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Effects of Winter Pruning and of Water Restriction on Fruit and Vegetative Growth, Water Potential and Leaf Gas Exchange during the Final Stage of Rapid Growth in an Early Maturing Peach Cultivar

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Summary

Three intensities of winter pruning and of water restriction were assessed in a three-year-old early maturing peach cultivar under orchard and pot training, respectively. Under increasing intensities of pruning, peach growth was not limited at fruit maturity, whereas peach growth was limited under increasing water restriction. Severe pruning and high water restriction contributed to reducing the total shoot length compared to the control trees. Stem water potential decreased under severe pruning and high water restriction, whereas leaf stomatal conductance and transpiration rate were enhanced under severe pruning and limited under high water restriction. Leaf temperature and sub-stomatal CO_2 concentration did not vary under different pruning intensities, whereas they increased and decreased, respectively, under increasing water restriction. Under the different pruning intensities, leaf stomatal conductance and transpiration rate were correlated to the shoot length per unit fruit-bearing shoot length, suggesting that vegetative growth could be an alternate sink to the one induced by fruit growth.

Key words. photosynthesis – *Prunus persica* – stomatal conductance – water status – water stress

Introduction

The impact of tree pruning on peach cropping has already been explored in view of improving fruit production (Mika 1986; Walcroft et al. 2002). In particular, considering the effect of pruning on tree water status, the positive incidence of summer pruning on peach water potential and leaf gas exchange has been established (Li et al. 2003). Branch removal was also reported to improve tree water status under arid conditions (Marsal et al. 2006). However, references are lacking about the incidence of winter pruning on peach tree water status and leaf gas exchange. Because fruit crop load is also likely to influence peach tree water status (Blanco et al. 1995), the assessment of winter pruning effects alone would make it necessary to perform different combinations of fruit-bearing shoot (FBS) numbers and fruit numbers per FBS resulting in the same total fruit load per tree. This issue has already been explored in peach trees, but fruit quality and crop value had only been investigated at harvest (Marini 2003), so that information was lacking on winter pruning effects during the period of vegetative and fruit growth, and particularly during the crucial period of rapid fruit growth (Grossman and DeJong 1995).

With this aim in mind, we first proposed assessing the effects of the intensity of winter pruning on fruit and vegetative growth, water potential and leaf gas exchange in orchard peach trees with similar fruit loads as well as de-fruited trees. It could be interesting to compare these winter pruning effects to those induced by different intensities of water restriction so as to better investigate the different physiological responses of peach trees to cultural practices. Therefore, an irrigation trial was performed at the same time as the pruning trial with similar peach trees. To better control the water restrictions in the irrigation trial, the trees were grown in pots, whereas the trees used for the pruning trial were grown in a neighbouring orchard. For these two experiments, an early peach variety was chosen. Finally, two experiments were performed with three-year-old 'Alexandra' peach trees; orchard-grown trees were used for the pruning trial in Experiment I and pot-grown trees were used for the irrigation trial in Experiment II.

Materials and Methods

Plant materials and experimental design

This study was performed at the INRA Gotheron Experimental Station near Valence in the Middle Rhône Valley in France. The peach trees (cv. 'Alexandra', grafted on GF 305 rootstock) used for Experiment I had been cultivated in an orchard since 1998, and the peach trees used for Experiment (Exp.) II had been cultivated separately outdoors in 130 L containers next to this orchard. This experimental design had already been used to study the influence of pruning and water restriction intensities on peach

quality at harvest. In Exp. I, each of the six treatments was laid out in four blocks, as already described (Bussi et al. 2005) with two of these blocks reserved for the present study. In Exp. II, each of the three treatments was laid out in six blocks, as already described (Mercier et al. 2009), with two of these blocks reserved for the present study. The homogeneity of the experimental trees in each experiment was checked by measuring tree trunk circumferences before differentiating the treatments. This was done in 2000, i.e., the first year of fruit production.

All the trees received routine horticultural care except for pruning in Exp. I and irrigation in Exp. II. Full bloom occurred on 20 and 15 March in Exps. I and II, respectively. Experiment time was generally expressed in number of days after full bloom (DAFB).

Experimental treatments

In the first experiment – two blocks of six treatments –, three pruning intensities were compared: light (T1, T4), medium (T2, T5) and severe (T3, T6), with trees bearing the same fruit load of approximately 100 fruits (T1, T2, T3), or de-fruited trees (T4, T5, T6). The lightly pruned fruit-bearing tree treatment (T1) was considered as the control. For the three increasing pruning intensities, the number of fruit-bearing shoots (FBS) left on the trees after pruning was 40, 30 and 20, respectively.

In the second experiment, a control irrigation treatment was compared to a light and a high water restriction. The six trees in the experiment – two blocks of three treatments – bore around 100 fruits each. The irrigation programmes were deduced from micromorphometric data. Control (T7), light water restriction (T8) and high water restriction (T9) trees were irrigated so that maximum daily shrinkage was maintained between 10 and 30 μm, 50 and 100 μm, 150 and 300 μm, respectively (Huguet et al. 1992).

Measurements

At the beginning of the growing season, around 60 DAFB, five FBS were marked on each of the six trees that bore fruits in Exps. I and II. The cheek diameters of the peaches on these tagged FBS in Exps. I and II were measured twice a week, between 8:00 and 10:00 a.m., in order to monitor the fruit growth pattern until harvest. The fruits were picked when their growth curve displayed a saturation pattern. Vegetative growth was assessed in Exps. I and II by measuring total shoot lengths on all the FBS of the trees on two dates: 56 and 117 DAFB, corresponding to the beginning and the end of the final stage of rapid fruit growth, respectively. At the last date, the shoot length of 'Alexandra' cv. was considered to be fully expanded, thereby providing an estimate of final shoot elongation (Bussi et al. 2005). FBS length was also evaluated so as to calculate shoot length per meter FBS, representative of tree vigour (Li et al. 1994).

In Exps. I and II, the effects of the treatments on stem and leaf water potential (Ψ stem and Ψ leaf) were monitored on the 12 and six trees in the experiment, respectively. In order to measure Ψ stem, leaves were shaded for one day before being excised from the tree for Ψ measurement. Ψ stem and leaf were measured using a Scholander pressure chamber (Scholander et al. 1965) on mature leaves from the middle of shoots at four time points on the measurement date (between 9 h and 15 h TU), using three samples at each measurement. Measurement dates were: 7 June for Ψ stem, 7, 14 and 27 June (79, 86 and 99 DAFB) for Ψ leaf in Exp. I, and 8 June (85 DAFB) for Ψ stem and leaf in Exp. II. Leaf photosynthesis was evaluated using a portable, infrared gas analyser equipped with a leaf chamber (model LCA-4). Leaves were sampled from the canopy of the same trees, just as for Ψ measurements, at four time points on the measurement date (between 9 h and 15 h TU). Each photosynthesis measurement was the mean of ten measurements performed successively on the same leaf by the analyser. Photosynthetic photon flux density (PPFD), stomatal conductance, transpiration rate, leaf temperature and sub-stomatal CO_2 concentration were obtained at the same time that photosynthesis was measured. Measurements for leaf photosynthesis and relative parameters were performed on the same dates as for Ψ leaf in Exp. I, and on 8 and 15 June in Exp. II. Data averaged for the different measurement dates were presented.

Statistical analysis

A classical analysis of variance was used. Before data analysis, homogeneity of variance was tested by Bartlett's test. The comparison of treatments was carried out using Fisher's test (Statgraphics® Plus software). Relationships were fitted to a simple linear equation.

Results

Fruit and vegetative growth

For both experiments, the first picking took place on 21 June, i.e., 93 and 98 DAFB in Exps. I and II, respectively. Seasonal changes in peach diameters showed that the curves obtained under severe pruning and high water restriction were generally lower than those under the controls (Fig. 1). From 81 to 95 DAFB, peach diameter was significantly greater under T1 than under T2 and T3 (Fig. 1), but no significant difference was detected thereafter. From 86 DAFB, peach diameter was greater under T7 than under T9, and this difference increased as fruit grew. Increasing pruning intensity contributed to decreasing shoot growth: total shoot length in FBS tree^{-1} in T2 and T3 (71 and 57 m long, respectively) was lower than in T1 (89 m long) on 56 DAFB, and this trend was confirmed on 117 DAFB: 156 (T2) and 126 (T3) *vs* 170 (T1) m long, respectively (Fig. 2). Nevertheless, increasing pruning intensity contributed to increasing shoot length per m FBS: 6.0, 8.5 and 10.7 m per m FBS on 117 DAFB in T1, T2 and T3, respectively. Total shoot length in FBS per tree in T8 and T9 (55 and 45 m long, respectively) was lower than the length measured in T7 (57 m long) on 56 DAFB. This trend was confirmed on 117 DAFB: 119 (T8) and 95 (T9) *vs* 124 (T7) m long, respectively (Fig. 2).

Water potential and leaf gas exchange

In Exps. I and II, Ψ stem decreased under increasing intensities of pruning (−17 % under severe pruning compared to control pruning) and under increasing water restriction (−52 and −14 % under T9 and T8, respectively,

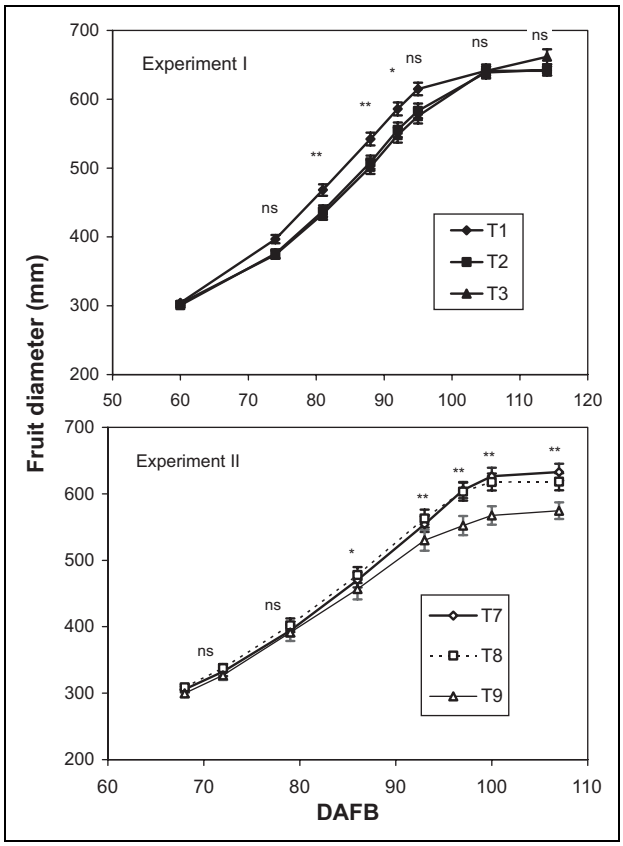


Fig. 1. Time-course of 'Alexandra' peach as related to the pruning and irrigation treatments. See the legend in Table 1. Vertical bars denote standard error of the averaged peach diameters. * and ** indicate significant differences at $P \leq 0.05$ and $P \leq 0.01$; ns, not significant.

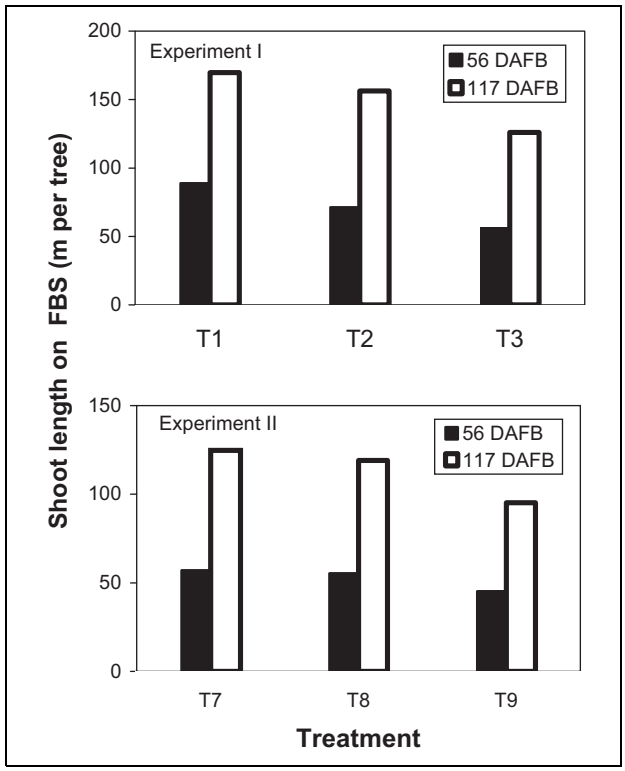


Fig. 2. Shoot length per tree of 'Alexandra' peach into all the FBS on two dates: 56 and 117 DAFB, as related to the pruning and irrigation treatments. See the legend in Table 1.

compared to T7) (Table 1). Leaf photosynthesis did not differ under various intensities of pruning, but significantly decreased under increasing water restriction (−17 % under T9 compared to T7) (Table 1). At the same time, stomatal conductance increased under increasing pruning intensity (+44 and +28 % under severe and medium pruning, respectively, compared to control pruning). The leaf transpiration rate was also higher under severe and medium pruning compared to control pruning (+25 and +24 %, respectively), but leaf temperature and sub-stomatal CO_2 concentration did not vary. Under increasing water restriction, stomatal conductance decreased, but the differences were greater than with leaf photosynthesis since it reached −36 % under T9 compared to T7 (Table 1). Leaf transpiration rate and sub-stomatal CO_2 concentration were also lower under T9 than under T7 (−20 and −12 %, respectively); in contrast, leaf temperature was above 34 °C under T9, whereas it was limited to around 32 °C under T7 and T8 (Table 1). Concerning fruit load effect, no difference in tree water status and leaf gas exchange was detected with de-fruited trees compared to fruited trees (Table 1).

Under the different pruning intensities, no relationship between leaf gas exchange and fruit diameter was detected (data not shown), whereas leaf stomatal conductance and transpiration rate measured on 99 DAFB were linearly related to shoot length per meter FBS measured on 117 DAFB (Fig. 3A and B). Under the same conditions, leaf photosynthesis and Ψ foliar were not significantly related to shoot length per meter FBS (data not shown).

Discussion

Since vegetative growth reduction usually limits carbon assimilation at the level of the fruit tree canopy (Corelli-Grappadelli et al. 1996), assimilates devoted to fruit production and, consequently, fruit growth and yield would be expected to decrease in Exp. I under severe pruning compared to those under control pruning. However, the leaf stomatal conductance and transpiration rate enhancement observed under severe pruning compared to that under control pruning was possibly responsible for maintaining the available assimilates throughout the whole canopy at a similar level under both conditions (Giuliani et al. 1997). Vegetative growth decrease under increasing pruning severity was likely to induce root growth decrease, in accordance with the theory of the shoot-root balance (Blasing et al. 1990) that might explain the trend towards a concomitant lower Ψ stem observed under high pruning severity (Mac Fadyen et al. 1996). Furthermore, Li et al. (2003) reported that Ψ stem was enhanced under summer pruning, therefore contributing to the limitation of the detrimental drought effect. So as compared to summer pruning, winter pruning would be likely to increase peach tree sensitivity to water stress. This assumption could not be confirmed under our

Table 1. Tree water potential, photosynthetic photon flux density (PPFD), net photosynthesis and relative physiological responses of leaves in 'Alexandra' peach trees as related to the pruning (Experiment I) and irrigation (Experiment II) treatments. No significant interaction was detected between pruning and fruit load treatments in Exp. I, so that their respective results were separately presented. P value is given by Fisher's test.

Experiment	Treatment	Stem water potential (Mpa)	Foliar water potential (Mpa)	PPFD (μmol m^{-2} s^{-1})	Photosynthesis (μmol m^{-2} s^{-1})	Stomatal conductance (mol m^{-2} s^{-1})	Transpiration (mmol m^{-2} s^{-1})	Temperature (°C)	Substomatal CO2 (μmol mol^{-1})
I	T1, T4	−0.78	−1.50	1169	14.3	0.32	4.74	29.7	237
	T2, T5	−0.84	−1.66	1325	15.6	0.41	5.89	30.6	231
	T3, T6	−0.92	−1.73	1193	14.0	0.46	5.93	30.3	232
	P-value	0.039	0.043	0.228	0.170	0.009	0.012	0.195	0.580
	T1, T2, T3	−0.86	−1.68	1246	15.3	0.41	5.66	30.0	234
	T4, T5, T6	−0.84	−1.65	1210	14.8	0.38	5.43	30.3	233
	P-value	0.490	0.450	0.380	0.380	0.090	0.170	0.450	0.670
II	T7	−1.02	−1.79	1501	17.1	0.35	5.57	32.3	214
	T8	−1.16	−1.87	1515	17.8	0.37	5.72	32.8	231
	T9	−1.55	−1.79	1483	14.1	0.22	4.48	34.2	188
	P-value	0.002	0.300	0.490	0.028	0.001	0.016	0.019	0.008

Intensity of pruning was light (T1, T4), medium (T2, T5) or severe (T3, T6), with fruited (T1, T2, T3), or de-fruited trees (T4, T5, T6).T7, T8 and T9 represented control irrigation, light and high water restriction, respectively.

experimental conditions because trees were not water-deprived in summer.

Under high water restriction, vegetative growth and leaf gas exchange decreased, as already mentioned (Girona et al. 1993). Those decreases probably contributed to the significant yield and average fruit weight reductions under high water restriction (Koundouras et al. 2008). According to Tardieu and Davies (1993), a decrease in root water potential of plants under drought conditions is accompanied by a root signal that tends to decrease stomatal conductance. This concept that correlates the control of stomatal conductance to water availability in the soil highlights plant water potential as a sensitive indicator of plant water stress (Robinson and Barritt 1990; Naor 1998). Under our conditions, because stem water potential and stomatal conductance were similarly limited under high water restriction, whereas foliar water potential did not considerably vary, stomatal closure was assumed to correspond primarily to stem rather than to leaf water potential decrease (Erf and Proctor 1989).

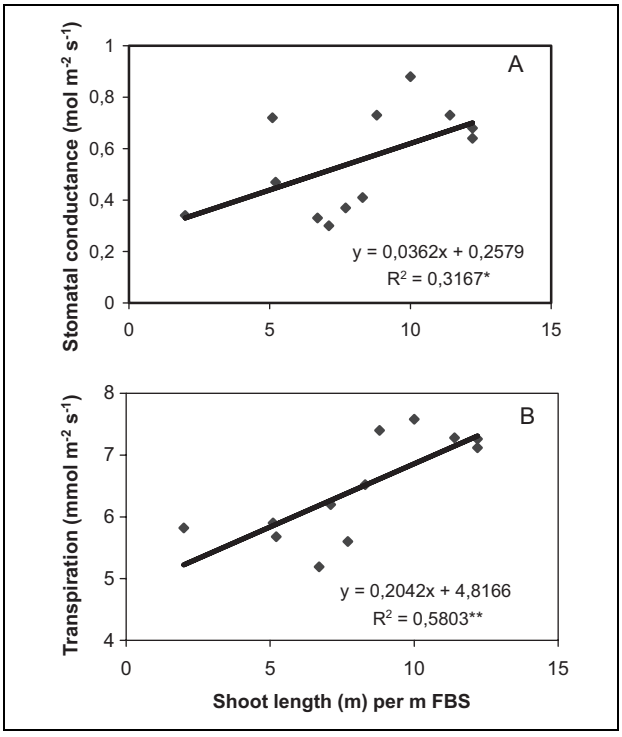


Fig. 3. Leaf stomatal conductance (A) and transpiration rate (B) of 'Alexandra' peach as related to shoot length per meter FBS. Each tree of Exp. I was represented (See "Materials and Methods").

Leaf transpiration rate normally decreases as a classic response to the progressive decline of stomatal conductance (Kilili et al. 1996), subsequently inducing an increase in leaf temperature (Gimenez et al. 1997). Leaf temperature was pinpointed as a possible factor modulating leaf photosynthesis, particularly under various water status of the fruit tree (Li et al. 2001; Guerfel et al. 2007). In our study, a strong limitation in leaf photosynthesis was concomitant with leaf temperatures reaching 34 °C under water restriction. However, this limitation was reported to not be just a response to leaf temperature (Centritto et al. 2005); decline of leaf sub-stomatal CO_2 concentration is also considered as an important factor (Flexas and Medrano 2002). Under various pruning severities, leaf temperature did not significantly vary. However, in contrast to the effect of increasing water restriction, increasing pruning severity contributed to increasing leaf stomatal conductance and leaf transpiration rate, a possible response to a simultaneous sink effect increase. The

lack of significant variations in leaf gas exchange under de-fruited trees compared to fruited trees suggested that the fruit sink effect was moderate in three-year-old peach trees bearing approximately hundred fruits. The correlation of the leaf stomatal conductance and, even more so, the correlation of the leaf transpiration rate with the shoot length per meter FBS suggested that vegetative growth could be an alternate sink to fruit growth, contributing to increasing the photosynthesis rate to its maximum level (MAHHOU et al. 2005; WÜNSCHE et al. 2005). This result ought to be confirmed with older trees bearing higher crop loads.

In conclusion, leaf stomatal conductance and transpiration rate were enhanced under severe pruning and limited under high water restriction during the last stage of rapid fruit growth. Leaf stomatal conductance was shown to be particularly sensitive to environmental factors (water availability) under various intensities of water restriction, and to plant factors (sink effect) under various pruning intensities. Peach growth appeared to vary under the different treatments, in conformity with variations in vegetative growth and leaf gas exchange.

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