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Comparison of the susceptibility of several cultivars of avocado to the persea mite, *Oligonychus perseae* (Acari: Tetranychidae)

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Abstract

We compared the susceptibility of seven cultivars of avocado, *Persea americana*, to feeding by *Oligonychus perseae*. Based on the percentage of leaf area damaged by mites in February 1998, cultivars were categorized into three groups: Hass and Gwen were 'susceptible', Fuerte, Lamb Hass and Reed were 'resistant', Esther, and Pinkerton were of 'intermediate' susceptibility. A life table study in the laboratory showed no difference in mortality and rate of development of *O. perseae* of either the first or second generation reared on either Hass, Pinkerton or Lamb Hass cultivars. Although *O. perseae* exhibited no difference across cultivars with respect to reproductive rates when reared on leaves collected in late spring (April) and early summer (June), net reproduction and intrinsic rate of increase were significantly higher on Hass avocados in mid summer (July). A corresponding increase in percentage leaf area damaged by mite feeding was also observed in the field on Hass in July. We suggest that seasonal changes in the nutritional quality of leaves may be the major factor determining susceptibility of avocado cultivars to *O. perseae*. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Olygonychus perseae*; *Persea americana*; Host plant resistance; Cultivars; Life table; Jack-knife

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1. Introduction

Historically, Californian avocados have been free of economically serious arthropod pests. However, in 1990 the tetranychid mite, *Oligonychus perseae* Tuttle, Baker and Abatiello, was first recorded in San Diego County, CA, and rapidly spread throughout all avocado growing areas in California (Bender, 1993; Thompson, 1993). At present this mite is the most serious foliar pest affecting avocados in California. Adult and immature *O. perseae* live on the undersides of leaves where they build silk nests mainly along the mid-rib and veins. Characteristic necrotic spots appear on leaves as a result of mite feeding within the nests (Aponte and McMurtry, 1997). Damage caused by large populations of mites induces premature leaf drop which opens the tree canopy and increases the risk of sunburn to young fruit and tree trunks. Trees stressed in this manner may abort developing fruit (Bender, 1993; Faber, 1997).

The avocado, *Persea americana* Miller (Lauraceae), is native to tropical North America (Scora and Bergh, 1990). The species is conventionally divided into three races, Mexican, Guatemalan and West Indian (Popenoe, 1915), which contain several hundred varieties (Condit, 1932). The most abundant avocado cultivar grown in Californian orchards is ‘Hass’, a hybrid of unknown origin (Anon., 1974). This cultivar is highly susceptible to *O. perseae* whereas anecdotal field evidence indicates that other cultivars may be more resistant to feeding by this pest (Faber, 1997).

The goal of this study was to compare the susceptibility of seven commercial avocado cultivars to *O. perseae* mite by (i) quantifying leaf damage on these cultivars from field collected samples, and (ii) quantifying demographic parameters of *O. perseae* in the laboratory on ‘susceptible’ and ‘resistant’ cultivars identified from (i).

2. Materials and methods

2.1. Cultivar susceptibility to *O. perseae*

The susceptibility of seven avocado cultivars to *O. perseae* was assessed by measuring feeding damage on leaves collected from avocado trees grown in a single plot of mixed cultivars at the South Coast Field Station in Irvine, CA, USA. In February 1998, 10 leaves were collected from each of three trees for each of the following cultivars: Esther, Fuerte, Gwen, Hass, Lamb Hass, Pinkerton, and Reed. Leaves were picked randomly at shoulder height and returned to the laboratory. Petioles were removed from leaves and abaxial leaf surfaces were scanned individually on a flat bed scanner. *O. perseae* feeding damage on leaves was measured from these scanned color images with the automated image analysis software SigmaScan^{TM} Pro 4.02 (Jandel Corporation, 1995). This software was used to identify damaged areas based on their color and to measure the extent of feeding by *O. perseae* as the percentage of leaf area damaged. A detailed description and evaluation of this technique for measuring mite feeding damage may be found elsewhere (Kerguelen and Hoddle, 1999a,b). Damage measured in February 1998 was caused by *O. perseae* feeding over summer in the 1997 growing season.

2.2. Mite development and life table construction

O. perseae were reared in the laboratory on foliage of three avocado cultivars and life tables were constructed to calculate demographic parameters. Lamb Hass, Pinkerton and Hass which showed respectively, low, intermediate and high levels of susceptibility to *O. perseae* feeding in the susceptibility study above were used (see Section 3).

Leaves were collected at South Coast Field Station from the same trees that were used in the susceptibility study. Leaf disks 22 mm diameter were cut with a cork borer from collected leaves and disks were placed abaxial side up on water saturated foam pads held in stainless steel pans. *O. perseae* eggs collected on Hass avocados in a commercial orchard (Camarillo, CA, USA) or from a greenhouse colony maintained on Hass avocados were placed individually on these disks. Thirty six eggs were set up simultaneously for all three cultivars. These constituted the initial cohorts for birth females from which horizontal life tables were constructed to estimate demographic growth parameters.

Leaf disks and *O. perseae* were maintained at $25 \pm 1^{\circ}$C under a long day light cycle (Light:Dark, 16:8) and mites were checked every 24 h and survivorship and developmental stage were recorded. Upon emergence, adults were sexed and young males (<24 h old) were transferred to leaf disks with young females (<24 h old). Leaf disks were checked daily and the number of eggs laid and immature mites born on each disk were recorded until all females died, and all eggs had either hatched or died. In the event a leaf disk started to deteriorate during the study, mites were moved to healthy leaf disks that were cut at the beginning of the trial but upon which no mites had been reared. This experiment was repeated at three different times through the 1998 growing season. The first trial was started on April 17, the second trial started on May 27, and the third trial started on July 16, 1998.

For each trial and each cultivar we calculated the net reproductive rate (R_0) and intrinsic rate of natural increase (r_m) as follows (Southwood, 1978):

$$R_0 = \sum l_x m_x \quad \text{and} \quad \sum_x e^{-r_m x} l_x m_x = 1$$

with x pivotal age, l_x number surviving to age x, m_x age-specific fecundity.

During the second trial, 36 larvae born on each cultivar (June 18–June 26) were transferred to fresh leaf disks. Larvae were reared to adulthood under the same conditions as previously described to estimate mortality and development rate of the second generation on each cultivar.

2.3. Leaf damage: 1998 growing season

Damage due to *O. perseae* feeding on trees at South Coast Field Station during the 1998 growing season was measured in April, May, July, and November 1998. Five leaves were collected on each of three trees of Hass, Lamb Hass and Pinkerton and the percentage of leaf area damaged was measured with automated image analysis software as described previously.

2.4. Statistical analysis

All statistical procedures were performed in SAS ver. 6.12 (Statistical Analysis System, Cary, NC). Mean percentages of leaf area damaged were compared among treatments with a nested design ANOVA performed on arcsine-transformed data. Mortality rates for each developmental stage of *O. perseae* were compared among cultivars with a Chi square test for each trial. In order to maintain the experimentwise level of significance at $\alpha = 0.05$, the level of significance for each of the three tests was adjusted to $a' = [0.05/3] = 0.017$. Duration of development from larva to adult, female longevity, and female fecundity were compared among cultivars and across trials with a two-way ANOVA (trial $\times$ cultivar). Average duration of development from larva to adult for the second generation was compared among cultivars with an ANOVA.

Estimates of the means and their standard errors of the net reproductive rate (R_0) and of the intrinsic rate of natural increase (r_m) on each cultivar were computed with a Jacknife procedure (Efron, 1981; Meyer et al., 1986). Both R_0 and r_m were compared among cultivars and across trials by means of a two-way ANOVA (trial $\times$ cultivar).

3. Results

3.1. Cultivar susceptibility to O. perseae

Mean percentage of leaf area damaged on leaves collected from seven cultivars at South Coast Field Station in February was significantly different among cultivars ($p = 0.001$). Average leaf area damaged was categorized as low on Fuerte, Lamb Hass and Reed (13%, 17%, and 17%, respectively), and high on Gwen and Hass (37% and 38%, respectively). Damage was intermediate on

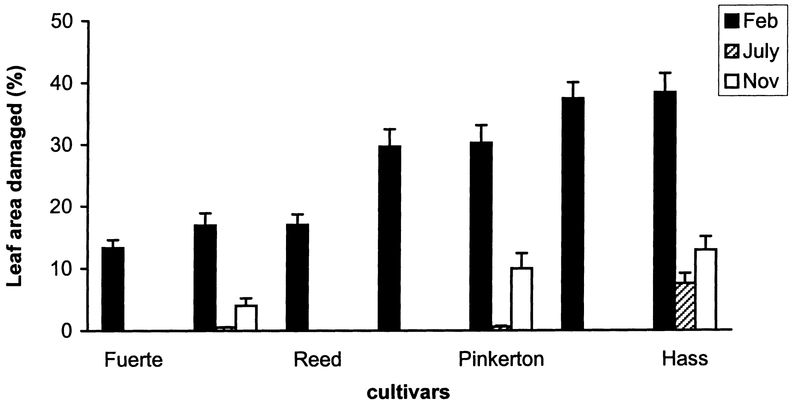

Fig. 1. Mean (+ s.e., $n = 30$) percentage leaf area damaged by *O. perseae* feeding on mature leaves of seven cultivars of avocado collected at South Coast Field Station in February, July and November 1998.

Esther and Pinkerton at 30% each (Fig. 1). Maximum leaf area damaged measured on leaves was 66% on Gwen and Hass, 63% and 65% on Esther and Pinkerton, respectively, and 35%, 36% and 37% on Fuerte, Lamb Hass and Reed, respectively.

3.2. Mite development and life table construction

3.2.1. Survival

Mite survival from larva to adult on leaf disks varied through the season on all three cultivars tested (Table 1). Survival was significantly different across the three cultivars in April ($p = 0.006$), when overall survival was the lowest. In April, survival was highest on Lamb Hass and lowest on Hass. No significant difference among cultivars was observed on later dates ($p = 0.94$ in May, and 0.58 in July).

Stage-specific mortality of *O. perseae* on leaf disks varied through time on all cultivars for all developmental stages (Fig. 2). However, neither larval mortality nor deutonymph mortality differed significantly among cultivars. Larval mortality was 35% in April ($n = 86$), decreased to 7% in May ($n = 96$) and increased again to 30% in July ($n = 46$) (Fig. 2a). Similarly, deutonymph mortality decreased from 20% in April ($n = 56$) to 7% in May ($n = 82$) but then remained at 7% in July ($n = 30$) (Fig. 2c). Protonymph mortality was significantly different among cultivars ($\chi^2 = 11{,}17$; $\mathrm{df} = 2$; $p = 0.004$). In April, 44% of protonymphs died on Hass ($n = 16$), 28% died on Pinkerton ($n = 18$), and none died ($n = 22$) on Lamb Hass. Protonymph mortality was similar on all cultivars in May (7%, $n = 89$) and July (6%, $n = 32$) (Fig. 2b).

Table 1
Percentage survival and mean duration (±s.e.) in days of development of first generation (F_1) and second generation (F_2) of *O. perseae* from larva to adult at 25°C on leaves of three cultivars of avocado collected at South Coast Field Station, California, in April, May and July 1998 (sample sizes are indicated in parentheses)

	Cultivars	April		May		July	
		Survival (%)	Duration of development	Survival (%)	Duration of development	Survival (%)	Duration of development
F_1	Hass	20.7 (29)	10.5 ± 0.42 (6)	81.8 (33)	9.7 ± 0.18 (27)	63.2 (19)	9.9 ± 0.08 (12)
	Lamb Hass	62.1 (29)	9.9 ± 0.28 (18)	78.8 (33)	9.7 ± 0.16 (26)	65.0 (20)	10.9 ± .18 (13)
	Pinkerton	39.3 (28)	10.9 ± 0.36 (11)	76.7 (30)	10.6 ± .24 (23)	42.9 (7)	11.3 ± 0.62 (3)
F_2	Hass	–	–	36.1 (36)	11.6 ± 0.85 (13)	–	–
	Lamb Hass	–	–	47.2 (36)	10.8 ± 0.18 (17)	–	–
	Pinkerton	–	–	33.3 (36)	10.1 ± 1.25 (12)	–	–

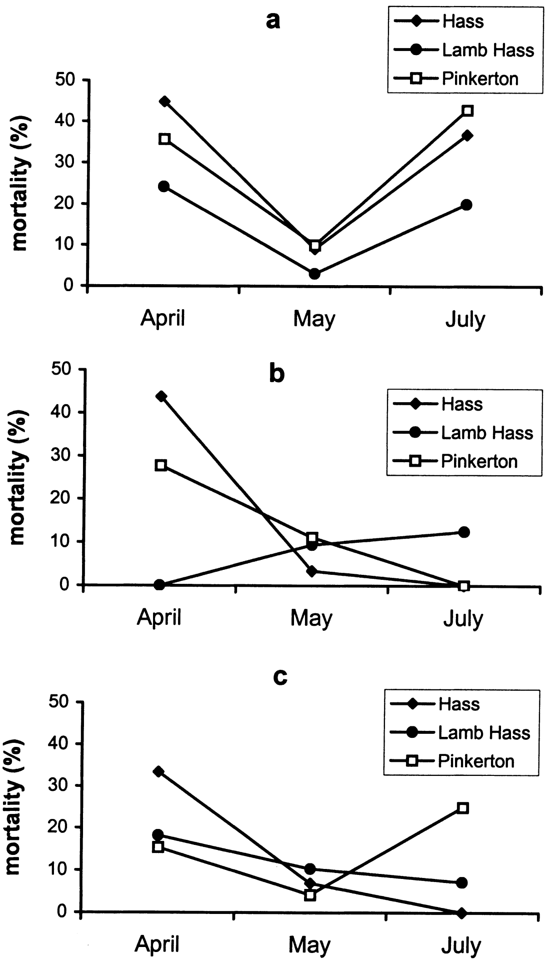

Fig. 2. Mortality of larvae (a), protonymphs (b), deutonymphs (c) of *O. perseae* at 25°C on leaf disks of three cultivars of avocado collected at South Coast Field Station in April, May, and July 1998.

3.2.2. Development

Development on leaf disks from larva to adult took approximately 10 days on all cultivars across all trials (Table 1). Longevity of adult female *O. perseae* differed significantly among cultivars ($p = 0.011$) and across trials ($p = 0.0001$) (Fig. 3a). On Hass, mean female longevity increased by 100% from 12 days in May ($n = 6$) to 24 days in July ($n = 11$). The increase of female longevity was lower on Pinkerton (+73% from April to May) and lowest on Lamb Hass (Fig. 3a). On Lamb Hass, mean female longevity initially increased from April to May (+ 70%) but then decreased in July (−44%). Since only one female reached

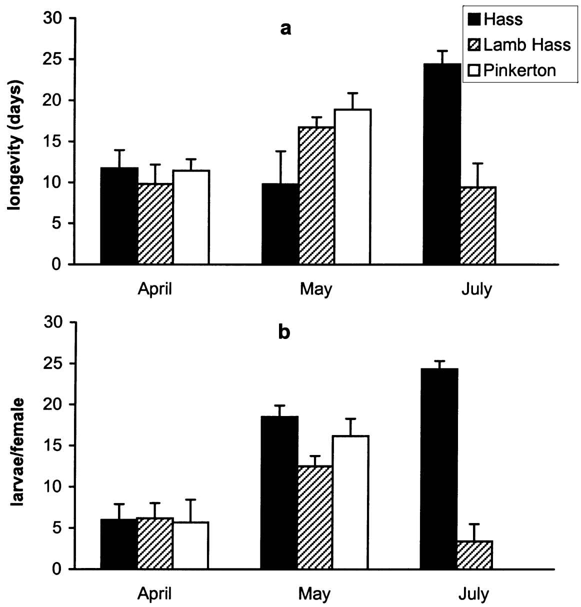

Fig. 3. Mean (+ s.e.) longevity in days (a) and mean (+ s.e.) fecundity in larvae/female (b) of adult female *O. perseae* at 25°C on leaf disks of three cultivars of avocado collected at South Coast Field Station in April, May, and July 1998.

adulthood on Pinkerton in July, no data on longevity, fecundity and demographic parameters are available. Mean fecundity was significantly different among female *O. perseae* reared on different cultivars ($p = 0.0001$) and across trials ($p = 0.0001$) (Fig. 3b). Fecundity of females on leaf disks in May increased greatly compared with that observed in April (3, 2 and 2.6 fold on Hass, Lamb Hass and Pinkerton, respectively). Fecundity then decreased in July on Lamb Hass (four-fold) while it increased further on Hass (+26%) when compared with May (Fig. 3b).

Survival of larvae to adulthood as well as duration of development from larva to adult for *O. perseae* reared from eggs laid on leaf disks (F_2) was similar on all cultivars ($p = 0.44$ and 0.25, respectively). However, compared to the parent generation survival was reduced on average by 50% and on Hass and Lamb Hass development tended to be slower (Table 1).

3.2.3. Demographic parameters

Mean net reproductive rate (R_0) and intrinsic rate of natural increase (r_m) varied significantly through time ($p = 0.0001$ for both) and among cultivars ($p = 0.0001$ for both) (Fig. 4). On all cultivars R_0 and r_m increased in May and decreased in July. In April, R_0 and r_m were highest on Lamb Hass. However, in May and July, R_0 and r_m were highest on Hass. The largest difference between Lamb Hass and

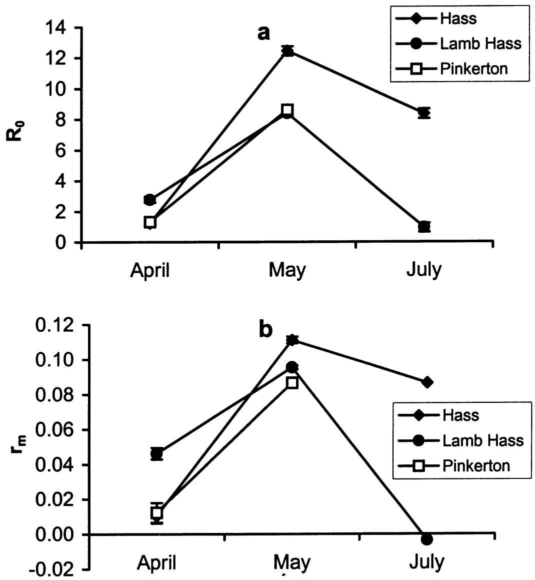

Fig. 4. (a) Net reproductive rate (R_0) and (b) intrinsic rate of natural increase (r_m) of *O. perseae* at 25°C on leaf disks of three cultivars of avocado collected at South Coast Field Station in April, May, and July 1998.

Hass for both $R_0$and r_m was observed in July when negative population growth was observed on Lamb Hass (Fig. 4b).

3.3. Leaf damage: 1998 growing season

No measurable leaf damage due to feeding by *O. perseae* in the 1998 growing season was observed until July. At this time, average percentage of leaf area damaged was significantly higher on Hass than on either Lamb Hass or Pinkerton ($p = 0.0117$). On average, 8% of the leaf area was damaged on Hass, while only 0.5% and 0.6% of the leaf area was damaged in July by *O. perseae* on Lamb Hass and Pinkerton, respectively (Fig. 1). In November, leaf damage had increased to 13% on Hass, 10% on Pinkerton and 4% on Lamb Hass and damage was significantly different across cultivars: ($p = 0.0028$).

4. Discussion

Comparison of visible damage among selected avocado cultivars showed significant and quantifiable differences in susceptibility to *O. perseae* feeding. At South Coast Field Station, Hass and Gwen cultivars showed about twice as much leaf area damaged as Fuerte, Lamb Hass, and Reed avocados while damage on Esther and Pinkerton was intermediate. Since leaf damage caused by mite feeding stresses trees by disturbing photosynthesis and transpiration (Sances et al., 1982), Hass and Gwen cultivars appeared to be very susceptible and suffered the most from mite infestation whereas stress was minimum on Fuerte, Lamb Hass and Reed cultivars which were more resistant.

Mite feeding damage also causes premature leaf drop (Bender, 1993; Faber, 1997); however, it is unknown whether all cultivars shed damaged leaves in response to the same levels of damage. Thus, lower average percentage of leaf area damaged on leaves collected on trees could possibly indicate more leaf drop on those trees. In this study we did not quantify leaf drop and therefore cannot definitely answer this question. However, we did not observe any obvious difference in leaf drop or secondary leaf flush on the various cultivars. Furthermore, on Hass avocados, although there is no known finite threshold of damage that causes leaf drop, the probability of leaf drop in early summer increases dramatically when percentage leaf area damaged exceeds 8% (Kerguelen and Hoddle, 1999a,b). Thus, if the cultivars with the lowest average leaf area damaged (i.e. Fuerte, Lamb Hass, and Reed) were shedding leaves with less damage, they would be shedding leaves with extremely little damage (less than 8% leaf area damaged) which seems unlikely.

In addition, in the laboratory, female longevity, female fecundity, and population growth of *O. perseae* (R_0 and r_m) on young mature leaves collected in July were significantly higher on the most susceptible cultivar (Hass) relative to the resistant cultivar (Lamb Hass). However, no such difference was observed on leaves collected in April or May. Thus the intrinsic quality of leaves seems to change through time in the susceptible cultivar so that summer leaves become particularly favorable to *O. perseae* reproduction. Mid-summer outbreaks of *O. perseae* are typical in commercial orchards that are infested with this pest in southern California (Hoddle et al., 1999; Kerguelen and Hoddle, 1999a,b). Our laboratory results suggest that *O. perseae* mid-summer outbreaks on Hass may be driven by the changing susceptibility of the Hass cultivar to *O. perseae* feeding rather than by other factors.

Conceptually, avocado cultivars could be resistant to *O. perseae* through the production of either constitutive or induced compounds detrimental to *O. perseae* longevity or fecundity. Avocado leaves have been reported to be toxic to various insects (Murakoshi et al., 1976; Chang et al., 1975; Sneh and Gross, 1981; Stein and Klingauf, 1990), mammals (Appleman, 1944; McKenzie and Brown, 1991; Craigmill et al., 1992) and birds (Burger et al., 1994). Furthermore, there are differences in leaf chemistry and biochemistry among cultivars. Avocado cultivars vary in their terpene levels (Bergh et al., 1973), phenol constituents and phenol biosynthesis enzyme activities and isozyme patterns (Brune and Van Lelyveld, 1982).

We observed neither increased mortality nor slower development of *O. perseae* on resistant cultivars (Lamb Hass and Pinkerton). Rather, the susceptible cultivar (Hass) was characterized by increased reproductive rates of *O. perseae*. Starting in the May 1998 bioassay, the average number of offspring per female was the highest on Hass, and the difference among cultivars increased in July 1998. Not only did females live longer on Hass and therefore laid more eggs, but they also produced offspring at a faster rate. In July, females produced on average a larva every day on Hass, whereas on average females produced one larva every second day on Lamb Hass. These results suggest that the observed difference of cultivar susceptibility to *O. perseae* is due to seasonal differences in nutritional quality of cultivars as no difference was observed across cultivars before this time.

The nutritional requirements of phytophagous mites are still not fully understood. Numerous studies have shown that the population density and fecundity of various tetranychids on various hosts are dependent on plant quality. Tetranychids pierce the parenchyma tissue of leaves with their stylets and siphon out the cells' contents (Van der Geest, 1985; Jeppson et al., 1975). Consequently, mite nutrition is directly affected by the chemical composition of ingested fluids. Plant quality is modified directly by fertilizers and indirectly by pesticide treatments which can induce hormoligosis (Rodriguez, 1964; Huffaker et al., 1969; Jesiotr et al., 1979). Although results are not always consistent, tetranychids are sensitive to the chemical composition of the host, particularly to nitrogen contents. Studies on *Tetranychus urticae* (Acari: Tetranychidae) have demonstrated a positive correlation between population growth and leaf sugar concentrations of several host plants (Rodriguez et al., 1960; Rodriguez and Cambell, 1961). Conversely, an over abundance of amino acids in the diet can be detrimental to *T. urticae* as excess amino acids induces excessive osmotic pressure in the hemolymph (Sun, 1963). No conclusive results have been obtained regarding the relationship between some vitamins in host plants and tetranychid population growth (Rodriguez and Rodriguez, 1952).

The chemical composition of sap and leaves of avocados varies both with time of year and cultivar. Nitrogen content of Hass avocado leaves growing in the spring increases through the summer and then drops in the fall and winter (Lahav et al., 1989). Increased nitrogen levels could explain why populations of *O. perseae* increase on Hass over summer. However, the same pattern of variation of nitrogen content was observed for Fuerte, a cultivar that is resistant to *O. perseae*. Thus it is unlikely that nitrogen content of leaves is fully responsible for observed differences in susceptibility among cultivars. Amino acid content in Hass avocados has been reported to drop from a maximum level in May to a minimum level in August before increasing again in the fall (El-Hamalawi and Menge, 1995). These variations are consistent with nutritional studies that indicated that an excess of amino acids was detrimental to tetranychid mites (Sun, 1963). However, no comparable data on amino acid cycles are available for the resistant cultivars we studied.

Starch and sugar content of avocado trees vary through the growing season. Sugar and starch levels are maximum in late-winter–early-spring and drop through the summer to reach minimum levels in the fall (Cameron and Borst, 1938; Scholefield et al., 1985; El-Hamalawi and Menge, 1995). Thus, if *O. perseae* population densities are correlated with carbohydrate contents in the trees, the correlation is a negative one. Similar starch and sugar cycles have been observed on susceptible (Hass) and resistant (Fuerte) cultivars, suggesting that cycling carbohydrate contents alone may not be responsible for differences in susceptibility to *O. perseae*.

When leaf damage was measured in February 1998 at the end of the 1997 growing season and again late in the 1998 season (November 1998) percentage leaf area damaged on Pinkerton was intermediate between damage on Lamb Hass and damage on Hass. However, at mid-season (July 1998) damage on Pinkerton was low and similar to damage on Lamb Hass. Thus, if the same change in nutritional quality of leaves is responsible for susceptibility to *O. perseae* on Hass and Pinkerton, it is evidently delayed on Pinkerton. This observation will guide future efforts to identify which biochemical processes may determine susceptibility to *O. perseae* through examining changes in nutritional quality that occur at different times on Hass and Pinkerton cultivars.

Further work is required to determine if the chemical composition of resistant and susceptible cultivars and seasonal variation of these compounds affects the longevity and fecundity of *O. perseae*. A better understanding of the biochemical processes that may mediate cultivar resistance to *O. perseae* will assist with breeding efforts designed to select for resistance to this pest. Furthermore, other factors not addressed in this study may contribute to observed resistance of cutivars to *O. perseae*. For example, hairs on the underside leaves are noticeably denser on Lamb Hass than on Hass and Pinkerton. Thus, lower feeding damage on Lamb Hass in the field may be due in part to the plant being more suitable for natural enemies (Walter, 1996; Agrawal, 1997).

Acknowledgements

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