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How does winter pruning affect peach tree–*Myzus persicae* interactions?

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Abstract

Winter tree pruning is a cultural practice known to modify vegetative growth, which is likely to affect the development of pests. However, it has been poorly addressed as a cultural control method for diminishing the population levels of the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae), in peach [*Prunus persica* (L.) Batsch (Rosaceae)] orchards. In this study, we conducted a 2-year, on-station experiment to evaluate how winter pruning affects peach–*M. persicae* interactions, by examining tree vegetative growth, aphid population dynamics, and crop yield and fruit quality. We collected data under an insect-proof shelter on adult peach trees submitted to various levels of pruning and artificially infested with aphids. Our results showed that pruning enhanced shoot growth due to the proportion of growing shoots, which increased exponentially (10–60%), whereas the growth rate of growing shoots was not affected. The degree of infestation of peach trees increased with increasing pruning intensity. This effect was mainly due to the increase of the proportion of growing shoots, on which aphids developed better than on rosettes. In turn, the higher the aphid infestation, the higher the aphid-induced shoot-tip damage, leaf curling, and leaf fall that disturbed the growth of growing shoots. However, aphids did not considerably reduce fruit quality at harvest. They did not affect fresh fruit weight, and the refractometric index (indicator of sugar content) was reduced by only 3–4%. The relevance of winter pruning as a cultural method for pest control in orchards conducted under integrated fruit production guidelines is discussed.

Introduction

Aphids, the largest group of plant phloem feeders, are known to depress plant growth and cause extensive loss of crop productivity (Veen, 1985; Davies et al., 2004; Singh et al., 2004; Gironse et al., 2005). As phloem feeders, aphids are considered to be external sinks for assimilates. Assimilate withdrawal can in part explain plant growth reduction. In infested plant stems, aphids not only intercept a part of the assimilate flow but also change the pattern of assimilate partitioning. They can induce redirection of the

movement of assimilates to their own advantage and can convert normal nitrogen sink tissues into nitrogen source tissues (Gironse et al., 2003, 2005). Aphids also damage new growth by inducing top-roll symptoms and chlorosis. It has been suggested that photosynthesis is inhibited in leaves showing such symptoms (Veen, 1985). Aphids produce honeydew on which sooty moulds grow, disturbing leaf photosynthesis. In addition to direct damage, aphids transmit several plant viruses.

Myzus persicae (Sulzer) (Homoptera: Aphididae) is a major pest of the *Prunus persica* (L.) Batsch (Rosaceae) peach crop in Europe. In a temperate climate, *M. persicae* is a holocyclic and dioecious species that overwinters on *Prunus* species as primary host plants. Aphids infest peach trees from the time that winter eggs hatch until the end of spring, when alate fundatrigeniae fly away to secondary

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host plants. In autumn, aphids return to their winter hosts. In peach orchards, *M. persicae* can cause direct damage by assimilate removal, foliage symptoms, fruit distortion, and/or fruit drop of previously punctured flowers, and indirect damage by the transmission of the plum pox virus, the causal agent of sharka disease. Because of its worldwide distribution and its economic importance for many cultivated plant species, the biology, ecology, and control of *M. persicae* have been widely studied. However, such studies have been mainly conducted on secondary host plants (Kennedy & Stroyan, 1959; Van Emden et al., 1969).

Chemicals have been used for many years to control aphids in orchards. Growers are now facing restrictions on the use of broad-spectrum insecticides and the increasing development of resistance to pesticides in aphid populations (Mazzoni et al., 1999; Guillemaud et al., 2003; Anstead et al., 2005). They therefore need aphid management alternatives to simple reliance on pesticide use. In most European countries, the concept of integrated fruit production (IFP) has been promoted since the late 1980s (Sansavini, 1997). The objective defined by IFP guidelines is to achieve high-quality economical production while safeguarding the environment and human health (Cross et al., 1997). To reduce the quantity of chemical inputs used to protect crops from fruit tree pests, IFP gives priority to natural, cultural, and biological control methods. However, most of the emphasis until now has been placed on descriptors of the sampling distribution of pest counts to develop decision-making guidelines and improve insecticide usage (Nyrop & Lakso, 2006). Integrated fruit production implementation needs to focus more on understanding the interactions between components of the crop–pest system and how they are affected by the environment and by management practices (Getz & Gutierrez, 1982). Although studies have been carried out (Leclant & Remaudière, 1970), pest–crop interactions and damage to fruit production remain poorly documented in the peach tree–*M. persicae* system.

Cultural practices can be used to create conditions unfavourable to pest development, and constitute a major component of fruit pest management. An important field of interest is cultural practices involved in plant vigour. The plant vigour hypothesis proposed by Price (1991) predicts that herbivorous insects will perform better on vigorously growing plants. Several studies have confirmed (Inbar et al., 2001; De Bruyn et al., 2002; Teder & Tammaru, 2002) or contradicted (Johnson et al., 2003) this hypothesis. Variations in insect responses, both among insect feeding guilds and within the sucking guild (Koricheva et al., 1998), highlight the complexity of plant–insect interactions. The susceptibility response of insect herbivores to plants greatly depends on the plant and insect species. Several

aphid species, including *Rhopalosiphum padi* (L.), *Aphis citricola* (van der Goot), and *Aphis pomi* (de Geer), have a preference for succulent terminal shoots of cherry or apple trees (Takeda, 1979; Brown & Welker, 1992; Sandström, 2000; Whitaker et al., 2006). On the other hand, *M. persicae* has been predominantly found on the mature leaves of potato plants (Jansson & Smilowitz, 1986). On the peach tree–*M. persicae* system, we have observed that this aphid species preferentially colonizes apices of peach shoots in spring, which agrees with field observations from growers and farm advisers. But references to the aphid's behaviour on peaches in the scientific literature are lacking.

Winter pruning is a training practice used in all fruit orchards to shape fruit trees or to partially adjust crop load. It is generally seen as a means of controlling tree vegetative growth and vigour (Faust, 1989; Marini, 2002), and as such, may also influence aphid performance. However, as far as we know, there are few references in the literature to the response of *M. persicae* to peach tree vigour and to the use of winter pruning as a possible alternative technique of aphid management. The aim of this study was to improve our understanding of the peach–*M. persicae* interactions in relation to winter pruning. We investigated (i) the regulation of aphid populations in relation to vegetative growth, (ii) the responses of trees (i.e., vegetative growth and damage) to aphid attacks and their effects on fruit quality, and (iii) the response of the whole system to winter pruning. The advantages of pruning as a cultural control strategy in IFP systems are presented.

Materials and methods

Experimental orchard

We collected data in 2005 and 2006 in an experimental orchard planted in 1998 with the mid-August peach cultivar Suncrest, grafted onto 'GF 677' rootstock, with 4 × 4.5 m spacing between rows. The experimental plot was located at the INRA Centre of Avignon (southeastern France: 43°9'N, 4°8'E). It consisted of two rows of 10 trees each. The trees were goblet trained. The alleys between rows were sown with grass. As of February 2005, the trees were placed under an insect-proof shelter in order to prevent pests and predators in the surrounding environment from entering the orchard. Sticky bands (20 cm wide) were placed around the trunks in order to prevent ants and other insects from climbing the trees.

Experimental design

We split the orchard into 12 aphid-infested trees (AI) and eight aphid-free trees (non-AI). In 2005, aphids emerged from winter eggs. In autumn of 2005, the insect-proof shelter prevented aphids from flying back to the orchard

Table 1 Characterization of the 20 peach trees and treatments. AI, *Myzus persicae* aphid infested; non-AI, non aphid infested; IP, pruning intensity (%). Groups of IP are defined as follows: LP, IP<30% (2005) and IP<40% (2006); MP, 30<IP<=55% (2005) and 40<IP<=60% (2006); and HP, IP>55% (2005) and IP>60% (2006)

Aphids	IP group	Tree no.	2005		2006	
			IP	Fruit load ¹	IP	Fruit load ¹
AI	LP	1	4.3	680	11.3	479
		2	14.8	888	20.8	295
		3	24.3	509	35.7	344
		4	25.8	819	38.4	247
	MP	5	32.1	477	49.3	444
		6	33.9	648	46.4	271
		7	39.3	416	49.1	539
		8	48.1	511	54.2	324
		9	49.0	332	56.4	389
	HP	10	56.0	289	62.9	341
		11	60.6	371	72.7	254
		12	65.5	476	67.7	231
Non-AI	LP	13	4.8	482	14.5	385
		14	9.9	800	24.6	418
		15	19.0	998	33.9	413
		16	28.2	692	35.8	360
	MP	17	39.4	540	48.8	344
		18	54.0	404	56.5	287
	HP	19	64.4	383	65.9	330
		20	65.4	260	76.6	340

¹Fruit load is the total number of fruits per tree.

and laying eggs on trees. Therefore, the trees of the AI treatment were manually infested in April and May 2006 with aphid colonies reared in the laboratory. A total of 176 aphids were deposited on 24 shoots per tree. To prevent aphid infestation, non-AI trees were regularly sprayed with insecticides (pirimicarb and imidacloprid) from the green-tip stage until the end of the aphid infestation period (mid-June), for a total of four applications in 2005 and three applications in 2006.

We completed pruning in February, which consisted of thinning out 1-year-old wood. Pruning intensity (IP) was defined as the percentage of mass of 1-year-old wood pruned on total 1-year-old wood. The mass of the non-pruned 1-year-old wood was assessed by measuring its length and using the empirical relationship

$$W = a \times L + b \times L^3,$$

where W (in g) and L (in cm) are, respectively, the fresh mass and the length of 1-year-old wood [2005: a = 0.108 ± 0.021 (mean ± SE), b = 6.84 × 10⁻⁵ ± 1.87 × 10⁻⁶,

R² = 0.96; 2006: a = 0.126 ± 0.015, b = 4.33 × 10⁻⁵ ± 1.82 × 10⁻⁶, R² = 0.96]. Pruning intensities ranged from 0 to 80%, and were slightly higher in 2006 than in 2005. Pruning treatments were randomly assigned to both infested and non-infested trees in 2005. The resulting ranking of trees in terms of IP was maintained in 2006.

Trees were managed according to normal commercial practices. They were fertilized with 60 units N/ha divided into three applications (in April, May, and June), and they were spray irrigated (only the ground was irrigated) about twice a week from mid-May to mid-August. Hand-thinning was carried out in mid-May to reduce fruit load. One fruit per 28 and 30 cm of 1-year-old wood was left in 2005 and 2006, respectively. Consequently, the number of fruits per tree varied depending on pruning treatments. Data characterizing the treatments applied to the 20 trees are summarized in Table 1.

Sampling and monitoring

At bud burst, we randomly selected and tagged 60 shoot buds per tree from all over the crown. Aphid populations were monitored at 7-day interval from mid-April until the period when no more aphids were observed on trees (about mid-June). All 60 tagged shoots were described using a classification of infestation degree (Leclant & Remaudière, 1970) adapted by Chen (1997) from tree level to colony level (Table 2). These degrees of infestation (d) were used to calculate an index of relative infestation (IF) for each tree with the following formula:

$$IF = \frac{\sum_{d=0}^5 (d \times f_d)}{5 \times \sum_{d=0}^5 f_d},$$

where d is the degree of infestation [d ∈ {0,1,2,3,4,5}], and f_d is the frequency of shoots with degree of infestation d.

Table 2 Definition of the degrees of infestation (d) used to describe shoot infestation of peach trees by *Myzus persicae*

d	Visual symptoms on the shoot	Number of aphids (n)
0	No aphids on the shoot	n = 0
1	Shoot is slightly infested	1<n≤5
2	Shoot is clearly infested	5<n≤25
3	Top 2–3 leaves become curled	25<n≤125
4	Three to five leaves curled; aphids crowd the top of the shoot	125<n≤625
5	Aphids crowd all over the top of the shoot and more than five leaves	n>625

The presence of winged aphids and predators on the shoot was also recorded.

We monitored vegetative growth on 36 of the tagged shoots by measuring the number of leaves per shoot every 15 days from mid-April to August. At the same time, the number of curled leaves and damaged shoot tips were recorded to evaluate aphid damage. Total shoot length on one main scaffold at the end of the growing season was also measured. A peach tree canopy is composed of two shoot types, which we categorized as rosette shoots (RS) or growing shoots (GS), also known as long shoots. Rosette shoots are less than 2 cm long, whereas GSs have elongated stems of more than 2 cm long. At the end of the growing season, about 150 shoots sampled around the tagged shoots were observed and classified into the two shoot types.

A sample of 36 fruits per tree near the tagged shoot was selected. At maturity, fruits were harvested and total yield was measured. Fruit quality was assessed on the sampled fruits by measuring their size, fresh weight, flesh water content, and refractometric index (RI, °Brix). The RI is the main indicator of quality used in the fruit industry. It is positively correlated with sugar content. Flesh water content and RI were measured on fruit pieces sampled from three locations that were longitudinally equidistant.

In 2006, European earwigs, *Forficula auricularia* (L.) (Dermaptera: Forficulidae), reported as opportunist aphid feeders, were observed in the orchard. They were monitored using strips of corrugated cardboard as artificial refuges. Two strips per tree were rolled around the main scaffolds. Earwigs occupying refuges during the day were counted once a week for 7 weeks.

Data analysis

Trees of AI and non-AI treatments were differentiated into three groups corresponding to different levels of intensity of pruning: high (HP), moderate (MP), and low (LP). In 2005, groups of IP were defined as follows: HP, $IP > 55\%$, MP, $30 < IP \leq 55\%$, and LP, $IP \leq 30\%$. As IP was slightly higher in 2006 than in 2005, group boundaries were increased from 30 and 55% in 2005 to 40 and 60% in 2006, so that the same trees belonged to the same group both years (see Table 1). We used the definitions to graphically describe growth patterns of shoots and aphids under the influence of winter pruning, not for statistical analysis. Time was expressed in Julian Days (JD). Pruning treatment consisted of a gradient of intensity without repetitions. When data were analysed with regression models, the tree was the statistical unit and regressions were applied on the average value of sample measurements. All statistical analyses were performed using R software (R Development Core Team, 2006).

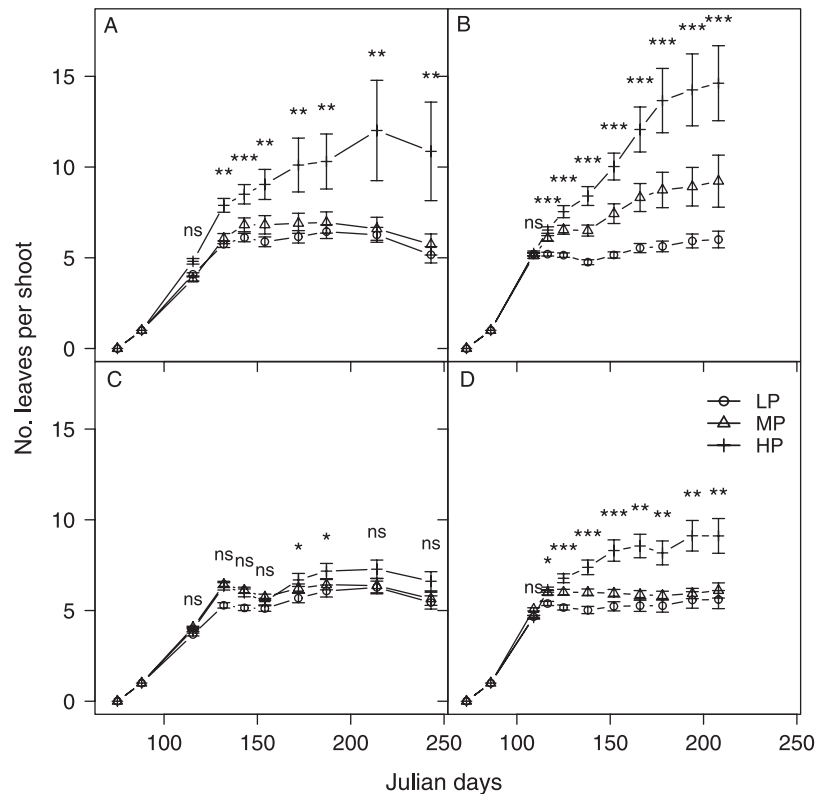
Effect of pruning intensity on tree vegetative growth. The relationship between winter IP and vegetative growth (expressed as the number of leaves per shoot) was estimated with linear regression. At each monitoring date, the linear regression was fitted between the log-transformed mean number of leaves per shoot and the squared IP of the trees from AI and non-AI treatments. We also tested, with a linear model, the effect of IP on the mean GS length measured at the end of the season. Then, the relationship between IP and the proportion of GS of each tree was fitted by a non-linear model on pooled data from both aphid treatments in 2005 and 2006, using a non-linear least-squares method based on the Gauss–Newton algorithm.

Aphid dynamics and predator abundance. The maximal IFs of the trees (i.e., the maximal IF value over time per tree) in 2005 and 2006 were compared with a two-sample Student's t-test. The percentage of infested shoots with at least one winged aphid and the number of predators per shoot were calculated at each monitoring date by averaging the measurements on all the shoots of all the trees of AI treatment. In 2006, analysis of variance (ANOVA) was used to determine significant differences between trees for the number of earwigs caught per day, with the monitoring date as replication. If significant differences were found, a Tukey multiple comparison test with a 95% family-wise confidence level was used to separate means.

Effect of pruning intensity and vegetative growth on aphid dynamics. We used linear models to analyse the relationships between the level of infestation of the trees (maximal IF and IF measured at each monitoring date) and IP, and between IF measured at each monitoring date and the proportion of GS. A χ^2 -test of independence was used to test, at all monitoring dates, whether or not shoot infestation was related to shoot type (i.e., GS and RS).

Effect of aphids on shoot growth and fruit quality. A two-sample Student's t-test was performed on the mean GS lengths of the trees from AI and non-AI treatments. We calculated shoot growth rates for each tree by differentiation of the mean number of leaves per shoot, interpolated on a daily basis using a local polynomial regression fitting method. The proportion of curled leaves per shoot was averaged per tree and monitoring date. The lowest value of shoot growth rate and the highest proportion of curled leaves per shoot over the period of aphid infestation were selected for each tree. By pooling data from 2005 and 2006, relationships between these values and highest IF were analysed with linear models. An average value of the RIs measured along the three directional orientations was considered for each fruit. Refractometric indices of non-AI

Figure 1 Seasonal measurements of the number of leaves per shoot of an average shoot of (A) non-aphid-infested peach trees in 2005, (B) non-aphid-infested trees in 2006, (C) *Myzus persicae* aphid-infested trees in 2005, and (D) aphid-infested trees in 2006 under low (LP), medium (MP), and high (HP) pruning intensity. Vertical bars represent standard error (SE) of group means. Asterisks represent P-values of the F-statistic of linear regressions between the number of leaves per average shoot (log-transformed) and pruning intensity (squared) performed at each monitoring date on all trees of each aphid treatment × year combination; ns, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.



and AI treatments were compared by a two-sample Student's t-test. Fresh weight of fruits of non-AI and AI treatments were compared by testing nested linear models. Full models (i.e., including aphid infestation and fruit load as predictive variables) and reduced models (i.e., only including fruit load as a predictive variable) were compared using a Fisher test.

Results

Effect of pruning intensity on tree vegetative growth

Pruning intensity influenced the time course of shoot growth, expressed as the number of leaves per shoot. On non-AI trees, the shoots of the HP group maintained their growth throughout the season, whereas those of the LP group stopped their active growth early in the season. In the case of the MP group, active shoot growth was maintained only in 2006, but at a lower rate than the HP group (Figure 1). In both years, the relationship between the number of leaves per shoot and IP of non-AI trees was significant at all monitoring dates ($R^2 = 0.76\text{--}0.97$, $F_{1,6} = 19.4\text{--}174.2$, all $P < 0.01$), except the first one. These results indicate that shoot growth increased exponentially with IP. Linear regression indicated no significant relationship between IP and the length of GS measured at the end of the season (2005: $R^2 = 0.22$, $F_{1,6} = 1.71$, $P = 0.24$; 2006: $R^2 =$

0.08 , $F_{1,6} = 0.53$, $P = 0.49$). Pruning intensity modified the relative proportion of GS and RS of the trees. Growing shoots represented about 10% of the total number of shoots in the least pruned trees, and reached about 60% in the most heavily pruned trees, independently of infestation (Figure 2). The percentage of shoots developing into GS can be predicted by the following model:

$$\%GS = a \times e^{b \times IP},$$

where $a = 7.496 \pm 1.337$ (SE) and $b = 2.547e-02 \pm 3.012e-03$ (SE).

Aphid dynamics and predator abundance

Aphid infestation varied in a synchronous way among trees for both years, but differently between years (Figure 3). The index of relative infestation increased more slowly and reached lower levels ($t = 2.81$, d.f. = 18.3, $P < 0.05$) in 2006 (IF = 0.175) than in 2005 (IF = 0.302). Aphid populations collapsed a few days after peak occurrence in both years. The number of aphids ultimately fell to 0 at 186 JD in 2005 and 194 JD in 2006. The percentage of shoots infested with at least one winged form was highest at 145 JD (76%) in 2005 and 178 JD (73%) in 2006. However, no relationship was found on these dates between the proportion of

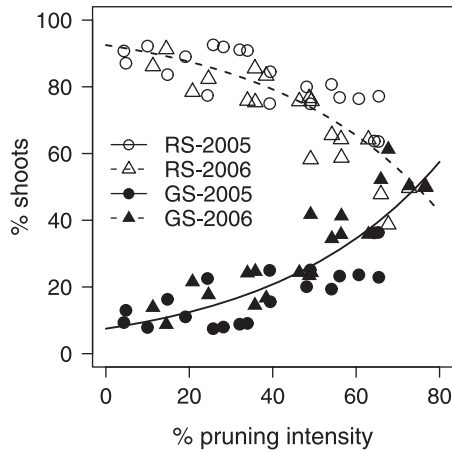


Figure 2 Proportion of rosette (RS) and growing shoots (GS) per peach tree in relation to pruning intensity of non-aphid-infested (non-AI) and *Myzus persicae* aphid-infested (AI) trees in 2005 and 2006. The lines are due to model adjustment (percentage of GS as an exponential function of pruning intensity) for GS (—) and RS (100 minus the GS percentage, ---).

winged forms and the index of aphid density per tree. Premature leaf senescence of infested leaves occurred around 130–150 JD in 2005, and 160–180 JD in 2006 (see next section). Aphids that had fallen with these leaves were prevented from upward migration by the sticky bands on the trunks. At the end of June, we observed higher aphid mortality, and this was in part associated with high temperatures. From about 165 JD, the maximum daily temperature exceeded 30–32 °C in both years.

Despite the insect-proof shelter, predators were occasionally observed on the trees. Coccinellids and syrphids were observed as of 158 JDs in 2005 and 178 JDs in 2006 (with a peak number of individuals per shoot below 0.04 in 2005 and 0.01 in 2006). In 2006, parasitism was observed

as of 157 JD. Earwigs were present in the orchard throughout the season. The number of earwigs differed between trees ($F_{11,72} = 11.4, P < 0.001$). A Tukey multiple comparison test indicated that the two trees at the limit of the insect-proof shelter had significantly higher numbers of earwigs (the cumulated numbers from 149 to 191 JDs were 870 and 950, respectively) than the other trees (on average 200). Aphid colonies did not develop on these two trees. Thus, these two border trees were excluded from the rest of the study. The feeding activity of earwigs was considered to be the same on the remaining trees.

Effect of pruning intensity and vegetative growth on aphid dynamics

Aphid populations reached higher levels with increasing IP in both 2005 and 2006 (Figure 3). In 2005, MP and LP groups were not very different. Positive linear relationships between peak IF and IP were significant in 2006 ($R^2 = 0.69, F_{1,8} = 17.5, P < 0.01$) and in 2005, after removing one tree from the analysis ($R^2 = 0.41, F_{1,9} = 6.28, P < 0.05$). This tree (no. 3, Table 1) had a high proportion of GS (23%) despite a moderate IP (24%), and it had the highest initial value of IF (data not shown). Significant positive relationships between IF and IP were recorded on five dates out of nine ($R^2 = 0.46–0.75, F_{1,9} = 7.52–26.6, \text{all } P < 0.05$) in 2005 (without tree no. 3; Figure 3A) and on seven dates out of 11 ($R^2 = 0.50–0.68, F_{1,8} = 8.17–17.2, \text{all } P < 0.05$) in 2006 (Figure 3B).

Shoot infestation was related to shoot type. The proportion of infested shoots was significantly higher for the GS type than for the RS type on almost all dates (2005: $\chi^2 = 14.0–40.9, \text{d.f.} = 1, \text{all } P < 0.001$; 2006: $\chi^2 = 3.9–28.4, \text{d.f.} = 1, \text{all } P < 0.05$) (Figure 4). Moreover, infestation degrees reached lower levels on RS than on GS. All along the monitoring period, the percentage of infested shoots that reached an infestation degree greater than or equal to 2 was higher for the GS type (59% in 2005 and 42% in 2006) than

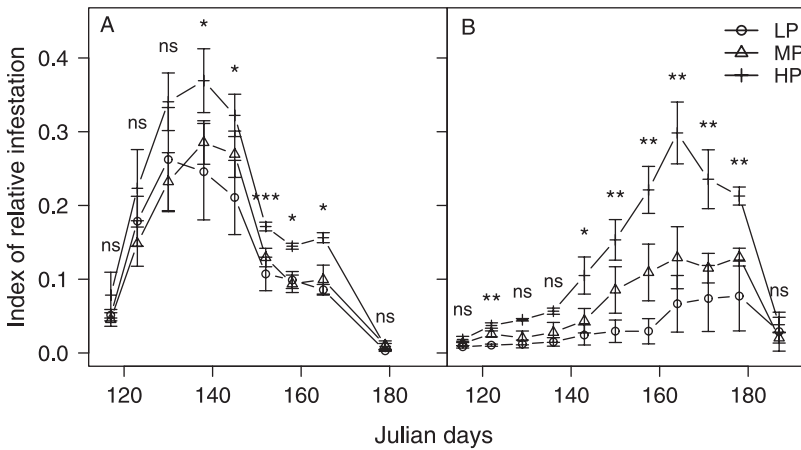
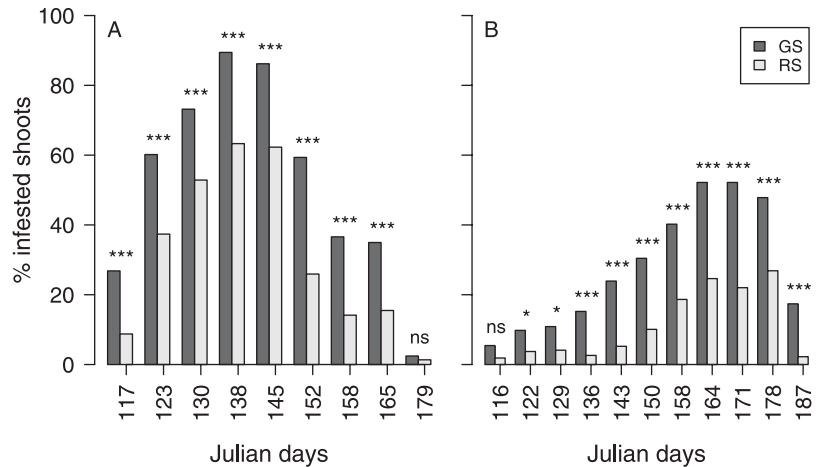


Figure 3 Seasonal measurements of the index of relative infestation of *Myzus persicae* aphid-infested (AI) peach trees in (A) 2005 and (B) 2006 under low (LP), medium (MP), and high (HP) pruning intensity. Vertical bars represent standard error (SE) of group means. Asterisks represent P-values of the F-statistic of linear regressions between the index of relative infestation and pruning intensity performed at each monitoring date on all trees of AI treatments (without tree no. 3 in 2005 and trees no. 1 and 11 in 2006); ns, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

Figure 4 Seasonal measurements of the proportion of *Myzus persicae* aphid-infested peach shoots depending on the type of shoot in (A) 2005 and (B) 2006. GS, growing shoots; RS, rosette shoots. P-values of the χ^2 -test performed at each monitoring date are indicated; ns, $P>0.05$, $*P<0.05$, $***P<0.001$.



for the RS type (36% in 2005 and 24% in 2006) in both years. Positive and significant linear relationships between IF and the proportion of GS were found from the third to the sixth monitored date ($R^2 = 0.43-0.78$, $F_{1,10} = 7.53-36.2$,

all $P<0.05$) in 2005, and from the fifth to the tenth monitored date ($R^2 = 0.44-0.54$, $F_{1,8} = 6.37-9.53$, all $P<0.05$) in 2006.

Effect of aphids on shoot growth and fruit quality

The average length of GS at the end of the season was significantly lower in the AI treatment (10.8 cm in 2005, 21.5 cm in 2006) than in the non-AI treatment (16.6 and 26.1 cm, respectively) (2005: $t = 5.61$, d.f. = 12.87, $P<0.001$; 2006: $t = 2.13$, d.f. = 14.55, $P = 0.05$). It was reduced by 35% in 2005 and 18% in 2006. In addition, the relationship between the number of leaves per shoot and IP for the AI treatment was significant at all dates except the first one in 2006 ($R^2 = 0.56-0.85$, $F_{1,8} = 10.2-43.7$, all $P<0.05$), but only at the fifth and sixth monitoring dates in 2005 ($R^2 = 0.37$, $F_{1,10} = 5.78$, $P<0.05$ and $R^2 = 0.45$, $F_{1,10} = 8.22$, $P<0.05$). The relationship was not as good as for the non-AI treatment (Figure 1), indicating that it was disturbed by aphid infestation, especially in 2005, as characterized by higher IF. From around 130–150 JD in 2005 and 160–180 JD in 2006, the number of leaves per shoot of infested trees decreased (Figure 1C,D), due to a premature fall of curled leaves, resulting in a negative shoot growth rate of almost all the trees (Figure 5A). By pooling data from 2005 and 2006, a linear decreasing relationship was observed between the lowest value of shoot growth rate and the highest value of IF during the period of aphid infestation ($R^2 = 0.65$, $F_{1,22} = 41.1$, $P<0.001$; Figure 5A). A linear positive relationship was also observed between the highest proportion of curled leaves per shoot and peak IF ($R^2 = 0.69$, $F_{1,22} = 49.7$, $P<0.001$; Figure 5B). In 2005, after leaf fall, the shoot growth rate of infested trees increased. In 2006, this regrowth tendency was only observed in the HP group (data not shown). Nevertheless, at the end of the growing period, the number of leaves per shoot of AI trees remained low compared to that of non-AI trees (Figure 1).

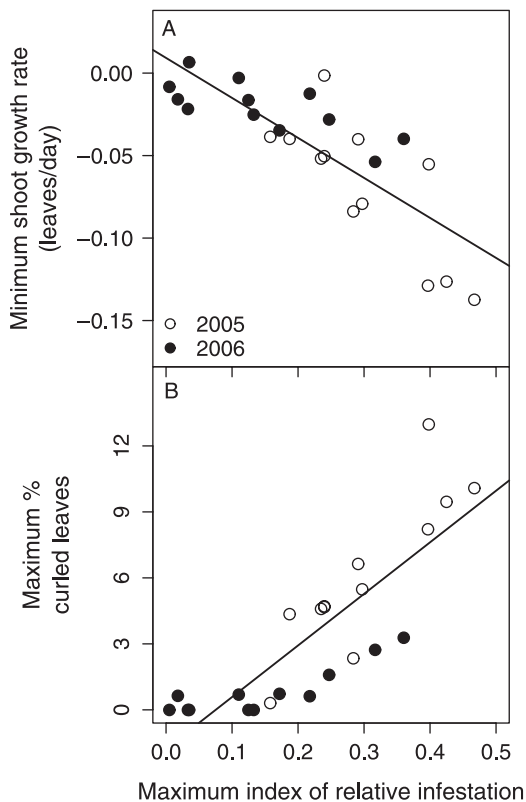


Figure 5 Relationship between the (A) minimum peach shoot growth rate or (B) the maximum proportion of curled leaves of an average shoot and the peak index of relative infestation of *Myzus persicae* aphid-infested trees in 2005 and 2006. Each point represents one tree.

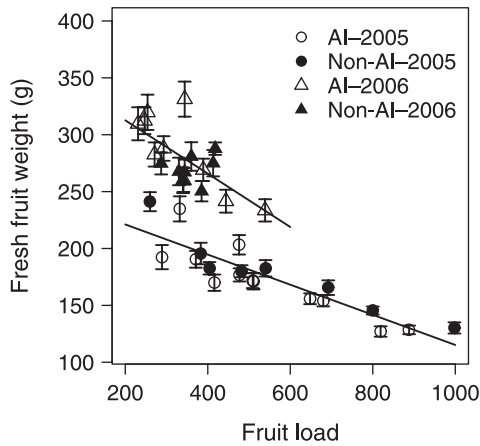


Figure 6 Relationship between average fresh fruit weight (g) and fruit load of non-aphid-infested (non-AI) and *Myzus persicae* aphid-infested (AI) peach trees in 2005 and 2006. Lines are linear regression models. Vertical bars represent SEM.

Fruit weights and the RI were higher in 2006 than in 2005. A close linear relationship between fresh fruit mass and fruit load was observed. The relationship was not significantly affected by aphid infestation (2005: $F_{2,16} = 1.13$, $P = 0.35$; 2006: $F_{2,16} = 2.38$, $P = 0.13$) (Figure 6). The average RI of fruits was 8.7 and 10.2 °Brix on infested trees, and 9.0 and 10.6 °Brix on non-infested trees, in 2005 and 2006, respectively. RI was significantly reduced by aphid infestation in 2005 and 2006 (2005: $t = 2.30$, d.f. = 566.2, $P < 0.05$; 2006: $t = 2.83$, d.f. = 573.4, $P < 0.01$; Figure 7). Nevertheless, the losses due to aphids were only about 3–4% of °Brix in both years.

Discussion

Aphid dynamics and the effect of pruning

The present study shows that severe winter pruning applied to peach trees increased the abundance of *M. persicae* aphids. This effect is mediated via an enhancement of vegetative growth. In addition, comparison between years indicates that a more differentiated shoot growth resulted in a more marked effect of pruning on aphid densities. The observed preference of aphids for growing shoots as compared to rosettes supported the plant vigour hypothesis. Based on this study, *M. persicae* can be classified as a preferential flush feeder on peach trees in the spring. Vegetative growth enhancement induced by severe pruning has been widely observed on fruit trees (Schneider & McClung, 1957; Lakso, 1984; Forshey & Marmo, 1985). However, the mechanisms underlying growth modifications are still not clear. Our study indicates that pruning shifts the distribution of shoot growth from rosettes to extension

shoots. Rosettes stopped their growth early in the season (at about 130 JD), when a number of preformed leaves had extended, while growing shoots could maintain their growth throughout the season, producing newly formed leaves. Due to a higher proportion of growing shoots, pruning prolongs the period of active vegetative growth. In addition, contrary to other studies on apple and peach trees (Schneider & McClung, 1957; Forshey & Marmo, 1985), we did not observe an effect of pruning on mean growing shoot length. The location and the type of cuts applied to the tree, as well as tree age, could explain variations observed between studies (Faust, 1989). Peach trees have a high capacity for new leaf formation (Gordon et al., 2006), which allows a high degree of plasticity of the canopy in response to current environmental conditions or manipulations such as pruning. As shown in the present study, severe pruning enhanced the proportion of suitable plant parts (i.e., the growing shoots) available to aphids. The mechanisms involved in the higher performance of *M. persicae* on flush leaves compared to mature leaves and, more generally, the preference of some aphid species for vigorous plant parts is still open to discussion.

In the 2 years of the study, the seasonal pattern of aphid dynamics was not affected by winter pruning. Despite the different timing of peak occurrence, aphid extinction in peach orchards appears to be a relatively regular event (186 JDs in 2005 and 194 JDs in 2006). The delay of peak occurrence and the different levels of infestation between the 2 years could be explained by two main factors. The first one was

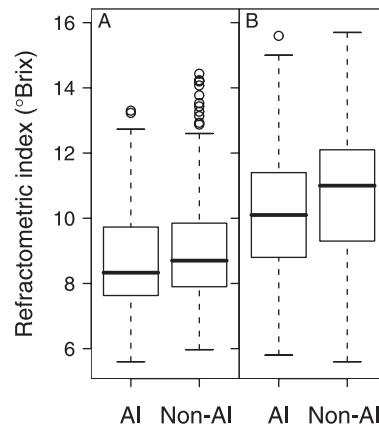


Figure 7 Boxplot distribution of refractometric index of the fruits sampled on peach trees of *Myzus persicae* aphid-infested (AI) and non-aphid-infested (non-AI) treatments in (A) 2005 and (B) 2006. Lower line, first quartile; line dividing the box, median; upper line, third quartile; open dots, outliers, that is, values that are more than 1.5*IQR lower than the first quartile and 1.5*IQR higher than the third quartile, where IQR is the interquartile range.

the type of infestation, that is, controlled vs. natural. When controlled (in 2006), infestation may be less effective because of a later infestation, a lower quantity of inoculum, and the need to acclimate the aphids from optimal laboratory conditions to variable climatic conditions. The second factor was the presence of the generalist European earwig predator in the orchard early in the 2006 season. This insect feeds on a range of orchard pests, including the green peach aphid (Lenfant & Sauphanor, 1992). It has been reported as a principal control agent of the woolly aphid (Mueller et al., 1988; Nicholas et al., 2005). Therefore, its presence can explain the difficulties involved in establishing the aphid population.

Processes commonly reported to explain the drop in aphid populations include enhanced emigration and lower fecundity of winged forms, depressed performance, and elevated mortality of aphids (Van Emden et al., 1969; Dixon, 1987; Karley et al., 2004). Factors presumed to be involved in these processes are plant nutritional quality, crowding, temperature, day-length, and predation (Van Emden et al., 1969; Sandström, 2000; Muller et al., 2001; Awmack & Leather, 2002). Our data were insufficient to draw clear conclusions on the relative importance of these ecological factors and on whether or not their effects are modified by winter pruning. Nevertheless, they confirmed that winged induction and mortality induced by temperature and predation (although reduced with partial exclusion of predators) are involved in population decline. But they did not clearly confirm the role of crowding in wing induction at the tree level, and the respective role of crowding and plant quality as affected by winter pruning on aphid seasonal patterns could not be identified. Results suggested complex interactions among the different factors. In addition, this study identified premature leaf fall as another process that could explain population decline.

Effect of aphids on shoot growth and fruit quality

In our study, aphid infestation reduced the average stem elongation of growing shoots. Similar effects have been reported for other aphid–plant systems and were attributed to both nutrient withdrawal and apical sink strength reduction through signals triggered by aphid feeding (Girousse et al., 2003, 2005). In this study, one of the main sources of damage was distortion of the leaves, causing premature senescence. Our results showed that defoliation intensity was related to aphid densities. Similar relationships were obtained by Straw et al. (2005) on the green spruce aphids–Stika spruce system. A recent study of the *Arabidopsis*–*M. persicae* system by Pegadaraju et al. (2005) indicated that premature senescence was not due to cell damage but instead to an increase in the expression of senescence-associated genes induced by aphid feeding.

Naturally senescent leaves or premature chlorotic leaves are generally of good quality for aphids (Awmack & Leather, 2002; Johnson et al., 2003). Induced chlorosis could be considered as a manipulation of host physiology that is beneficial to the insect, as it improves host quality. However, hypersenescence also contributed to limiting aphid infestation so that, from this point of view, it is beneficial to the host (Pegadaraju et al., 2005).

Despite aphid-induced foliage damage, fruit growth and fruit quality were hardly reduced. In 2006, a lower fruit load and a higher vegetative growth (resulting in a higher leaf:fruit ratio) explained a higher fruit growth and RI value, when compared to 2005. Shoots were highly capable of at least partially recovering the canopy biomass after premature defoliation. Because the study was conducted on a late maturing cultivar (harvested at around 220 JD), the period of fruit enlargement and sugar accumulation (stage III; from 80 days after full bloom, at about 160 JD, to harvest) occurred at the time when aphid populations had disappeared and vegetative regrowth had started. In the case of an early maturing cultivar, higher production losses could be expected because aphid damage occurs when the leaf area index is low and because fruits and leaves are highly competitive sinks, both of which lead to resource-limited growth conditions (DeJong et al., 1987). Our results raise questions about the processes involved in the capacity of fruit trees to support relatively high aphid infestations. The capacity of regrowth allowed by the plasticity of the canopy, the growth dynamics of vegetative and reproductive parts, and the kinetics of carbon reserve replenishment in the perennial parts of the tree should be of particular interest for future studies.

Relevance of winter pruning as a method of aphid control in integrated fruit production

Our results did not support the hypothesis that peach trees need to be totally protected from aphids if they are not involved in sharka epidemic. However, resident aphids such as *M. persicae* should be less involved in the spread of the sharka disease than migratory aphid species (Gottwald et al., 1995). Results highlight the relevance of studying winter pruning as a potential complementary method of aphid control in orchards, given the relative capacity of peach trees to tolerate a certain level of aphids without major production losses, as was demonstrated in this study, thus confirming results of Leclant & Remaudière (1970). Indeed, the levels of aphid infestation were of the same order of magnitude as those observed on untreated trees in the field by Karagounis et al. (2006). In French peach orchards and when indirect damage is not taken into account (i.e., transmission of the sharka disease), it is recommended to apply insecticide when more than 7% of

the shoots are infested (ACTA, 1974). Based only on direct damages, our results led us to question the relevance of such thresholds, as did those of Candolfi et al. (1993), who shed doubts on the empirically defined economic injury level used by grape growers for the European red mite.

Pruning performed in our study was slightly different from standard practices concerning the choice of fruiting shoots, but our highest pruning treatments were rather close to conventional pruning (Giauque, 2003) as far as IP is concerned. Slight pruning treatments reduced aphid populations, mainly through a reduction in plant vigour and in the proportion of growing shoots. However, low pruning reduced the wood rejuvenation capacity of new shoots due to an increase of the proportion of rosettes. This could be a problem, as growers need to maintain fruiting wood throughout the tree canopy; ideal fruiting shoots from the viewpoint of agronomic performance are moderately vigorous shoots, whereas short shoots tend to produce small fruits (Marini, 2002). Additionally, low pruning may render crop load adjustment difficult.

Integrated fruit production gives priority to alternatives over chemical methods of pest control. Henceforth, IFP implementation needs to consider not crop and pest management separately but crop–pest management. Until now, few studies have dealt with the impact of one or a set of practices on both agronomical and ‘pest’ performances. Among them are studies of the combined effect of irrigation and pruning on peach yield, quality, and susceptibility to brown rot (Mercier et al., 2008). Our study is of particular interest in this context as we investigated the effect of winter pruning on aphid dynamics as well as tree growth, and fruit yield and quality. An ideal winter pruning should provide a trade-off between the need for production of fruiting shoots, fruit yield and quality enhancement, and the regulation of aphid populations.

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