GAS EXCHANGE CHARACTERISTICS OF APPLE AND PEACH LEAVES AS INFLUENCED BY EUROPEAN RED MITE AND TWOSPOTTED SPIDER MITE

by

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(ABSTRACT)

Three densities of European red mite (ERM) (Panonychus ulmi Koch) and twospotted spider mite (TSM) (Tetranychus urticae (Koch)) were maintained on greenhouse-grown 'Imperial Delicious' apple (Malus domestica) and 'Redhaven' peach (Prunus persica) leaves. As ERM- and TSM-days increased, apple leaf net photosynthesis (Pn), transpiration (Tr), and chlorophyll content (TCHL) decreased linearly. TSM was more damaging to apple leaf gas exchange than ERM. Apple water use efficiency (WUE) declined similarly with increasing mite-days for both mite species. Apple specific leaf weight (SLW) decreased with ERM-days and increased with TSM-days. Peach Pn, Tr, and TCHL declined linearly for both ERM and TSM. Both mite species were equally damaging to peach leaf gas exchange. Peach WUE decreased with increasing ERM and TSM-days. There was no mite effect on peach SLW. The results from separate apple and peach studies indicate that peach may be more tolerant to mite feeding than apple.

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INTRODUCTION

The heavy use of DDT during the 1940's and 1950's, and other pesticides since, killed natural mite predators and allowed mite populations to increase. Mites are major economic pests of horticultural and agronomic crops due to their inherent ability to produce several generations per season and rapidly acquire resistance to pesticides.

Mite feeding indirectly affects plant growth and productivity. Piercing mouthparts allow mites to penetrate the cuticle and to damage epidermal and mesophyll cells of host leaves. Mite feeding has varied detrimental effects on physiological characteristics of leaves for several plant species.

Virginia orchards annually encounter both European red mites (ERM) (*Panonychus ulmi* (Koch))and twospotted spider mites (TSM) (*Tetranychus urticae* Koch), in the same orchard at the same time. Present pest management programs assume that these mite species are equally destructive. However, Flaherty and Huffaker (1970) and Youngman et al. (1986) demonstrated that mite species can affect host plants differently. As tree-fruit pest control research becomes more focused on pest and host-plant interactions, the evaluation of mite species and their effects on orchard crops becomes more important.

LITERATURE REVIEW

Tetranychid mites are regarded as annual pests in commercial orchards. European red mites are the dominant mite pest in Virginia orchards. Twospotted spider mites are of lesser importance. The brick-red appearance of ERM distinguish them from the slightly larger TSM, which are pale yellow with two dark marks on their bodies (Alford, 1984, p.234-236).

Both ERM and TSM have worldwide distribution, however, the range of host plants differs. TSM is one of the most polyphagous species of the Tetranychidae family. Its host plants include a wide range of pome and stone fruits, vegetable crops, strawberry, gooseberry, walnut, ornamental shrubs and trees, glasshouse crops and weeds (van de Vrie et al., 1972). For ERM, the primary food sources are apple, plum, and less frequently cherry, pear, gooseberry, loganberry and walnut (van de Vrie et al., 1972).

Mite Life History. In late summer ERM mate and deposit overwintering eggs on shoots, buds, branches, bark and spurs. Egg hatch coincides with spur leaf emergence the following spring. Motile larvae colonize the new foliage and pass through several developmental stages before reaching the adult, reproductive stage (Cagle, 1946). ERM lay summer eggs on both leaf surfaces. Summer eggs deposited by mated females produce both male and female offspring, while unmated females produce only male offspring. The rate of development of immature stages is influenced by temperature, humidity and food quality (van de Vrie et al., 1972). Five to ten generations are usually produced per season in Virginia.

In early fall, overwintering-female-forms of TSM are produced in response to short days. After mating, these females overwinter in organic matter on the orchard floor or in cracks in the soil. After reactivation by the warm, spring temperatures, surviving females move up the tree trunk to the underside of the new foliage where summer eggs are laid (Alford, 1984, p.236).

The immature TSM is motile from birth and must pass through several developmental stages before it is capable of reproduction. As with ERM, mated TSM females produce male and female offspring, but unmated females produce only male offspring. Generally, there are seven overlapping generations per season (Alford, 1984 p. 236).

Both ERM and TSM are frequently dispersed by wind and by instinctive migration to food and oviposition sites. ERM have the ability to produce a thread by which they can lower themselves onto another leaf or be carried several miles by air currents (Marle, 1951). TSM are not known to be dispersed in this manner.

Mite Quantification. Visible leaf injury does not accurately reflect the size of the mite population or the length of infestation. Several methods have been used to quantify mite populations since quantification is critical to the implementation of integrated pest management programs. Pest management practices are based on pest density and span of infestations.

In early field studies, researchers assumed that trees treated with acaracides were mite-free and compared them to trees infested with mites. Later, experimenters attempted to quantify mite populations. Over the years mite quantification methods were modified to provide a more representative indication of mite populations. Mite population data have been recorded as mites/leaf (Chapman et al., 1952 and Lienk et al., 1956), mites/cm^2 leaf area (Briggs and Avery, 1968 and Avery and Briggs, 1968b), mite days (Hall and Ferree, 1975, Sances et al., 1981 and McClernan and Marini, 1986), and mite days/cm^2 leaf area (Sances et al., 1979).

The mite day concept quantifies mite populations over time (Sances et al., 1981). It integrates the actual mite numbers on a leaf with the length of time that the mites remain on the surface using the following equation (Hall and Ferree, 1975).

$$MD=(\#\text{ mites day}_1+\#\text{ mites day}_2)/2 * (\#\text{ days between } 1\&2)$$

This concept assumes that 10 mites on the leaf surface for 10 days equals 100 mites on the leaf surface for 1 day. It also assumes that mites feed for equal time-periods. Sances et al. (1981) reported that net photosynthesis (Pn) and yield of strawberry on mite-stressed plants were strongly correlated with mite-day accumulations.

Mite Effect on Tree Growth and Yield. Although data conflict, high populations of mites have been detrimental to growth and fruiting. ERM densities of 1-2 mites/cm^2 of leaf area decreased the rate of shoot extension on potted, nonbearing 'Brompton' plum, yet 0.5 mites/cm^2 of leaf area increased shoot growth rate (Avery and Briggs, 1968a and Briggs and Avery, 1968). Shoot lengths of container-grown crabapple C and M.4 rootstocks were reduced by mite densities of 3.9 mites/cm^2 and 4.9 mites/cm^2 of leaf area, respectively. However, 2.6 mites/cm^2 had no effect on shoot length of M.1, a rootstock which exhibited bronzed foliage.

Vegetative growth of field trees has been mildly affected by mites. Zwick et al. (1976) reported that shoot growth of vigorous, nonstressed 'Newtown' and 'Golden Delicious' apple trees was not influenced by 70 ERM/leaf. Klopfenstein and Holdsworth (1978) reported no differences in trunk circumference and shoot extension of spur-type 'Delicious' apple trees resulting from a range of ERM densities. However, Lienk et al. (1956) reported that trunk girth increments were greatest for uninfested

'Cortland' and 'Red Delicious' apple trees. In Pennsylvania, Beers and Hull (1987) reported that shoot length, trunk girth and leaf number of three apple culctivars were only slightly affected by high ERM populations over a three year period. Peach vegetative growth was not affected by accumulations of 8900 mite-days (McClernan and Marini, 1986).

Fruit quality can be reduced by mite feeding. Smaller apple size has been reported by Briggs and Avery (1968), Light and Ludlam (1972), and Beers et al. (1987). Hoyt et al. (1979) found that 120 mites/leaf suppressed cumulative apple growth. However, Klopfenstein and Holdsworth (1978) and Zwick et al. (1976) reported that up to 70 mites/leaf had no effect on apple size. Kovach and Gorsuch (1985) reported that fruit size was not reduced on 'Redhaven' peach trees that accumulated 852 mite-days/leaf prior to harvest. Preharvest fruit drop was positively associated with mite level, but fruit red color, soluble solids, and leaf phosphorous and calcium concentrations were negatively related to mite level (Lienk et al., 1956 and Ames et al., 1984).

Yield reductions have been reported for mite damaged trees. Lienk et al. (1956) reported that high mite populations reduced apple yield. Beers et al. (1987) and Beers et al. (1987) reported reduced return bloom on limbs that accumulated 930 ERM-days/leaf. Flower bud formation was reduced 74 and 34% for 'Cortland' and 'Delicious', respectively (Lienk et al., 1956). Forty to fifty TSM/leaf on 'Wight' peaches did not adversely affect yield, fruit size, preharvest drop, or fruit set the following year (Bailey, 1979).

Factors Influencing Mite Injury. The effect of mites on growth and productivity of tree crops is influenced by many factors including: weather, time of mite attack, fruit load, tree species, and cultivar. Temperature is a principal factor governing the size of mite populations. Tanigoshi et al. (1975a) found that the number of days required to complete the life cycle for female McDaniel spider mite _Tetranychus_ _mcdanieli_ McGregor, decreased with increasing temperatures. Tanigoshi et al (1975a) reported an increase in _T_. _mcdaneili_ developmental and oviposition rates with temperature increases.

Early season infestations are most detrimental to fruit production (Lienk and Minns, 1980, Light and Ludlam, 1972, and Hoyt et al., 1979). Ames et al. (1984) reported that increasing the fruit load magnified detrimental mite effects on fruit quality of 'Miller Sturdeespur Delicious' apple. However, Beers et al. (1987) reported that mites reduced fruit size, regardless of leaf to fruit ratios of 'Rome Beauty'/MM.111 and 'Yorking'/M.26.

Tolerance to mite stress varies tremendously among tree species. Pear species are regarded as some of the more sensitive host plants. Dustan and Stevenson (1961) reported enhanced leaf scorching of three pear cultivars with less than three ERM/leaf and 'D'Anjou' growth and yield were reduced by low densities of TSM (Westigard et al., 1966). Net photosynthesis (Pn) of 'Mission' almonds was reduced 19.1% by 150 Tetranychus pacificus, McGregor mite-days (Youngman et al., 1986). Barnes and Moffitt (1978) reported that high populations of ERM caused a 40% reduction in yield of Persian walnut in the third year of the study. Barnes and Andrews (1978) reported 13 to 19% lower yields on almond trees the year following infestation with Pacific spider mite. Strawberries appear quite tolerant to TSM, since 7100 TSM-days/leaf were required to reduce Pn (Sances et al., 1981).

Apple cultivars demonstrate differential susceptibility to mite injury. Downing and Moillet (1967) reported greater ERM populations and more severe visible leaf damage to 'Red Delicious' than to 'Spartan' or 'McIntosh'.

Mite Feeding. Immature and adult mites of both species feed by inserting a stylet into the leaf and drawing out cell contents. Jeppson et al. (1975) defined mite injury as the puncture of epidermal tissue and subsequent removal of cell contents. Liesering (1958) reported that a TSM inserted it's stylet and removed cellular contents from 18 to 20 cells per minute.

Avery and Briggs (1968b) indicated that initial feeding injury was predominantly associated with damage to the palisade and spongy mesophyll near the veinlets and the parenchyma of the bundle sheath cells. ERM damage appeared as light, small speckles on a green leaf. Histological studies by Avery and Briggs (1968b) showed that visual injury symptoms increased with the number of injured cells. As ERM feeding intensity increased, speckling increased and leaves exhibited a dull green color which eventually turned brown or bronzed. Bronzing was characterized by damage to much of the palisade tissue between the veinlets. Sances et al. (1979) observed that depth of injury was greatest at high mite populations suggesting that TSM may revisit areas to feed at greater tissue depths. Prolonged feeding induced premature defoliation of apple and plum (Avery and Briggs, 1968b and Beers and Hull, 1987).

Avery and Briggs (1968b) reported that ERM injury to the mesophyll of apple and plum leaves varied with the leaf surface used for feeding. Feeding on the lower surface damaged spongy mesophyll cells and in some cases the lowest palisade cell layer. Measurements of mite stylet length revealed that the stylets were too short for mites feeding from the lower surface to damage upper palisade cells. Mite feeding from the upper surface injured all of the palisade layers and occasionally the adjacent spongy mesophyll cells.

Cytological studies identified physical mite damage to leaf mesophyll cells. Tanigoshi and Browne (1981) found direct and indirect changes in leaf cells of 'Delicious' apple attacked by T.mcdanieli. Direct injury that led to death of the mesophyll cells was characterized by punctures in the cell wall, coagulation of protoplasts, and degeneration of organelles. Indirect injury of non-punctured cells was manifest in structural changes that may have altered the function of the chloroplast.

Mite injury apparently goes beyond physical damage to cells and removal of cell contents. Avery and Briggs (1968a) reported that cells adjacent to ERM-injured cells of expanding leaves did not develop normally, indicating a direct or indirect disturbance of growth. Storms (1971) reported that salivary excretions of TSM were translocated to growing regions of bean plants, however, the chemical structure and the specific effects were unknown. Avery and Briggs (1968a) showed that radioactive tracers were injected into leaves of apple and plum by ^{14}C-labeled ERM.

Mite damage may interfere with the biosynthesis or balance of plant growth substances. Avery and Lacey (1964) reported that ERM-damaged tissue of 'Brompton' plum contained more gibberellin-like substances and less auxin-like substances except for indoleacetic acid (IAA). Similar amounts of IAA were found in expanding leaves of infested and control plants, however, significantly less IAA was detected in the internodes of mite damaged trees.

Severely injured leaves exhibit little or no recovery following mite removal. Chapman et al. (1952) observed no recovery of ERM-damaged leaves during mid-season. The absence of visible recovery suggests that the leaf is not functioning properly and may be permanently impaired.

Mite feeding removes cellular substances required for proper leaf function. Hall and Ferree (1975) reported significant differences in leaf color of 'Franklin' apple leaves inoculated with four levels of TSM. Reductions in leaf chlorophyll have been reported for apple (Boulanger, 1958, Chapman et al., 1952, Lathrop, 1951, and Zwick et al., 1976), plum (Avery and Briggs, 1968b), strawberry (Sances et al., 1979) and almond (Andrews and LaPre, 1979). Sances et al. (1979) and DeAngelis et al. (1983) reported that chlorophyll concentration was well correlated to percent of leaf area damaged by the mites.

Mite Effects on Leaf Physiology. Mite feeding dramatically reduced Pn and Tr of almond (Andrews and LaPre, 1979 and Youngman et al., 1986), apple (Hall and Ferree, 1975 and Avery and Briggs, 1968b), strawberry (Sances et al., 1981) and peppermint (DeAngelis et al., 1983).

The level of injury required to impair leaf physiology is unclear. Hall and Ferree (1975) investigated the effects of TSM on leaves attached to winter-grown 'Franklin' apple trees. Populations of 60 mites/leaf for 3 days (180 mite-days), 30 mites/leaf for 9 days (270 mite-days), and 15 mites/leaf for 16 days (240 mite-days) reduced Pn. As mite-days per leaf increased , the reductions in Pn also increased. Reductions in Pn occurred prior to visible leaf injury. In almond 150 mite-days reduced Pn (Youngman et al., 1986). Sances et al. (1981) reported that strawberry Pn was reduced by early-season populations of 3100 TSM mite-days/leaflet and late-season infestations of 7100 TSM mite-days/leaflet. With TSM-damaged peppermint leaves DeAngelis et al. (1983) found a negative linear regression between Pn and the leaf injury index (0 = no injury, 20 = bronzed).

Reductions in Tr have been detected before reductions in Pn occurred (Sances et al., 1981). Tr has been reduced by TSM on apple (Ferree and Hall, 1981), strawberry (Sances et al., 1981), and almond (Youngman and Barnes, 1986). Suppressed Tr has been attributed to stomatal closure and injury to mesophyll tissue (Sances et al., 1979). Differences in degree of stomatal opening categorized as open (turgid guard cells), intermediate (turgid guard cells but stomates not open), and closed (flaccid guard cells) occurred between mite damaged and protected tissue (Sances et al., 1979). The mite-infested tissue had more closed stomates and fewer open stomates than mite-free tissue.

Ferree and Hall 1980 reported that 420 TSM-days reduced the leaf water potential of Delicious apple. This may indicate that mite feeding alters the leaf water status. In the same study, Delicious leaf nitrogen and nonstructural carbohydrate levels were reduced by 300 TSM-days.

The effects of mites on leaf physiological functions have not been resolved. A greater understanding of the interaction between mites and their host plants is necessary to improve orchard pest management techniques. Although more than one mite species may pose a threat within an orchard, few reports compare different mite species. The objectives of this study were to compare the influence of TSM and ERM on photosynthesis, transpiration, stomatal conductance, specific leaf weight, and leaf chlorophyll of one-year-old, greenhouse-grown apple and peach trees.

MATERIALS AND METHODS

The apple experiment and peach experiment were conducted during the summer of 1988. Experimental methods were similar for each tree species. Twelve one-year-old 'Imperial Delicious' apple trees on MM.111 rootstock were moved into the greenhouse on 13 April. Leaf gas exchange measurements began on 19 May and ended on 8 June. Mite treatments were applied on 20 May. Twelve one-year-old 'Redhaven' peach trees on Halford rootstock were moved into the greenhouse on 17 May. Leaf gas exchange measurements began on 9 July and ended on 22 August. Mite treatments were applied on 10 July.

All trees were planted in 3.7-liter pots in a medium of equal parts peat, perlite, and vermiculite (v/v/v). Each tree was fertilized with soluble fertilizer (20%N-8.2%P-15%K) 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. One foliar application of magnesium sulfate at 12.5 g/liter was applied 29 days after planting for apple and 40 days after planting for peach.

Both apple and peach trees were trained to one vigorous shoot. Pesticides were applied according to the spray program in Appendix A to ensure that all trees were pest-free prior to application of mite treatments.

For both the apple and peach experiments, six single-tree-replicates were used for each mite species in a randomized complete block design. Three leaves of similar age per tree were tagged. Tack trap^R was applied to the stem above and below the petiole of each treatment leaf to confine mite populations to individual leaves. 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. 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 two to three days for each mite species, using the equation described by Hall and Ferree (1975).

$$MD=(\#\text{ mites day}_1 + \#\text{ mites day}_2)/2 *(\#\text{ days between day 1\&2})$$

Net photosynthesis (Pn), transpiration (Tr), and stomatal conductance (Cs) were determined for each tagged apple leaf at 0, 6, 13, 17, and 20 days after treatment (DAT) and for each tagged peach leaf at 0, 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 infrared gas analyzer in an open system as described by Schaffer et al. (1986). Tr was determined from dew point hygrometer readings, measured before and after air passed through the leaf chamber. Pn and Tr values were used to determine water use efficiency (WUE). At the conclusion of each experiment, the test leaves were harvested and leaf area was determined with a Li-Cor model LI-3000 portable leaf area meter. Leaf dry weight was recorded after 72 h at 70C in a forced-air drying oven. SLW was calculated as mg of dry weight per cm^2 of leaf area. Chlorophyll content (TCHL) was determined for each leaf at the conclusion of the experiment by acetone extraction as described by Arnon (1949). Four leaf disks totaling 1.26 cm^2 were collected, two from each side of the leaf midrib. Concentrations of chlorophyll a and chlorophyll b were determined from absorption values obtained at 645 and 663 nm respectively, with a Shimadzu spectrophotometer (model UV-160).

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

RESULTS AND DISCUSSION

Discrete mite densities within mite species, and similar densities for both mite species were maintained for apple and peach leaves (Tables 1 and 2).

Apple Gas Exchange. There was a significant mite species by mite density by DAT interaction for apple Pn, and Tr. Therefore, regression analyses were performed for each mite species using cumulative mite-days as the independent variable over the entire experiment.

Net photosynthesis was negatively related in a linear manner to cumulative mite days for ERM and TSM (Figure 1A). Intercepts and slopes differed from zero for each mite species. Slopes for mite species differed (p=0.01). The slope for TSM was nearly twice as steep as the slope for ERM, indicating that TSM caused greater reductions in Pn than ERM. This effect is clearly shown by comparing the number of mite-days required for each mite species to cause a similar reduction in Pn. A 45% reduction in Pn was estimated at 900 mite-days for TSM and 1750 mite-days for ERM. Even though TSM reduced Pn at a greater rate than ERM, visible injury was detected earlier for ERM damaged leaves.

To account for random variation due to measurement date often encountered in photosynthetic studies (Hall and Ferree, 1975), Pn data were expressed as percent of the control and regressed on mite-days (Table 3). This approach strengthened the relationship between apple Pn and ERM- and

TSM-days, however, these models are not intended for predictive purposes.

Although Tr declined linearly with increasing mite-days for both mite species, data were more variable for ERM as indicated by the lower R^2 value in (Figure 1B). Intercepts and slopes differed from zero 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. An 8% reduction in Tr was predicted at 300 TSM-days and 1741 ERM-days.

In the apple experiment, TSM was more damaging per individual than ERM in terms of Pn, and Tr. These results concur with a study by Youngman et al. (1986) that compared the effects of equal numbers of Panonychus citri (McGregor), P. ulmi, T. urticae, and T. pacificus for the same length of time on gas exchange of almond leaves. Tetranychus species were more damaging than Panonychus species. Gas exchange characteristics were affected equally within mite genera.

Apple WUE did not differ between mite species. However, it did decline with increasing ERM and TSM-days (Figure 1C). The declines in Pn and Tr for increasing mite-days were not the same for each mite species. However, when expressed as a ratio, WUE reductions are similar for ERM and TSM. Pn reductions were greater than Tr reductions for both mite species, therefore as mite days increased, WUE declined.

Chlorophyll content decreased linearly with cumulative mite-days for TSM and ERM (ERM, $Y=17.6 - 0.0026md$ $R^2=0.59$ TSM, $Y=16.9 - 0.0033md$ $R^2=0.66$). There was no mite species by mite day interaction (Table 4). Boulanger (1958), Chapman et al. (1952), Lathrop (1951) and Zwick et al. (1976) also found that mite feeding reduced leaf chlorophyll content. SLW was related negatively to ERM, but positively to TSM populations (Table 4). The increase in SLW by TSM may represent a disturbance of growth by altering amounts of growth promoting substances (Avery and Lacey, 1964).

To characterize the reduction of Pn, stepwise regression models, using first and second order terms for TCHL and Tr, were developed for each mite species (Table 5). Apple Pn reductions were characterized differently for each mite species. For ERM, stepwise regression indicated that TCHL was the most significant term in the model ($R^2=0.69$). The addition of the Tr term did not contribute greatly to the explanation of Pn reduction. In contrast, both Tr and TCHL explained Pn reductions for TSM. The Tr term ($R^2=0.70$) accounted for most of the variation. The addition of $TCHL^2$ to the model increased the R^2 value to 0.83. Youngman et al. (1986) reported similar results suggesting injury varies with genera of mite.

Peach Gas Exchange. Analysis of variance indicated a significant mite density by DAT interaction for Pn ($p=0.01$). Pn declined linearly with increasing cumulative ERM and TSM mite-days (Figure 2A). Intercepts and slopes differed significantly from zero, but not between mite species. Therefore at a given mite-day each mite species reduced Pn equally. A 50% reduction in Pn was calculated at 3100 ERM and TSM-days.

To account for random fluctuations in Pn values (Hall and Ferree, 1975) and leaf aging, Pn data were expressed as percent of the control and regressed on mite-days (Table 3). This approach improved the relationship between peach Pn and ERM- and TSM-days, however, these models are not intended for predictive purposes.

Transpiration 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 (Figure 2B). Intercepts and slopes differed significantly from zero for Tr, but did not differ between mite species.

Peach WUEs pooled across mite species declined with mite days, but were not different for ERM and TSM (Figure 2C) since Pn and Tr were affected similarly by both mite species. As with apple, greater reductions in Pn than Tr resulted in WUEs that declined with increasing mite days.

Peach TCHL was negatively related to mite days and there was no mite species by mite day interaction (ERM, $Y=25.2 - 0.0033md$ $R^2=0.81$ TSM, $Y=23.2 - 0.0025md$ $R^2=0.66$). Peach SLW was not influenced by mite species or mite day (Table 4).

Peach Pn reductions were characterized for both mite species by stepwise regression models, using first and second order terms for Tr and TCHL (Table 5). Stepwise regression models indicated that both TCHL and Tr explained Pn reductions for ERM and TSM. TCHL was the first significant term and 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, $TCHL^2$ accounted for most of the variation (R^2=0.68), while the addition of Tr^2 strengthened the relationship (R^2=0.80). The 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 were characterized by 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 a difference in tree species tolerance to mites. Peach leaves were more tolerant of mite feeding than apple leaves. Results showed that 2900 mite-days were required for a 45% reduction in peach Pn, however, only 1750 ERM-days and 900 TSM-days were required to cause a 45% reduction in apple Pn.

The literature indicates that tolerance to mites varied with host plant. Although response to mite feeding was highly variable (Downing and Moillet, 1967), apple was generally regarded as fairly tolerant to mite feeding. Zwick et al. (1976) reported that 70 ERM/leaf had no adverse effects on apple tree growth or yield, but Ferree and Hall (1975) found significant reductions in Pn of greenhouse-grown apple trees after only 450 mite-days. Peach trees appeared very tolerant to mite infestations since yield and growth of 'Cresthaven' trees were not affected by 3600 and 8900 ERM-days, respectively (McClernan and Marini, 1986). Densities of 40-50 mites/leaf did not affect yield of 'Wight' peach (Bailey, 1979).

The physical surface features of leaves may be a principal factor governing the damage potential of tree species. Neilson (1958) found that McDaniel spider mites preferred sweet cherry, sour cherry, and 'Delicious' apple leaves to the more pubescent pear, apricot, and peach leaves. ERM caused more damage on smooth-surfaced 'Delicious' than hairy-surfaced 'Spartan', or 'McIntosh' leaves (Downing and Moillet, 1967).

Clearly, the physiological effects of ERM and TSM vary for apple and peach trees. Consideration of mite species, tree species and their interactive effects would aid the development and implementation of more accurate orchard pest management programs.

CONCLUSIONS

Two important effects of ERM and TSM on 'Redhaven' peach and 'Imperial Delicious' apple leaf physiology have been determined from this experiment. First, different mite species can affect gas exchange characteristics of apple differently. TSM reduced photosynthesis, and transpiration of apple leaves more than did ERM. Second, the effect of mites varied with tree species. For apple, physiological differences were observed between mite species. In contrast, no mite species differences were determined on peach.

Table 1. Mite-day (MD) accumulations for each density of European red mite (ERM) and twospotted spider mite (TSM) on 'Imperial Delicious' apple, 1988.

		MD at following days after treatment			
Mite species	Mite density	6	13	17	20
ERM	Control	0^{z}a	0 a	0 a	0 a
ERM	Low	49 b	198 b	548 b	784 b
ERM	High	214 c	785 c	1333 c	1741 c
TSM	Control	0 a	0 a	0 a	0 a
TSM	Low	42 b	215 b	536 b	776 b
TSM	High	234 c	763 c	1332 c	1756 c
Significance		p-values			
Mite spp.		0.21	0.86	0.50	0.78
Mite density		0.01	0.01	0.01	0.01
Mite spp. x mite density		0.01^{Y}	0.24	0.72	0.51
SE (overall mean)		4.3	11.5	8.0	9.6

[z] Means were separated within column and mite species by Tukey's HSD, 5% level.

[Y] In the event of a significant interaction, treatment means were separated within mite species

Table 2. Mite-day (MD) accumulations for each density of European red mite (ERM) and twospotted spider mite (TSM) on 'Redhaven' peach, 1988.

		MD at following days after treatment			
Mite species	Mite density	4	13	26	44
ERM	Control	0[z] a	0 a	0 a	0 a
ERM	Low	73 b	338 b	1607 b	3116 b
ERM	High	285 c	976 c	2555 c	4309 c
TSM	Control	0 a	0 a	0 a	0 a
TSM	Low	72 b	390 b	1742 b	3058 b
TSM	High	270 c	999 c	2543 c	4206 c
Significance		p-value			
Mite spp.		0.51	0.23	0.41	0.52
Mite density		0.01	0.01	0.01	0.01
Mite spp. x mite density		0.68	0.51	0.41	0.88
SE (overall mean)		10.1	10.1	60.2	101.5

[z] Means were separated within column and mite species by Tukey's HSD, 5% level.

Table 3. 'Imperial Delicious' apple and 'Redhaven' peach net photosynthetic (Pn) values expressed as percent of the control regressed on European red mite (ERM) and twospotted spider mite (TSM) mite-days.

Regression model	Model R^2
Apple	
%Pn = 98.1 - 0.025 ERM-days	0.79
%Pn = 97.9 - 0.046 TSM-days	0.85
Peach	
%Pn = 100.2 - 0.012 ERM-days	0.81
%Pn = 98.6 - 0.012 TSM-days	0.79

Table 4. Tree species and mite species interaction means for chlorophyll content (TCHL) and specific leaf weight (SLW) of 'Imperial Delicious' apple and 'Redhaven' peach leaves on final measurement date, 1988.

	Apple			Peach		
Mite species	MD	TCHL (ug/cm2)	SLW (mg/cm2)	MD	TCHL (ug/cm2)	SLW (mg/cm2)
ERM	0	17.6	6.5 a^{z}	0	25.7	6.3
ERM	738	15.6	6.5 a	3116	13.8	6.0
ERM	1741	13.1	6.3 b	4309	11.8	6.1
TSM	0	17.0	6.5 a	0	23.3	6.6
TSM	776	14.1	7.0 b	3058	15.9	6.2
TSM	1755	11.2	7.1 b	4206	12.4	6.3
Significance			p-values			
Mite spp.	0.78	0.04	0.01	0.52	0.94	0.13
Mite days	0.01	0.01	0.08	0.01	0.01	0.16
M x 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^{y}		L	NS,Q^{x}		L	NS
R^2		0.59	0.46		0.74	--

z Interaction means separated within mite species by Tukey's HSD, 5% level.

y Statistical 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 analyzes. Coefficients of determination (R^2) are for the combined regression model for TCHL vs MD and SLW vs MD.

x There was a nonsignificant relationship for SLW vs ERM-days, however, there was a significant quadratic relationship for SLW vs TSM-days.

Table 5. Stepwise regression models for 'Imperial Delicious' apple and 'Redhaven' peach net photosynthesis (Pn) using the variables chlorophyll content (TCHL) and transpiration (Tr), 1988.

Model variables	Model R^2
	Apple
	ERM
TCHL*	0.67
TCHL*, Tr^2	0.68
TCHL, TCHL^2, Tr^2	0.68
TCHL, TCHL^2, Tr^2, Tr	0.68
	TSM
Tr*	0.70
Tr*, TCHL^2*	0.83
TCHL^2, TCHL, Tr*	0.83
TCHL^2, TCHL, Tr, Tr^2	0.83
	Peach
	ERM
TCHL*	0.69
TCHL*, Tr^2*	0.81
TCHL*, TCHL^2, Tr^2*	0.83
TCHL*, TCHL^2, Tr^2, Tr	0.84
	TSM
TCHL^2*	0.68
TCHL^2*, Tr^2*	0.80
TCHL^2*, Tr^2, Tr	0.80
TCHL^2, TCHL, Tr, Tr^2	0.80

*Indicates variable was significant at the 15% level.

Figure 1. Linear regression models relating cumulative European red mite (ERM) and twospotted spider mite (TSM) mite-days with apple (A) ERM, Pn = 19.2 - 0.0049md R^2 = 0.47 TSM, Pn = 19.4 - 0.0094md R^2 = 0.84, (B) ERM, Tr = 1.32 - 0.000061md R^2 = 0.02 TSM, Tr = 1.25 - 0.00035md R^2 = 0.42, and (C) WUE (umol CO_2 m^{-2} sec^{-1}/mmol H_2O m^{-2} sec^{-1}) ERM, WUE = 14.8 - 0.0032md R^2 = 0.23 TSM, WUE = 15.7 - 0.0049md R^2 = 0.51.

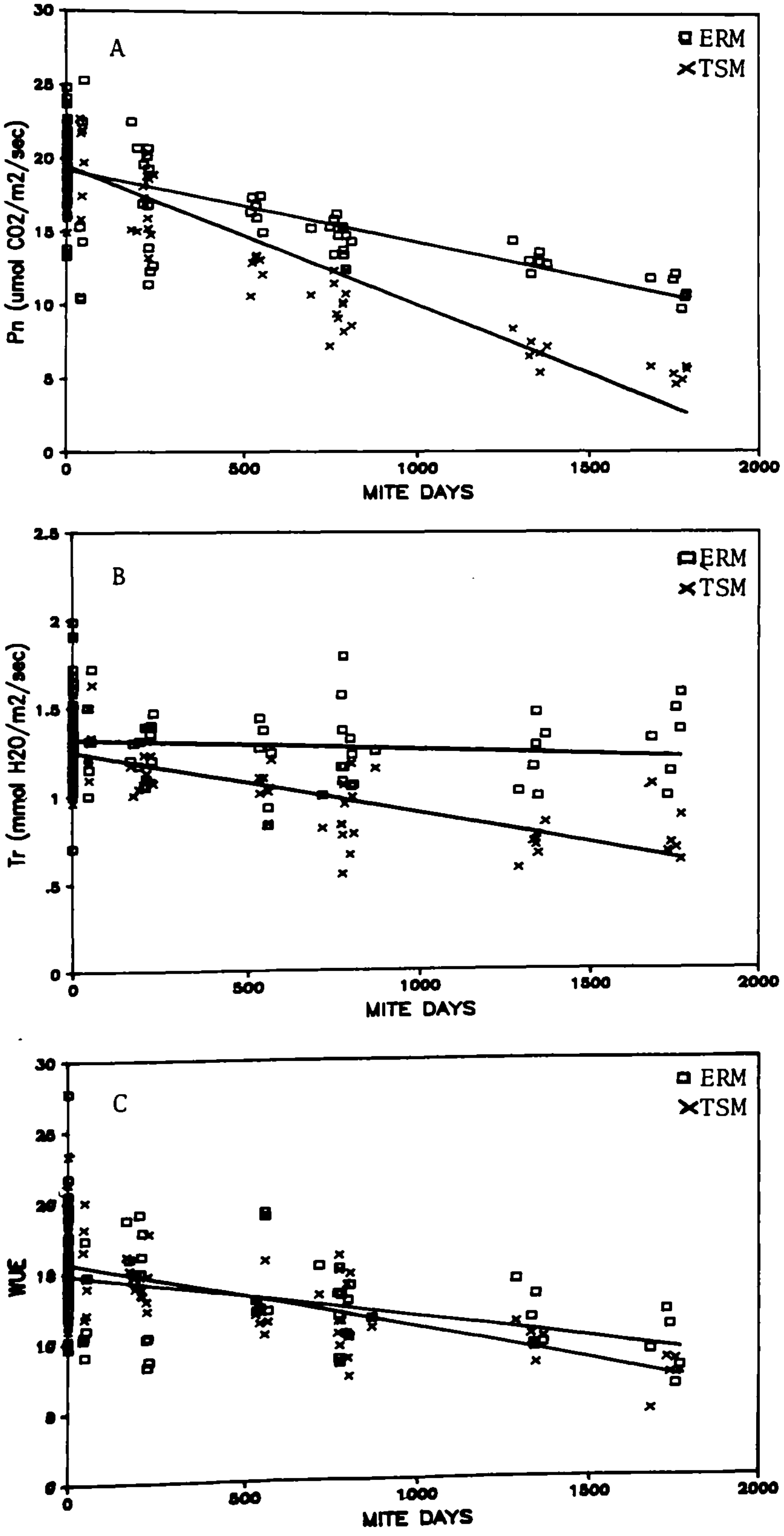
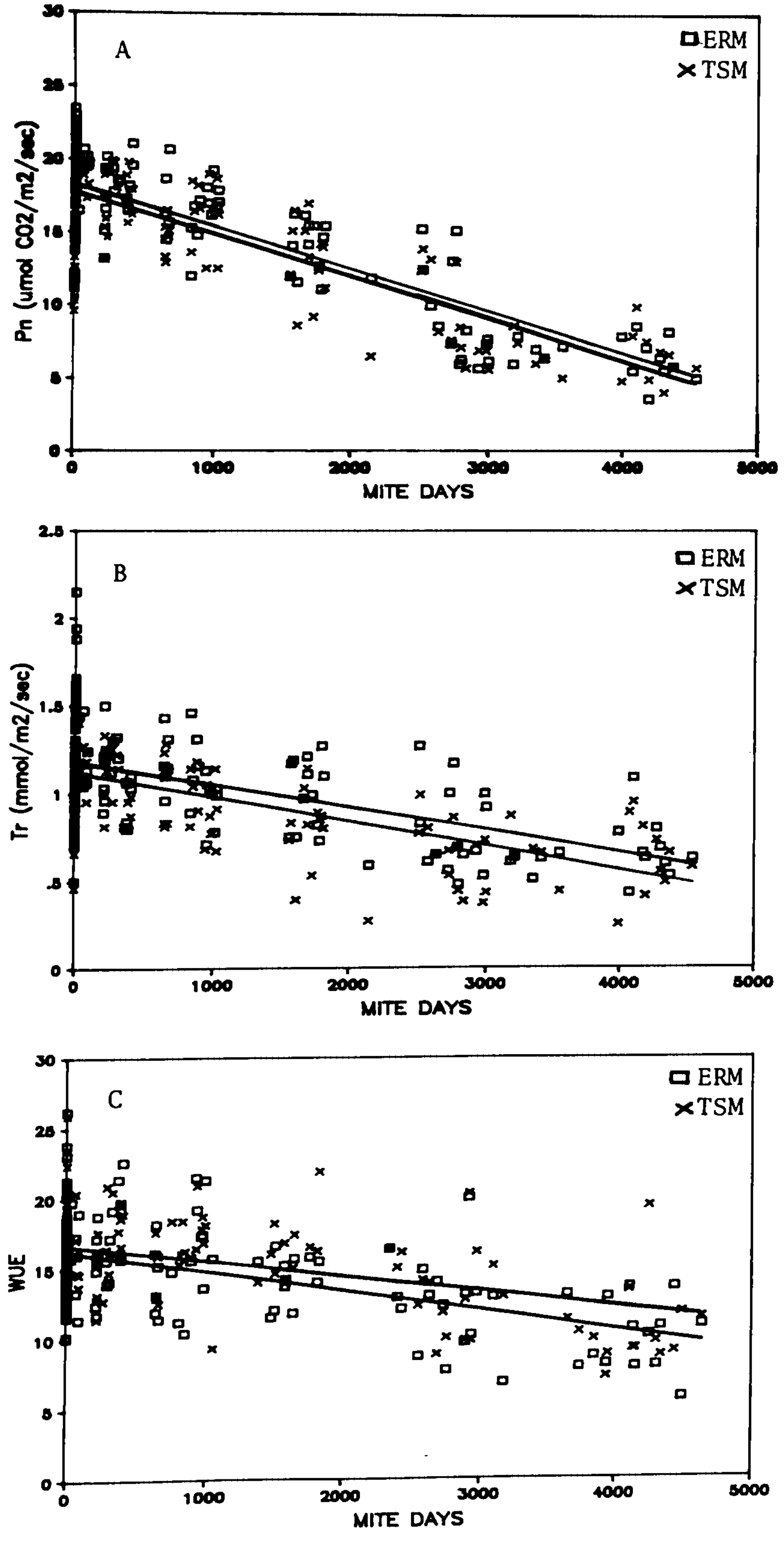

A
ERM
TSM
Pn (umol CO2/m2/sec)
0
5
10
15
20
25
30
0
500
1000
1500
2000
MITE DAYS
B
ERM
TSM
Tr (mmol H2O/m2/sec)
0
.5
1
1.5
2
2.5
0
500
1000
1500
2000
MITE DAYS
C
ERM
TSM
WUE
0
5
10
15
20
25
30
0
500
1000
1500
2000
MITE DAYS

Figure 2. Linear regression models relating cumulative European red mite (ERM) and twospotted spider mite (TSM) mite-days with peach (A) ERM, Pn = 18.3 - 0.0029md R^2 = 0.68 TSM, Pn = 17.7 - 0.0029md R^2 = 0.68, (B) ERM, Tr = 1.21 - 0.00013md R^2 = 0.32 TSM, Tr = 1.12 - 0.00014md R^2 = 0.39, and (C) WUE (umol CO_2 m^{-2} sec^{-1}/mmolH_2O m^{-2} sec^{-1}) ERM, WUE = 16.2 - 0.0014md R^2 = 0.27 TSM, WUE = 16.6 - 0.0011md R^2 = 0.21.


A
ERM
TSM
Pn (umol CO2/m2/sec)
0
5
10
15
20
25
30
0
1000
2000
3000
4000
5000
MITE DAYS
B
ERM
TSM
Tr (mmol/m2/sec)
0
.5
1
1.5
2
2.5
0
1000
2000
3000
4000
5000
MITE DAYS
C
ERM
TSM
WUE
0
5
10
15
20
25
30
0
1000
2000
3000
4000
5000
MITE DAYS

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APPENDIX A

1988 SPRAY SCHEDULE

Pests	Chemical	Concentration	Date of application
Apple			
Whiteflies, aphids	Methomyl	0.4 ml/l	5/11
Whiteflies, aphids	Methomyl	0.4 ml/l	5/20
Aphids	Methomyl	0.4 ml/l	5/25
Mite predators	Carbaryl	2.4 g/l	5/25
Aphids	Methomyl	0.4 ml/l	6/3
Mite predators	Carbaryl	2.4 g/l	6/3
Peach			
Whiteflies, aphids	Methomyl	0.4 ml/l	6/2
Mites	Cyhexatin	0.45 g/l	6/5
Mites	Cyhexatin	0.45 g/l	6/24