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Heterogeneity in fruit distribution and stem water potential variations in peach trees under different irrigation conditions

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SUMMARY

The hypothesis that different fruit loads between ‘scaffold branches’ of a tree can induce water status differences was evaluated. Two different experiments were carried out, one under full irrigation conditions and the other under conditions in which peach trees were deficit irrigated (50%). Thinning treatments were applied in both experiments at the beginning of Stage III of fruit development: 1) EVEN-max with fruits distributed evenly with maximum crop, not thinned, 2) EVEN-min with fruits distributed evenly with minimal crop (< 90 fruit tree⁻¹), and 3) UNEVEN with fruits distributed unevenly by totally defruiting half of the available main (scaffold) branches per tree and leaving the other half unthinned. Stem water potential (Ψ_{stem}) was measured with a pressure chamber at solar noon, and midday leaf conductance (g_l) using a portable steady state porometer. UNEVEN trees always had intermediate Ψ_{stem} values between EVEN-max and EVEN-min, independent of irrigation treatments. Maximum fruit load differences between trees (EVEN-max compared to EVEN-min) produced Ψ_{stem} differences of 0.12 MPa and 0.25 MPa for full irrigation and deficit irrigation experiments, respectively. Although the magnitude of change in Ψ_{stem} was larger for deficit irrigated conditions, extreme differences in fruit load between main branches within an UNEVEN peach tree only induced differences in leaf conductance and had no effect on the water potential of scaffold branches independent of the irrigation experiment. Fruit load effects on branch water status were governed mainly by tree fruit load rather than scaffold branch fruit load. These results indicate that there is either little hydraulic isolation between the main stems, irrespective of tree water status, or an improved hydraulic efficiency associated with defruiting.

Branch junctions are important components in sap flow in plants and have been studied as segmentation points, so that branches are conceived as small independent units rooted in the main bole (Tyree, 1988). The anatomical evidence supporting this point of view suggests the existence of an hydraulic isolation of branches, produced by vascular constrictions (Tyree and Ewers, 1991; Sachs *et al.*, 1993). When considering water loss from branches, there is general agreement that water loss from one branch has little impact on the water potential of other branches of a tree. This fact has been used to support the existence of branch autonomy for water relations (Sprugel *et al.*, 1991). However, there appears to be some level of variability between species in the isolation between portions of the xylem (Schulte and Brooks, 2003), and Tyree and Ewers (1991) speculated that branch vascular constrictions for some species are not as relevant, compared to total plant resistance.

On the other hand, fruits can alter tree water status balance during periods of maximum fruit sink strength (i.e., Stage III of fruit development in peach trees), and increasing their number can increase photosynthesis and leaf conductance, and decrease leaf water status (DeJong, 1986; Mimoun *et al.*, 1996; Marsal and Girona, 1997). As a result, if branches have some independent

behaviour from a water transport point of view, an extreme change in fruit load between two main branches of a tree could produce significant variations in water potential between branches. The extent of these changes would depend on the degree of isolation between branches and perhaps also on the tree water status that could act as a response modifier. If this were the case, not only could there be the potential for carbon availability and transport to reduce fruit growth when fruits are densely located on a branch (Wardlaw, 1990; DeJong and Grossman, 1995) – which is the reason for fruit thinning – but also there could be a water relations limitation involved in causing differential fruit growth on a stem.

This study was undertaken to evaluate the hypothesis that different fruit loads on the main scaffold branches, trained according to horticultural practices in a commercial orchard, can induce water status differences within the tree.

MATERIALS AND METHODS.

One experiment was carried out in 2001, under full irrigation conditions, while the other experiment, in 2003, was under deficit irrigation conditions in which trees were irrigated to 50% of full irrigation requirements as estimated from a water budget method (Goldhamer and Snyder, 1989).

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Full irrigation experiment

The full irrigation experiment was carried out in a block at UC Davis, Wolfskill Experimental Orchard, Winters, California. Twenty-four trees from eleven rows of 10 year-old ‘Elegant Lady’ peach (*Prunus persica* L.) trees, on ‘Lovell’ rootstock, were selected for uniformity. The orchard was planted in a high density formation (5.5 × 2 m spacing) and trained to a Kearney perpendicular-V with two main scaffold branches per tree. The trees were irrigated twice weekly by microjet sprinklers, receiving 100% replacement of reference evapotranspiration (ET_o; data obtained from the California Irrigation Management System recorded at Winters). Rainfall was absent during the experimental period.

Deficit irrigation experiment

The deficit irrigation experiment was carried out in 2003 in a commercial orchard at Lleida, Spain. Twelve trees from 5 rows of 20 year-old ‘O Henry’ peach (*P. persica* L.) trees, on seedling rootstock, were selected for uniformity. The orchard was planted in a traditional density formation (5 × 4 m spacing) and trained to a vase system with four main scaffold branches per tree. The trees were irrigated daily by a drip system with double-pipes per tree row, and the studied trees received 50% replacement of crop evapotranspiration (ET_c) during Stage III of fruit development, and 100% ET_c during other developmental phases (ET_c = ET_o × K_c; data obtained from the Xarxa Agrometeorologica de Catalunya). Rainfall was absent during Stage III of fruit development.

Thinning treatments

Fruit thinning treatments were applied in both experiments at the beginning of Stage III of fruit development (on May 15 and July 1, for the full and deficit irrigation experiments, respectively). There were four scaffold thinning treatments: (1) EVEN-max, all scaffold branches on a tree were left unthinned resulting in fruit distributed evenly within a tree and a maximum crop; (2) EVEN-min, all scaffold branches on a tree were

heavily thinned with fruit distributed evenly within a tree and a minimal crop (< 90 fruit per tree); (3) UNEVEN-F, fruited (unthinned) scaffold branches that were adjacent to defruited scaffold branches on the same tree; and (4) UNEVEN-DF, defruited scaffold branches that were adjacent to fruited (unthinned) scaffolds on the same tree. Because scaffold branches were used as the reference unit for comparisons, the number of trees in the UNEVEN treatment was doubled (12 and 8 trees for the full and deficit irrigation experiment, respectively) compared to EVEN treatments (6 and 4 trees for the full and deficit irrigation experiment, respectively).

Measurements

Midday stem water potential (Ψ_{stem}) was measured with a pressure chamber (Model 3005; Soil Moisture Equipment Corp., Santa Barbara, CA, USA), following procedures outlined by McCutchan and Shackel (1992). Measurements were made at solar noon on covered leaves located in the lowest portion of each scaffold. Midday leaf conductance (g_l) was measured only in the full irrigation experiment under natural light conditions, greater than 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, using a portable steady state porometer (Model LI-1600, LI-COR Inc., Lincoln, NE, USA). Ψ_{stem} and g_l were measured on one or two leaves per scaffold branch, respectively, in all trees. All measurements were repeated on four different occasions at key points during Stage III fruit development (just after fruit thinning, early-mid-Stage III, late-mid-Stage III, and a week before harvest).

Fruit load was determined by harvesting fruits 1 week before commercial maturity in the full irrigation experiment (July 2), to avoid significant fruit drop; and at commercial maturity in the deficit irrigation experiment (August 30). All fruit were removed from each scaffold branch and counted in one pick.

Statistical analysis.

Data were analysed by repeated measures analysis of variance (SAS Institute Inc., 1988), and means separated using Duncan's multiple range test at the 0.05 level of significance.

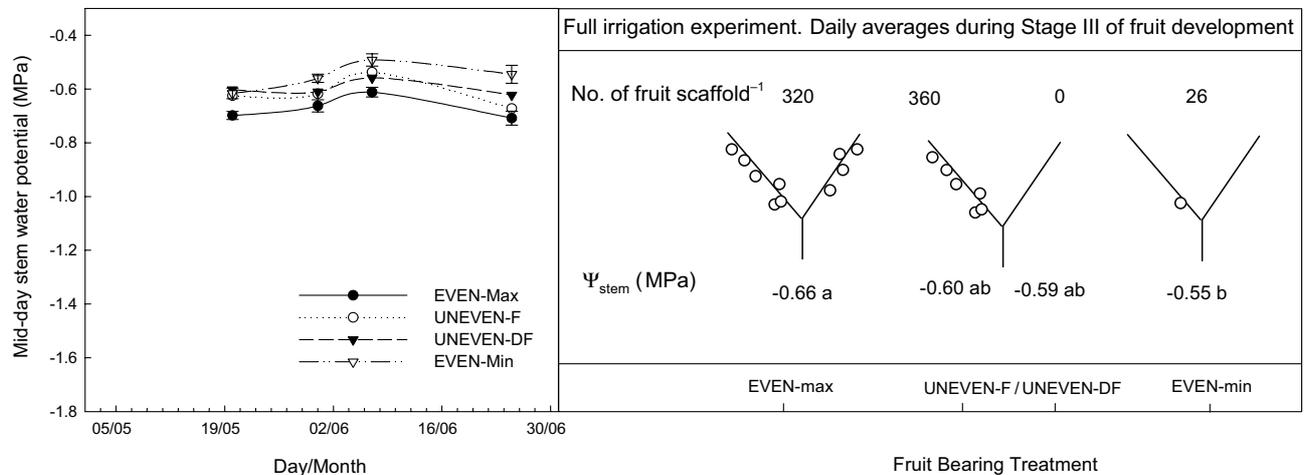


FIG. 1

Daily patterns of mid-day stem water potential (MPa) (left panel), scaffold branch fruit load and daily average mid-day stem water potentials (Ψ_{stem} ; -MPa) (right panel) in the various fruit bearing treatments in the full irrigation experiment during Stage III of fruit development. Error bars (left panel) denote (\pm standard error). Values followed by the same letter (right panel) are not significantly different ($P = 0.05$)

TABLE I

Effects of fruit bearing treatments on average leaf conductance during Stage III, and on water sprout fresh weight at harvest in the full irrigation experiment

Bearing treatments	g_l ($\text{mol m}^{-2} \text{s}^{-1}$)	Water sprout fresh weight (kg)
EVEN-Max	*324 a	0.961 c
UNEVEN-F	303 a	1.166 bc
UNEVEN-DF	277 b	1.734 ba
EVEN-Min	257 b	2.012 a
<i>P</i>	0.0001	0.0019

*Mean values followed by the same letter in each column are not significantly different at $P = 0.05$ (see text).

RESULTS

Full irrigation experiment

Unthinned trees (EVEN-max) had an average of 640 fruits per tree and UNEVEN trees had about half that load (360 fruits per tree), while EVEN-min trees had an average of 51 fruits per tree. At the whole tree level, fruit load significantly affected tree average Ψ_{stem} and g_l . Ψ_{stem} and g_l of EVEN-max trees were significantly lower than those of EVEN-min trees (i.e., reduced by 0.11 MPa and 67 $\text{mmol m}^{-2} \text{s}^{-1}$, respectively; Figure 1 and Table I). Fruit load at the scaffold branch level in UNEVEN trees affected only g_l , with UNEVEN-DF having very slight, but consistently lower values (about 25 $\text{mmol m}^{-2} \text{s}^{-1}$) than UNEVEN-F (Figure 1 and Table I). Ψ_{stem} did not vary significantly in accordance with fruit load at the scaffold branch level within UNEVEN trees (Figure 1). On the other hand, both Ψ_{stem} and g_l in UNEVEN trees had intermediate values between those corresponding to EVEN-max and EVEN-min trees (Figure 1 and Table I).

Water sprout fresh weight was initially measured in this study to observe if the effect of fruiting on Ψ_{stem} diminished with time, and if this could be due to a larger development in leaf area. Total water sprout fresh weight decreased with tree fruit load and EVEN-max trees had one-half the fresh weight of EVEN-min trees (Table I). Water sprout fresh weight was not significantly different between UNEVEN-F and UNEVEN-DF scaffold branches, but differences in the absolute values between those scaffolds were large and equal to 54% of the differences between EVEN-min and EVEN-max trees, indicating substantial variability among trees.

Deficit irrigation experiment

Unthinned trees (EVEN-max) had an average of 508 fruits per tree and UNEVEN trees, in which half of the scaffold branches were defruited, had about half that load (247 fruits per tree). EVEN-min trees had slightly more cropping than the pre-planned levels (137 fruits per tree), but still very low crop values at the scaffold branch level (32 fruits per scaffold branch).

Deficit irrigation resulted in substantial decreases in Ψ_{stem} values over the period of the experiment. At the onset of deficit irrigation, values were similar to those of a fully irrigated orchard (-0.7 MPa), and then gradually declined to minimum values of -1.7 MPa for EVEN-max trees at the end of Stage III (Figure 2). The maximum differences in fruit load achieved between EVEN-max and EVEN-min scaffold branches significantly influenced Ψ_{stem} , resulting in an average decrease of 0.25 MPa for the high fruit load treatments (Figure 2). Although UNEVEN-F scaffold branches had fruit numbers similar to EVEN-max scaffold branches, their average Ψ_{stem} values were significantly different. UNEVEN-F scaffold branches had higher Ψ_{stem} values than EVEN-max scaffold branches, therefore showing the significant influence of being adjacent to a defruited scaffold branch (Figure 2). Average Ψ_{stem} values of EVEN-min scaffolds and UNEVEN-DF were not significantly different (Figure 2). Ψ_{stem} values between UNEVEN-F and UNEVEN-DF scaffold branches also were not significantly different (Figure 2).

DISCUSSION

Water stress increased the effect of fruit load on Ψ_{stem} , and differences of 0.25 MPa were observed between thinning treatments in the deficit irrigated experiment, while maximum differences were only 0.11 MPa between thinning treatments in the fully irrigated experiment, despite the fact that higher fruit loads were achieved in the fully irrigated experiment (640 fruits per tree in two scaffold branches that were allotted less space than the 508 fruits per tree among four scaffold branches in the deficit irrigated experiment). Besides irrigation and cropping, other growing conditions differed between the

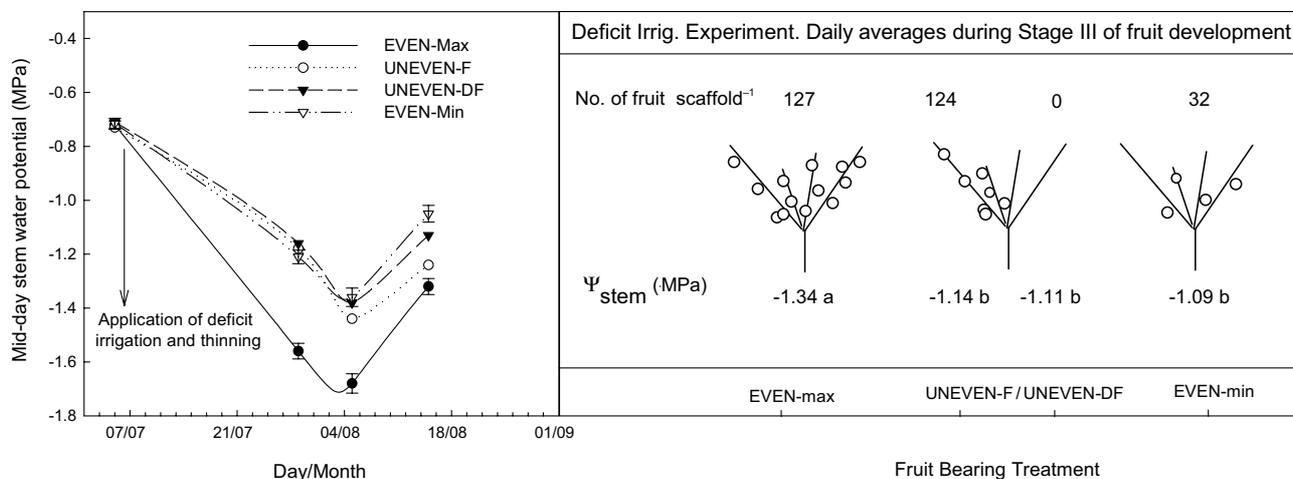


FIG. 2

Daily patterns of mid-day stem water potential (MPa) (left panel), scaffold branch fruit load and daily average mid-day stem water potentials (Ψ_{stem} ; -MPa) (right panel) in the various fruit bearing treatments in the deficit irrigation experiment during Stage III of fruit development. Error bars (left panel) denote (\pm standard error). Values followed by the same letter (right panel) are not significantly different ($P = 0.05$)

two experiments such as tree training conditions (V system, in contrast to a vase system), and peach cultivar. However, the fact that the crop loads of trees in the deficit irrigation experiment were actually lower, on a per tree and land area basis, while the difference in Ψ_{stem} between scaffold branches in the same tree were greater in the deficit irrigation experiment, indicates that the irrigation factor was the most important difference between the two experiments.

Although water stress increased the response of fruit load to water status, the response of Ψ_{stem} to the heterogeneity in fruit distribution within a tree was somewhat similar between experiments. The effect of large differences in fruit load between adjacent scaffold branches in UNEVEN trees was not significant (Figures 1 and 2). This lack of fruit distribution effect within a tree indicates that crop load effects on Ψ_{stem} are governed mainly by fruit load on a tree basis, rather than on a scaffold branch basis. However, g_1 seemed to behave differently from Ψ_{stem} , and, under full irrigation conditions, scaffold branches with similar fruit load (UNEVEN-F and EVEN-max, or UNEVEN-DF and EVEN-min) had average g_1 values that were not significantly different from each other, but were different from scaffold branches with different fruit loads (Table I). This indicates that g_1 was influenced more by scaffold branch fruit load than by tree fruit load. The mechanism by which g_1 responds to decreased fruit load is thought to be related to a decrease in photosynthesis (DeJong, 1986; Gucci *et al.*, 1991; Palmer, 1992), which in turn may be driven by a down-regulation of leaf photosynthesis as a result of reduced assimilate demand from fruits (Ben Mimoum *et al.*, 1996). Since large branches are thought to be highly autonomous for photo-assimilates after the Spring vegetative growth period (Sprugel *et al.*, 1991) and carbohydrate produced in a defruited branch does not supply dry matter for the fruits in adjacent branches (Marsal *et al.*, 2003), the demand for dry matter is probably sensed at a local level (i.e., at units smaller than a branch). It is therefore logical that the effects of scaffold branch fruit load on leaf conductance become manifest in close proximity to fruit sinks.

Vegetative growth, as indicated by water sprout fresh weight at harvest, was significantly reduced by increasing fruit load, and reflected the dependence of vegetative growth on carbon availability. However, vegetative growth is also considered to be highly sensitive to water stress (Hsiao, 1972; Bradford and Hsiao, 1982). In this experiment, stem water potential was not as well correlated as g_1 to water sprout fresh weight (Figure 3), indicating that differences in vegetative growth were probably driven more by dry matter availability at the scaffold branch level than scaffold branch water status. It was also observed that the larger development of water sprouts for EVEN-min scaffold branches under full irrigation conditions did not over-ride the effect of fruit

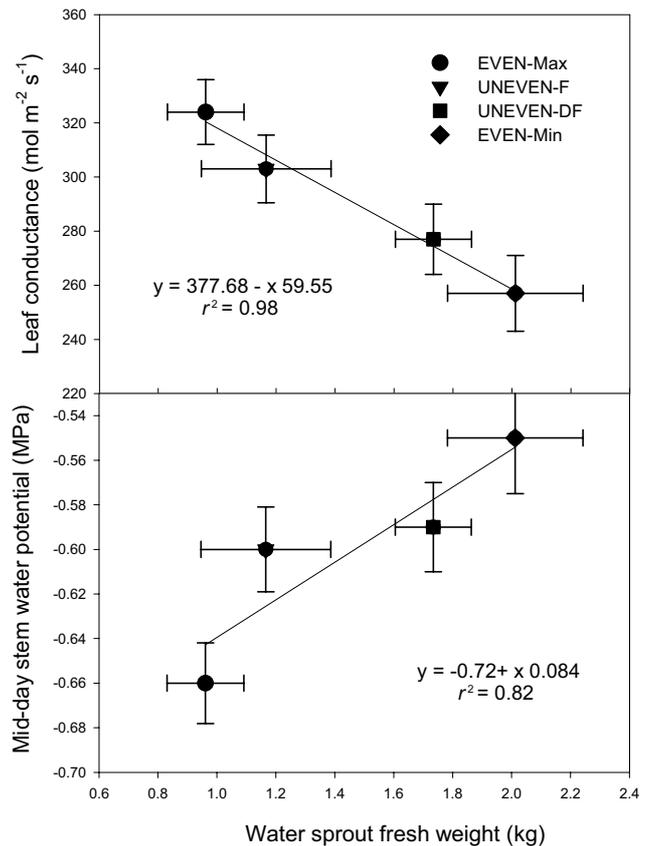


FIG. 3 Relationship between water sprout fresh weight (kg) and leaf conductance (top panel), or mid-day stem water potential (Ψ_{stem} MPa; bottom panel) for the full irrigation experiment. Observations represent treatment averages. Error bars denote (\pm standard error).

load on Ψ_{stem} , and the influence over time (i.e., during Stage III), if any, was in the direction toward increasing fruit load effects on Ψ_{stem} (Figures 1 and 2).

In summary, any process that is closely driven by variations in dry matter availability (i.e., leaf conductance and, perhaps to lesser extent, vegetative growth) seemed to be autonomous at the branch level. On the other hand, processes that are related primarily to water transport such as tension in the xylem vessels, as indicated by stem water potential, showed little branch autonomy. The lack of Ψ_{stem} variation within UNEVEN peach trees appears to result from an absence of hydraulic isolation between the main scaffold branches, or possibly an increase in hydraulic conductance for those large branches with a heavy crop load compared to defruited branches. A recent study (Basile *et al.*, 2003) supports the notion of strong hydraulic continuity in the vascular system of peach trees, since the hydraulic resistance of trunks and stems was remarkably small and represented only about 10% of total tree resistance.

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