cultivars (Levin et al. 2020, Plavcová et al. 2023). Therefore, plant-based indicators that utilise plants as biosensors of water deficit appear as promising tools for more efficient irrigation scheduling (Jones 2004, Fernández 2017).

Several plant-based indicators have been identified as useful descriptors of plant water status. Among them, midday stems water potential (Ψ_{stem}) measured with a Scholander-type pressure chamber is arguably the most widely used plant-based water status indicator (Naor et al. 1995, Shackel et al. 1997), although its measurements are labour intense and restricted to discrete sampling dates. Ψ_{stem} responds dynamically

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to changing soil and atmospheric conditions and integrates the effect of plant water uptake, transport and loss. Values of Ψ_{stem} provide a useful indication of the level of drought stress experienced by the plant and should be related to hydraulic thresholds such as turgor loss point or the onset of run-away xylem cavitation (Meinzer et al. 2009, Plavcová et al. 2023).

Stomatal conductance (g_s) has also been suggested as a suitable plant-based indicator because stomatal closure belongs to the first response to water stress, at least in isohydric species. Apple trees, which are the focal tree species of this study, were considered as isohydric species with a stringent stomatal control (Lakso 1994, Lauri et al. 2016), although more recent study reported anizohydric behaviour and very narrow hydraulic safety margins in young high-yield apple trees (Beikircher et al. 2013). While stomata close in response to low soil water and high vapour pressure deficit (Fernández et al. 2011, Ahumada-Orellana et al. 2019), stomatal conductance was found to be a less sensitive water status indicator than Ψ_{stem} and maximal diurnal trunk shrinkage (MDS) in apple trees (Doltra et al. 2007).

In horticultural crops, tree water use is also strongly affected by crop load, with higher yield being associated with greater water demands (Wünsche et al. 2000, Naor et al. 2008). Therefore, trees with higher crop loads typically have lower water potential values (Naor et al. 2008), although leaf water potential was not affected by crop load in adult lemon trees (Ortuño et al. 2009). The explanation for the lower water potential values in heavily cropping trees is sought in their higher leaf gas exchange rates because ample fruits cause high demands for assimilates (Wünsche et al. 2000).

This study aimed to evaluate the effect of five irrigation treatments on fruit yield and size calibre and relate these yield parameters to midday stem water potential and leaf gas exchange during four consecutive years. We expected that non-irrigated trees will bear less fruits and/or smaller fruits compared to the irrigated ones. We also expected Ψ_{stem} and g_s to be lower in non-irrigated than irrigated trees. By linking yield parameters with plant-based indicators of water stress, we will be able to refine irrigation scheduling in apple orchards and, by extension, utilise limited water irrigation reservoirs more efficiently.

MATERIAL AND METHODS

Plant material. Apple trees (*Malus* × *domestica* Borkh.) cv. Red Jonaprince planted in 2013 at the experimental plots of Research and Breeding Institute of Pomology Holovousy Ltd., Czech Republic (15°34'48''E, 50°22'24''N) were used for the measurements. The scions were grafted on semi-dwarfing M9 rootstock and spaced 3.5 m between rows and 1.2 m between trees. The trees were trained as slender spindles combined with "Klik" pruning. The final height of the trees was 3.2 m. The measurements occurred during four consecutive growing seasons from 2019 to 2022. The orchard site experiences a temperate mild climate with a mean annual temperature of 8.4 °C and mean precipitation of 664 mm. The soil texture composition on the site was 22.2% clay, 69.1% silt and 8.7% sand based on laboratory analyses using Kopeckeho o-rings. Hence, the soil was classified as silty loam Luvisol soil of medium fertility according to WRB classification (IUSS Working Group WRB 2015). Based on the soil texture, soil water content at field capacity was established at 34.2 vol. %, and the permanent wilting point was at 15.9 vol. %. To regulate fruit set to optimal crop density, hand thinning at BBCH 72 (fruit diameter of 20 mm according to Meier 2001) was carried out with the aid of Equilifruit disc (Kon and Schupp 2013) for the cultivar Red Jonaprince the maintained number of fruit per branch cross-section area was estimated as $\delta + 1$, where δ is the recommended optimal bearing. The plant protection and fertilisation followed the rules of integrated fruit production. Herbicides were applied to maintain the row weed free. The inter rows were covered with grass and periodically mown.

Irrigation treatments. Five different irrigation treatments were applied to sectors consisting of 17 adjacent trees grown in five neighbouring north-south oriented rows. The sectors were not rotated during the four consecutive seasons of the experiment; hence, the effect of irrigation compounded over the four years. The trees were drip-irrigated with the dripline placed within the tree row at the height of 0.5 m above the soil surface. The drippers had a flow capacity of 2.3 L/h and were placed in 0.5 m spacing. Crop evapotranspiration was estimated according to the Penman-Monteith equation (Allen et al. 1998), with later updates by Allen and Pereira (2009). First, reference evapotranspiration (ET_0) was calculated using the Penman-Monteith equation. ET_0 was then multiplied by the crop coefficient that varied from 0.5 to 1.2 throughout the season, reflecting the canopy development. The calculation used micrometeorological data measured within the orchard at 2 m above ground. The measured micro-

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meteorological variables included air temperature (DS18B20, Dallas Semiconductor, Dallas, USA), air humidity (HIH-4000, Honeywell, Charlotte, USA), wind direction and speed (W2, Tlusťák, Prague, Czech Republic), solar radiation (SG002, Tlusťák, Prague, Czech Republic) and rainfall totals (Small Rain Gauge 100.053, Pronamic, Skjern, Denmark). The data were further validated against the official meteorological data by Czech Hydrometeorological Institute measured in the station situated 500 m from the orchard. The orchard data agreed well with the official meteorological data, and we used the orchard data for all our analyses. Soil moisture was measured within the root zone of the trees using three sensors (VIRRIB, Fiedler AMS, České Budějovice, Czech Republic) per plot placed in soil depths of 10, 30 and 60 cm. The VIRRIB sensors measure soil moisture based on soil electric conductivity. They were placed in the middle between two neighbouring trees in the row directly under the drip line, thus measuring the wetted soil volume. Measured soil volumetric water content was converted to the saturation proportion of available soil water content (ASWC) calculated as the difference in soil water content between the field capacity and the wilting point.

In total, five irrigation treatments were administered. These included ET-100, ET-50 and non-irrigated control ET-0, in which 100% or 50% or none of the estimated evapotranspiration was supplied after accounting for natural rainfall. These treatments applied irrigation during the whole growing season from 1st April to 30th September. The other two irrigation treatments were regulated deficit irrigation (RDI) RDI-50 and RDI-50a, in which 50% of the estimated evapotranspiration was replaced during the rapid phase of fruit growth (BBCH 72–77 according to Meier 2001), while full replacement of evapotranspiration was done outside of these phenological stages. RDI-50 had an optimal crop load as determined using a hand-thinning gauge (Equilifruit). In the RDI-50a treatment, the fruit load was regulated to 60% of the optimal crop load of the cultivar. Irrigation scheduling was based on soil moisture criterium, and the goal was to prevent ASWC to decline below 0.7 in fully irrigated ET-100 treatment. Thus, irrigation volumes and frequencies varied depending on soil moisture and were between 4 to 11 mm per dose applied 2–3 times per week during the dry periods.

Fruit yield and size calibre. For these measurements, 10 trees in each irrigation treatment with similar flowering intensity and growth vigour were selected at the beginning of the experiment in 2019 and used throughout the whole 4-year period. At the end of each growing season, fruits were manually picked, sorted and weighed using a portable scale with an accuracy of 0.01 kg. Total annual fruit yield (kg/tree), fruit count and fruit distribution within three size categories (small: < 65 mm, medium: 65–75 mm, large: > 75 mm) were determined.

Midday stems water potential. Midday stems water potential was measured on sunny days in 2-week intervals from June to September. The measurements were done on four tree individuals per irrigation treatment that were selected at the beginning of each growing season to have homogeneous flower density and hence expected bearing. For each tree, two fully expanded healthy leaves on the current year extension shoots that faced the sun were selected and covered with an aluminium bag to prevent transpiration. Ψ_{stem} was measured after at least 30 min of equilibration. The covered leaves were excised between 11:00–13:00 h and measured immediately using a portable Scholander pressure chamber (1505D-EXP, PMS Instrument Company, Albany, USA). We used the average calculated from the two measurements per tree for statistical analyses.

Leaf gas exchange. Leaf gas exchange parameters were measured on the same days, and trees were used for Ψ_{stem} measurements. The measurements were carried out during 11:00–13:00 h using a portable infra-red gas analyser (LI-6800P, Li-Cor Inc., Lincoln, USA). A healthy mature leaf was inserted into the measuring cuvette, and the leaf gas exchange reading was taken after reaching a steady state, which typically took 2–3 min. The irradiance was set to a constant of 1 800 μmol/m^2/s, close to the ambient irradiance on sunny days when the measurements were done and corresponded to light-saturated photosynthetic conditions. Reference CO_2 concentrations were 400 ppm, the flow rate was 300 μmol/s, and the fan speed was 10 000 rpm. The chamber's air temperature and relative air humidity were set to follow the ambient conditions. Matching of reference and sample infrared gas analysers was done after each measurement. Out of all measured leaf gas exchange parameters, leaf stomatal conductance was selected and used for analyses as it affects leaf water loss and leaf carbon gain.

Statistical analyses. The difference in flower density and yield was analysed by fitting linear regression models, which a one-way ANOVA followed up to test for the effect of irrigation treatment. Poisson regression models were fitted and followed with ANOVA-type

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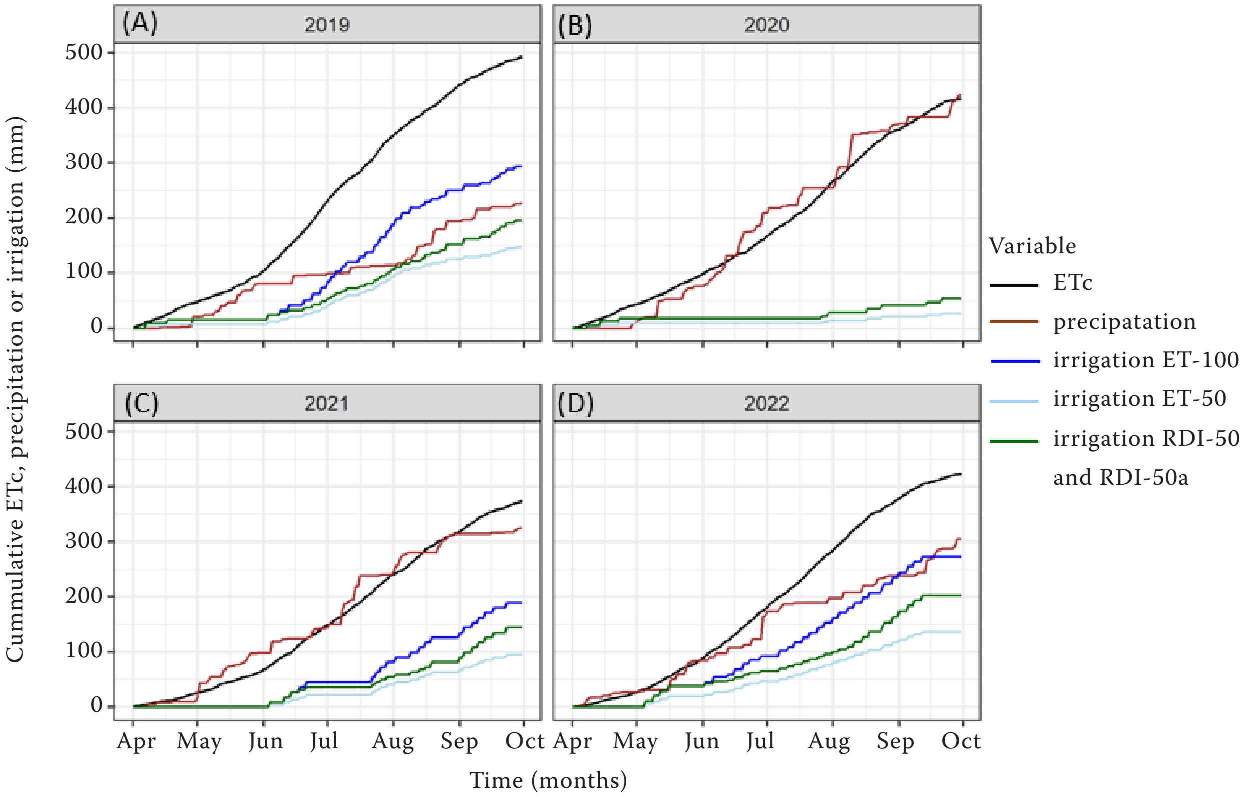

Figure 1. Cumulative reference evapotranspiration (ET_C), precipitation and irrigation in ET-100, ET-50, RDI-50 and RDI-50a treatments during four consecutive growing seasons. In 2020, the irrigation was the same for in RDI-50, RDI-50a and ET-100

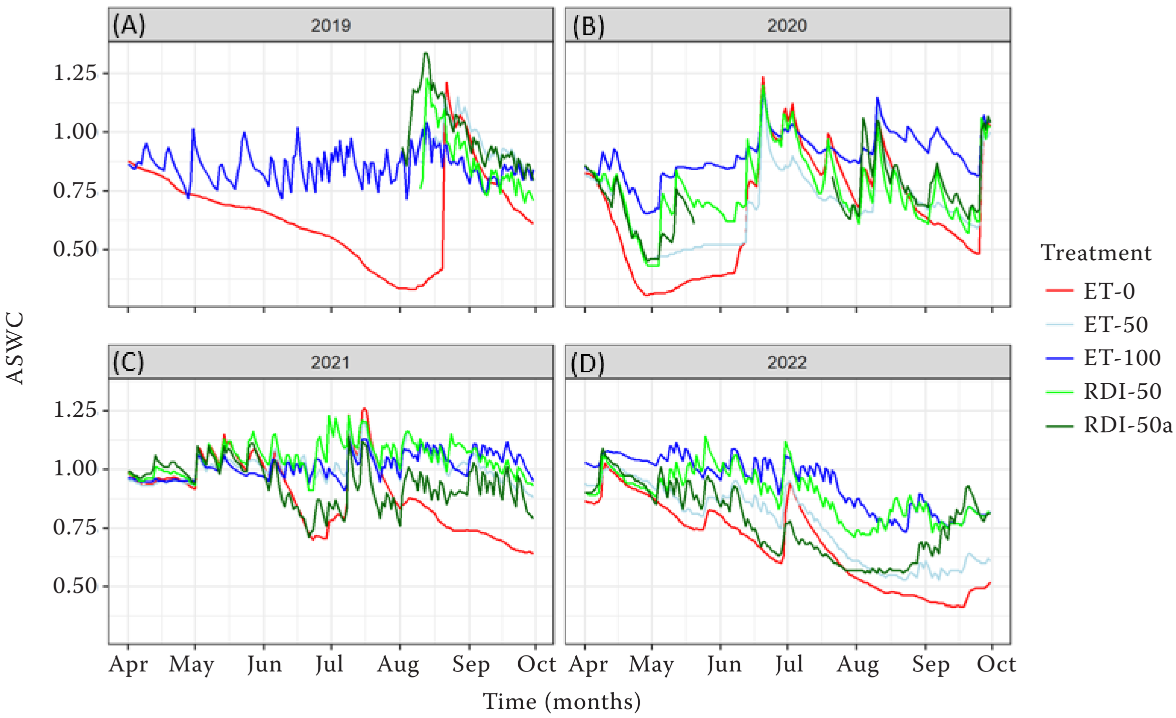

Figure 2. Available soil water content (ASWC) in four irrigation treatments (ET-50, ET-100, RDI-50, RDI-50a) and a non-irrigated control (ET-0) during four consecutive years

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λ^2-tests for the number of fruits in three size categories. Linear regression models with treatment and date as factors followed by ANOVA *F*-tests were used to analyse differences in Ψ_{stem} and g_s. The models were fitted separately for each of the four studied years. At each measuring date within the season, individual treatment means were separated from the non-irrigated control (ET-0) by pairwise contrasts using the means function from the means package (Lenth et al. 2019). Bonferroni correction was used to adjust the *P*-values for multiple comparisons. Simple linear regression assessed the relationship between Ψ_{stem}, g_s and climatic conditions and yield. All analyses were carried out using R (R Development Core Team 2010).

RESULTS

Microclimatic conditions. The year 2019 was the driest and hottest of the four studied years. Cumulative evapotranspiration reached 492 mm, while precipitation during May–September period was only 228 mm, with very little rain during the peak of vegetation season from June to August (Figure 1A). Hence, an irrigation water supplement of 294 mm was applied in fully irrigated treatment ET-100. In contrast, 2020 and 2021 were relatively wet, and precipitation was the main water input, with irrigation only 54 mm and 189 mm in fully irrigated treatment ET-100 in 2020 and 2021, respectively (Figure 1B, C). The year 2022 was relatively dry, with an exceptional rainfall event of more than 40 mm at the end of June. In total, 273 mm of irrigation water was applied in fully irrigated treatment (Figure 1D).

Available soil water content was generally the lowest in non-irrigated control ET-0, the highest in fully irrigated treatment ET-100, and medium in ET-50 and RDI treatments, although the measurements were variable in response to precipitation events (Figure 2).

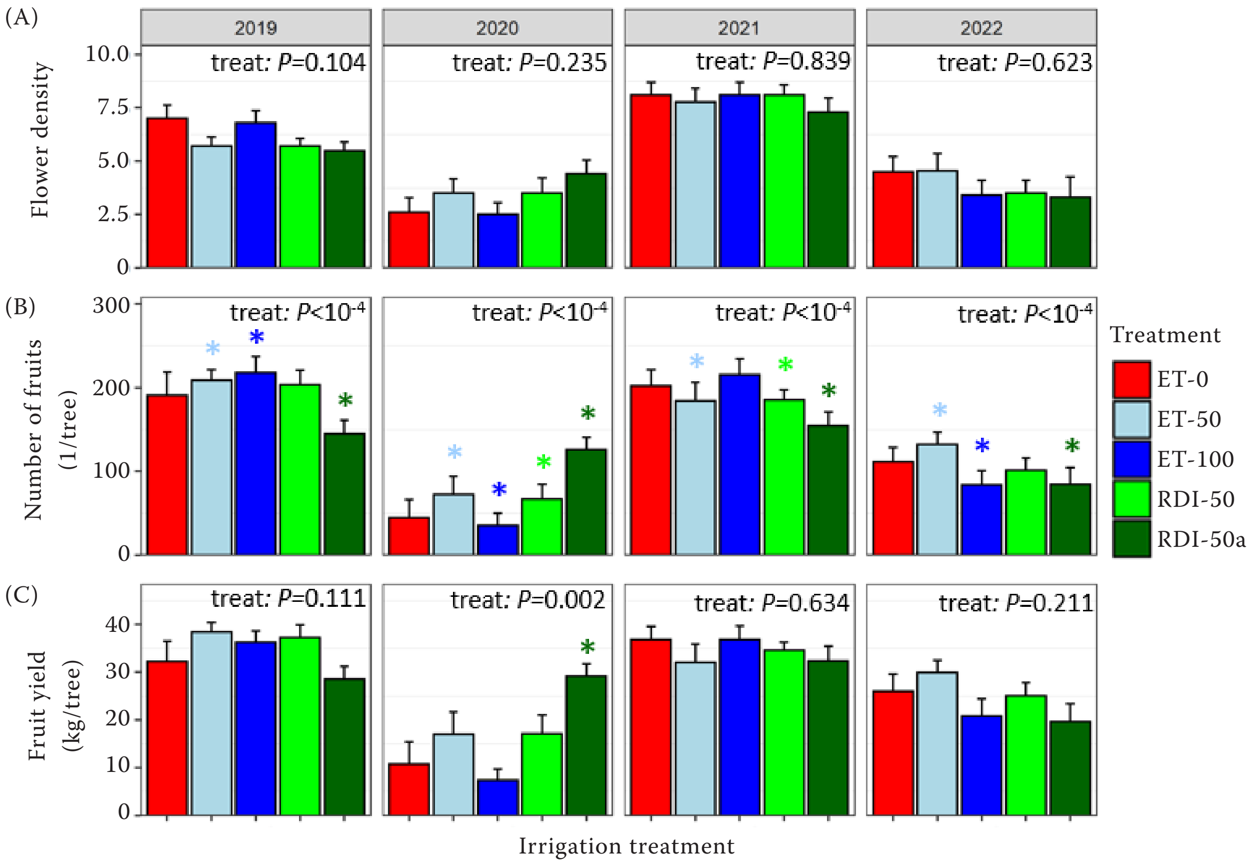

Figure 3. (A) Flower density; (B) number of fruits and (C) fruit yield of apple trees subjected to four irrigation treatments (ET-50, ET-100, RDI-50, RDI-50a) and a non-irrigated control (ET-0) during four consecutive years. The bars are means, and the error bars are standard errors (n = 10). *P*-values of ANOVA-type *F*-tests (flower density, yield) or λ^2-tests (number of fruits) are shown. Significant differences between individual treatments and ET-0 are indicated with an asterisk

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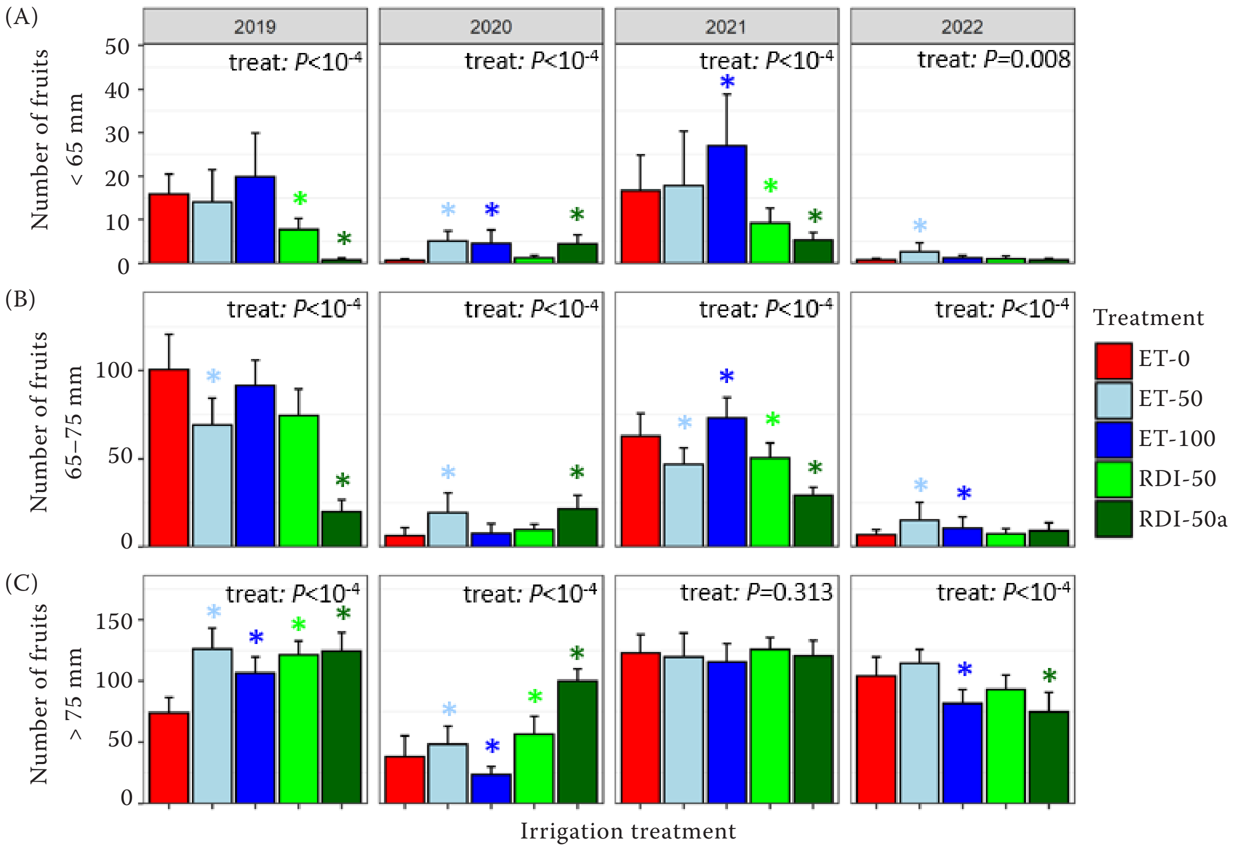

Figure 4. Number of fruits per tree in three size classes (smaller than 65 mm; between 65 and 75 mm; and larger than 75 mm) in apple trees subjected to four irrigation treatments (ET-50, ET-100, RDI-50, RDI-50a) and a non-irrigated control (ET-0) during four consecutive years. The bars are means, and the error bars are standard errors (n = 10). P-values of ANOVA-type λ^2-tests are shown. Significant differences between individual treatments and ET-0 are indicated with an asterisk

In 2020, the rather wet conditions during the period from June to August were evidenced by the small difference between ET-0 and ET-100 (Figure 2B). In contrast, the difference between these treatments was rather high during most of the seasons of 2019 and 2022 (Figure 2A, D) and parts of the season 2021 (Figure 2C). In 2021 and 2022, there was a notable divergence of values between RDI-50 and RDI-50a, irrigated in the same regime and with the same amount of water (Figure 2C, D).

Fruit yield. Flower density showed signs of alternate bearing behaviour, with 2019 and 2021 being years with high flowering, whereas 2020 and 2022 were years with low flowering (Figure 3A). The biennial pattern in flower density was also reflected in the number of fruits at harvest and annual fruit yield (Figure 3B, C). Within years, there were no statistically significant differences in flower density among the five irrigation treatments (Figure 3A). In contrast, there were statistically significant differences in the number of fruits among the five treatments, although there was no clear pattern of one irrigation treatment being consistently better or worse in each of the four studied years (Figure 3B). A notable pattern is the lack of alternate bearing in the irrigation treatment combined with the fruit thinning (RDI-50a), which is evident from a relatively high number of fruits and high fruit yield in 2020 (Figure 3B, C).

The distribution of fruits in three size classes was also quite variable among years and irrigation treatments (Figure 4). In low crop years (2020 and 2022), there was a low number of small fruits (< 65 mm) and a high number of large fruits (> 75 mm) per tree in all five irrigation treatments (Figure 4). The differences in fruit size due to irrigation treatment were variable, with no clear, consistent pattern across years. No clear pattern among treatments was observed either when the number of fruits in each size

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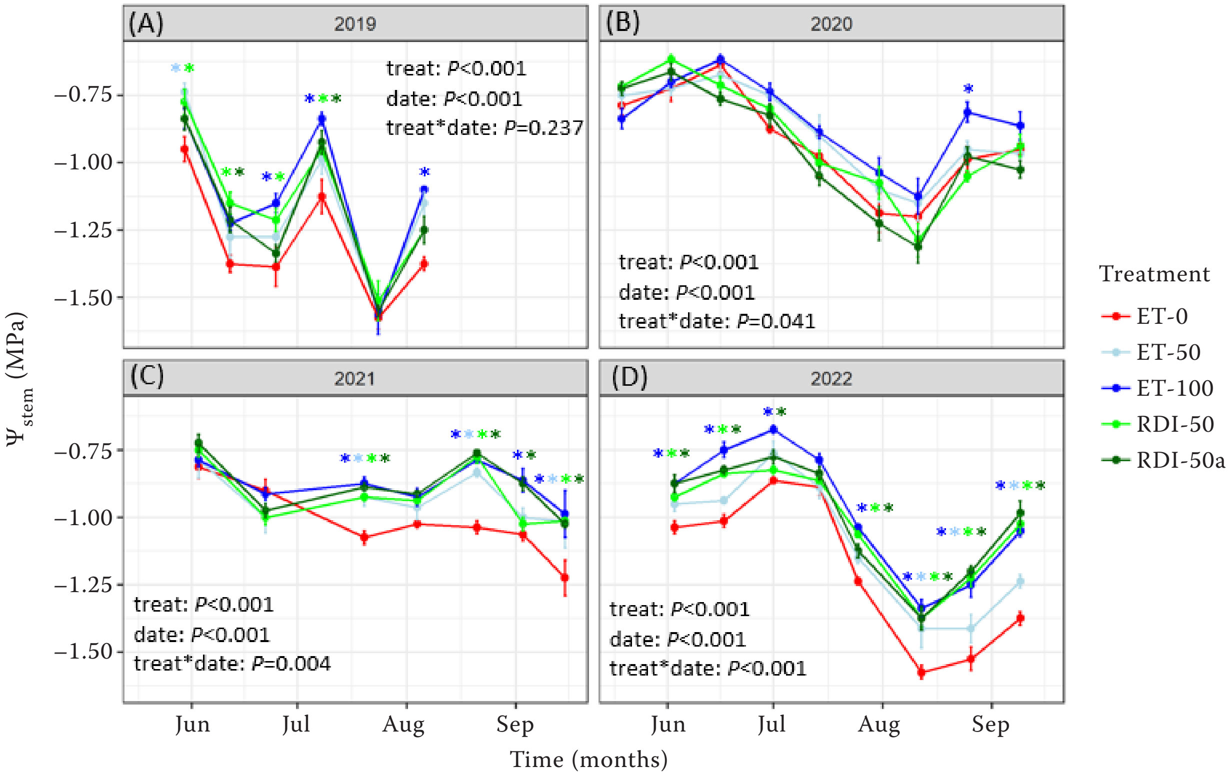

Figure 5. Seasonal course of midday stems water potential (Ψ_{stem}) in apple trees subjected to four irrigation treatments (ET-50, ET-100, RDI-50, RDI-50a) and a non-irrigated control (ET-0) during four consecutive years. The points are means, and the error bars are standard errors (n = 4). P-values of ANOVA-type F-tests are shown. Significantly different treatment *vs* control (ET-0) pairwise comparisons are indicated with an asterisk and colour-coded according to the treatment that was significantly different from the non-irrigated control (ET-0)

category was expressed as relative fractions of the total number of fruits (data not shown).

Midday stems water potential. The measured Ψ_{stem} values were between –0.6 and –1.7 MPa across dates and irrigation treatments (Figure 5). In three out of the four years of measurements, the non-irrigated control (ET-0) had significantly lower values of Ψ_{stem} than fully irrigated trees on most of the measured days (Figure 5). The difference in Ψ_{stem} between ET-0 and the fully irrigated treatment (ETC-100) was –0.32 MPa at the maximum and –0.16 MPa on average. The differences among treatments were the lowest in season 2020, which was also particular in that the RDI-50a treatment had the lowest Ψ_{stem} values out of all five treatments.

Leaf stomatal conductance. The g_s values ranged from 16.4 to 672.5 mmol/m^2/s across dates and irrigation treatments (Figure 6). There were no significant differences among treatments in seasons 2019 and 2021. In 2020, there was a clear pattern of higher g_s in RDI-50a treatment, with the difference being the highest in the middle of the growing season. In 2022, the fully irrigated treatment (ET-100) had slightly higher values of g_s compared to the non-irrigated control (ET-0). This difference was the highest at the end of the growing season.

Relationships between physiological parameters, microclimatic parameters and fruit yield. Both physiological parameters, Ψ_{stem} and g_s, were significantly and positively related to ASWC across all measured days (Figure 7A, C). R^2 was 0.125 for the ASWC *vs* Ψ_{stem} relationship and 0.061 for the ASWC *vs* g_s. In contrast, both physiological parameters were significantly negatively related to daily crop evapotranspiration (ET_C) across all measured days, with the R^2 being 0.341 for ET_C *vs* Ψ_{stem} and 0.106 for ET_C *vs* g_s relationship (Figure 7B, D). There was a significant negative relationship between minimal seasonal Ψ_{stem} and annual fruit yield when excluding 2021 (Figure 8A), implying that more negative Ψ_{stem} was associated with a higher fruit yield (R^2 = 0.734). There was also a significant positive association

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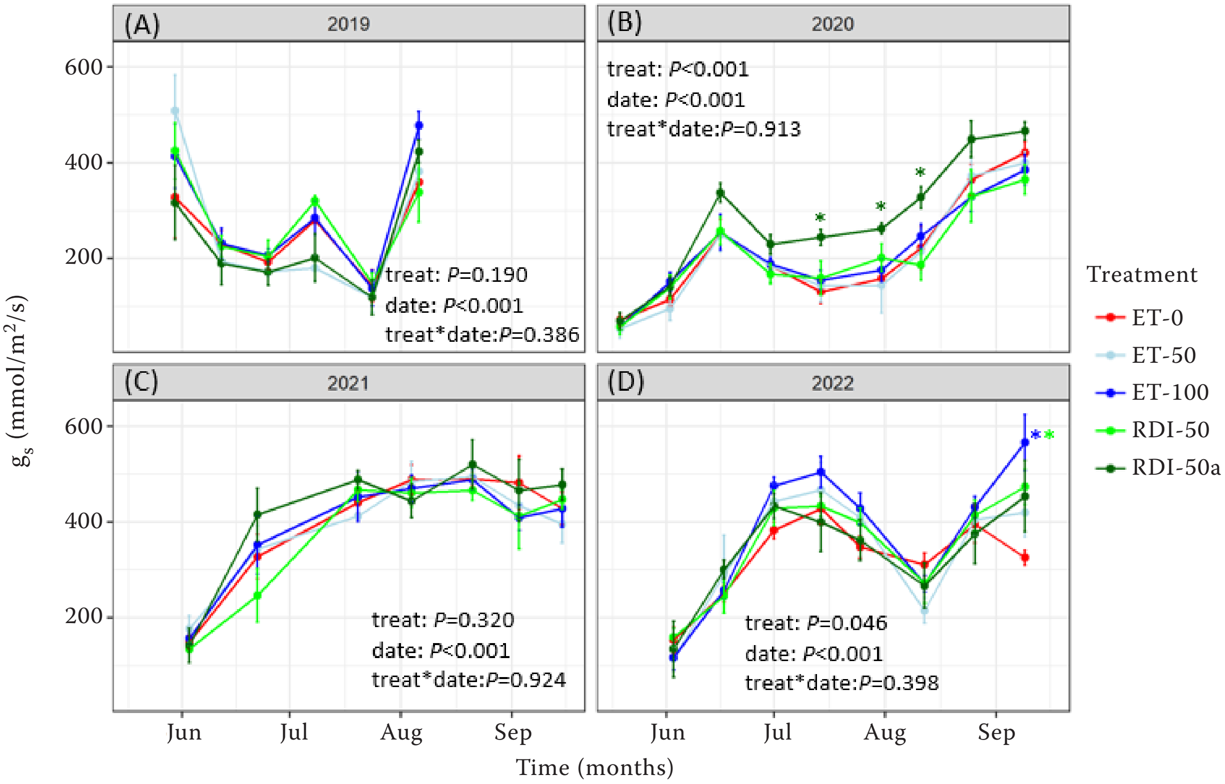

Figure 6. Seasonal course of leaf stomatal conductance (g_s) in apple trees subjected to four irrigation treatments (ET-50, ET-100, RDI-50, RDI-50a) and a non-irrigated control (ET-0) during four consecutive years. The points are means, and the error bars are standard errors (n = 4). P-values of ANOVA-type F-tests are shown. Significantly different treatment *vs* control (ET-0) pairwise comparisons are indicated with an asterisk and colour-coded according to the treatment that was significantly different from the non-irrigated control (ET-0)

between minimal seasonal g_s and annual fruit yield, with R^2 being 0.678 (Figure 8B).

DISCUSSION

This study monitored fruit yield, midday stem water potential and stomatal conductance for four consecutive years in apple trees cv. Red Jonaprince was subjected to five irrigation treatments (Figures 1 and 2). Despite the significantly lower Ψ_{stem} in non-irrigated trees throughout most of the growing seasons, there was neither a reduction in the overall fruit yield (Figure 3) nor a consistently significant effect on fruit size (Figure 4). These results suggest that the yield parameters of cv. Red Jonaprince apple trees were robust against cumulative but mild drought stress. Our results contrast with some other studies that found a significant fruit size reduction in apple trees that received no or low irrigation (Naor et al. 1995, 2008, Robinson et al. 2019). In our study, yield parameters were more affected by the intrinsic interannual variation expressed as alternate bearing behaviour in a biennial cycle. Thus, producing small fruits was associated with higher crop loads during "on" years rather than reduced soil water availability.

Irrigation resulted in less negative values of midday stem water potential compared to non-irrigated trees (Figure 5). The mean observed difference in Ψ_{stem} between fully irrigated and non-irrigated trees of 0.16 MPa was not large but sustained in three out of four growing seasons monitored (i.e., in 2019, 2021, 2022). Similar values of Ψ_{stem} and similar differences between irrigated and non-irrigated treatments were reported for apple trees grown in North East Spain (Doltra et al. 2007) and in the Golan Heights in Israel (Naor et al. 1995), which are both characterised by much drier climate compared to our study site. The seasonal minima of Ψ_{stem} ranged from –1.0 to –1.6 MPa, which can be considered no or mild drought stress (De Swaef et al. 2009, Robinson et al. 2019). Our observation that non-irrigated trees experienced only mild drought stress agrees with the non-significant effect on yield components.

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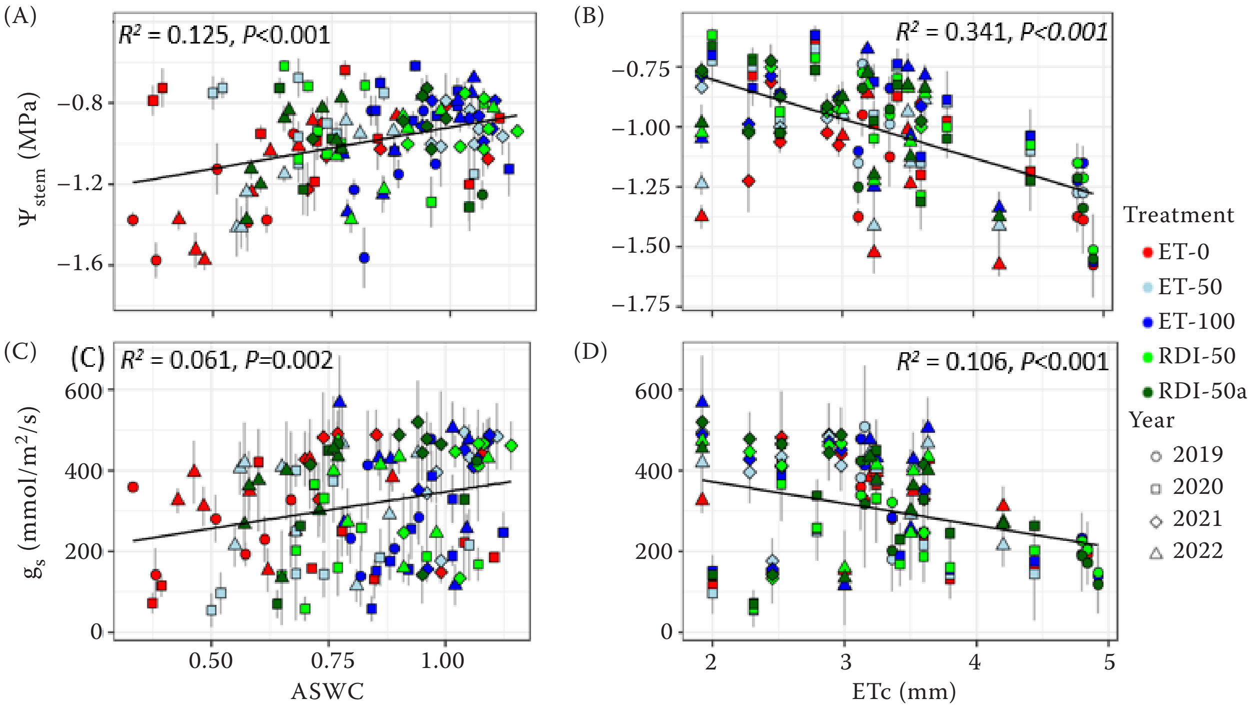

Figure 7. Relationship between (A) available soil water content (ASWC) and midday stem water potential (Ψ_{stem}); (B) crop evapotranspiration (ET_C) and Ψ_{stem}; (C) ASWC and leaf stomatal conductance (g_s); (D) ETC and g_s across all measuring dates and irrigation treatments. The points represent irrigation treatment means per each date, and the error bars represent standard error (SE). n = 4 for Ψ_{stem} and g_s. The lines are linear regressions to the data. Corresponding R^2 and P-values are provided. n = 129 for ASWC; n = 150 for ET_C

Leaf stomatal conductance did not differ much among the irrigation treatments, with the exception of a clearly higher g_s in RDI-50a treatment in season 2020 (Figure 6). The higher values of g_s in RDI-50a can be linked with its higher crop load compared with the other four treatments. Due to fruit thinning in RDI-50a, the trees did not over-cropped in 2019 and did not show as strong signs of alternate bearing as the other four treatments. The high sensitivity of g_s to crop load have been previously reported in apple trees (Palmer et al. 1997, Wünsche et al. 2000) and demonstrates that trees upregulate their leaf gas exchange to match the higher carbon demands of growing and ripening fruits (White et al. 2016).

Similar g_s values between irrigated and non-irrigated trees, while Ψ_{stem} differed, suggest that the apple trees exhibit anizohydric rather than isohydric behaviour. During anizohydric response, trees do not close their stomates during drought stress and tolerate certain declines in water potential (Klein 2014). Our results are in agreement with Beikircher et al. (2013), who found late stomatal closure and, consequently, negative hydraulic safety margins in three high-yield apple cultivars. The relative insensitivity of g_s to irrigation means that g_s is a less suitable plant-based water stress indicator than $\Psi_{stem,}$ at least for cv. Red Jonaprince. However, the extrapolation of these results to other apple tree cultivars should be done with caution because the stomatal response and the degree of izo/anizohydry may differ among cultivars (Beikircher et al. 2013, Levin et al. 2020).

Both physiological parameters Ψ_{stem} and g_s were responsive to atmospheric water demands (Figure 7), which makes the separation of soil- and atmospheric-drought difficult for irrigation practice. While the soil water availability and atmospheric water demands are typically tightly coupled on monthly to seasonal scales (Torres et al. 2013, Jupa et al. 2022), atmospheric water demands and high air temperatures may have negative impacts on plant hydraulic integrity even under the conditions of non-limiting soil water (Schönbeck et al. 2022). This means that there are situations in which water stress on trees cannot be relieved by supplying irrigation.

Seasonal minimal Ψ_{stem} was negatively correlated with annual fruit yield when one year (2021) was excluded (Figure 8A). 2021 was wet in the early growing season, and flower density in spring was

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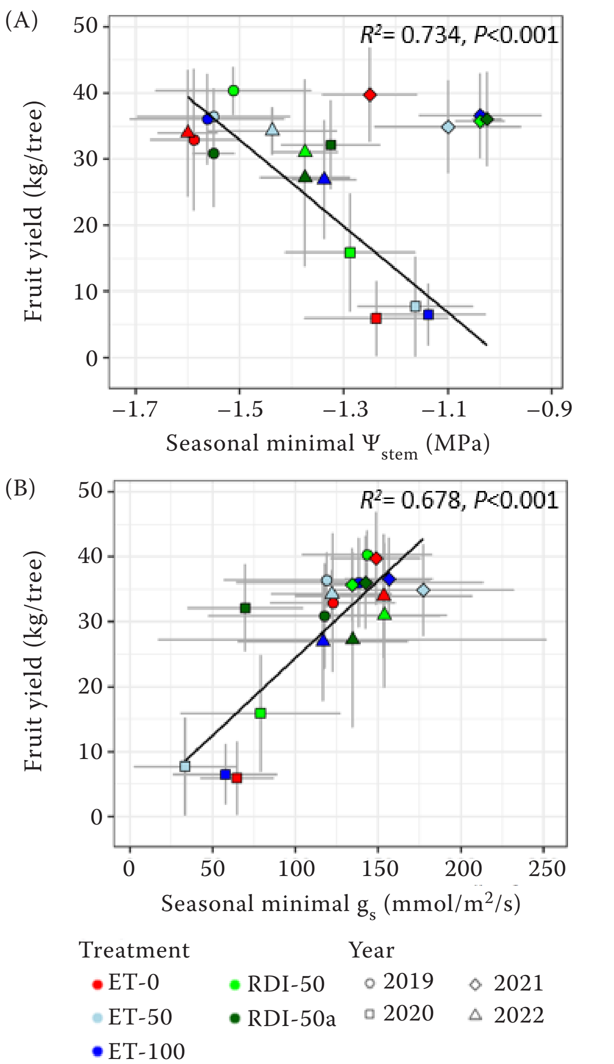

Figure 8. Relationship between (A) seasonal minimal midday stem water potential (Ψ_{stem}) and annual fruit yield and (B) seasonal minimal leaf stomatal conductance (g_s) and annual fruit yield across all four measured years and five irrigation treatments. The points represent irrigation treatment means per each year, and error bars represent standard error (SE); *n* = 10 for fruit yield, *n* = 4 for Ψ_{stem} and g_s. The lines are linear regressions to the data. Corresponding R^2 and *P*-values are provided

high. A positive correlation was also found between minimal seasonal g_s and annual fruit yield across all four years (Figure 8B). These results point to a close association between fruit yield and tree water and carbon relations. High fruit load requires high carbon assimilation rates to meet the high sink demands of growing fruits. Therefore, trees leave their stomata open, resulting in high g_s. Consequently, the trees also experience high evaporative water loss, leading to lower Ψ_{stem}.

Our data shed more light on two commonly measured plant-based indicators of tree water status. It was found that Ψ_{stem} was more sensitive to differences in irrigation than g_s, which suggests that Ψ_{stem} is a better plant-based indicator for irrigation scheduling than g_s. Differential irrigation and the resulting differences in tree water status did not affect yield parameters, and hence, irrigation necessity cannot be proved by yield data under mild-humid climatic conditions. Such non-significant differences are frequently not reported in the scientific literature, which can lead to an unwanted publication bias (Dwan et al. 2008).

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REFERENCES

Ahumada-Orellana L., Ortega-Farías S., Poblete-Echeverría C., Searles P.S. (2019): Estimation of stomatal conductance and stem water potential threshold values for water stress in olive trees (cv. Arbequina). Irrigation Science, 37: 461–467.

Allen R.G., Pereira L.S. (2009): Estimating crop coefficients from a fraction of ground cover and height. Irrigation Science, 28: 17–34.

Allen R.G., Pereira L.S., Raes D., Smith M. (1998): Crop evapotranspiration – guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper 56. Rome, Food and Agriculture Organisation, 300(9), D05109.

Bauerle T.L., Smart D.R., Bauerle W.L., Stockert C., Eissenstat D.M. (2008): Root foraging in response to heterogeneous soil moisture in two grapevines that differ in potential growth rate. New Phytologist, 179: 857–866.

Beikircher B., De Cesare C., Mayr S. (2013): Hydraulics of high-yield orchard trees: a case study of three *Malus domestica* cultivars. Tree Physiology, 33: 1296–1307.

Campbell G.S., Campbell M.D. (1982): Irrigation scheduling using soil moisture measurements: theory and practice. Advances in Irrigation, 1: 25–42.

Cancela J.J., Cuesta T.S., Neira X.X., Pereira L.S. (2006): Modelling for improved irrigation water management in a temperate region of northern Spain. Biosystems Engineering, 94: 151–163.

De Swaef T., Steppe K., Lemeur R. (2009): Determining reference values for stem water potential and maximum daily trunk shrinkage in young apple trees based on plant responses to water deficit. Agricultural Water Management, 96: 541–550.

Dodd I.C. (2007): Soil moisture heterogeneity during deficit irrigation alters root-to-shoot signalling of abscisic acid. Functional Plant Biology, 34: 439–448.

Doltra J., Oncins J.A., Bonany J., Cohen M. (2007): Evaluation of plant-based water status indicators in mature apple trees under field conditions. Irrigation Science, 25: 351–359.

https://doi.org/10.17221/160/2023-PSE

Dwan K., Altman D.G., Arnaiz J.A., Bloom J., Chan A.-W., Cronin E., Decullier E., Easterbrook P.J., Elm E.V., Gamble C., Ghersi D., Ioannidis J.P.A., Simes J., Williamson P.R. (2008): Systematic review of the empirical evidence of study publication bias and outcome reporting bias. PloS One, 3: e3081.

Fernández J. (2017): Plant-based methods for irrigation scheduling of woody crops. Horticulturae, 3: 35.

Fernández J.E., Torres-Ruiz J.M., Diaz-Espejo A., Montero A., Álvarez R., Jiménez M.D., Cuerva J., Cuevas M.V. (2011): Use of maximum trunk diameter measurements to detect water stress in mature 'Arbequina' olive trees under deficit irrigation. Agricultural Water Management, 98: 1813–1821.

Hanson B.R., Orloff S., Peters D. (2000): Managing irrigation water on the farm. California Agriculture, 54: 38–42.

IUSS Working Group (WRB. 2015): World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. Rome, Food and Agriculture Organisation.

Jones H.G. (2004): Irrigation scheduling: advantages and pitfalls of plant-based methods. Journal of Experimental Botany, 55: 2427–2436.

Jupa R., Mészáros M., Hoch G., Plavcová L. (2022): Trunk radial growth, water and carbon relations of mature apple trees on two size-controlling rootstocks during severe summer drought. Tree Physiology, 42: 289–303.

Klein T. (2014): The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Functional Ecology, 28: 1313–1320.

Kon T.M., Schupp J.R. (2013): Thinning tall spindle apple based on estimations made with a hand-thinning gauge. HortTechnology, 23: 830–835.

Lakso A.N. (1994) Apple. In: Schaffer B., Andersen P.C. (eds.): Handbook of Environmental Physiology for Fruit Crops. Florida, CRC Press, 2–42. ISBN: 0-8943-0175-0

Lauri P.-É., Barigah T.S., Lopez G., Martinez S., Losciale P., Zibordi M., Manfrini L., Corelli-Grappadelli L., Costes E., Regnard J.-L. (2016): Genetic variability and phenotypic plasticity of apple morphological responses to soil water restriction in relation with leaf functions and stem xylem conductivity. Trees, 30: 1893–1908.

Lenth R., Singmann H., Love J., Buerkner P., Herve M. (2019): Package 'emmeans'. Available at: http://cran.r-project.org/package=emmeans

Levin A.D., Williams L.E., Matthews M.A. (2020): A continuum of stomatal responses to water deficits among 17 wine grape cultivars (*Vitis vinifera*). Functional Plant Biology, 47: 11–25.

Meier U. (2001): Growth stages of mono- and dicotyledonous plants. BBCH Monograph. Bonn, Federal Biological Research Centre for Agriculture and Forestry.

Meinzer F.C., Johnson D.M., Lachenbruch B., McCulloh K.A., Woodruff D.R. (2009): Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Functional Ecology, 23: 922–930.

Naor A., Klein I., Doron I. (1995): Stem water potential and apple size. Journal of American Society of Horticultural Science, 120: 577–582.

Naor A., Naschitz S., Peres M., Gal Y. (2008): Responses of apple fruit size to tree water status and crop load. Tree Physiology, 28: 1255–1261.

Ortuño M.F., Brito J.J., García-Orellana Y., Conejero W., Torrecillas A. (2009): Maximum daily trunk shrinkage and stem water potential reference equations for irrigation scheduling of lemon trees. Irrigation Science, 27: 121–127.

Palmer J.W., Giuliani R., Adams H.M. (1997): Effect of crop load on fruiting and leaf photosynthesis of 'Braeburn'/M.26 apple trees. Tree Physiology, 17: 741–746.

Plavcová L., Mészáros M., Jupa R., Scháňková K., Kovalíková Z., Náměstek J., Mahrová A. (2023): Yield and water relations of two apple cultivars under irrigation. Irrigation Science, doi.org/10.1007/s00271-022-00839-2

R Development Core Team (2010): R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Robinson T., Lordan J., Francescatto P. (2019): Irrigation of apples in a humid climate in wet and dry years. In: Proceeding of the IX International Symposium on Irrigation of Horticultural Crops 1335, Matera, 477–482.

Schönbeck L.C., Schuler P., Lehmann M.M., Mas E., Mekarni L., Pivovaroff A.L., Turberg P., Grossiord C. (2022): Increasing temperature and vapour pressure deficit lead to hydraulic damages in the absence of soil drought. Plant, Cell and Environment, 45: 3275–3289.

Shackel K.A., Ahmadi H., Biasi W., Buchner R., Goldhamer D., Gurusinghe S., Hasey J., Kester D., Krueger B., Lampinen B., McGourty G., Micke W., Mitcham E., Olson B., Pelletrau K., Philips H., Ramos D., Schwankl L., Sibbett S., Snyder R., Southwick S., Stevenson M., Thorpe M., Weinbaum S., Yeager J. (1997): Plant water status as an index of irrigation need in deciduous fruit trees. HortTechnology, 7: 23–29.

Torres G.M., Lollato R.P., Ochsner T.E. (2013): Comparison of drought probability assessments based on atmospheric water deficit and soil water deficit. Agronomy Journal, 105: 428–436.

White A.C., Rogers A., Rees M., Osborne C.P. (2016): How can we make plants grow faster? A source-sink perspective on growth rate. Journal of Experimental Botany, 67: 31–45.

Wünsche J.N., Palmer J.W., Greer D.H. (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.

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