Egg Production and Population Growth of the Citrus Red Mite (Acari: Tetranychidae) on Differentially Irrigated Citrus Trees

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ABSTRACT We determined the effect of moderate (20%), continuous water stress of citrus trees on the egg production and population growth of the citrus red mite, Panonychus citri (McGregor). We also measured differences in individual and total free amino acids, soluble protein, total nitrogen, and percentage of soluble nitrogen to determine if water stress influenced the concentration of soluble nitrogenous compounds. Although this level of water stress can reduce yield directly, we observed no consistent effect of irrigation on concentrations of nitrogenous compounds. Temporal or ontogenetic variation among trees more strongly affected concentration of plant nitrogenous compounds than irrigation. The three citrus cultivars examined—Citrus limon (L.) Burman f. cv. Eureka, and Citrus sinensis (L.) Osbeck cv. Valencia and cv. Washington Navel—also varied in sensitivity to differential irrigation; lemon was least sensitive and 'Washington Navel' orange was most. Egg production rates were independent of irrigation level. Mite population growth on commercial, differentially irrigated 'Washington Navel' trees also was independent of irrigation level. When P. citri activity is expected to be greatest, differential irrigation is expected to have minimal influence on P. citri populations. The direct effects of suboptimal irrigation on yield probably are of more economic importance than any indirect effects of altering host tree suitability to mites.

KEY WORDS Arachnida, Panonychus citri, water stress, fecundity

The hypothesis that water stress increases the susceptibility of plants to phytophagous arthropods has been explored many times in the last few years. Supporting evidence is largely circumstantial, however, and several counter-examples also are known (see Mattson & Haack [1987] for a recent review). One physiological explanation postulates that the more soluble and (presumably) more assimilable forms of nitrogen increase in response to stress (White 1984). However, detailed quantitative chemical analyses of the various forms of nitrogen available to arthropods in stressed plants, especially in conjunction with measurements of arthropod survival, growth, or reproduction, have rarely been performed.

In this study, we investigated the effect of moderate, continuous water stress on the susceptibility of potted and mature Citrus trees on egg production and population growth of the citrus red mite, Panonychus citri (McGregor). We also quantified variation in individual and total free amino acids, soluble protein, and total nitrogen content among three citrus cultivars subjected to differential irrigation and determined if variation in either mite egg production or population growth on trees in different irrigation treatments was related to the variation in these nutritionally important phytochemicals.

Materials and Methods

Potted Trees. Sixty 2-yr-old citrus trees about 1.5 m in height (20 each of 'Eureka' lemon (Citrus limon (L.) Burman), 'Valencia' and 'Washington Navel' orange (Citrus sinensis (L.) Osbeck) were repotted in the spring of 1986 in 57-liter plastic containers and placed outside at the University of California Citrus Research Center, Riverside. An automated, battery-powered irrigation system (IBOC-10, Irri-Trol Mfg., Valencia, Calif.) was installed with nine independently controlled water lines with drip emitters calibrated to deliver water at the rate of 3.78 liters (1 gal)/h, one emitter per tree.

Water needs for commercial citrus are calculated from the rate of evaporation of water from an open pan (ETo) (obtained in this study from a weather station less than 200 m from the experimental site), a crop coefficient describing the overall resistance of leaves to evaporation relative to an open pan (0.75 for citrus), and the surface area of the leaf canopy (Kriedemann & Barrs 1981). Evapotranspiration (ET) treatments of 80% ET ("stressed"), 100% ET, and 120% ET ("overwatered") were maintained during the irrigation sea-
son (April–October). These irrigation treatments were chosen for their expected direct effects on plant physiology and yield (Marsh 1973). These treatments caused an average ±17% variation in leaf photosynthesis rates during the growing season (Hare et al. 1989) and have affected tree yields in contemporary studies. For example, mean (±SEM) yields from a commercial grove in the 1986 growing season were 142 ± 18 kg per tree in the 80% ET treatment, 157 ± 17 kg per tree in the 100% ET treatment, and 183 ± 21 kg per tree in the 120% ET treatment (C. Coggins, personal communication).

The time necessary to deliver the calculated quantity of water per day for each cultivar was determined and used for the 100% ET treatment. Irrigation time for the 80% ET treatment was reduced 20% and that for the 120% ET treatment was increased 20%, to the nearest minute. Irrigation times were recalculated each week on the basis of the previous week’s mean daily ET, value and canopy growth. Trees were watered automatically every 24 h, commencing at 0100 hours (PDST). All treatments received natural precipitation during the winter (November–March) rainy period. A flow meter also was installed to ensure that the irrigation system was working properly while unattended.

Accuracy of irrigation calculations was monitored with soil tensiometers (0.3 m) inserted into the soil of three trees per treatment per cultivar to measure soil suction. Tensiometers were read three times per week at 1300 hours (PDST) (i.e., at the midpoint between irrigation cycles). Readings for the 100% ET treatment were expected to be between 10 and 25 kilopascals (kPa) (Marsh 1981). Actual irrigation times were modified from those calculated if consistent deviations from this range occurred. When readings were in the 10–25-kPa range for the 100% ET treatments, readings were usually between 5 and 10 kPa in the 120% ET treatments and between 60 and 80 kPa in the 80% ET treatments. Values in the latter range have been correlated with reduced tree and fruit growth (Marsh 1973).

Mites used to monitor egg production were originally collected in 1986 from lemon trees at Riverside. Mites were maintained in a growth chamber at a constant temperature of 26°C and a photoperiod of 14:10 (L:D) using procedures identical to those of Munger & Gilmore (1963). Three times a week, motile stages were transferred to fresh lemon fruit, leaving behind a cohort of eggs within 48 h of the same age. Eggs on old fruit were returned to the incubator where immatures were allowed to eclose and develop. Adults were not used in experiments until egg production was noted.

Fifteen trees per cultivar (five trees per irrigation treatment) were randomly selected in September 1986. A single adult female mite from the laboratory colony was placed in a cage clipped to one leaf of the current flush per tree (one mite per cage, one cage per tree, five trees per treatment for each of the three cultivars). Cages were located in the north quadrant of each tree and, whenever possible, entirely on one side of the leaf midrib. Cages were checked three times per week, and daily egg production rate was calculated for each mite using procedures described by Hare (1988). Dead and missing mites were replaced after moving cages to a fresh leaf. Cages with surviving mites were routinely moved weekly to a new leaf to avoid significant reductions in larval leaf quality from previous feeding.

Observations were continued from 17 September until 24 November in 1986 and from 4 May until 27 July in 1987, when adult mortality caused by high daily temperatures became excessive. Native mite populations and other potential arthropod pests did not colonize experimental trees and were absent during both time periods. A total of 367 mites was used in 1986 and 574 in 1987.

Mature Trees. Experiments on full-sized trees were conducted in a commercial grove of ‘Washington Navel’ oranges on rough lemon rootstocks planted in 1947 near Woodlake, Calif. This plot is part of an ongoing project that includes three irrigation and three fertilization treatments. The experiments described below were done on trees receiving normal fertilization (i.e., fertilization levels based upon leaf analysis [Embleton et al. 1978]), no pesticide applications, and no growth regulator applications (48 trees in 1986 and 24 trees in 1987).

Trees also were irrigated at 80, 100, and 120% of calculated ET levels. The irrigation system included low-volume nonrotating sprinklers (one sprinkler per tree) on individual, pressure-regulated water lines, each line serving six trees. All trees were irrigated simultaneously for 24 h; the quantity of water delivered was varied among treatments by varying flow rates. The interval between irrigations varied according to evapotranspiration demand and any rainfall since the previous irrigation. Timing of irrigations was determined from State of California Department of Water Resources weekly crop water use reports issued for the southern San Joaquin Valley. These data include daily measured evapotranspiration, normal, and forecast evapotranspiration for citrus. When mites were active, irrigations were made at 5–7-d intervals, during highest evapotranspiration periods, irrigations occurred at 4-d intervals. External manifestations of water stress were rarely observed except in the 80% ET treatment. Other arthropod pests were absent, and the trees were not subjected to any other known abiotic stresses.

Mite densities were monitored at 1-4 wk intervals from 19 February through 18 June 1986 and from 11 February through 17 June 1987 (i.e., from before population development through population collapse) using procedures described by Hare & Youngman (1987). Monitoring was stopped when mite populations crashed because of the onset of high (>40°C) temperatures. After mite populations declined, mite-days were calculated for each tree.
as the area under the mite density curve as described by Hare & Youngman (1987). Differences in the mean number of mite-days among trees within irrigation treatments were analyzed by a two-factor analysis of variance (ANOVA) (Sokal & Rohlf 1981).

Chemical Analyses. Samples of leaves from the same age class and exposure upon which mites were monitored were taken at 2-wk intervals from potted trees during both experimental periods and at 3-wk intervals during the spring from the commercial grove. Two five-leaf terminals each were removed from the north and south sides of each experimental tree, bagged, packed in ice, and immediately returned to the laboratory. Leaves from replicate terminals were pooled, divided into three subsamples, weighed, then frozen at -10°C until analyzed.

Soluble protein was quantified using methods described by Jones et al. (1989). Values are reported as milligrams ribulose diphosphate carboxylase equivalent protein per gram (fresh weight) of foliage. Free amino acids were extracted and quantified after forming o-phthalaldehyde (OPA) derivatives using procedures described by Hare (1988). Total nitrogen (percentage of dry wt) was analyzed using the micro-Kjeldahl technique (McKenzie & Wallace 1954), except that we replaced the mercuric oxide catalyst with copper and potassium sulfate and used bromocresol green and methyl red instead of methylene blue as the indicator. A relative index of soluble nitrogen was calculated first by converting percentage of nitrogen (N) on a dry-weight basis to total nitrogen concentration on a fresh-weight basis (TN, mg/g) as follows:

$$\text{TN} = (\text{N} - (\% \text{ H}_{2}\text{O}/100)) \cdot 10.$$  

Then total soluble nitrogen (SN, mg/g fresh wt) was calculated from total free amino acids (TAA, mg/g fresh wt) and soluble protein content (P, mg/g, fresh wt) as follows:

$$\text{SN} = (\text{TAA} + P)/6.25,$$

where 6.25 is a widely used factor to convert from percentage of nitrogen to protein. Finally, percentage of soluble nitrogen was calculated from the ratio of SN to TN.

Statistical Analyses. Fecundity data from the potted trees were grouped into 2-wk periods centered on the date of foliage chemical analysis. Both studies on potted and mature trees were done using a split-plot ANOVA design. The error terms for evaluating the effects of whole plots (citrus cultivars and irrigation levels), subplots (sampling period), and their interactions were chosen accordingly. Variation among cultivars, among irrigation treatments, and their interaction was tested over the variation among trees within irrigation-by-cultivar combinations. Variation over time, the two- and three-way interactions involving time, and variation among trees within irrigation-by-cultivar combinations was tested over the pooled within-tree error. Variation in total nitrogen, soluble protein, total and individual free amino acid concentration, and percentage soluble nitrogen was analyzed by ANOVA using a similar design. Analyses were carried out on all cultivars combined and on each cultivar individually.

Results

Potted Trees. In the fall 1986 experiments, no significant effect of irrigation on the “summary” nitrogen parameters of total amino acid content, soluble protein content, percentage of total nitrogen, or percentage of soluble nitrogen was detected from the overall data analysis (Table 1). However, fourteen of the 20 amino acids, total amino acid content, soluble protein content, and percentage of soluble nitrogen differed significantly because of the cultivar-by-irrigation treatment interaction, suggesting that there was substantial variation in the responses of the three Citrus cultivars to irrigation.

The only factor significantly affected by irrigation level in lemon trees was total nitrogen content ($F = 6.00; \text{df} = 2, 12; P < 0.05$); it was consistently lowest in the 120% ET irrigation treatment (Fig. 1). In ‘Washington Navel,’ fourteen individual amino acids, including proline (all significant, $F \geq 4.81; \text{df} = 2, 12; P \leq 0.03$), total amino acid content ($F = 6.18; \text{df} = 2, 12; P < 0.05$), soluble protein content ($F = 7.20; \text{df} = 2, 12; P < 0.01$), and percentage of soluble nitrogen content ($F = 5.19; \text{df} = 2, 12; P < 0.05$) differed significantly among irrigation treatments. In general, ‘Washington Navel’ trees in the 120% irrigation treatment were richest in the soluble forms of nitrogen (Fig. 1). In ‘Valencia,’ only three of the individual free amino acids (alanine, leucine, and proline) differed significantly among irrigation treatments (all significant, $F \geq 3.89; \text{df} = 2, 12; P \leq 0.05$), although none of the summary nitrogen parameters differed among irrigation treatments (Fig. 1).

Therefore, our 1986 data fail to support the hypothesis that reduced irrigation during the previous summer consistently increased concentrations of soluble nitrogenous compounds in potted citrus trees. On the contrary, ‘Washington Navel’ trees (slightly overwatered) had higher concentrations of soluble nitrogen than did drought-stressed trees.

In spring 1987, in contrast to the results from the previous autumn, concentrations of total amino acids, soluble protein, and total nitrogen all differed significantly among irrigation treatments in the overall analysis (Table 2), and each was highest in the 80% ET treatment, intermediate in the 120% treatment, and lowest in the 100% ET treatment. All summary parameters also varied over time (Table 2), and all declined as the season progressed (Fig. 2). However, as in the previous fall, the effect of the cultivar-by-irrigation treatment interaction...
Table 1. Fall 1986 F statistics for *P. citri* on potted trees

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Total amino acids</th>
<th>Soluble protein</th>
<th>% Total nitrogen</th>
<th>% Soluble nitrogen</th>
<th>Daily egg production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irrigation</td>
<td>2</td>
<td>0.30</td>
<td>0.93</td>
<td>0.03</td>
<td>1.27</td>
<td>0.84</td>
</tr>
<tr>
<td>Cultivar</td>
<td>2</td>
<td>15.31***</td>
<td>40.24***</td>
<td>28.16***</td>
<td>19.05***</td>
<td>2.74</td>
</tr>
<tr>
<td>Irrigation x cultivar</td>
<td>4</td>
<td>3.02**</td>
<td>4.10**</td>
<td>2.42</td>
<td>3.85*</td>
<td>0.16</td>
</tr>
<tr>
<td>Trees within irrigation x cultivar)</td>
<td>36</td>
<td>2.20***</td>
<td>2.31***</td>
<td>5.11***</td>
<td>1.84**</td>
<td>2.19***</td>
</tr>
<tr>
<td>Time</td>
<td>4</td>
<td>25.40***</td>
<td>10.19***</td>
<td>4.19**</td>
<td>21.46***</td>
<td>11.72***</td>
</tr>
<tr>
<td>Cultivar x time</td>
<td>8</td>
<td>1.06</td>
<td>2.78**</td>
<td>1.25</td>
<td>2.02*</td>
<td>0.05</td>
</tr>
<tr>
<td>Irrigation x cultivar x time</td>
<td>16</td>
<td>2.40***</td>
<td>1.78*</td>
<td>0.93</td>
<td>2.70***</td>
<td>1.32</td>
</tr>
<tr>
<td>Error mean squares*</td>
<td>78</td>
<td>0.78</td>
<td>6.89</td>
<td>0.03</td>
<td>33.15</td>
<td>1.67</td>
</tr>
</tbody>
</table>

* P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001.

was significant for five individual free amino acids, total free amino acid concentration, soluble protein concentration, and total nitrogen concentration (Table 2).

Only one free amino acid, lysine, differed significantly (*F* = 5.31; df = 2, 12; *P* ≤ 0.05) among irrigation treatments in lemon, and none of the summary nitrogen parameters was significantly af-

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**Fig. 1.** Fall 1986: Comparisons of lemon and 'Valencia' and 'Naval' orange foliage from potted trees irrigated at 80, 100, or 120% ET. Values are cultivar means (±SEM) based on five tree means for each cultivar-by-treatment combination and two determinations per tree.
Table 2. Spring 1987 F statistics for *P. citri* on potted trees

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Total amino acids</th>
<th>Soluble protein</th>
<th>% Total nitrogen</th>
<th>% Soluble nitrogen</th>
<th>Daily egg production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irrigation</td>
<td>2</td>
<td>7.28***</td>
<td>4.78*</td>
<td>5.47***</td>
<td>2.21</td>
<td>0.40</td>
</tr>
<tr>
<td>Cultivar</td>
<td>2</td>
<td>60.76***</td>
<td>64.89***</td>
<td>44.51***</td>
<td>50.35***</td>
<td>0.59</td>
</tr>
<tr>
<td>Irrigation x cultivar</td>
<td>4</td>
<td>6.83***</td>
<td>4.48**</td>
<td>4.01**</td>
<td>1.94</td>
<td>1.02</td>
</tr>
<tr>
<td>Trees within (irrigation x cultivar)</td>
<td>36</td>
<td>1.20</td>
<td>2.91***</td>
<td>4.60***</td>
<td>1.82**</td>
<td>2.27***</td>
</tr>
<tr>
<td>Time</td>
<td>5</td>
<td>39.28***</td>
<td>6.96***</td>
<td>23.44***</td>
<td>33.45***</td>
<td>8.55***</td>
</tr>
<tr>
<td>Irrigation x time</td>
<td>10</td>
<td>1.59</td>
<td>1.38</td>
<td>1.59</td>
<td>1.04</td>
<td>0.59</td>
</tr>
<tr>
<td>Cultivar x time</td>
<td>10</td>
<td>5.83***</td>
<td>1.95*</td>
<td>5.90***</td>
<td>3.26***</td>
<td>1.23</td>
</tr>
<tr>
<td>Irrigation x cultivar x time</td>
<td>20</td>
<td>2.42***</td>
<td>1.54</td>
<td>1.77*</td>
<td>1.18</td>
<td>2.13**</td>
</tr>
<tr>
<td>Error mean squares</td>
<td>180</td>
<td>3.25</td>
<td>14.07</td>
<td>0.09</td>
<td>79.60</td>
<td>2.38</td>
</tr>
</tbody>
</table>

*, P ≤ 0.05; **, P ≤ 0.01; ***, P ≤ 0.001.

Degrees of freedom = 180 for all chemical parameters and 1,201 for daily egg production rate.

In contrast, in 'Washington Navel,' 14 individual amino acids differed significantly among irrigation treatments (all significant, \( F \geq 4.91; \) df = 2, 12; \( P \leq 0.05 \)), as did total free amino acid content (\( F = 29.91; \) \( P \leq 0.001 \)), soluble protein content (\( F = 29.91; \) \( P \leq 0.001 \)), and daily egg production rate (\( F = 8.55; \) \( P \leq 0.01 \)).

![Fig. 2. Spring 1987: Comparisons of lemon and 'Valencia' and 'Navel' orange foliage from potted trees irrigated at 80, 100, or 120% ET. Values are cultivar means (±SEM) based on five tree means for each cultivar-by-treatment combination and two determinations per tree.](image-url)
Table 3. Spring 1987 F statistics for field-grown ‘Washington Navel’ trees

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Total amino acids</th>
<th>% Total nitrogen</th>
<th>% Soluble nitrogen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Irrigation</td>
<td>2</td>
<td>3.94*</td>
<td>2.15</td>
<td>0.34</td>
</tr>
<tr>
<td>Trees within irrigation</td>
<td>21</td>
<td>0.87</td>
<td>1.42</td>
<td>1.25</td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>36.82***</td>
<td>37.38***</td>
<td>77.88***</td>
</tr>
<tr>
<td>Irrigation × time</td>
<td>6</td>
<td>0.39</td>
<td>0.36</td>
<td>0.38</td>
</tr>
<tr>
<td>Error mean squares</td>
<td>63</td>
<td>1.06</td>
<td>4.81</td>
<td>0.04</td>
</tr>
</tbody>
</table>

", P \leq 0.05; ***, P \leq 0.001.

The concentration of amino acids, soluble protein, total nitrogen, and soluble nitrogen were significantly different among irrigation treatments. The highest concentrations of total amino acids, soluble protein, and total nitrogen occurred in the 100% ET treatment, whereas the 80% ET treatment had the highest percentage of soluble nitrogen. The 120% ET treatment had an overall higher percentage of soluble nitrogen than the other irrigation treatments.

Mature Trees. Results from mature, field-grown ‘Washington Navel’ trees contrast with those from potted ‘Washington Navel’ trees. Only the concentration of proline differed significantly (F = 8.38; df = 2, 21; P \leq 0.01) because of irrigation at the field site. Highest concentrations generally occurred in the 100% ET treatment until the last sampling period, at which time highest concentrations occurred in the 80% ET treatment. Of the summary nitrogen parameters, only total free amino acids and percentage soluble nitrogen differed significantly because of irrigation treatment (Table 3); highest concentrations of both generally occurred in the 100% ET treatment (Fig. 3). All parameters showed substantial variation over time (Table 3, Fig. 3).

Mite Reproduction Rates. In general, results presented in Fig. 4 agree with previous field studies showing daily oviposition rates ranging from one to three eggs per female per day (Hare 1988). In the overall analyses, daily oviposition rates were independent of irrigation level on all cultivars in both the fall 1986 and spring 1987 experiments (Tables 1 and 2, Fig. 4). The lack of significant variation in egg production rates among cultivars in the spring is similar to the results reported by Hare (1988), showing that new, spring-flush leaves of lemon and mandarin orange do not differ significantly for egg production by P. citri when spring mite populations are active.

Fig. 3. Spring 1987: Comparisons of foliage from field-grown ‘Navel’ orange trees irrigated at 80, 100, or 120% ET. Values are means (±SEM) of eight tree means for each treatment and two determinations per tree.
In general, mite populations achieved a relatively high density (more than three times the conventional treatment threshold of two adults per leaf [Pehrson et al. 1984]). In 1986, mite densities differed significantly among treatments only on 23 April ($F = 5.28; \text{df} = 2, 45; P \leq 0.01$), but densities were highest in the 120% ET treatment and lowest in the 80% ET treatment (Fig. 5). In 1987, mite densities never differed significantly among treatments (all $F \leq 2.48; \text{df} = 2, 21; P \geq 0.10$; Fig. 5). Total mite-days did not differ significantly among irrigation treatments in either year ($F = 0.34; \text{df} = 2, 45; P > 0.50$ in 1986 and $F = 1.04; \text{df} = 2, 21; P > 0.25$ in 1987) (Fig. 5).

**Discussion**

We noted substantial variation among the three citrus cultivars in how their nitrogen metabolism was altered by differential irrigation when grown in pots. 'Washington Navel' orange was the most sensitive and lemon was the least among the three cultivars examined. However, full-sized, field-grown 'Washington Navel' orange trees showed little change in concentration of nitrogenous compounds in response to differential irrigation.

We considered the possibility that differential irrigation at the beginning of the season would have less effect on plant nitrogen metabolism and sus-
ceptibility of trees to mites than at the end of the irrigation season. Because trees in all treatments were equally exposed to winter rains, winter rainfall may have replenished the soil water reservoir and nullified the differences between treatments before the growth of mite populations. Thus, the lack of strong differences among treatments in either potted or field-grown trees for mite reproduction or population growth in the spring was not unexpected. We had anticipated that it might require several weeks more of differential irrigation, especially on field-grown trees, before treatment effects would become sufficiently large to affect mite population growth.

Neither the data on mite egg production nor plant nitrogen characteristics in the fall 1986 experiments indicate that water-stressed trees were more suitable for mite reproduction after a full season of under-irrigation than in the spring. Thus, we conclude that during the periods when citrus red mite activity is expected to be greatest differential irrigation of host trees has little consistent effect on either mite egg production or population growth.

The effect of water stress on any particular plant-arthropod association depends upon the physiological changes occurring in stressed plants and the abilities of arthropods to exploit those changes (Mattson & Haack 1987). Previous studies showing reductions in plant suitability for growth of populations of mites following water stress include the European red mite, Panonychus ulmi (Koch), on apple (Specht 1965) and the twospotted spider mite, Tetranychus urticae Koch, on soybean (Mellors et al. 1984).

Recently, Youngman et al. (1988) showed that Tetranychus pacificus McGregor produced more eggs on potted almond trees subjected to variable water stress (e.g., heavy watering when wilting was observed) than on trees subjected to continuous water stress (e.g., just enough water to keep wilted leaves alive) or control (well-watered) trees. They argued that these differences in egg production may contribute at least in part to the increases in mite densities on water-stressed almond trees (Youngman & Barnes 1986). These authors reviewed several other examples showing increases in mite populations on drought-stressed crops.

In reconciling these different results of water stress on mite reproduction and population growth, we must consider that most views of herbivore nutrition assume that nitrogen is more limiting than energy; that energy content of food is usually not a good predictor of performance, and that proteolysis, either within the plant or during digestion by the herbivore, is unlikely to be a rate-limiting step in herbivore nutrition (Brodbeck & Strong 1987).

The assumption that "predigested" proteins (i.e., free amino acids) are metabolically more useful than amino nitrogen in the form of protein probably needs to be reevaluated. For example, diets containing all nitrogen in the form of amino acids were not better for oviposition by Anthonomus grandis Boheman than diets containing all nitrogen as protein (Vanderzant 1963). Naylor (1964) found that survival and developmental rates of Tribolium confusum Jacquelin du Val were highest when protein supplied at least one-third of dietary nitrogen than when all nitrogen was provided as crystalline amino acids. Egg production by T. urticae and P. citri were highest when all dietary nitrogen was provided as protein rather than (in whole or in part) by free amino acids (Kantaratanakul & Rodriguez 1979, Hare & Bethke 1988). Uniform hydrolysis of proteins to their individual free amino acids in response to water stress, therefore, may be a minor component in changes in the suitability of drought-stressed plants for phytophagous arthropods (Naylor 1972, Brodbeck & Strong 1987). Mattson & Haack (1987) discuss other factors in addition to plant nitrogen metabolism that also may influence the behavioral acceptability and physiological suitability of foliage from water-stressed plants for herbivorous insects.

It would not be appropriate to extend our results to other pests of citrus. First, because of the seasonal abundance of P. citri, plant analyses were continued only until mid-June on field-grown trees and

![Fig. 5. Mean (±SEM) number of adult female citrus red mites on field-grown 'Navel' orange trees irrigated at 80, 100, or 120% ET during 1986 and 1987. Means based on 16 trees per treatment in 1986 and eight trees per treatment in 1987. In 1986 mean (±SEM) mite-days were 337.3 ± 28.7 in the 80% ET treatment, 358.7 ± 42.8 in the 100% ET treatment, and 376.3 ± 26.7 in the 120% ET treatment. In 1987, values were 433.3 ± 65.9, 602.0 ± 119.2, and 450.1 ± 100.3, respectively.](image-url)
mid-July on potted trees. Thus, we cannot speculate on the effect of differential irrigation on population growth of arthropod species that are abundant on citrus outside our experimental periods.

Second, because *P. citri* has been shown to be only slightly affected by within-cultivar seasonal variation in concentrations of nitrogenous plant compounds (Hare 1988), even the lowest levels found in this study may be sufficient to satisfy the nutritional needs of *P. citri*. Arthropods species more sensitive to the physiological condition of the host plant might show greater responses to differential irrigation of citrus than does *P. citri*.

Nevertheless, variation in irrigation level sufficient to have caused direct yield reductions in other studies had no consistent, significant effect on *P. citri* population growth. There may be higher levels of water stress that would perhaps promote *P. citri* population growth; however, we expect the direct effects of water stress on yield also to be greater. Thus, within the practical limits of differential irrigation to which most commercial citrus would be subjected, water stress of host trees has minimal influence on growth of *P. citri* populations.

Acknowledgment

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