Gas Exchange Characteristics of Apple and Peach Leaves Infested by European Red Mite and Twospotted Spider Mite

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Abstract. Greenhouse-grown 'Imperial Delicious' apple (*Malus domestica* Borkh.) and 'Redhaven' peach (*Prunus persica* Batsch.) trees were inoculated during the summer with three densities of European red mite (ERM) (*Panonychus ulmi* Koch) and twospotted spider mite (TSM) (*Tetranychus urticae* Koch). As ERM- and TSM-days increased, net photosynthesis (Pn), transpiration (Tr), and total chlorophyll content (TCHL) of apple leaves decreased linearly. At similar densities, TSM was more damaging than ERM to apple leaf gas exchange. Water-use efficiency (WUE) of apple declined similarly with increasing mite-days for both mite species. Specific leaf weight (SLW) of apple increased with TSM-days. Pn, Tr, TCHL, and WUE of peach declined linearly with increasing ERM- and TSM-days, and the rates of decline were similar for both mite species. Mites did not affect peach SLW. These results indicate that greenhouse-grown peach is more tolerant than apple to mite feeding.

Present pest management programs assume that mite species are equally destructive. However, Flaherty and Huffaker (1970) and Youngman et al. (1986) demonstrated that mite species can affect host plants differently. Therefore, the evaluation of each mite species on orchard crops becomes more important.

Traditionally, researchers focused on screening chemicals for mite control on fruit trees; however, with the re-evaluation and removal of standard pesticides, such as cyhexitin (plictran), interest in host plant-tetranychid mite interactions has been renewed.

Leaf gas exchange of apple, cherry, peach (Ferree et al., 1986), strawberry (Sances et al., 1981), and almond (Andrews and LaPre, 1979) were adversely affected by mite feeding. Pn was progressively reduced as TSM populations increased (Andrews and LaPre, 1979; Hall and Ferree, 1975; Sances et al., 1981). Tr generally decreased with mite feeding (Ferree and Hall, 1981), but results were more variable than for Pn (Ferree et al., 1986; Sances et al., 1981).

Several greenhouse studies (Ferree and Hall, 1981; Ferree et al., 1986; Hall and Ferree, 1975) showed reductions in apple leaf Pn and Tr after moderate mite feeding injury, but similar data for peach are lacking. However, peach yield and growth were not influenced by large ERM (McClernon and Marini, 1986) or TSM (Bailey, 1979) populations, suggesting that field-grown peach trees may be more tolerant of mite feeding.

The purpose of this study was to compare the influence of TSM and ERM on Pn, Tr, SLW, and TCHL of leaves on 1-year-old, greenhouse-grown apple and peach trees.

Materials and Methods

One-year-old 'Imperial Delicious' apple trees on MM. 111 rootstock were placed in the greenhouse on 13 Apr. One-year-old 'Redhaven' peach trees on 'Halford' rootstock were placed in a greenhouse on 17 May. Experimental methods were similar for each tree species. Each species was considered an experiment.

All trees were planted in 3.7-liter pots in a medium of equal parts (by volume) peat, perlite, and vermiculite. At planting, every tree received one application of micronutrients in the form of soluble trace elements mix at 600 mg-liter⁻¹. Each tree was fertilized with soluble fertilizer (20N-8.2P-15K) (Peters Fertilizer Products, W.R. Grace and Co., Allentown, Pa.) at 200 mg N/liter at 18, 25, and 32 days after planting for apple and 14, 24, and 41 days after planting for peach. In preliminary studies, Mg deficiency was observed; therefore, MgSO₄ at 12.5 g-liter⁻¹ was applied foliarly 29 and 40 days after planting for apple and peach, respectively.

Both apple and peach trees were trained to one vigorous shoot. Methyl N-[[[(methylamino) carbonyl]oxy]ethanimidothioate (methomyl; Lannate 50W) at 1.2 g a.i./liter controlled aphids and whitefly. Tricyclohexylhydroxystannane (cyhexitin; Plictran 50W) at 225 mg a.i./liter controlled mites before treatments began. 1-Naphthalenyl methylcarbamate (carbaryl; Sevin 50W) was applied during the experiment at 1.2 g a.i. /liter to eliminate mite predators.

For both experiments, six single-tree replicates were used per mite species in a randomized complete-block design. Three leaves of similar age per tree were tagged. Tack trap (Necessary Trading Co., New Castle, Vs.) was applied to the stem above and below the petiole of each treatment leaf to confine mite populations. Mite densities of 0, 10, or 40 mites per leaf, representing control, low, and high densities, respectively, were randomly assigned to one tagged leaf per tree. For each experiment, six trees were inoculated with ERM, and six trees were inoculated with TSM. Adult ERM and TSM were collected from field and greenhouse sources and deposited on the upper surface of the leaf. Mites were added or removed daily to maintain population differences. Mite days (MD) were determined every 2 or 3 days by averaging the number of mites per leaf between two counting dates and multiplying by the number of 24-hr periods that had elapsed (Sances et al., 1981).

Pn and Tr were determined for each tagged apple leaf at 0 (19 May), 6, 13, 17, and 20 DAT and for each tagged peach

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Abbreviations: DAT, days after treatment; ERM, European red mite; Pn, net photosynthesis; SLW, specific leaf weight; TCHL, total chlorophyll; Tr, transpiration; TSM, twospotted spider mite; WUE, water-use efficiency.

Fig. 1. Mite-day accumulations for low and high mite densities for apple (A) and peach (B) trees at various days after mite placement.

leaf-at 0 (9 July), 4, 9, 13, 19, 26, 39, and 43 DAT. Trees were transported to the laboratory the evening before measurement. Pn was determined with an Anarad model Ar-600 infrared gas analyzer (Anarad, Santa Barbara, Calif.) using chambers similar to those described by Syvertsen and Smith (1983). Westinghouse (500 R/3 FL) lamps provided a photosynthetic photon flux of $1050 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. Air temperature in the chamber was $28 \pm 2^\circ\text{C}$ and relative humidity was maintained at $60\% \pm 5\%$. Tr was determined with a General Eastern 1100AP model dewpoint hygrometer (General Eastern Instruments, Watertown, Mass.). Pn and Tr values were used to estimate WUE. The test leaves were harvested at the conclusion of each experiment. Four leaf disks, two from each side of the midrib, totaling 1.26 cm^2 , were used to determine TCHL for each leaf by acetone extraction, as described by Arnon (1949) and modified by Marini (1986). Absorbance at 645 and 663 nm was measured with a Shimadzu spectrophotometer (model UV-160; Shimadzu Scientific Instruments, Columbia, Md.). Leaf area was determined with a LI-COR model LI-3000 portable leaf area meter (LI-COR, Lincoln, Neb.). Leaf dry weight was recorded after 72 hr at 70°C in a forced-air drying oven.

Data were tested by analysis of variance and regression. Mean separation was by Tukey's HSD at the 5% level.

Results and Discussion

Mite densities did not differ between mite species; therefore, species data were pooled. A control treatment with no mites

Fig. 2. Net photosynthesis (Pn), transpiration (Tr), and water-use efficiency (WUE) of apple leaves as influenced by varying European red mite (ERM)- and twospotted spider mite (TSM)-days. (top) ERM, $P_n = 19.2 - 0.0049 \text{ MD}$, $R^2 = 0.47$; TSM, $P_n = 19.4 - 0.0094 \text{ MD}$, $R^2 = 0.84$; (center) ERM, $Tr = 1.32 - 0.000061 \text{ MD}$, $R^2 = 0.02$; TSM, $Tr = 1.25 - 0.00035 \text{ MD}$, $R^2 = 0.42$; (bottom) WUE ($\mu\text{mol CO}_2/\text{m}^2 \text{ per sec}/\text{mmol H}_2\text{O per m}^2 \text{ per sec}$); ERM, $WUE = 14.8 - 0.0032 \text{ MD}$, $R^2 = 0.23$; TSM, $WUE = 15.7 - 0.0049 \text{ MD}$, $R^2 = 0.51$.

and two discrete mite densities were maintained for both apple (Fig. 1A) and peach (Fig. 1B) leaves.

Apple gas exchange. There was a significant mite species $\times$ mite density $\times$ DAT interaction for apple Pn and Tr. Therefore, regression analyses were performed for each mite species using mite-days per leaf as the independent variable. As ERM- and

Table 1. Tree species and mite species interaction means for TCHL and SLW of 'Imperial Delicious' apple and 'Redhaven' peach leaves on final measurement date, 1988.

Mite species	Apple			Peach		
	Mite days	TCHL ($\mu\text{g}\cdot\text{cm}^{-2}$)	SLW ($\text{mg}\cdot\text{cm}^{-2}$)	Mite days	TCHL ($\mu\text{g}\cdot\text{cm}^{-2}$)	SLW ($\text{mg}\cdot\text{cm}^{-2}$)
ERM	0	17.6	6.5	0	25.7	6.3
	738	15.6	6.5	3116	13.8	6.0
	1741	13.1	6.3	4309	11.8	6.1
TSM	0	17.0	6.5	0	23.3	6.6
	776	14.1	7.0	3058	15.9	6.2
	1755	11.2	7.1	4206	12.4	6.3
Significance			<i>P</i> values			
Mite spp.	0.78	0.04	0.01	0.52	0.94	0.13
Mite days (MD)	0.01	0.01	0.08	0.01	0.01	0.16
M $\times$ MD	0.51	0.68	0.01	0.87	0.22	0.92
SE (overall mean)		0.3	0.02		0.5	0.2
Regression ²		L	Q ^y		L	NS
R ²		0.59	0.46		0.74	---

²Statistical significance levels were assessed at $P \leq 0.05$ ($n = 36$); NS represents nonsignificance and L and Q represent significant linear and quadratic terms, respectively. In the event of a nonsignificant interaction, mite species were pooled for regression analyses. Coefficients of determination (R^2) are for the combined regression model for TCHL vs. MD and SLW vs. MD. Where was a nonsignificant relationship for SLW vs. ERM-days; however, there was a significant quadratic relationship for SLW vs. TSM-days ($n = 18$).

TSM-days increased, Pn declined linearly (Fig. 2, top). Intercepts and slopes differed from zero for each mite species. Slopes for mite species differed ($P \leq 0.01$); the slope for TSM was nearly twice as steep as the slope for ERM. It took 900 mite-days for TSM to reduce Pn by 45%, whereas 1750 ERM-days were required to cause a similar effect. In sharp contrast, visible injury was detected earlier for ERM-damaged leaves than for TSM-damaged leaves (data not shown).

Although Tr declined linearly with increasing mite-days for both mite species, data were more variable for ERM than TSM, as indicated by the lower R^2 value (Fig. 2, center). Intercepts and slopes differed from zero ($P < 0.05$) for each mite species, and slopes for mite species differed ($P = 0.01$). As with Pn, Tr was reduced more by TSM than by ERM. Tr was reduced by 8% with 300 TSM-days and 1741 ERM-days.

Apple Pn and Tr were damaged more per individual with TSM than ERM. These results concur with a study by Youngman et al. (1986) that compared the effects of *Panonychus citri* (McGregor), *P. ulmi*, *Tetranychus urticae*, and *T. pacificus* on gas exchange of almond leaves. *Tetranychus* spp. were more damaging than *Panonychus* spp. Gas exchange characteristics were affected equally within mite genera.

Although apple WUE declined with increasing ERM- and TSM-days (Fig. 2, bottom), it did not differ between mite species. Pn was reduced more than Tr for both mite species; therefore, as mite days increased, WUE declined.

Chlorophyll content decreased linearly with increasing mite-days and there was no mite species $\times$ mite-day interaction (Table 1). Boulanger (1958) and Zwick et al. (1976) also found that mite feeding reduced leaf chlorophyll content. SLW was not affected by ERM, but was positively related to TSM populations (Table 1). The basis of the increase in SLW induced by TSM is not understood; however, these results are in agreement with Campbell et al. (1989).

To characterize the reduction of Pn, stepwise regression models, using Tr and TCHL as first- and second-order terms, were developed for each mite species. Apple Pn models differed for

each mite species. For ERM, TCHL was the most significant term in the model ($R^2 = 0.67$). Addition of the Tr term did not contribute greatly ($R^2 = 0.68$) to the explanation of Pn variation. In contrast, both Tr and TCHL explained a significant amount of variation in Pn for TSM. The Tr term ($R^2 = 0.70$) accounted for most of the variation. The addition of TCHL² to the model increased the R^2 value to 0.83. Youngman et al. (1986) also reported that mite genera altered leaf physiology differently.

Peach gas exchange. There was a significant mite density $\times$ DAT interaction for Pn ($P \leq 0.01$). Pn declined linearly with increasing ERM and TSM mite-days (Fig. 3, top). Intercepts and slopes differed significantly from zero, but not between mite species.

To account for random variation often encountered in photosynthetic studies due to measurement date (Hall and Ferree, 1975) and to account for the gradual decline in Pn as leaves age (Ferree and Barden, 1971), Pn data were expressed as the percent of the control for each measurement date and regressed on mite days (Table 2). This approach improved the relationship between Pn and MD for ERM, but not for TSM on apple, and improved the relationship for both mite species on peach.

Tr was influenced by mite density, DAT, and mite species, but there were no interactions. Tr declined linearly with increasing mite-days for both mite species (Fig. 3, center). Intercepts and slopes differed significantly from zero, but did not differ between mite species.

Peach WUES declined with increasing mite days, but were not different for ERM and TSM (Fig. 3, bottom). As with apple, greater reductions in Pn than Tr resulted in WUES that declined with increasing mite days.

Peach TCHL was negatively and linearly related to mite days and there was no mite species $\times$ mite-day interaction (Table 1). Peach SLW was not influenced by mite species or mite days (Table 1).

Peach Pn reductions were characterized for both mite species by stepwise regression models, using first- and second-order

Fig. 3. Net photosynthesis (Pn), transpiration (Tr), and water-use efficiency (WUE) of peach leaves as influenced by varying European red mite (ERM)- and twospotted spider mite (TSM)-days. (top) ERM, $Pn = 18.3 - 0.0029 MD$, $R^2 = 0.68$; TSM, $Pn = 17.7 - 0.0029MD$, $R^2 = 0.68$; (center) ERM, $Tr = 1.21 - 0.00013MD$, $R^2 = 0.32$; TSM, $Tr = 1.12 - 0.00014MD$, $R^2 = 0.39$; (bottom) WUE ($\mu\text{mol CO}_2/\text{m}^2$ per sec/ $\text{mmol H}_2\text{O}$ per m^2 per sec); ERM, $WUE = 16.2 - 0.0014MD$, $R^2 = 0.27$; TSM, $WUE = 16.6 - 0.0011 MD$, $R^2 = 0.21$.

terms for Tr and TCHL. Both TCHL and Tr explained significant amounts of variation in Pn for both mite species. TCHL explained the majority of the variation ($R^2 = 0.69$) for ERM. The addition of Tr^2 increased the R^2 to 0.81. For TSM, TCHL² accounted for most of the variation ($R^2 = 0.68$), and the addition of Tr^2 strengthened the relationship ($R^2 = 0.80$). The

Table 2. Regression equations of net photosynthesis, expressed as the percent of the control, on ERM and TSM mite-days.

Tree species	Regression equation ²	R^2
Apple	$\%PN = 98.1 - 0.025 \text{ ERM-days}$	0.79
	$\%PN = 97.9 - 0.046 \text{ TSM-days}$	0.85
Peach	$\%PN = 100.2 - 0.012 \text{ ERM-days}$	0.81
	$\%PN = 98.6 - 0.012 \text{ TSM-days}$	0.79

²Regression equations were significant at $P < 0.0001$ ($n = 60$ for apple and $n = 92$ for peach).

³PN percentages (%PN) were calculated for each mite-infested leaf as $(PN_{ck}/PN_{ij}) \times 100$, where PN_{ck} is the mean PN value of six control leaves on the jth measurement date, and PN_{ij} is the PN value of the ith mite-infested leaf on the jth measurement date.

peach results indicate that both TCHL and Tr are important terms for 'the characterization of Pn reductions by ERM and TSM. In contrast, apple Pn reductions by ERM and TSM were related to TCHL for ERM, and Tr and TCHL for TSM.

Although the apple and peach experiments cannot be statistically compared, some comparisons are meaningful. Results from these studies and a preliminary study (data not shown), indicate that peach leaves were more tolerant of mite feeding than apple leaves. For a 45% reduction in peach Pn, 2900 ERM- or TSM-days were required; however, only 1750 ERM-days and 900 TSM-days were required for a similar reduction in apple.

In addition, these results indicate that greenhouse experiments do not relate well with orchard data. Mite studies with orchard trees show greater tolerance to mite feeding. Zwick et al. (1976) reported that 70 ERM/leaf had no adverse effects on apple tree growth or yield. 'Cresthaven' peach trees appeared tolerant to mite infestations, since yield and growth were not affected by 3600 and 8900 ERM-days, respectively (McClernan and Marini, 1986). Densities of 40 to 50 mites/leaf did not affect yield of 'Wight' peach (Bailey, 1979). Campbell et al. (1990) concluded that greenhouse-grown leaves are more susceptible to mite feeding than field-grown leaves, and that compared to greenhouse-grown apple leaves, greenhouse-grown peach leaves are more tolerant to ERM feeding.

In conclusion, consideration of mite species, tree species, growing conditions, and their interactive effects would improve the accuracy of orchard pest management programs.

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