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DETERMINING THE SUSCEPTIBILITY OF AVOCADO CULTIVARS TO FEEDING BY THE PERSEA MITE, *Oligonychus perseae* (ACARI: TETRANYCHIDAE)

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SUMMARY

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 feeding on leaves in 1997, cultivars were categorized in 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*.

KEY WORDS: *Persea americana* Mill., host plant resistance, genotypes, life tables, Jack-knife, pest, arthropod.

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, California, USA, 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 and it infests 90% of avocado growing acreage. 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 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 resulting in reduced yields (Bender, 1993; Faber, 1997).

The avocado, *Persea americana* Miller (Lauraceae), is native to tropical North America (Scora and Bergh, 1990). The species is divided in three races, Mexican, Guatemalan and West Indian (Popenoe, 1915; Bergh and Ellstrand, 1986; Nakasone and Paull, 1998), 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).

MATERIALS AND METHODS

Quantifying cultivar susceptibility to *Oligonychus 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, California, U.S.A. In February 1998, 10 leaves were collected from each of three trees for each of the following: '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. *Oligonychus perseae* feeding damage on leaves was measured from these scanned color images with the automated image analysis software SigmaScan™ 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, 1999). Damage measured in February 1998 was caused by *O. perseae* feeding over summer in the 1997 growing season.

Mite development and life table construction

Oligonychus 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 Results section).

Leaves were collected at South Coast Field Station from the same trees that were used in the susceptibility study and used for mite demographic studies. 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. *Oligonychus perseae* eggs collected on 'Hass' avocados in a commercial orchard (Camarillo, California, U.S.A) 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 ± 1°C under a long day light cycle (Light:Dark, 16:8) and mites were checked every 24 hours and survivorship and developmental stage were recorded. Upon emergence, adults were sexed and young males (<24 hours old) were transferred to leaf disks with young females (<24 hours 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, 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):

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

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

During the second trial, thirty-six larvae born on each cultivar (June 18 to June 26, 1998) 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.

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 3 trees of ‘Hass’, ‘Lamb Hass’ and ‘Pinkerton’ and the percentage of leaf area damaged was measured with automated image analysis software as described previously.

Statistical analysis

All statistical procedures were performed in SAS v 6.12 (Statistical Analysis System, Cary, N.C.). 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 $P \leq 0.05$, the level of significance for each of the three tests was adjusted to $P=[0.05/3]=0.017$. Duration of development from larva to adult, female longevity, and female fecundity were compared among cultivars and across trials with a 2-way ANOVA (trial x 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 2-way ANOVA (trial x cultivar).

RESULTS

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 ($P \leq 0.001$). 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 'Esther' and 'Pinkerton' at 30% each (Figure1). 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.

Oligonychus perseae development and life table construction

<u>Survival</u>

Oligonychus perseae 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 (Figure 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) (Figure 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) (Figure 2c). Protonymph mortality was significantly different among cultivars (x^2= 11.17; 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) (Figure 2b).

<u>Development</u>

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' (Figure 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 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) (Figure 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' (4 fold) while it increased further on 'Hass' (+26%) when compared with May (Figure 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 (F2) was similar on all cultivars (x^2= 1.64; df= 2; *P*= 0.44 and F= 1.41; df= 2, 39; *P*= 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).

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

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 (Figure 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).

DISCUSSION

Comparison of visible damage among selected avocado cultivars showed significant quantifiable differences in susceptibility to *O. perseae* feeding. At South Coast Field Station, Hass and Gwen cultivars exhibited approximately twice as much leaf area damaged as 'Fuerte', 'Lamb Hass', and 'Reed' avocados while damage on 'Esther' and 'Pinkerton' was intermediate.

Mite feeding damage can cause premature leaf drop if severe enough (Bender, 1993; Faber, 1997). However, it is unknown whether all cultivars studied here drop damaged leaves in response to similar levels of damage. Thus, lower average percentage leaf area damaged estimates on leaves collected from "resistant" trees may indicate leaf drop on those trees as heavily damaged leaves have been shed and less damaged leaves were retained which resulted in low damage estimates. We did not quantify leaf drop by each cultivar studied. However, no obvious differences in leaf drop or secondary leaf flush on cultivars studied was noticed when leaves were collected from South Coast

Field Station. For the Hass cultivar, there is no known finite threshold of damage that causes leaf drop. However, the probability of leaf drop in early summer increases when percentage leaf area damaged by *O. perseae* feeding exceeds 8% (Kerguelen and Hoddle, unpublished). Thus, if cultivars with the lowest average leaf area damaged (i.e. ‘Fuerte’, ‘Lamb Hass’, and ‘Reed’) were shedding slightly damaged leaves, leaf drop would occur when less than 8% of leaf area was damaged by mite feeding. Shedding leaves with such low levels of damage is probably unlikely.

In the laboratory, female longevity and fecundity, and population growth (R_0 and r_m) estimates for *O. perseae* reared 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. It is possible that the intrinsic quality of avocado leaves may change through time so that by summer leaves on the Hass cultivar become particularly favorable to *O. perseae* survival and reproduction. Mid-summer outbreaks of *O. perseae* are observed in commercial orchards infested with this pest in southern California. Our laboratory results suggest that *O. perseae* outbreaks in mid-summer on ‘Hass’ may be facilitated by a chemical change within leaves that causes the ‘Hass’ cultivar to become conducive to *O. perseae* reproduction.

Avocado leaves are 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, differences in leaf chemistry and biochemistry among cultivars have been demonstrated. For example, avocado cultivars vary in their terpene levels (Bergh et al., 1973), phenol constituents, 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 one 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 levels. 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 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 may be unlikely that nitrogen content of leaves is fully responsible for observed differences in susceptibility among the cultivars examined in this work. 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 and we can not speculate on the role of excess amino acid production as a resistance mechanism.

Starch and sugar content of avocado trees can also vary through the growing season. Sugar and starch levels are maximal 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 cultivar 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*. Secondary plant compounds like avocado furans in idioblasts oil cells in leaves have been shown to have insecticidal properties and may be important in avocado resistance to *O. perseae* (Rodriguez-Solana and Trumble, 1998; Rodriguez-Solana *et al*., 1998). Correlative studies determining relationships between avocado furans and *O. perseae* demographics would be a first step to ascertain if changes in these compounds throughout the year affect *O. perseae* development. If correlations were detected intensive bioassay-driven tests to identify the exact resistance compounds could then be undertaken. 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 cultivars 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 having domatia suitable as refuges for natural enemies (Walter, 1996; Agrawal, 1997).

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

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

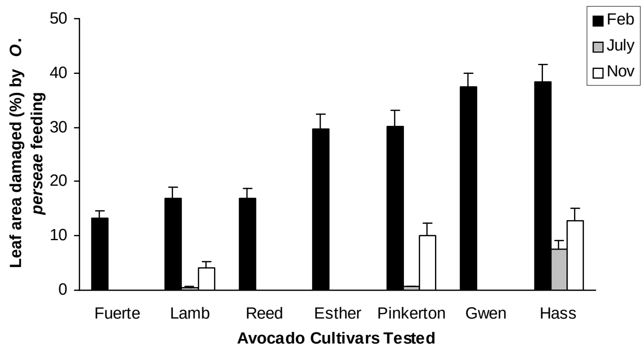


Figure 1. Mean (± s.e., n=30) percentage leaf area damaged by *Oligonychus perseae* feeding on mature leaves of seven cultivars of avocado collected at South Coast Field Station in February 1998, July and November 1998.

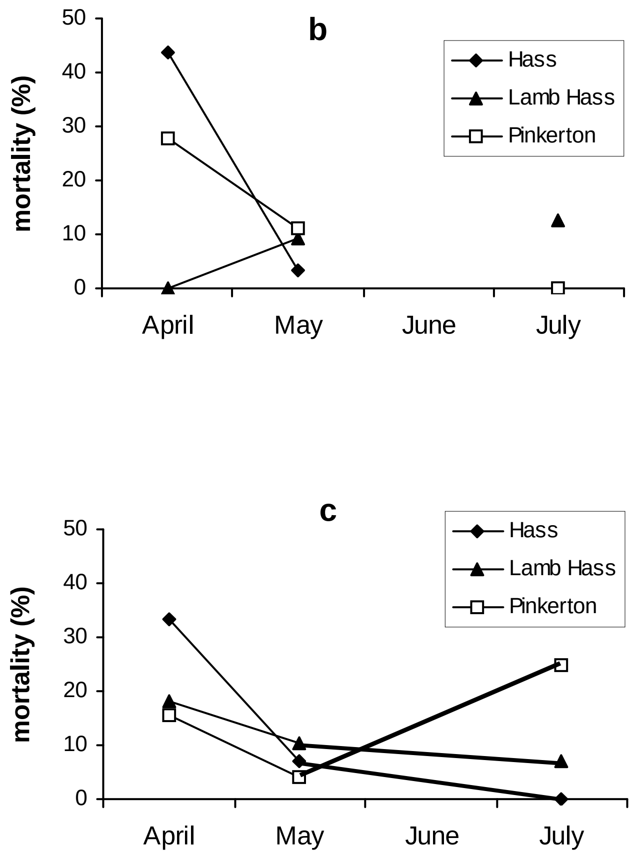
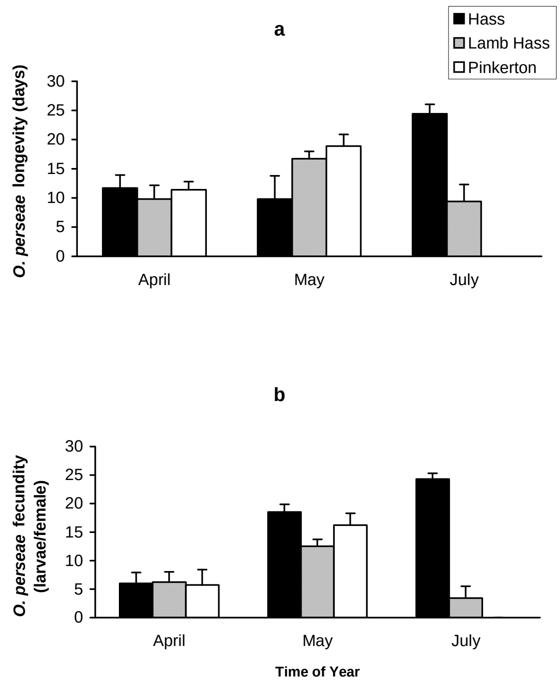


Figure 2. Mortality of larvae (a), protonymphs (b), deutonymphs (c) of *Oligonychus perseae* at 25ºC on leaf disks of three cultivars of avocado collected at South Coast Field Station in April, May, and July 1998.



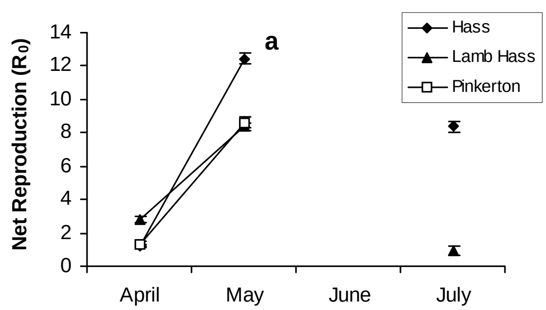


Figure 3. Mean (± s.e.) longevity in days (a) and mean (± s.e.) fecundity in larvae/female (b) of adult female *Oligonychus perseae* at 25ºC on leaf disks of three cultivars of avocado collected at South Coast Field Station in April, May, and July 1998.

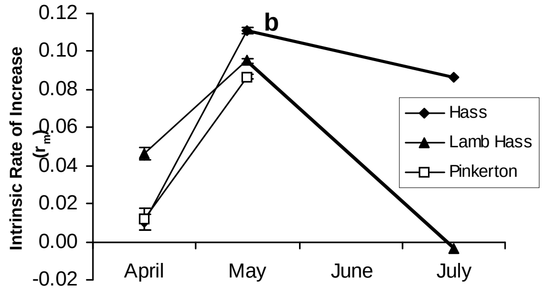


Figure 4. (a) Net reproductive rate (R_0) and (b) intrinsic rate of natural increase (r_m) of *Oligonychus perseae* at 25ºC on leaf disks of three cultivars of avocado collected at South Coast Field Station in April, May, and July 1998.