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MANIPULATING VINEYARD IRRIGATION AMOUNTS TO REDUCE INSECT PEST DAMAGE

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Abstract. Insect herbivore densities can respond to changes in host plant vigor. While many basic studies have described the generalized patterns and mechanisms of host plant influence on herbivore densities and biological traits, fewer studies have shown practical applications for the observed ecological patterns. We assessed the effect of different irrigation amounts on grapevine (*Vitis vinifera* L., cv. Thompson Seedless) condition and the resulting changes to an insect herbivore (the variegated leafhopper, *Erythroneura variabilis* Beamer). Water amounts delivered to vines were manipulated with respect to amounts delivered in a weighing lysimeter: 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, and 1.4 times that used by vines in the lysimeter. We then followed plant growth measurements and leafhopper density and biological traits throughout the growing season. By August and September, midday leaf water potential, mean shoot length, vegetative growth, and pruning mass were a positive linear function of applied water amounts. The amount of N per unit leaf area decreased as applied water amounts increased. Similar to measured levels of vine growth, there was a seasonal response of leafhopper density to applied water amounts. By August and September, leafhopper density was a positive linear function of applied water amounts. Dry mass of fifth instar leafhoppers, the numbers of marked and recaptured adults, and leafhopper egg deposition were also positively correlated to irrigation amounts. Our results indicate that the greatest influence of manipulated vine growth and irrigation amounts may be due to differences in adult leafhopper movement and reproductive potential, which has implications for dispersal of pests between vineyards. We demonstrated that applied irrigation amounts to vines can be manipulated to suppress insect herbivore density without negatively influencing crop yield. We discuss our results of insect herbivore response to changes in plant water stress within the context of the plant vigor hypothesis.

Key words: *agroecosystems; California, USA;* Erythroneura variabilis; *host plant quality; insect–plant interactions; leafhopper; plant stress and plant vigor hypotheses; plant water deficits for pest management;* Vitis vinifera.

INTRODUCTION

Insect herbivore life-history traits, such as growth, fecundity, and dispersion, are often influenced by host plant quality (Mattson 1980, Herms and Mattson 1992, Waring and Cobb 1992, Leather 1994, Koricheva et al. 1998). Two contrasting hypotheses suggest that changes in host plant quality result in generalized patterns of herbivore attack. In the first, stressed or slow-growing plants are more suitable as food for insect herbivores (White 1974, 1984, Mattson and Haack 1987). Support is found mostly in field studies of natural ecosystems (Hacker and Bertness 1995), such as herbivorous insect species that increase in density following natural periods of host plant stress such as drought (White 1974). Other evidence comes from plant biochemical changes associated with plant stress that can improve insect performance, such as increased nitrogen (N) and lowered defensive chemicals (Feeney 1970, Rhoades 1979). The second hypothesis suggests that vigorous plant growth will favor herbivores, especially those that are intimately associated with their host plant (Price 1991). Support for this hypothesis comes largely from studies showing insect herbivore preference and increased performance on young plants or plants with longer shoots (Coley 1983, Karban 1987, Lightfoot and Whitford 1987, Price et al. 1987, Byrne and Draeger 1989).

Price (1991) suggests that these two hypotheses present not a dichotomy in nature, but opposing ends to a continuum. Indeed, the great variation in insect species responses to plant condition may preclude a generalized description of herbivore–plant vigor patterns. For example, while numerous studies show that galling insects prefer vigorous plants or plant modules (Craig et al. 1986, Preszler and Price 1988, Prado et al. 1999), some gall-forming species have shown either no preference (McKinnon et al. 1999) or less preference to vigorously growing plants (De Bruyn 1995). Although most research supporting both the plant stress and plant vigor hypotheses has been conducted in either natural

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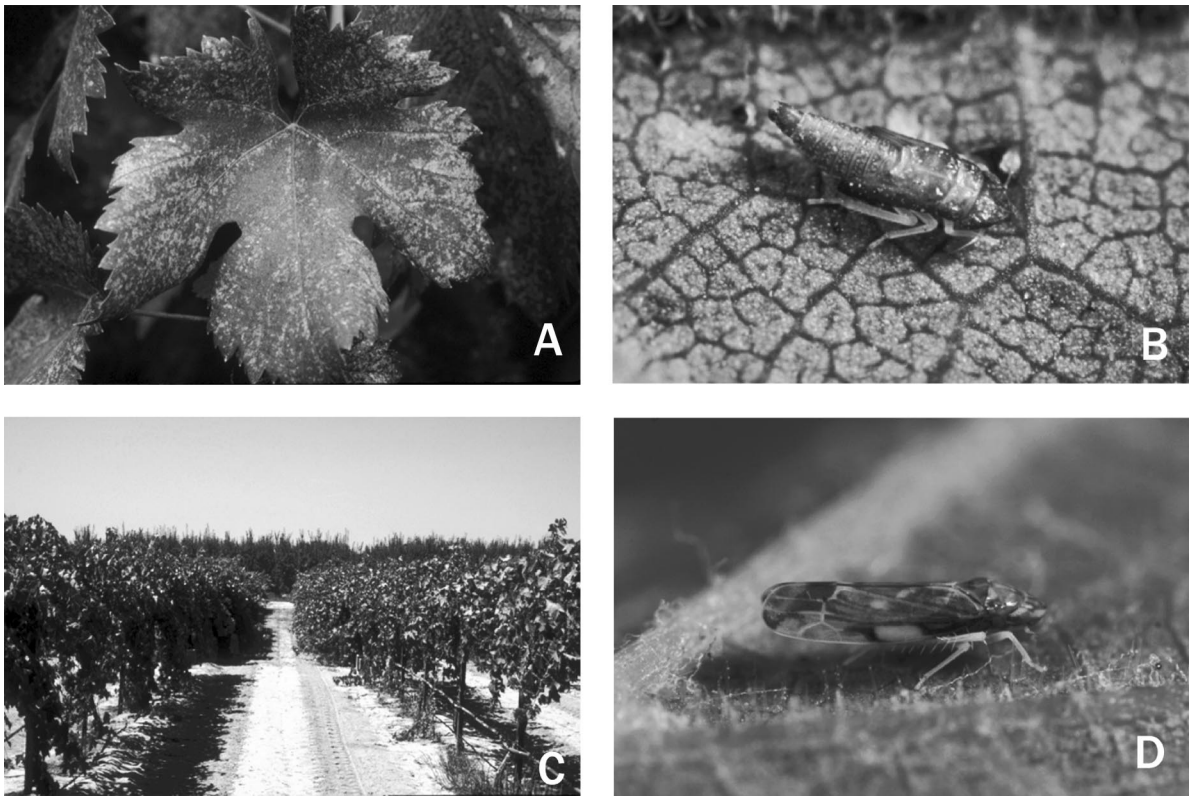

PLATE 1. Variegated leafhopper (*Erythroneura variabilis*) damage on a single leaf showing damage to individual leaf mesophyll. (B) A fifth instar variegated leafhopper nymph. (C) The lysimeter block, with vines receiving 0.0 and 0.2 ET applied irrigation amounts in the foreground and 1.2 and 1.4 ET applied irrigation amounts in the background. (D) An adult variegated leafhopper.

ecosystems or the laboratory, insect herbivore response to host plant condition can have considerable economic importance in agroecosystems. Furthermore, changes in plant quality in natural ecosystems are often associated with uncontrolled changes in climate or soil quality, while in agroecosystems manipulation of water and mineral levels is often an essential component of crop production. Therefore, management of plant vigor levels to suppress pest densities in agroecosystems provides opportunity to test ecological hypotheses in applied systems.

We investigated the manipulation of irrigation amounts to change host plant quality and improve insect pest management. Waring and Cobb (1992) report that most insect herbivores studied (68% of 75 cases) respond positively to naturally water-stressed plants, while there was no clear pattern when plants were artificially water stressed (51% of 99 cases). Still, applied irrigation amounts are one of the more essential and often manipulated components in irrigated agroecosystems, and water conservation has become an essential crop management and environmental factor in many semiarid agricultural regions. We manipulated irrigation amounts in a block of 'Thompson Seedless' vines, to determine the response of the variegated leafhopper, *Erythroneura variabilis* Beamer, to changes in plant vigor. This cicadellid was the primary vineyard pest in California's San Joaquin Valley in the 1990s (Settle and Wilson 1990, Wilson et al. 1992). *Erythroneura variabilis* feeds on leaf mesophyll cells and can cause chlorotic spotting and defoliation, thereby reducing leaf photosynthesis (see Plate 1A). The relationship between vineyard irrigation amounts and leafhopper density was first described by Trichilo et al. (1990). These researchers showed that reduced irrigation amounts lowered leafhopper densities (*E. variabilis* and *Erythroneura elegantula* Osborn). The mechanisms causing this reduction were not determined and leafhopper densities in the test plots were far below reported economic injury levels, which are between 10–20 nymphs per leaf (Wilson et al. 1992). Therefore, it was unclear whether irrigation amounts could be manipulated to reduce economically damaging *E. variabilis* densities while maintaining healthy vines and high yields. Our goals were to: (1) validate the influence of applied water amounts on *E. variabilis* density, (2) determine the underlying mechanism for *E. variabilis* response to vine growth as a function of irrigation, and (3) ascertain the feasibility of manipu-

lating irrigation amounts to improve pest management while maintaining a viable commercial vineyard.

METHODS

Description of study site

A weighing lysimeter was installed at the University of California, Kearney Agricultural Center (Parlier, California, USA) in the San Joaquin Valley in 1986. Two *Vitis vinifera* L. (cv. ''Thompson Seedless'' clone 2A) grapevine cuttings were planted in the lysimeter on 9 April 1987. Cuttings were also planted in the 1.4-ha (168 × 82 m) vineyard surrounding the lysimeter with vine and row spacings of 2.15 and 3.51 m, respectively (7.55 m^2 per vine). Row direction was east/west. The soil was a Hanford fine sandy loam (coarse-loamy, mixed, nonacid, thermic Typic Xerorthent) of uniform depth throughout the vineyard. The vine trellis consisted of a 2.13-m wooden stake onto which a 0.6- or 1.2-m cross-arm was placed with wires attached at either end to support the vine's fruiting canes. The trellis for the vines in the lysimeter was self-contained to ensure it was part of the lysimeter mass.

The soil container of the lysimeter was 2 × 4 m (width × length) and 2 m deep. The tank was weighed with a balance beam and load cell configuration, with most of the mass being eliminated using counter masses. The calibrated accuracy of the lysimeter was ±0.025 mm of water, and the overall resolution of the system was 400 g or 0.05 mm of water. The hourly loss of mass by the lysimeter was assumed to be due to the water loss by transpiration, soil evaporation, and drainage. A more detailed description of the lysimeter can be found in Phene et al. (1991).

Vines within the lysimeter and the surrounding vineyard were irrigated with 4 L/h in-line drip emitters, spaced every 0.30 m. The drip tubing was attached to a wire suspended 0.4 m above the soil surface. Irrigation water for the lysimeter was supplied from two 300-L water tanks suspended on the weighbridge supporting the lysimeter (to ensure this water was a part of the lysimeter's mass). The lysimeter was weighed hourly to determine evapotranspiration (ET_c) of the two vines, and the change in mass was compared with a 16-L (8 L/vine) threshold value of water loss. When the threshold was exceeded, the lysimeter was irrigated. At midnight the water tanks were refilled, the inflow was measured with a flow meter and recorded electronically, and the new lysimeter mass was used as a baseline for the next day. A Campbell Scientific 21× Micrologger (Campbell Scientific, Logan, Utah, USA) was used to monitor and control the system and to communicate with a computer at the USDA-ARS Water Management Research Laboratory (WMRL) in Fresno, California, USA. Data were downloaded to the WMRL computer and processed daily at midnight. The number of irrigations applied each day during the 1991, 1992, and 1993 growing seasons ranged from 0 to 7.

The irrigation pump for the rest of the vineyard was connected to the lysimeter's datalogger. Whenever the lysimeter was irrigated, the vineyard pump was activated and an irrigation event took place. The irrigation treatments were applied water amounts at various fractions of lysimeter water use. Vines were irrigated at 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, and 1.4 times that used by the lysimeter (see Plate 1C). Each row was 38 vines in length and each irrigation treatment plot consisted of 19 vines down a row. The irrigation treatments within each block were set up as a line source, going from lowest to highest irrigation amounts. Treatments were replicated eight times (eight blocks) and the line-source direction was randomized in each block. Two rows separated each block. The duration that the solenoid valves at the head of each row were activated was used to provide the differing fractions of applied water. In-line water meters downstream from the solenoid valves were used to measure actual applied water amounts. Water application amounts were within 3% of the target value (specific fraction of lysimeter water use) for each irrigation treatment.

Measuring vine water status and growth parameters

Midday leaf water potential (Ψ_l) readings were measured according to the procedures of Williams and Araujo (2002). Specifically, midday measurements of Ψ_l were taken between 1230 and 1330 hours, using a pressure chamber (PMS Instruments Company, Corvallis, Oregon, USA). Leaf blades for Ψ_l determinations were covered with a plastic bag, quickly sealed, and petioles then cut within 1–2 s. The time between leaf excision and chamber pressurization was generally <15 s. Leaves chosen for midday Ψ_l determinations were fully expanded, mature, exposed to direct solar radiation, and located on the south side of the east/west rows. A single leaf from a minimum of five individual vine replicates per irrigation treatment was measured on each sample date. The Ψ_l values reported herein are the means of weekly readings taken during August in 1991 ($n = 4$), August and the first week of September in 1992 ($n = 5$), and biweekly in August in 1993 ($n = 2$).

Leaf area was determined on a single vine in three blocks of selected irrigation treatments in August of 1991 and 1992 and the first week of September in 1993. At this time, lengths of all shoots on each vine were also measured. All leaves were removed from each vine, fresh mass measured and subsampled. The area of the subsample was determined with a LI-COR model 3100 area meter (LI-COR, Lincoln, Nebraska, USA). After their area was measured, leaves were subsampled and dried at 70°C in forced-air ovens until no further decrease in mass was measured. Total N concentration was measured on the samples of ground leaf tissue by the Kjeldahl procedure. Values of leaf N were expressed on a dry mass and area basis. Fresh pruning masses (an indicator of the current season's vegetative

growth) were measured during the dormant season (after the leaves have fallen). The mass of four vines was recorded within each treatment and block combination ($n = 8$).

Measuring leafhopper density and biological traits

Nymph density.—*Erythroneura variabilis* densities were determined at periods of peak nymph densities in each generation. In the central San Joaquin Valley, *E. variabilis* generations typically peak in late May to early June (first generation), mid-to late July (second generation), and early September (third generation) (Wilson et al. 1992). The timing of sample dates was more precisely determined by weekly monitoring nymph densities and egg hatch on 30 leaves collected throughout the lysimeter block. To sample peak nymph densities, leaves were collected from the middle vines of each plot at node positions 1–3, 4–6, and 5–10 for the first, second, and third *E. variabilis* generations, respectively (as described by Daane and Costello 2000). In each study year, the number of leaves and blocks (replicates) sampled varied slightly, reflecting analysis of the previous season's data. In 1991, 20 leaves were sampled in each irrigation treatment of all eight blocks. In 1992, 40 leaves were sampled in each of four irrigation treatments (0.0, 0.4, 0.8, and 1.2) in each of six blocks. In 1993, 25 leaves were sampled in each of four irrigation treatments (0.0, 0.4, 0.8, and 1.2) in each of four blocks.

Nymph size.—The dry masses of fifth instar *E. variabilis* (see Plate 1B) were used to measure leafhopper size differences among irrigation treatments. In each sample, ~300 fifth instars were collected in each sampled plot and immediately frozen. Just before weighing, samples were oven-dried at 70°C for 2 h and then placed in a covered petri dish containing Drierite (W. A. Hammond Drierite Company, Xenia, Ohio, USA) to prevent reabsorbtion of moisture from the air. Nymphs were weighed in groups of three to the nearest 0.001 μg. Collections were made in the second and third *E. variabilis* generations in 1992 and the first, second, and third generations in 1993. For the second generation in 1992, *E. variabilis* were collected in the 0.0, 0.6, and 1.2 irrigation treatments from three blocks; on all other collection dates, all treatment levels were sampled in each of three blocks.

Nymph mortality.—To measure nymph mortality, we used small (0.5 × 0.25 m) organdy cages to isolate *E. variabilis* cohorts on three mature leaves. To begin, a shoot was put through the organdy cage (open at both ends), which was then tied in place over the selected leaves with the growing shoot tip outside the distal end of the cage. All cages were located on the north side of the vine to reduce direct sunlight from increasing temperatures inside the cages. The cages were established before the first *E. variabilis* generation, and the three isolated leaves showed no signs of *E. variabilis* presence or damage at that time. To inoculate the clean leaves, first and second instar *E. variabilis* were collected from vines in the 1.0 irrigation treatment. To induce the small nymphs to remove their mouthparts from the leaf, thereby preventing damage, we touched their abdomen with a camel hair brush until they began walking, and then transferred them with the camel hair brush to a clean, freshly excised leaf. These leaves were used to inoculate the organdy cages (10 nymphs/leaf or 30 nymphs/cage).

Cages were established in the 0.0, 0.4, 0.8, and 1.2 irrigation treatments, with five replicates per treatment, each in separate blocks. Some leafhoppers died immediately after transfer, which more likely reflects damage during inoculation. To account for this mortality, 3 d after inoculation we counted nymphs in each cage and, when necessary, second instar(s) were added to bring the total back to 30 nymphs/cage. Every 2–3 d thereafter, the cages were opened and nymph density was recorded by development stage. The experiment was undertaken during the second (3–30 July) and third (1 September–14 October) generations in 1993.

Adult movement.—The preference of adult *E. variabilis* (see Plate 1D) to disperse to vines in different irrigation treatments was determined in mark–release–recapture studies. Adults were collected from a vineyard outside the lysimeter block using a ''D-vac,'' a gasoline powered blower-vacuum (Echo, Lake Zurich, Illinois, USA) that had an intake rate of 15.3 m^3/min when fitted with a 10 cm diameter orifice. Collected adults were placed into 2-L plastic bags, anesthetized with CO_2 and marked with a florescent dye by adding a small amount (<0.2 g) to each plastic bag and shaking. Earlier trials found that this method marked >80% of the collected adults and the majority remained marked for 3 d. In each trial, the anesthetized and marked adults were divided equally into cardboard cups (5 cm deep × 8 cm wide), using a graduated cylinder to measure the volume and equally distribute adults. The cups were placed 5 m from the vineyard edge and at points that were equidistant from the beginning of each irrigation treatment for each sampled block. Soon after the cups were placed on the ground the fresh air revived the adults and they dispersed. During the mark–release process, efforts were made to prevent injury to the marked adults by making collections in the early morning hours, when ambient temperatures were lower, and using the florescent dye sparingly to reduce problems with flight. With these techniques, <2% of marked insects remained in the cups after the 1–2 min release period; it is not known whether they were unable to disperse because they were weak when collected, marked with too much dye, or damaged during the D-Vac process. The number of adults marked in each trial is estimated at ~4000 and ~9000 in the second and third generations, respectively, by measuring their volume while anesthetized. There was little or no measurable wind during the release.

At 1 and 3 d after the release, all 19 vines (both north and south sides) in each treatment plot were sampled with the D-Vac for either 30 or 60 s/vine in 1992 and 1993, respectively. The increase in sample time in 1993 (an additional 30 s/vine) was to collect more *E. variabilis*. Collected adults were placed in plastic bags, frozen, and later examined under an ultraviolet light to determine the number of marked adults. During this examination, the samples were cleaned of plant debris and the total number of adults was also determined. The first trial was conducted on 24–26 July 1992 in the 0.0, 0.4, 1.0, and 1.4 irrigation treatments in each of three blocks. The trial was repeated on 3–4 August 1992, 23–24 July 1993, and 4–5 August 1993 in all irrigation treatments in each of three blocks. These sample dates correspond to the natural presence of adults derived from the first and second *E. variabilis* generations in each year.

Adult egg deposition.—The number of eggs deposited per female was used to estimate the effect of irrigation treatments on adult reproductive potential. Two experiments were conducted concurrent with the egg deposition period for the third *E. variabilis* generation in 1993. In the first experiment, the tested adults were reared from first and second instars that had been isolated in organdy cages in the 1.0 irrigation treatment, using the same protocol to isolate clean leaves as described previously. From these rearing cages, newly molted adults were collected, sexed, and placed into trial cages, isolating five female and three male adults on three clean (no leafhopper eggs) leaves. The trial cages had been previously established in 0.0, 0.6, and 1.2 irrigation treatments in each of four blocks (replicates). In the second experiment, we reversed the order by rearing nymphs at 0.0, 0.6, and 1.2 irrigation treatments and moving adults into the 1.0 treatment level, using the same protocols as in the first trial. In both experiments, all adults died after 4 wk and the number of live, hatched, and dead *E. variabilis* eggs were recorded on all leaves in all cages by viewing the leaves through a dissecting microscope.

Statistical analysis

Data on grapevine water status and growth parameters and on *E. variabilis* density, mass, and egg deposition are presented herein as means per treatment (± 1 SE). Treatment influences on grapevine and *E. variabilis* parameters were separately analyzed for each year or experimental trial, using analysis of variance (ANOVA) and regression analysis, with treatment means separated using Tukey's hsd test (three or more treatments) or a *t* test (two treatments). With the exception of the ''nymph mortality'' study, all *E. variabilis* mean values and statistical analyses were determined from mean values of each replicate, which is a more rigorous analysis because of the lowered degrees of freedom. Treatment influence in the nymph mortality study was determined using repeated-measures ANOVA on *E. variabilis* nymph densities per leaf and adult densities per cage.

Results

Irrigation amounts, vine water status, and vegetative growth

Grapevine evapotranspiration (ET_c) from budbreak (mid-March) until the end of October was 6532, 6123, and 6472 L/vine (equivalent to 865, 811, and 857 mm of water) in 1991, 1992, and 1993, respectively. The amount of water actually applied to the vines in the lysimeter was less, because irrigations did not commence until the first week of May each year. Mean water use between budbreak and the first annual irrigation for vines in the lysimeter was 455 L/vine (61 mm). During this time, vines in all of the irrigation treatments were dependent upon rainfall or water obtained from the soil reservoir. Applied water amounts to the 1.0 irrigation treatment between the initiation of irrigation and the third generation of *E. variabilis* (the middle of September) was ~5100 L/vine (675 mm) each year. Vines in the other irrigation treatments received their designated fraction of this amount each year.

The initial measurements of vine water status taken early in the growing season resulted in minimal differences in midday Ψ_l among the irrigation treatments. Thereafter, midday Ψ_l gradually decreased throughout the growing season, especially for vines that were irrigated with applied water amounts $<100\%$ of lysimeter use. The seasonal minimums of Ψ_l for all irrigation treatments generally were obtained in August and September, when midday Ψ_l was a positive linear function of applied water amounts (Fig. 1A). Midday Ψ_l of vines that were irrigated at $\geq 100\%$ of ET_c in 1991 and 1992 were > -1.0 MPa in August and September, while in 1993 the Ψ_l of vines in the 0.6 irrigation treatment was > -1.0 MPa at that time (values < -1.0 MPa indicate vine stress [Grimes and Williams 1990]).

Vegetative growth measured late in the growing season was also a positive linear function of applied water amounts. Leaf area/vine was >30 m^2 for those irrigated at $\geq 100\%$ of ET_c in 1991 and 1993 (Fig. 1B). It is unknown why vines had less leaf area across all irrigation treatments in 1992. Mean shoot length had a similar positive linear increase as applied water amounts increased (data not given). Pruning mass (a measure of seasonal vegetative growth) also was a positive linear function of applied water amounts, up to the 1.2 irrigation treatment (Fig. 1C). The slight reduction in pruning mass at the highest irrigation treatment (1.4) may be due to water saturated soil that resulted in a lack of oxygen in the root zone. The amount of N per unit leaf area decreased as applied water amounts increased (Fig. 1D). The concentration of N in leaf tissue, expressed on a percentage dry mass basis,

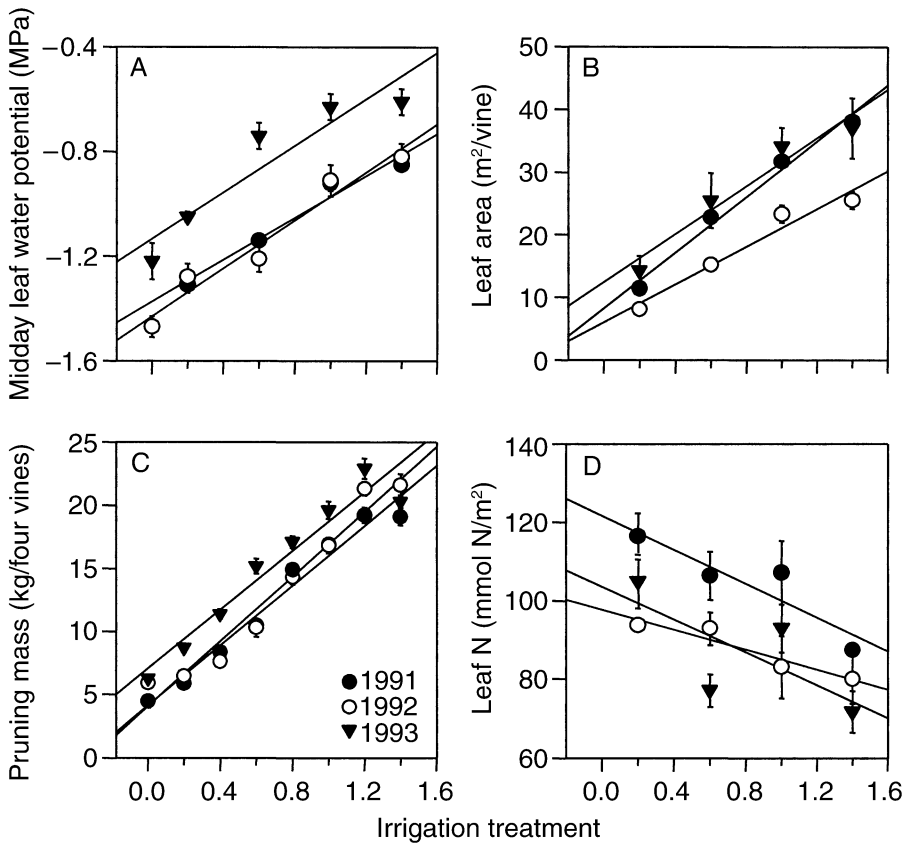

FIG. 1. Relationship of mean (±1 SE) (A) midday Ψ_l, (B) leaf area, (C) pruning mass, and (D) leaf N (mmol N/m² leaf area) to irrigation treatments, which are applied water amounts at fractions of lysimeter water use, in 1991 (solid circle), 1992 (open circle), and 1993 (solid triangle). See Table 1 for regression analysis parameters.

was not significantly affected by the irrigation treatments (data not given).

The highest yield across the three years of study was that of the 0.8 irrigation treatment: 46.9 ± 2.5 fresh mass/ha (mean ± 1 SE). The yields of the 0.0, 0.4, 0.6, 1.0, 1.2, and 1.4 irrigation treatments were 21, 37, 68, 95, 95, and 86, respectively, and 87%, that of the 0.8 irrigation treatment for the same time frame. These values are similar to those averaged across five years (Williams 2000).

Leafhopper biological traits

Nymph density.—Differences in *E. variabilis* densities among irrigation treatments became greater as the season progressed, reaching a maximum in August and September in each year. For example, there were no significant differences in *E. variabilis* numbers among the four irrigation treatments monitored during the first generation of 1993 ($F_{3,12} = 3.085$, $P = 0.068$; Fig. 2). At the second brood in 1993, only the *E. variabilis* density in the nonirrigated treatment was lower than the other treatments ($F_{3,12} = 3.821$, $P = 0.039$). By the third generation in September, *E. variabilis* densities in each treatment sampled were significantly different from one another ($F_{3,12} = 24.358$, $P < 0.001$; Fig. 2). Peak third generation densities were a positive linear function of applied water amounts in each year of study (Fig. 3).

We also sought to determine those changes in vine response to applied water amounts that most impact *E. variabilis*. A visual comparison of measured vine parameters regressed against applied water amounts (Table 1) indicates that pruning mass (closely related to shoot length), midday Ψ_l, and leaf area (in that order) responded similarly to nymph densities regressed against applied water amounts (Fig. 3). We tested this by regressing average nymph density against the averages of each vine growth parameter measured (for each treatment × year combination). This compared favorably to the visual assessment, with pruning mass, midday Ψ_l, shoot length, and leaf area with a positive linear relationship to nymph densities (Table 2). Leaf N (percentage dry mass or mmol N/m² leaf area) did not have a significant relationship to *E. variabilis* density (Table 2).

Nymph size.—The dry mass of fifth instar *E. variabilis* was a positive linear function of applied water amounts in the second and third generations in both years of study (Fig. 4). Only the dry mass of first generation *E. variabilis* was not significantly correlated to

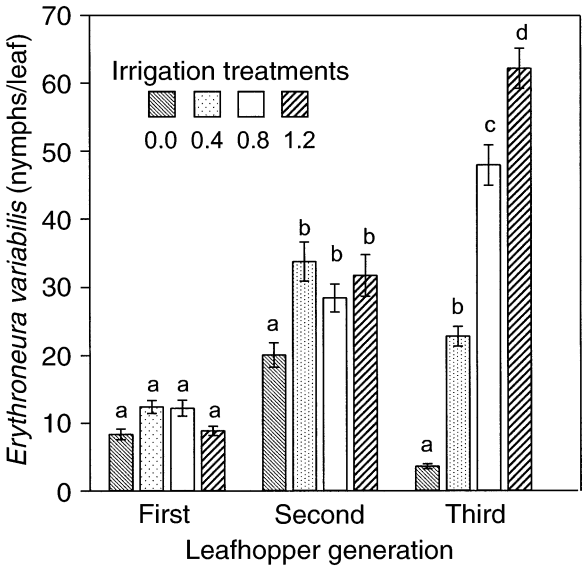

FIG. 2. Peak *E. variabilis* nymph densities (mean ± 1 SE) in each of the three summer generations (data collected on 4 June, 21 July, and 9 September 1993 for the first, second, and third generations, respectively) show that differences in *E. variabilis* densities among irrigation treatments, which are fractions of lysimeter water use, increased as the season progressed. Within each brood, treatment means separated by different letters are significantly different (Tukey's multiple comparison test, $P < 0.05$).

irrigation levels ($y = 0.097 + 0.0008x$, $r^2 = 0.023$; $F_{1,7} = 0.14$, $P = 0.719$). In both years, overall *E. variabilis* dry mass significantly decreased as the season progressed, with mean dry mass in 1992 at 0.094 ± 0.005 and 0.086 ± 0.003 μg in the second and third generations, respectively ($t = 3.471$, $P = 0.007$); and in 1993 at 0.098 ± 0.001, 0.090 ± 0.001, and 0.086 ± 0.001 μg in the first, second, and third generations, respectively ($F_{2,21} = 38.92$, $P < 0.001$; all means are significantly different from each other, Tukey's hsd test, $P < 0.01$).

Nymph mortality.—During the July trial, two cages in the 0.8 treatment were torn open and data from those cages have been excluded from the data analysis. There were no significant differences in nymph mortality among individual treatments, as indicated by the number of nymphs that reached the adult stage ($F_{3,48} = 2.01$, $P = 0.125$). To increase the number of replicates, data were combined from deficit (defined as midday Ψ_l values <-1.0 MPa in August, found in the 0.0 and 0.4 treatments) and adequate (defined as midday Ψ_l values >-1.0 MPa in August, found in the 0.8 and 1.2 treatments) applied water amounts; nymph density (by stage) was then plotted against sample date (Fig. 5A, B). Still, there were no significant treatment differences in season-long nymph density (repeated-measures ANOVA, $F_{1,50} = 5.263$, $P = 0.060$). This is reflected in the number of *E. variabilis* reaching the adult stage: 5.1 ± 2.3 and 7.0 ± 1.7 adults per leaf in deficit and adequate applied water amounts, respectively ($t = 1.89$, $P = 0.077$) (Fig. 5C). A visual comparison of stage mortality showed that most mortality occurred during the first and second nymphal stages, right after the leaves were inoculated (the later reduction in nymphs resulted from development to the adult stage, which were removed from the cages). There was no apparent difference in stage development. The lack of significant treatment difference may be due to a flawed experimental design, using cages that were too small (three leaves per cage) and with too few replicates.

In the second trial (1 September–14 October), many of the caged leaves had undetected *E. variabilis* eggs deposited before the leaves were isolated, resulting in more leafhoppers in the cages than were initially inoculated. This negated the validity of the experiment, and the data are not presented.

Adult movement.—There was a positive linear relationship between total adult *E. variabilis* collected and applied water amounts in 1992 during the adult flight at the beginning of the second (Fig. 6A) and third (Fig. 6B) *E. variabilis* generations. In 1993, the number of collected adults again had a linear relationship to applied water amounts during the adult flights at the beginning of the second and third generations ($y = 47.58 + 46.6x$, $r^2 = 0.41$, $F_{1,7} = 4.19$, $P = 0.086$ and $y = 220.5 + 288.9x$, $r^2 = 0.49$, $F_{1,7} = 5.987$, $P = 0.05$,

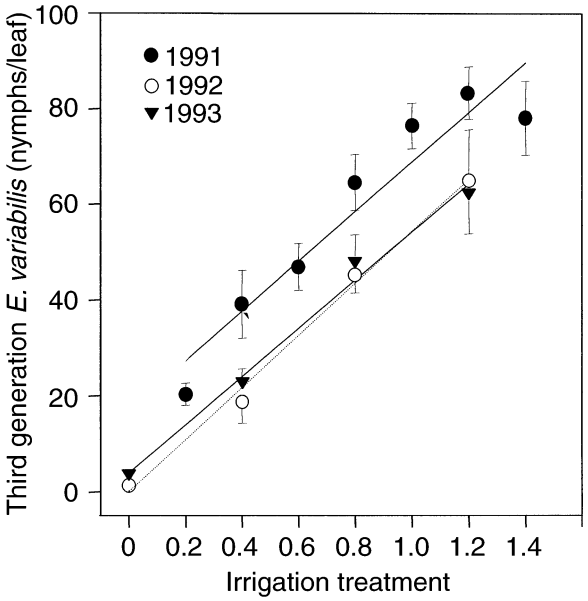

FIG. 3. Relationship of *E. variabilis* nymph densities (mean ± 1 SE) in the third *E. variabilis* generation (peak nymph densities) to irrigation treatments, which are fractions of lysimeter water use, in August 1991 (solid circle), September 1992 (open circle), and September 1993 (solid triangle). There was a positive and significant correlation in each year (regressions for 1991, $y = 16.84 + 51.95x$, $r^2 = 0.89$, $F_{1,5} = 50.71$, $P < 0.001$; 1992, $y = -0.008 + 54.29x$, $r^2 = 0.99$, $F_{1,2} = 349.76$, $P = 0.003$; 1993, $y = 3.88 + 50.17x$, $r^2 = 0.98$, $F_{1,2} = 200.27$, $P < 0.001$).

TABLE 1. Regression parameters for midday Ψ_1, leaf area, pruning mass, and leaf N (mmol N/m^2 leaf area) to irrigation treatments, which are fractions of lysimeter water use, in 1991, 1992, and 1993 on grapevines in the San Joaquin Valley, California, USA.

Growth parameter	Year	Slope and intercept	r^2	F	P
Midday Ψ_1	1991	$y = -1.37 + 0.40x$	0.95	56.89	0.017
	1992	$y = -1.43 + 0.46x$	0.96	64.53	0.004
	1993	$y = -1.13 + 0.44x$	0.83	21.03	0.019
Leaf area	1991	$y = 8.23 + 22.17x$	0.97	120.98	0.008
	1992	$y = 5.96 + 15.07x$	0.93	43.37	0.022
	1993	$y = 12.38 + 19.17x$	0.91	33.23	0.029
Pruning mass	1991	$y = 4.10 + 11.86x$	0.96	196.60	<0.001
	1992	$y = 4.04 + 12.84x$	0.95	142.67	<0.001
	1993	$y = 7.03 + 11.65x$	0.92	81.87	<0.001
Leaf N	1991	$y = 121.7 - 21.6x$	0.75	10.32	0.080
	1992	$y = 97.7 - 12.825x$	0.86	18.85	0.049
	1993	$y = 103.6 - 21.0x$	0.26	2.08	0.286

Note: For each year, degrees of freedom for midday Ψ_1, leaf area, and leaf N are 1, 2 and for pruning mass are 1, 6.

respectively). However, a visual comparison of data in Fig. 6C and D shows the adult density rose from 0.0 to a peak at the 0.8 irrigation treatment and then declined. For this reason, a simple two parameter, nonlinear model of an exponential rise to a maximum plateau was used to describe the data:

$$y = a\,(1 - b^x) \quad (1)$$

where a and b were regression parameters obtained from data. The nonlinear model better fit the data sets in the second (Fig. 6C) and third (Fig. 6D) generations than the linear model. While models that show a rise and decline would provide an even better fit, we believe there were similar or greater adult densities (per vine) in the higher irrigation treatment levels, as compared with the 0.8 level, and that the observed drop in adults collected may be an artifact of sample methodology, where the increased foliage at the higher irrigation treatments lowered sampling efficiency.

The number of marked and recaptured adults followed a clear pattern. In 1992 and 1993, there was a significant and positive linear relationship between *E. variabilis* adults marked and recaptured and irrigation treatments in each sampled generation (Fig. 7).

Adult egg deposition.—Results from the egg deposition study show that females deposited significantly more eggs on leaves in the 1.2 irrigation treatment (23.6 ± 4.5 eggs/female) than on leaves from the 0.6 irrigation treatment (15.2 ± 1.9 eggs/female) and no applied water (4.4 ± 1.0 eggs/female) ($F_{2,5} = 6.031$, $P = 0.022$). There were no significant differences in egg deposition in the cross experiment in which adults were on leaves in the 1.0 irrigation treatment but reared from nymphs in the 0.0, 0.6, or 1.2 irrigation treatments (20.3 ± 2.2, 33.8 ± 3.1, and 26.6 ± 6.6, respectively; $F_{2,6} = 1.835$, $P = 0.239$).

DISCUSSION

We showed that *E. variabilis* nymph density was positively related to applied water amounts in a Thompson Seedless vineyard. While applied water amounts greater than lysimeter water use increased nymph densities, it did not increase grape yields, which were maximized at the 0.8 irrigation treatment (reported herein and in Williams 2000). Our results indicate that vineyard irrigation amounts can be manipulated for leafhopper control without decreasing crop yield. This applied aspect of our research can be placed in context

TABLE 2. Relationship of third generation leafhopper densities to grapevine water status (Ψ_1), vegetative growth (leaf area and pruning mass), and leaf N (expressed on a dry mass and area basis) in the San Joaquin Valley, California, USA.

Vine vigor parameter	Slope	r^2	P
Pruning mass	$y = 4.32 + 0.210x$	0.979	0.006
Midday Ψ_1	$y = -1.37 + 0.008x$	0.973	0.001
Shoot length	$y = 1.23 + 0.020x$	0.943	0.018
Leaf area	$y = 3.83 + 0.370x$	0.924	0.025
N (mmol/m^2 leaf area)	$y = 109.2 - 0.303x$	0.349	0.247
N percentage dry mass	$y = 2.05 + 0.003x$	0.122	0.355

Note: Regression analysis was completed on *E. variabilis* mean density in each treatment (0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, and 1.4 times that used by vines in the weighing lysimeter) for each year of the study (1991, 1992, and 1993) against each vine growth parameter average in the same treatment and year.

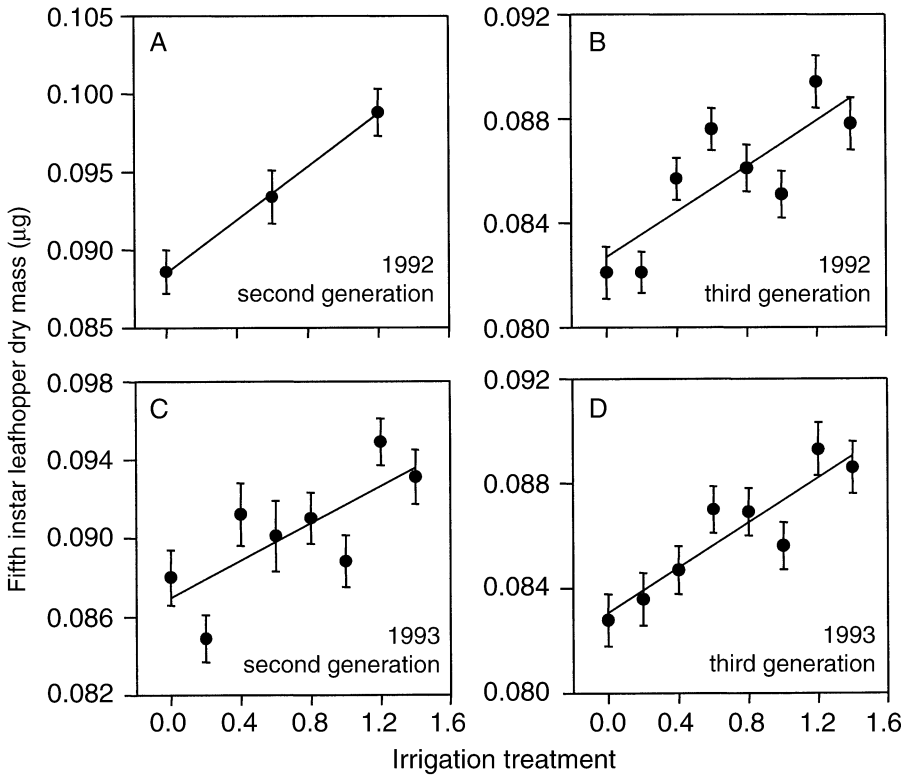

FIG. 4. The dry mass of fifth instar *E. variabilis* was significantly and positively correlated to irrigation treatments, which are fractions of lysimeter water use, in 1992 in the (A) second and (B) third generations ($y = 0.089 + 0.0085x$, $r^2 = 0.997$, $F_{1,2} = 929.2$, $P = 0.021$; $y = 0.082 + 0.0043x$, $r^2 = 0.605$, $F_{1,7} = 11.73$, $P = 0.014$, respectively) and in 1993 in the (C) second and (D) third generations ($y = 0.087 + 0.0048x$, $r^2 = 0.574$, $F_{1,7} = 8.09$, $P = 0.029$ and $y = 0.0831 + 0.0042x$, $r^2 = 0.819$, $F_{1,7} = 27.30$, $P = 0.002$, respectively).

with theoretical discussions of the impact of host plant quality on insect herbivore density. More importantly, while numerous studies of the plant vigor or plant stress hypotheses have been conducted in natural ecosystems following periods of stress (e.g., drought) or in small plots where nutrient or water levels are easily manipulated (Waring and Cobb 1992, Leather 1994), this study supplies further evidence that agricultural pest densities can be suppressed by manipulating levels of plant stress that are still within the boundaries of proper crop management.

We found that *E. variabilis* densities were a positive linear function of pruning mass, midday Ψ_l, shoot length, and leaf area, while *E. variabilis* density did not have a significant relationship to leaf N (Table 2). These vine growth parameters were measured to determine those changes in vine condition that most impact *E. variabilis* in order to manipulate vineyard management practices and vine condition for improved pest management. For example, McQuate and Connor (1990*a*) suggest that changes in soybean qualities in response to water deficits that could negatively affect Mexican bean beetle densities include increased leaf toughness and concentration of free amino acids. However, identifying specific host plant qualities in our study proved more difficult than we anticipated. First, the measured vine parameters were closely interrelated; for example, applied water amounts influence shoot lengths, which influences pruning mass and leaf area. Second, we can not separate out host quality from environmental quality because the influence of irrigation amounts on pruning mass, for example, also results in changes to the availability of young shoots, shade, temperature, and humidity. Therefore, while we discuss each of the measured vine growth parameters in context with their individual impact on host plant quality or insect growth parameters, the interrelationship of measured vine parameters and their overall impact on the vineyard environment should be considered.

Erythroneura variabilis density most closely followed pruning mass (Table 2). Increased vegetative growth (or shoot length) has been associated with increased herbivore densities, particularly for those insects closely associated with plant leaves or shoots. For example, Kimberling et al. (1990) studied the leaf-galling grape phylloxera *Daktulosphaira vitifoliae* (Fitch) on wild grape and found more galls on the longer shoots. As in our study, they found that these differences increased as the season progressed, but also suggested that the vigorous growth early in the season

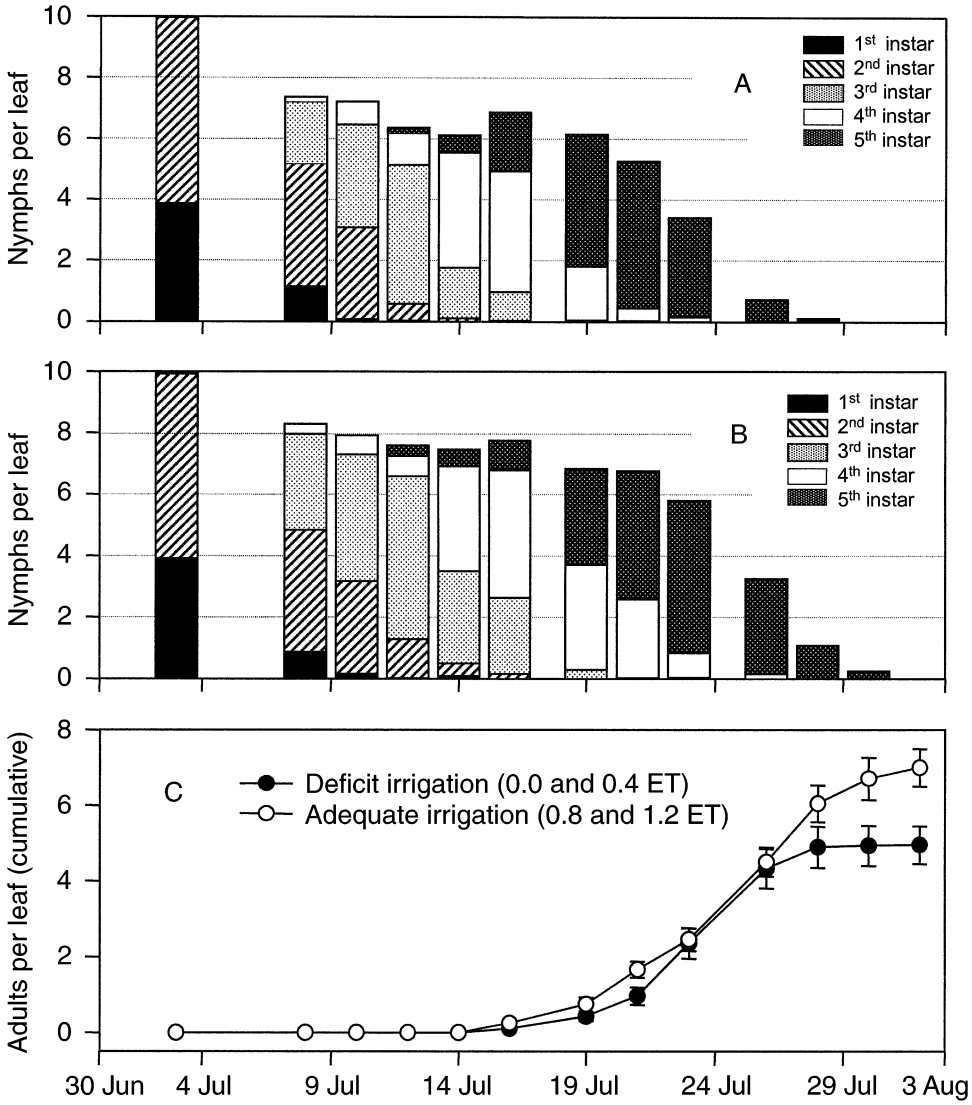

FIG. 5. *E. variabilis* nymph mortality was significantly greater in the deficit irrigation treatments (0.0 and 0.4) than in treatments receiving adequate irrigation amounts (0.8 and 1.2) (repeated-measures ANOVA, $F_{1,50} = 5.263$, $P = 0.06$). Irrigation treatments represent fractions of water applied to vines growing in the lysimeter.

provided better quality leaves for colonization. Another aspect of increased pruning mass is a corresponding increase in the amount of new foliage, which has also been associated with better survival of leaf-feeding herbivores (Larsson and Ohmart 1988, Spiegel and Price 1996, Floater 1997). This positive relationship between increased insect performance and younger leaf age is most often associated with leaf-chewing larvae, which can be negatively impacted by older or tougher foliage (Coley 1983, McQuate and Connor 1990*a*, *b*). Observations suggest that *E. variabilis* adults and nymphs can feed on quite mature leaves, as long as there is sufficient leaf water content (K. M. Daane, *personal observation*). However, there are numerous studies that show *Bemisia tabaci* (Gennadius) and *Bemisia argentifolii* Bellows and Perring have greater ovipositional preference or survival on young leaves (Byrne and Draeger 1989, Cardoza et al. 2000).

Another aspect of increased vegetative growth (as measured by pruning masses, shoot growth, and leaf area) is a corresponding decreased temperature and increased humidity within the canopy. Increased applied water amounts will increase grapevine stomatal conductance and transpiration (Williams et al. 1994). Canopy temperature of vines irrigated at values ≥100% of lysimeter water will be less than that of ambient temperature, while those of deficit-irrigated grapevines will be greater (Williams et al. 1994). For example, canopy temperature for the no applied water treatment can be up to 7°C higher than ambient and 10°C greater than vines irrigated at 100% of lysimeter water use. It should be pointed out that temperature of fully shaded

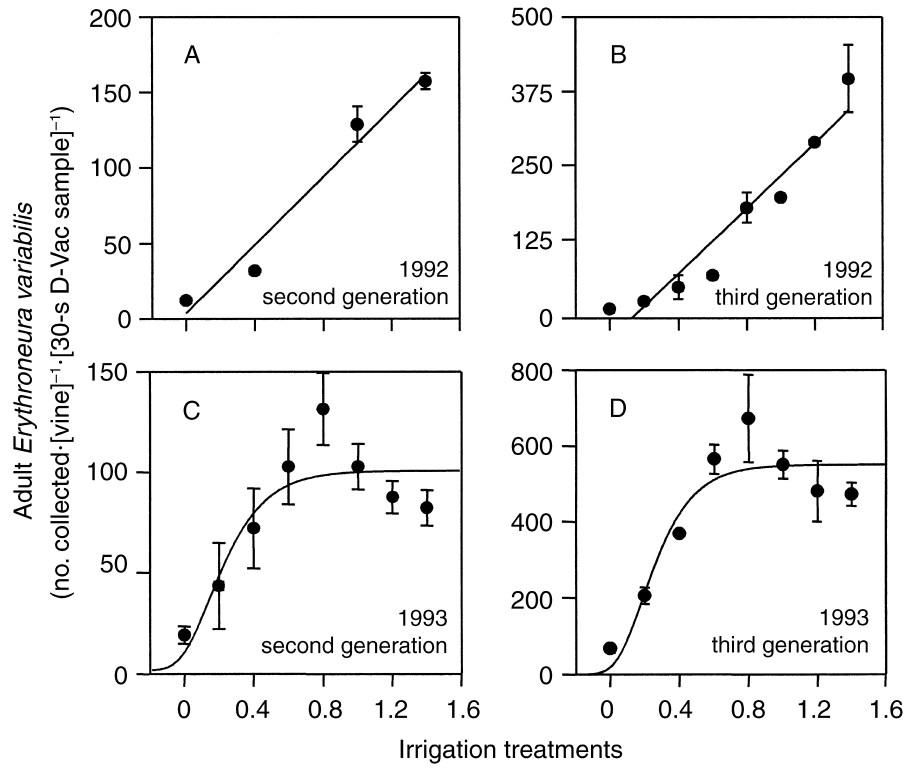

FIG. 6. Relationship of the number of adult *E. variabilis* collected from vines supplied with different irrigation treatments, which are fractions of lysimeter water use, shows a positive and significant linear correlation in 1992 during the adult flight at the beginning of the (A) second and (B) third generations ($y = 3.92 + 112.6x$, $r^2 = 0.965$, $F_{1,3} = 55.89$, $P = 0.017$ and $y = -34.31 + 270.5x$, $r^2 = 0.922$, $F_{1,7} = 71.17$, $P < 0.001$, respectively). A nonlinear regression model was used to describe the adults captured in 1993 at the beginning of the (C) second and (D) third generations ($y = 102.26\ [1 - 0.02^x]$, $r^2 = 0.73$, $F_{2,7} = 16.07$, $P = 0.007$ and $y = 558.42\ [1 - 0.03^x]$, $r^2 = 0.81$, $F_{1,7} = 26.35$, $P = 0.002$, respectively).

leaves among the different irrigation treatments do not differ significantly (L. E. Williams, *unpublished data*). Such great difference in exterior canopy microclimate can influence insect development and survival (Meyer and Root 1996, Skinner 1996*b*, Willmer et al. 1996). The development rates of *E. variabilis* eggs, nymphs, and adults are primarily driven by temperature (Wilson et al. 1992), although upper temperature thresholds are unknown for this species. As a comparison, Olsen et al. (1998) determined constant temperature development rates for nymphs of two leafhopper pests of grapes, *Erythroneura elegantula* Osborn and *E. ziczac* Walsh. They reported a rapid decline in development after 31–33°C, and *E. elegantula* nymphs failed to develop at 35°C. With mean high July temperature in the Central Valley at 37°C, temperatures in vines with water deficits might easily exceed the survival threshold for some or all of the *E. variabilis* development stages, resulting in mortality of nymphs or dispersal of adults. For example, water stress in an almond orchard was shown to change development times for mites, resulting in an increase in mite densities (Oi et al. 1989). It is possible that the increased temperatures in vineyards with water deficit could alter *E. variabilis* development; however, our cage studies of *E. variabilis* nymphal development and mortality did not show clear treatment effects. We believe that our cage studies need to be repeated to provide a better description of the confounding influence of water management on *E. variabilis* development and mortality.

Leaf water potential, which was also positively correlated to *E. variabilis*, is best described by midday Ψ_l, with values < -1.0 MPa indicating vine stress (Grimes and Williams 1990). According to our measurements of midday Ψ_l, the middle of July was the first time that vines in the nonirrigated treatment may have been stressed and this corresponds to the initial separation of nymph density among treatments. Lowered leaf water potential could influence *E. variabilis* egg and small nymph mortality, and in the caged study of nymph mortality, most mortality did occur within five days of inoculating leaves with first and second instar *E. variabilis*. We believe that important aspects of *E. variabilis* stage survival that were not examined in this study are the mortality of deposited eggs and recently hatched nymphs. *Erythroneura variabilis*' small (~0.6 mm), cigar-shaped eggs are inserted under several layers of leaf epidermal cells, commonly parallel to or within a leaf vein (Wilson et al. 1992). Because eggs are buried inside the leaf, leaf condition may greatly

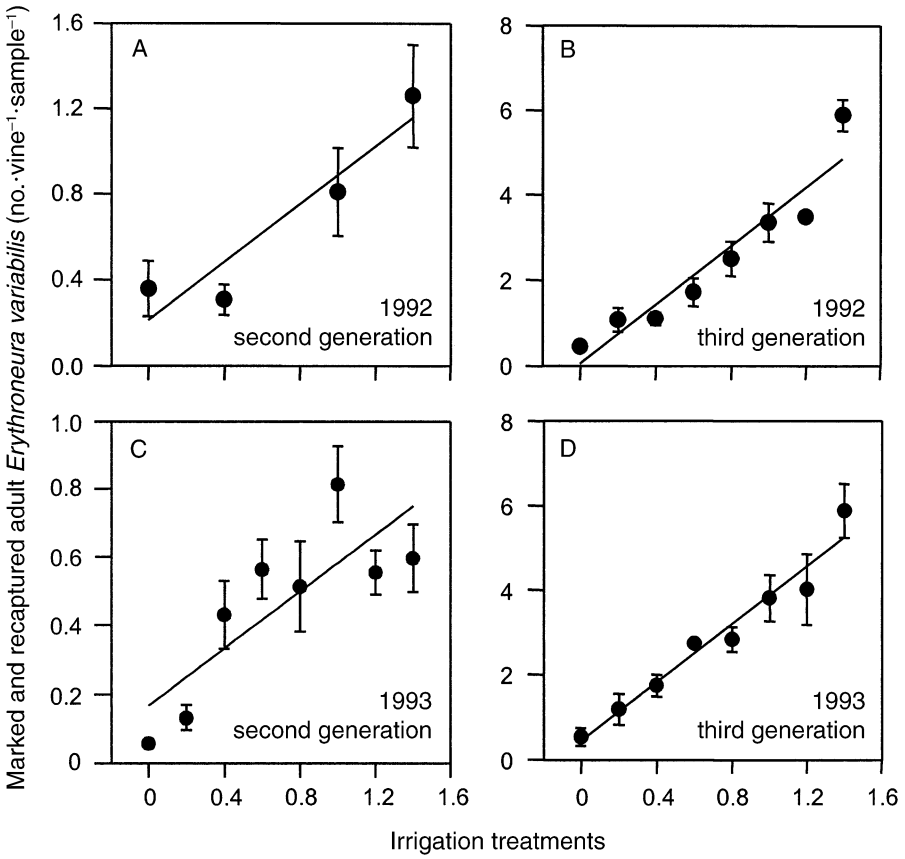

FIG. 7. Relationship of the number of marked, released, and recaptured adult *E. variabilis* collected from vines in different irrigation treatments, which are fractions of lysimeter water use, during the adult flight at the beginning of the (A) second and (B) third generations in 1992 and the (C) second and (D) third generations in 1993. There was a positive and significant correlation for each generation in both years (1992, second generation, $y = 0.21 + 0.67x$, $r^2 = 0.88$, $F_{1,3} = 15.42$, $P = 0.059$; 1992, third generation, $y = 0.05 + 3.42^x$, $r^2 = 0.901$, $F_{1,7} = 54.87$, $P < 0.001$; 1993, second generation, $y = 0.17 + 0.42x$, $r^2 = 0.67$, $F_{1,7} = 11.98$, $P = 0.013$; third generation, $y = 0.43 + 3.43x$, $r^2 = 0.96$, $F_{1,7} = 130.9$, $P < 0.001$).

influence their survival (Hinton 1981). Hoffman et al. (1990) report that eggs of the potato leafhopper, *Empoasca fabae* (Harris), which are also laid inside plant tissue, had increased mortality and development period when deposited in water-stressed alfalfa. Others have reported increased insect egg mortality under conditions of water stress (Castañé and Savé 1993), and though not measured in this study *E. variabilis* may be similarly affected by vine water stress.

Some studies supporting the plant stress hypothesis report a positive correlation between plant N levels and water deficits (McClure 1980). However, we did not find that N levels were dramatically affected by applied water amounts, with N expressed on a percentage dry mass basis showing no clear trend and millimoles of N per square meter showing a negative correlation. Correspondingly, there was no relationship of *E. variabilis* density to N levels, which ranged 1.7–2.7% dry mass across all treatments. These N levels may simply not have been low enough to limit *E. variabilis* (see Mattson 1980). For example, Ohmart et al. (1985) found no differences in a chrysomelid larva, *Paropsis atomaria* Oliver, reared on foliage with 1.7–3.0% dry mass, although there was a significant decrease in pupal mass and increase in development time below this level. There is also a species-specific response to changes in plant N. Strauss (1987) found that increased N fertilization of sagebrush (*Artemisia ludoviciana* Lutz.) resulted in greater numbers of phloem and seed feeding insects, but there was not a consistent change in the densities of chewing insects. While the most common response to N fertilization of the host plant is improved insect performance (demonstrated in nearly 60% of 186 studies reviewed by Waring and Cobb 1992), there is very little work on N requirement of leafhoppers (but see Prestidge 1982*a*, Brodbeck et al. 1996). Silvanima and Strong (1991) followed seasonal changes in planthoppers, *Prokelisia dolus* Wilson and *P. marginata* (Van Duzee), on salt marsh cord grass and found no correlation between these planthopper densities and increased foliar N, and Prestidge (1982*b*) found cicadellids were more common in unfertilized grasslands. The most probable influence of different N levels on *E. variabilis* is the movement of adults early and late

in the growing season. Dispersal and fecundity of adult sucking insects may be correlated with changes in leaf N, with herbivores feeding on some plant species in spring, when foliar N levels are high, and moving to new food sources during the season, as leaves age. In grapevines there is a seasonal progression from higher to lower leaf N (Williams 1987) that could cue changes in herbivore feeding and oviposition. Host quality (Hunter and McNeil 1997) and phenology (Mopper and Simberloff 1995) can influence herbivore diapause and performance, and it may be that the late-season reduction in N levels and new shoot growth cues cessation of fall *E. variabilis* oviposition that result in their sexual diapause during the dormant season.

In this study, *E. variabilis* density patterns would best fit the plant vigor hypothesis, with a positive linear response to applied water amounts and the corresponding changes in plant growth measurements. Researchers have shown increasing (Mattson and Haack 1987), decreasing (Kennedy and Booth 1959, Floater 1997), little to no effect (Ellsworth et al. 1992), and varying (English-Loeb 1989, Mopper and Whitham 1992) insect density responses to water deficits, depending on the insect and plant species studied (Meyer and Root 1996, Schowalter et al. 1999). Larsson (1989) and Waring and Cobb (1992) suggest that generalized trends can be found in the type of feeding guilds, reporting increased density responses to increased plant stress as follows: cambium feeders > sucking insects > mining insects > chewing insects > gall forming insects. Still, the density response of *E. variabilis*, a sucking insect, does not fit this generalized pattern as its densities were lowered with increased plant stress, as measured by vine growth parameters. Unlike some sucking insects like the phloem-feeding aphids, *E. variabilis* feeds on leaf mesophyll. Its interactions with the host plant may thus be more closely aligned with leaf-chewing or gall-forming herbivores. As with some gall-forming or leaf-mining insects, *E. variabilis* developmental stages are closely tied to the host plant leaf, from egg placement inside the leaf to the exclusive feeding on the leaf by nymphs and reproductive adults (Wilson et al. 1992).

The life-history traits that appeared most responsible for the observed treatment differences in *E. variabilis* densities were adult dispersal to and higher egg deposition on vines with greater applied water amounts. We found a positive correlation in the number of marked–recaptured adults to vines receiving more applied water amounts, with nearly a 10-fold difference between the 0.0 and 1.4 treatments in each trial. Movement of adult herbivores to hosts of better food quality is common (Leather 1994). Adult dispersal to better quality host plants is expected to be particularly applicable when mobile females choose oviposition sites close to where larvae will feed, and when the quality of the oviposition site greatly affects survival and future egg deposition of the offspring (Craig et al. 1989, Price 1991). For example, many aphid species respond to changes in host N levels by migrating to hosts of better food quality, or by reducing their growth, development rates, or fecundity (Mattson 1980, Leather 1994). Similar to N levels, plant water status can also affect dispersal, oviposition preference, and mortality. Adults of a stem-galling sawfly, *Euura lasiolepsis* Smith, sought potted willow plants with younger (Craig et al. 1986) and longer (Craig et al. 1989) shoots and higher water amounts (Preszler and Price 1988) to initiate gall formation and deposit an egg (Preszler and Price 1995).

That adult *E. variabilis* might seek out better quality environments is implied by their close association with grapevines; for example, the reproductive organs of overwintered *E. variabilis* adults do not mature until the adults feed on grape leaves (Wilson et al. 1992). Furthermore, once a vine and individual leaves are selected for egg deposition, there is little movement of the nymphs to new feeding sites. Therefore, egg and nymph survival depends on abiotic and biotic factors at or near the oviposition site. There is some evidence that host plant quality affects movement of other adult *Erythroneura*. In New York, the eastern grape leafhopper, *E. comes* (Say), overwinters in wooded areas next to vineyards; after the spring migration, oviposition is concentrated on vines adjacent to the wooded areas (first generation) but by the end of the summer (second generation) leafhoppers are evenly distributed throughout the vineyard (Martinson et al. 1994), suggesting an in-season movement and host plant selection by adults. Similarly, the adult potato leafhopper has a large host range and was found to discriminate in host plant species selection for oviposition (Roltsch and Gage 1990). In general, highly mobile adults are expected to move to plants of better quality for their survival (Kareiva 1982). However, examples of adult movement or oviposition preference can be found that support both the plant stress and plant vigor hypotheses (Mattson and Haack 1987, Lawton 1995, Skinner 1996*a*, Fritz et al. 2000) or neither (Craig et al. 1999, Finch and Collier 2000).

We found that *E. variabilis* deposited fewer eggs on leaves in the water deficit treatments and that these differences in egg deposition were determined primarily during the adult stage, after *E. variabilis* was placed on the host and regardless of where the adults fed as larvae. As evidence, there were no significant differences in the egg deposition of adults reared from nymphs on leaves in the 0.0, 0.6, and 1.2 irrigation treatments and then placed, as adults, on leaves in the 1.0 irrigation treatment. The decision to oviposit and the potential fecundity of some insect herbivores have been tied to host plant quality (Leather 1994). Once at the oviposition site, host plant condition can affect herbivore egg deposition in two ways; it can affect the fecundity of the adult arising from larvae feeding on the plant, or it can affect the egg deposition of the adult arriving at the plant for the first time (Leather 1994).

Our data on adult egg deposition might appear to contradict our studies on nymphal size, because we found a significant increase in leafhopper size, as measured by dry mass, with increased irrigation amounts and increased larval size is often correlated with increased adult egg deposition (Denno and McClound 1985). That this pattern did not apply to *E. variabilis* may be explained by its adult biology. *E. variabilis* adults can live for several weeks during the summer (and up to six months during the overwintering period) and are synovigenic. The poor food supply of the nymphs did not affect adults later provided with higher quality host material. Therefore, water-stressed leaves were either a poorer adult food source, resulting in lower egg deposition, created a less favorable environment for the adults, resulting in lower adult longevity (not measured) and potential for oviposition, or changed the leaf structure altering their preference as an oviposition substrate or reducing adult oviposition or feeding cues. Similarly, when the aphid *Rhopalosiphum padi* is moved from a poor quality to a better quality host plant, its fecundity is improved (Leather 1989). The aphid *Metopolophium dirhodum* reduces embryo growth and reabsorbs the youngest embryos in times of nutrient stress, which safeguards reproduction until conditions improve (Grüber and Dixon 1988). The ecological implication is that a proportion of adult *E. variabilis* on poor quality hosts should disperse to higher quality hosts to improve potential egg production and /or deposition; the practical implication is that vigorous vine growth will attract more leafhoppers and will not be compensated with increased crop yields.

Practical applications

Our goal was to determine whether irrigation practices could be used as a tool in vineyard pest management, as has been suggested for other agroecosystems (Perfect 1986). Specifically, can grapevine conditions be manipulated by applied irrigation amounts to suppress *E. variabilis* populations. We demonstrated that *E. variabilis* nymph density, nymph size, adult egg deposition, and adult movement are positively related to increasing amounts of applied irrigation. Furthermore, Williams (2000) showed that lowered irrigation amounts (0.6 to 1.0 ET) maximized yield. While commercial vineyards do not use a weighing lysimeter to determine applied irrigation amounts, the exacting manipulation of grapevine condition, as used in this study, for *E. variabilis* control may be used in commercial vineyards utilizing crop coefficients to determine vineyard irrigation amounts (Williams et al. 2003). This research provides evidence that application of appropriate irrigation amounts also has environmental benefits associated with water conservation and reduced insecticide use.

Still, there are potential confounding factors that we did not investigate. First, while vigorously growing vines tend to have more leafhoppers, they can withstand higher leafhopper densities with less economic damage; conversely, stressed vines may have fewer leafhoppers, but these low densities may cause greater economic damage (L. E. Williams and K. M. Daane, *unpublished data*). This increased tolerance of herbivore feeding in vigorously growing plants may be a trade-off to higher herbivore densities (Fineblum and Rausher 1995, Willis et al. 1999). Second, there was a strong seasonal response of *E. variabilis* density to applied water amounts with treatment differences most pronounced in the third leafhopper generation. Larsson (1989) suggests the seasonal timescale on which plant stress operates must be considered. In our study, early season shoot growth of vines among the different irrigation treatments can be similar (Williams et al. 1994) due to rainfall patterns and water availability in the soil profile. According to measurements of midday Ψ_l, the middle of July was the first time that vines in the nonirrigated treatment may have been stressed (values < -1.0 MPa). This is just before the second *E. variabilis* generation, when the influence of irrigation treatments on *E. variabilis* densities first became apparent. Significant differences in *E. variabilis* densities among all treatments were not apparent until the third generation, in August and September. Because insecticide treatment decisions are often made in the first or second leafhopper generation, there will be little evidence, at that time, of the full impact of deficit irrigation on host plant quality and *E. variabilis* densities. Third, our study focused on *E. variabilis*, yet host plant quality can have other, positive and negative, impacts on other arthropod species in the agroecosystem. Reduced grapevine growth due to water stress increased densities of the Pacific spider mite (*Tetranychus pacificus*) (Hanna et al. 1997). However, the influence of water stress on another mite pest, the twospotted spider mite (*Tetranychus urticae*), may be negative (Oloumi-Sadeghi et al. 1988) or nonlinear (English-Loeb 1989, 1990). Moreover, we do not believe that the levels of water deficits that maintain grape yields (applied water amounts of 80% of full ET_c, Williams 2000) suggested here would result in mite outbreaks. Fourth, we did not study parasitism or predation levels and poor leaf quality has been associated with slower herbivore development, which can lead to increased mortality from natural enemies (Clancy and Price 1987, Benrey and Denno 1997, Lill and Marquis 2001). Finally, our study on nymph mortality did not provide information on stage-specific mortality, and we did not study the impact of irrigation amounts on egg mortality or oviposition cues.

Water management programs have been suggested for insect pest control in rice (Mogi 1993), cotton (Slosser 1980, Beasley and Adams 1995, Slosser et al. 2001), soybean (Lambert and Heatherly 1995), onion (Kanman and Mohamed 2001), and turfgrass (Crutchfield et al. 1995). It has been most commonly used in cotton systems, where water stress usually increases whitefly

densities (Skinner 1996*a*) and nutrient stress (lower N) usually reduces whitefly densities (Bentz et al. 1995). Water amounts have been shown to influence both pest and natural enemy densities in row crops (Felland and Pitre 1991, Flint et al. 1994, 1996), and water management might also work in conjunction with other pest management practices. For example, the combined mortality from plant water deficits and natural enemies was shown to significantly reduce an armored scale insect (*Pseudaulacaspis pentagona*) on mulberry trees (Hanks and Denno 1993). In California vineyards, the adoption of deficit irrigation due to its positive effect on grape quality (Williams and Mathews 1990, Williams et al. 1994) will then assist in pest management and, combined with a more patient approach to insecticide use for leafhopper pests, result in lower applied irrigation and pesticide amounts.

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