ARTICLE

Precipitation and Temperature Effects on Populations of *Aedes albopictus* (Diptera: Culicidae): Implications for Range Expansion

BARRY W. ALTO[1] AND STEVEN A. JULIANO

Behavior, Ecology, Evolution, and Systematics Section, Department of Biological Sciences, Illinois State University, Normal, IL 61790–4120

J. Med. Entomol. 38(5): 646–656 (2001)

ABSTRACT We investigated how temperature and precipitation regime encountered over the life cycle of *Aedes albopictus* (Skuse) affects populations. Caged populations of *A. albopictus* were maintained at 22, 26, and 30°C. Cages were equipped with containers that served as sites for oviposition and larval development. All cages were assigned to one of three simulated precipitation regimes: (1) low fluctuation regime - water within the containers was allowed to evaporate to 90% of its maximum before being refilled, (2) high fluctuation regime - water was allowed to evaporate to 25% of its maximum before being refilled, and (3) drying regime - water was allowed to evaporate to complete container dryness before being refilled. Greater temperature and the absence of drying resulted in greater production of adults. Greater temperature in combination with drying were detrimental to adult production. These precipitation effects on adult production were absent at 22°C. Greater temperatures and drying treatments yielded higher and lower eclosion rates, respectively and, both yielded greater mortality. Development time and size of adults decreased with increased temperatures, and drying produced larger adults. Greater temperatures resulted in greater egg mortality. These results suggest that populations occurring in warmer regions are likely to produce more adults as long as containers do not dry completely. Populations in cooler regions are likely to produce fewer adults with the variability of precipitation contributing less to variation in adult production. Predicted climate change in North America is likely to extend the northern distribution of *A. albopictus* and to limit further its establishment in arid regions.

KEY WORDS *Aedes albopictus*, adult population size, mortality and eclosion rates, global climate change

RESEARCH ON THE North American distribution of *Aedes albopictus* (Skuse), a container-dwelling mosquito introduced via shipments of tires from Asia (Hawley 1988; Hawley et al. 1987), has focused on effects of biotic factors, such as interactions with other mosquito species (e.g., Livdahl and Willey 1991, Juliano 1998, Daugherty et al. 2000, Teng and Apperson 2000). It is likely, however, that regional differences in abiotic factors (e.g., temperature, precipitation, humidity) will have a major influence on its distribution in the United States (Teng and Apperson 2000), as is the case for most organisms (Dunson and Travis 1991). In temperate climates such as midwestern United States and Japan the active season for *A. albopictus* is late spring to early fall. Several studies have suggested that both winter and summer temperatures may affect population biology and distribution of this species (Nawrocki and Hawley 1987, Teng and Apperson 2000, Alto and Juliano 2001).

Effects of active season temperature on mosquito life-history traits are well documented. Higher temperatures decrease embryonic (e.g., Trpis et al. 1973) and larval (e.g., Teng and Apperson 2000) development times, and decrease size of adults (e.g., Rueda et al. 1990). Regional differences in precipitation are also likely to affect the distribution of *A. albopictus* in the U.S. Mosquito abundance is often positively related to precipitation (e.g., Ho et al. 1971, Lounibos 1981, Sulaiman and Jeffery 1986). Water levels in container habitats fluctuate, and in many instances containers may dry completely (Lounibos 1985, Bradshaw and Holzapfel 1988). As a container dries, density of larvae increases, potentially enhancing intraspecific competition and resource limitation, resulting in increased larval development time and mortality, decreased adult size (e.g., Lord 1998), and decreased adult longevity (Hawley 1985). Mosquitoes occurring in containers that dry completely are directly affected by increased egg (e.g., Sota and Mogi 1992a, 1992b) and larval (e.g., Bradshaw and Holzapfel 1988) mortality due to desiccation, and effects on development time (Juliano and Stoffregen 1994), and indirectly by reduced resource quality via resource drying (Aspbury and Juliano 1998). Because temperature and precipitation covary regionally, experiments manipulating both of these factors are needed to deter-

[1] Current address: Entomology and Nematology Department, University of Florida, P.O. Box 110620, Gainesville, FL 32611–0620 (e-mail: bwalto@ufl.edu).

mine accurately how these abiotic factors influence *A. albopictus.*

In addition, distribution of *A. albopictus* may be affected by anthropogenic changes in regional temperature and precipitation regimes. Fossil fuel combustion and deforestation have increased the amounts of greenhouse gases (e.g., CO_2, CH_4, NO, O_3) in the atmosphere and these atmospheric changes are likely to increase the global average temperature by 2–4.5°C by 2100 (IPCC 1995, Mitchell et al. 1995). Climate change is also likely to alter patterns of precipitation. Predicted changes in precipitation vary regionally, and have high uncertainty, but likely scenarios include the following: (1) greater annual precipitation, (2) more frequent summer droughts, (3) more precipitation in the cool season, and (4) more precipitation concentrated in major storms (e.g., IPCC 1995). Changes in both temperature and precipitation are likely to affect *A. albopictus* populations by altering reproductive and mortality rates (Lawton 1995, Sutherst et al. 1995), and may affect its distribution in the United States.

Exactly how current or future climate regimes affect *A. albopictus* (and other insects with complex life cycles) is difficult to predict because effects of climate may be stage dependent. For example, increased temperature results in increased probability of survival to adulthood and rapid larval growth and development (e.g., Teng and Apperson 2000), however adults tend to be smaller (e.g., Rueda et al. 1990), with correspondingly reduced fecundity (e.g., Nasci 1986, Packer and Corbet 1989, Day et al. 1990) and reduced longevity (e.g., Hawley 1985). Temperature also affects leaf litter decomposition and microbial activity in aquatic habitats (reviewed by Webster and Benfield 1986), and so affects resource availability to larvae. Interactions of effects of temperature and precipitation also render predictions of climatic effects on populations difficult. Thus, to predict effects of climate (or climate change) on spread and ultimate distribution and abundance of *A. albopictus* we need experiments examining the joint effects of temperature and precipitation across the entire life cycle.

Our objective was to test experimentally the hypothesis that temperature and precipitation regimes, acting across the entire life cycle of *A. albopictus*, affect population size and growth. Specifically, we predict that *A. albopictus* population growth will: (1) increase with temperature (due to more rapid larval growth and development); (2) increase as variability of water input to containers decreases; (3) and show nonadditive effects of temperature and precipitation, with combinations of high temperature and variable water input resulting in disproportionally low rates of population growth. This experiment will provide information on how regional differences in temperature and precipitation will affect the distribution of *A. albopictus* in temperate North America and may help to refine predictions about how climate change may affect the distribution of *A. albopictus.*

Materials and Methods

Laboratory Study

Source of Mosquitoes. *Aedes albopictus* used in this experiment were the F_1 progeny of field collected larvae from East St. Louis, IL. Field collected larvae were reared on bovine liver powder in large plastic tubs of tap water. Newly eclosed adults were identified and transferred to 0.6-m^3 cages maintained at 22–27°C and a photoperiod of 16:8 (L:D) h. Adults were allowed to mate freely and provided with continuous access to ≈10% sucrose solution and weekly blood meals from anesthetized laboratory mice (Juliano et al. 1993). Eggs from this colony were used to initiate the experiment.

Experimental Protocol. Experimental populations of *A. albopictus* were housed in 20-liter plastic bucket cages, each with a cloth sleeve, and the top (diameter = 22 cm) and two 19 by 22-cm side windows covered with 0.05-cm nylon mesh. Within each cage were four 200-ml plastic containers (5 cm in height). These served as sites for development of larvae and oviposition sites for adults. We used four containers per cage to maximize evaporation from the containers, thus facilitating application of the precipitation treatments (see below). Each container held 120 ml of a 2:1 mixture of water from tires:deionized water, and 1.50 ± 0.05 g (dry mass after 24 h at 60°C) of Black locust, *Robinia psuedoacacia* (L.), leaves, broken into 1-cm^2 pieces. Tire water and leaves were collected from a single site near Bloomington, IL. Tire water was mixed and filtered through a 70-μm filter before its addition to experimental containers. Leaves were allowed to soak for 3 d before the addition to each container of 25 first-instar (<24-h-old) *A. albopictus* hatched by the method of Novak and Shroyer (1978). These 100 larvae were the initial cohort of *A. albopictus* added to each cage, and we did not add individuals to cages after this initial cohort. Larvae grew within the four containers, pupated, emerged as adults, mated, took blood meals, and oviposited within each cage, and it is the dynamics of adult production within each cage that we monitored.

Cages were randomly placed in three environmental chambers (Percival I-35VL) set at constant temperatures 22, 26, and 30°C and a photoperiod of 16:8 (L:D) h. Positions of cages within each environmental chamber were systematically rotated each week to reduce effects of within-chamber variation in temperature. We measured relative humidity within each environmental chamber 22 times throughout the course of the experiment using humidity pens (Fisher) placed outside the cages. Mean relative humidities were similar for 22°C (mean ± SE = 83.77 ± 0.71%) and 26°C (84.05 ± 0.89%), and slightly lower for 30°C (72.77 ± 1.09%).

Equal number of cages within each temperature were randomly assigned to one of three precipitation regimes designed to simulate different regular inputs of precipitation to containers: (1) low fluctuation regime—water within the containers was allowed to evaporate to 90% of its maximum before containers

were refilled to 120 ml, (2) high fluctuation regime—water was allowed to evaporate to 25% of its maximum before containers were refilled to 120 ml, and (3) drying regime—water was allowed to evaporate to complete container dryness (=absence of water, even if leaf litter was moist). Containers remained dry for 5 d, then were refilled to 120 ml. Refilling containers with deionized water induced hatches of eggs oviposited on container walls and the resulting additional cohorts of larvae developed within containers. In the low fluctuation regime, eggs were submerged by water shortly after being oviposited, whereas in the high fluctuation or drying regimes, eggs remained on the walls of the containers for long periods before being inundated. We expect differences in the timing of refilling events to affect size of hatches, larval densities, age structure of larvae, and egg mortality. There were three replicates of each temperature-precipitation combination (9 cages per environmental chamber, 27 total cages).

Adults within cages were provided with ≈10% sucrose solution and weekly blood meals from anesthetized laboratory mice, using methods similar to those for our laboratory colony. The experiment ran for 105 d, long enough for the production of several overlapping generations of adults within each cage. The first cohort of adults produced was distinct, but as eggs were deposited and containers were flooded, cohorts of larvae overlapped, as did the cohorts of adults they eventually produced.

Data Collection and Analysis. We checked cages daily for pupal exuviae and dead adults, and we recorded any adults that escaped the cage (which were killed and treated as mortality). Sex of newly eclosed adults was determined by examining the pupal exuviae at 16× magnification. Some pupal exuviae, escaped adults, and dead adults may not have been recorded. A comparison of the actual versus estimated number of adults remaining at the end of the experiment showed that our estimates deviated from the actual number of adults by a mean ± SE of 21.22 ± 3.64%. For most cages, our estimate of number of adults was an overestimate, suggesting that some mortality went undetected. Cages subjected to drying yielded underestimates, perhaps due to failure to recover pupal exuviae from containers that frequently have low water levels, which may obscure pupal exuviae among the leaves.

In seven of the original 27 cages, there was massive mortality of larvae early in the experiment, and these cages failed to yield sufficient numbers of adult females to produce subsequent generations. These failures were not significantly related to temperature or to precipitation input (Fisher exact tests, $P > 0.10$). Therefore, these cages were excluded from the analysis and nine new cages were established and manipulated for 105 d using identical methods. For all analyses, we evaluated scatter plots of residuals versus predicted values and found no evidence that new and old cages differed for any measured variable (Draper and Smith 1966). We therefore combined old and new cages into a single analysis.

We analyzed this experiment using two-way analysis of variance (ANOVA) or multivariate analysis of variance (MANOVA), with temperature, precipitation, and interaction as effects. The main effect of temperature presented a statistical problem because temperature was manipulated for the entire environmental chamber, not for each cage. Because we lacked the facilities to replicate temperatures across multiple chambers we are forced to assume that interchamber variation (other than temperature) is negligible, to use error (i.e., variation among cages within the same temperature-precipitation combination) to test for the main effect of temperature. This assumption is often made in analyses of effects of temperature (e.g., Rueda et al. 1990, Teng and Apperson 2000). For all analyses, raw data met assumptions of normality and homogeneous variances unless otherwise stated. For ease of interpretation, raw data will be presented for any analysis requiring transformation. For all two-way analyses, significant interactions were further analyzed by univariate or bivariate (Scheiner 1993) pairwise contrasts of precipitation regime within temperature treatments (e.g., dry, 25%, and 90% regimes at 22°C) using the sequential Bonferroni method, with experimentwise $\alpha = 0.05$ (Rice 1989). Significant main effects in the absence of interaction were further analyzed by univariate or bivariate contrasts of pairs of main effect means (sequential Bonferroni for bivariate contrasts and Ryan-Einot-Gabriel-Welsch test for univariate contrasts, SAS Institute 1989).

Production of Adults. Two variables, the number of dead and escaped adults collected during the experiment (hereafter referred to as *During*), and the number of living adults remaining at the end of the experiment (referred to as *End*), were used in a MANOVA with profile analysis, with temperature and precipitation regime as fixed effects (SAS Institute 1989, Scheiner 1993, von Ende 1993). This MANOVA tested for differences in cumulative production of adults among treatments and also for differences in the pattern of adult production (i.e., relative numbers During and End). We determined which of the variables contributed most to significant MANOVA effects using standardized canonical coefficients as described by Scheiner (1993). Standardized canonical coefficients are scaled eigenvectors (analogous to a least-squares regression of multivariate means) that quantify the relative contribution of each dependent variable to multivariate effects and the relationship among dependent variables (positive or negative) (Scheiner 1993). We used profile analysis to test hypotheses concerning "parallelism" (i.e., is the difference During - End affected by treatments?) and "levels" (i.e., is the sum During + End affected by treatments?) (von Ende 1993).

Adult Mortality and Eclosion Rates. For all populations, eclosion of individuals in the first and second cohorts were separated by a distinct time gap of several days. For each replicate cage, we determined the overall mortality rate of adults (sexes pooled) from the start of emergence of the second cohort to the end of the experiment. We estimated number of adults per

cage on day t as $N_t = N_{t-1} + B_t - D_t$, where B_t = number of adults eclosing on day t (exuviae recovered from all four containers), and D_t = number of dead adults on day t (recovered bodies + any escapes). Per capita daily mortality rate was then D_t / N_{t-1}, and per capita daily eclosion rate was then B_t / N_{t-1}. A MANOVA with average daily mortality and eclosion rates (i.e., averaged over the course of the experiment) as the variables was used to determine how temperature and precipitation affect these variables. Mortality rate was reciprocally transformed to meet the assumption of normality.

Development Time and Size. For each replicate cage, we determined the median time to eclosion for males and females in the first cohort. For both sexes, median development times were log transformed to meet the assumption of normality and were analyzed by two-way ANOVA.

We determined the size of adult females by measuring wing lengths of a sample of adults obtained from each cage during the experiment (mean $n = 12$ females) and a sample of living adults at the end of the experiment ($n = 10$ females). Wing lengths were measured from the proximal edge of the costa to the distal end of the R^2 vein (adults dried for ≥24 h at 60°C). When possible, we used the mean of the right and left wing lengths, which were measured by a computer imaging system with Image-Pro Plus software (Media Cybernetics, L.P. version 3.0, 1993–1997). Due to the large number of damaged adults, the day on which adults were collected was highly variable. To account for variation in adult size due to the day on which adults were collected, we determined the residual wing length for those adults from a regression for wing length versus time (d). Next, we used a MANOVA with two variables (During and End) to detect any treatment effects on wing length. Mean residual wing length was used for the variable 'During' and mean wing length was used for the variable 'End.'

Egg Mortality. We determined egg mortality by sampling eggs remaining on the walls of the containers at the end of the experiment. We cut 0.5 by 5.0-cm vertical strips from each container (≈200 eggs per container, four containers per cage) and counted the number of unhatched eggs. These strips were then submerged in water to induce a hatch, using methods similar to those used in hatching the first cohort. After 24 h, the number of new hatchlings was subtracted from the number of unhatched eggs to obtain an estimate of egg mortality. Eggs were not examined for fertility. Therefore, our estimate of egg mortality may be greater than actual egg mortality. Proportion mortality for a cage was calculated as the sum of hatchlings produced subtracted from the sum of unhatched eggs, divided by the sum of unhatched eggs for the four containers. Because cumulative egg mortality was positively related to time of assay, we recorded the day on which eggs were assayed, with day 0 = the day the experiment was terminated. Egg mortality was significantly related to time of assay (see *Results*), and graphical analysis indicated a clearly nonlinear relationship. Therefore, we ran a logistic regression (Glantz and Slinker 1990) of proportion egg mortality versus time of assay (d) to obtain the residual mortality, which enabled us to remove any effect of assay time on egg mortality. Mean residual mortality for the four containers was then analyzed by a two-way ANOVA.

Cumulative Adult Production and Cumulative Water Volume. We determined the cumulative volume of water added to each cage (all four containers) and tested for a relationship across all cages between cumulative water added to a cage and cumulative number of adults produced. This analysis enabled us to determine whether or not adult production (per cage) was related to the amount of water treatments received. We ran a linear regression (all treatments) of cumulative adult production versus cumulative water volume added.

Interval of Time Between Water Addition. Most containers received water multiple times. For each cage, we determined the mean interval of time (d) between water additions for all four containers. Mean intervals between additions were analyzed by a two-way ANOVA.

Field Study

Study Site and Data Collection. We conducted a parallel field study to relate our temperature and precipitation treatments to the conditions encountered by *A. albopictus* in the midwest. We monitored weekly water temperature and drying rates at two sites in East St. Louis, IL, where *A. albopictus* immatures inhabit abandoned auto tires. Both sites consisted of ≈150–300 discarded tires in disorganized piles. We chose at random tires that were near the surface, and exposed to direct sun for most of the day. We included tires both at the center and at the edges of the tire pile. The first site was along a railroad right-of-way, with surrounding vegetation consisting mostly of small poplar, *Populus* sp., and poison sumac, *Rhus vernix* (L.), and was monitored from 1 to 29 July 1998. The second site was in a residential area, with the surrounding vegetation consisting of sugar maple, *Acer saccharum* (Marsh.), and willow, *Salix* sp., and was monitored from 17 August to 11 October 1998, after tires of the first site were removed in a clean-up program.

We chose at random 16 tires at site 1 and eleven tires at site 2, and removed their contents. We affixed plastic rulers to the inside of each tire, and then calibrated each tire, so that a given depth on the ruler corresponded to a known volume, by adding water in 250-ml increments and then recording the depth. We repeated this process until the tire was at its maximum volume. After tires had been calibrated, we returned the original contents. We checked tires weekly between 0900 and 1300 hours to record water depth and temperature. We also obtained mean daily ambient air temperature and precipitation records for this county from the Illinois State Climatologist office.

For each observed depth, we estimated volume by linear interpolation between calibration values, determined the corresponding percent of maximum wa-

Table 1. MANOVA results for production of adults, mortality and eclosion, and female wing length for 22, 26, and 30°C and 90%, 25%, and drying precipitation regimes

Analysis	Source	df	Pillai's trace	*P*
Production of adults	Temp	4	1.10	0.0001
	Precip	4	0.98	0.0001
	Temp*Precip	8	0.78	0.0063
	Error df	20		
Production of adults (Sum)	Temp	2	0.27	0.0438
	Precip	2	0.75	0.0001
	Temp*Precip	4	0.40	0.0312
	Error df	20		
Production of adults (Diff.)	Temp	2	0.89	0.0001
	Precip	2	0.25	0.0568
	Temp*Precip	4	0.41	0.0259
	Error df	20		
Mortality and Eclosion	Temp	4	0.80	0.0003
	Precip	4	0.45	0.0350
	Temp*Precip	8	0.51	0.1232
	Error df	20		
Size (female wing length)	Temp	4	0.83	0.0002
	Precip	4	0.42	0.0490
	Temp*Precip	8	0.41	0.2808
	Error df	20		

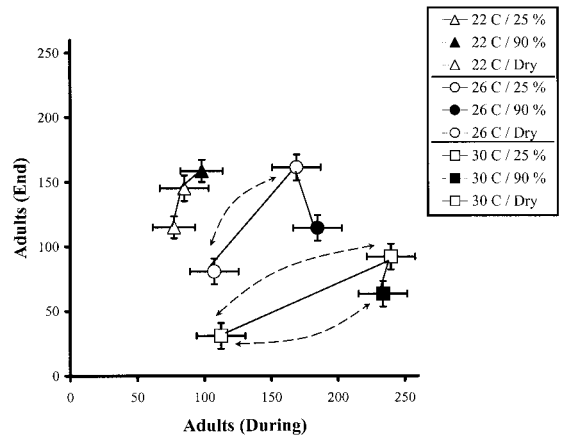

Fig. 1. Least squares means ± SE mean number of adults produced During and at the End of the experiment. Dashed lines indicate bivariate means that are significantly different from one another by multivariate pairwise comparisons (Scheiner 1993).

ter volume, and the interval of time (d) for tires to be reduced to 90 and 25% of maximum water volume, and to dry completely (no standing water). For each site, on a weekly basis, we determined the proportion of tires that had volumes of water ≥25%, ≥90%, and dry. We determined the mean water temperature for all tires for the duration of the monitoring period.

Results

Laboratory Study

Production of Adults. MANOVA indicated significant temperature, precipitation, and temperature-precipitation effects for adult production (Table 1). The magnitudes of standardized canonical coefficients (abbreviated SCC:During = 2.13, End = −0.59) showed that adults produced During the experiment contributed the most to the differences among temperature-precipitation combinations. The opposite signs of the SCC's showed that there was a negative relationship between numbers of adults produced During versus those remaining at the End of the experiment (Fig. 1). Bivariate pairwise contrasts showed that 26°C/25% regime had significantly greater production of adults than did 26°C/dry regime, with the number of adults remaining at the End of the experiment strongly contributing to this pairwise difference (SCC: During = 0.48, End = 2.42). Also, 30°C/25% and 30°C/90% regimes produced significantly more adults compared with 30°C/dry regime, with the number of adults produced During the experiment contributing most to the difference involving the 30°C/90% regime (SCC: During = 1.88, End = 0.77) and both the number of adults produced During and End contributing strongly to the difference involving the 30°C/25% regime (SCC: During = 1.48, End = 1.52) (Fig. 1). All other bivariate pairwise contrasts were not significant. In general, dry treatments produced fewer adults than did 25% or 90% treatments (Fig. 1), and 30°C yielded fewer adults at the End but more adults During the experiment compared with 22°C, with 26°C intermediate (Fig. 1).

Profile analysis on sum production of adults (During + End) also indicated significant temperature, precipitation, and temperature-precipitation effects (Table 1). The strongest effect on sum production of adults was that of precipitation (Table 1), and this is evident in the Fig. 1 by the location of bivariate means nearer the origin, indicating low numbers of adults both During and at the End of the experiment (dry), or farther from the origin, indicating high numbers of adults both During and at the End of the experiment (25% and 90%). Pairwise contrasts yielded results identical to those of the main MANOVA, with one additional significant effect: 26°C/90% regime had significantly greater production of adults compared with 26°C/dry regime.

Profile analysis on difference in production of adults (During - End) yielded significant effects of temperature and temperature-precipitation, but the effect of precipitation was marginally nonsignificant (Table 1). The strongest effect on the difference was that of temperature (Table 1) and this is evident in Fig. 1 by the location of bivariate means radially, either nearer to the vertical axis, indicating relatively more adults alive at the End of the experiment (22°C) or nearer to the horizontal axis, indicating relatively more adults recovered During the experiment (30°C). The only significant pairwise difference was between 30°C/90% and 30°C/dry regime.

Adult Mortality and Eclosion. Mortality and eclosion rate were significantly affected by temperature and precipitation treatments (Table 1). Greater temperatures resulted in greater mortality and eclosion rates (Fig. 2a). Bivariate contrasts showed that all three temperature treatments were significantly different from one another with mortality rate contributing the most to those differences (SCC: mortality =

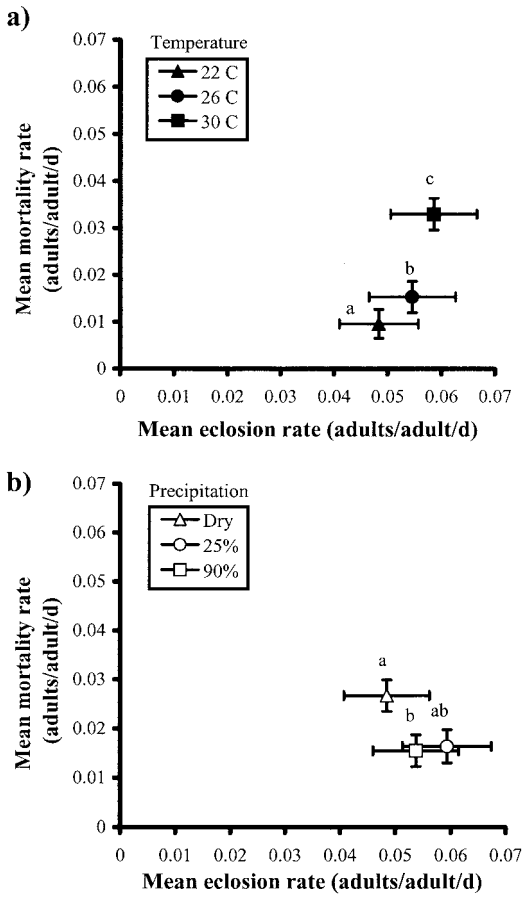

Fig. 2. Least squares means ± SE mean eclosion and mortality of adults. Letters denote bivariate means that are significantly different from one another by multivariate pairwise comparisons (Scheiner 1993).

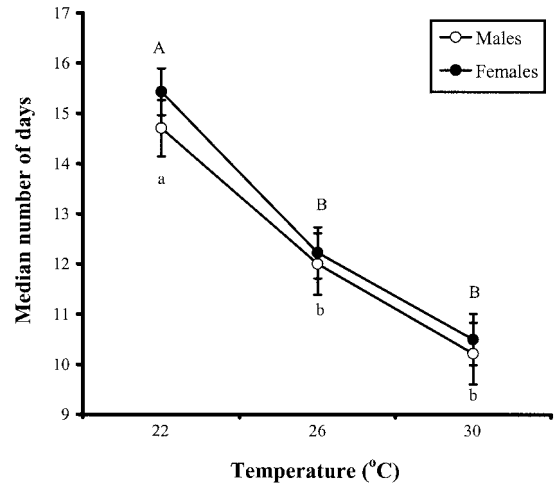

Fig. 3. Least squares means ± SE median days to development for the first cohort of males and females. Lower case and upper case letters denote significant differences based upon univariate pairwise comparisons among temperature treatments for males and females, respectively.

2.17, eclosion = −0.12). For the precipitation effect, bivariate contrasts showed that drying treatments yielded significantly greater mortality rates and lower eclosion rates than did 90% regime, with mortality rate contributing the most to the difference (SCC: mortality = 2.16, eclosion = 0.12) (Fig. 2b).

Development Time and Size. Median time to eclosion for the first cohort was significantly affected only by temperature for both males ($F = 15.53$; df = 2, 20; $P = 0.0001$) and females ($F = 27.03$; df = 2, 20; $P = 0.0001$). Univariate contrasts showed that both sexes developed significantly more slowly at 22°C compared with 26 and 30°C (Fig. 3). Precipitation and the interaction of temperature-precipitation effects were not significant.

Size of adult females was significantly affected by temperature and precipitation treatments (Table 1). Bivariate contrasts showed that all three temperature treatments were significantly different from one another with greater temperatures yielding smaller wing lengths (Fig. 4a). For the precipitation effect, bivariate contrasts indicated that females in the dry treatment had significantly larger wings than did females in the 90% precipitation regime (Fig. 4b). For both the temperature (SCC: During = 2.10, End = 0.18) and precipitation (SCC: During = 2.10, End = 0.19) effects, the residual wing length measured for those females collected During the experiment contributed the most to the effects.

Egg Mortality. Egg mortality was significantly related to the time of assay (logistic regression $\chi^2 = 107.1$, df = 1, $P = 0.0001$). Proportion egg mortality was significantly affected only by temperature ($F = 24.58$; df = 2, 20; $P = 0.0001$), with greater temperatures yielding greater proportion egg mortality. Univariate contrasts showed that all three temperatures were significantly different from one another (mean ± SE, 30°C = 0.90 ± 0.02, 26°C = 0.71 ± 0.05, 22°C = 0.50 ± 0.04). Precipitation and the interaction of temperature-precipitation effects were not significant.

Cumulative Adult Production and Cumulative Water Volume. Regression of cumulative adult production per cage versus cumulative water added per cage showed no significant relationship ($F = 1.17$; df = 1, 27; $P = 0.2893$; $r^2 = 0.0415$).

Interval of Time Between Water Addition. Timing of water additions was significantly affected by temperature ($F = 235.66$; df = 2, 20; $P = 0.0001$), precipitation ($F = 405.57$; df = 2, 20; $P = 0.0001$), and the interaction of temperature-precipitation ($F = 30.45$; df = 4, 20; $P = 0.0001$). Time between water additions decreased with temperature, and decreased in sequence from 90 to 25% to drying precipitation regimes (Fig. 5).

Field Study

Water Volume. For both sites, the periods of time required for tire water volume to be reduced to 90%, 25% of maximum, and for drying were within the same range

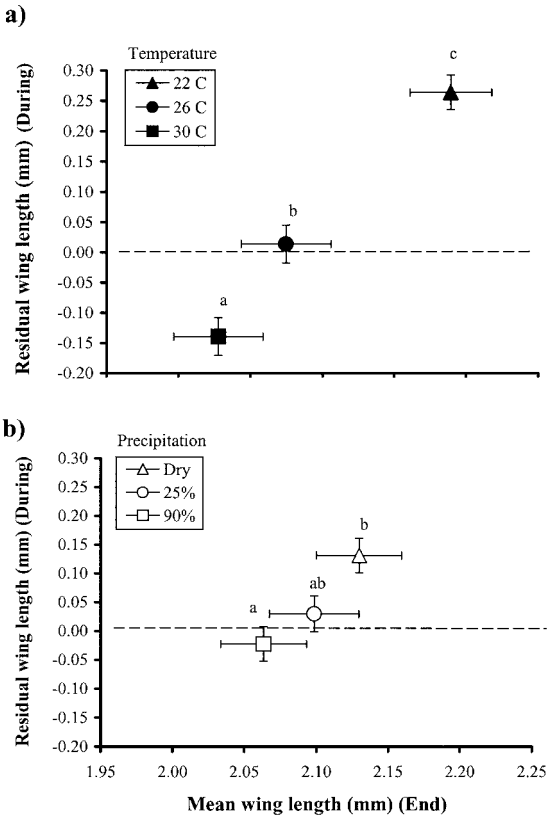

Fig. 4. Least squares means ± SE residual wing length (During) and mean wing length (End) for adult females. Dashed lines indicate residual wing lengths that are equivalent to the predicted value for the sample date. Letters denote significant differences among bivariate means.

as the corresponding intervals of time for containers in the laboratory study to be reduced to these volumes (Fig. 5). At site 1 in particular, mean temperature and drying times were very similar to those in the 30°C treatments in the laboratory (Fig. 5). At site 2, time to reach 90% was not estimable as water volumes were always <90%. At both sites, a high proportion of the tires had volumes >25%, and only a few weekly samples resulted in volumes exceeding 90% (Fig. 6). At both sites, complete drying of tires occurred, but the frequency of occurrence differed among sites. For site 1, >60% of tires went dry within a four-week period, whereas at site 2 a period of 8 wk elapsed before a small proportion of the tires went dry (Fig. 6).

Temperature. Daily ambient air temperature was closely related to weekly water temperatures at both sites (Fig. 7). For much of the sample period, temperatures fell within the range used in the laboratory study (Fig. 7).

Discussion

Results from this experiment clearly demonstrate that both temperature and precipitation affect population dynamics of *A. albopictus.* High temperatures resulted in greater production of adults during the experiment, but fewer adults remaining alive at the end of the experiment (Fig. 1). At low temperatures the reverse was true. These temperature-dependent differences in adult dynamics could be explained by temperature effects on either daily eclosion rates or daily adult mortality rates.

In this experiment, decomposing leaf litter that served as the resource base for larvae was added only once, simulating container habitats in the temperate zone, which typically receive a single large annual input of leaves (Kitching 1971). Because microbial activity and decomposition rate are positively related to temperature (Webster and Benfield 1986), the pattern of greater production of adults early and lower numbers late at high temperatures may be a result of more rapid microbial growth, and correspondingly more rapid depletion of resources at higher temperatures. Higher temperature

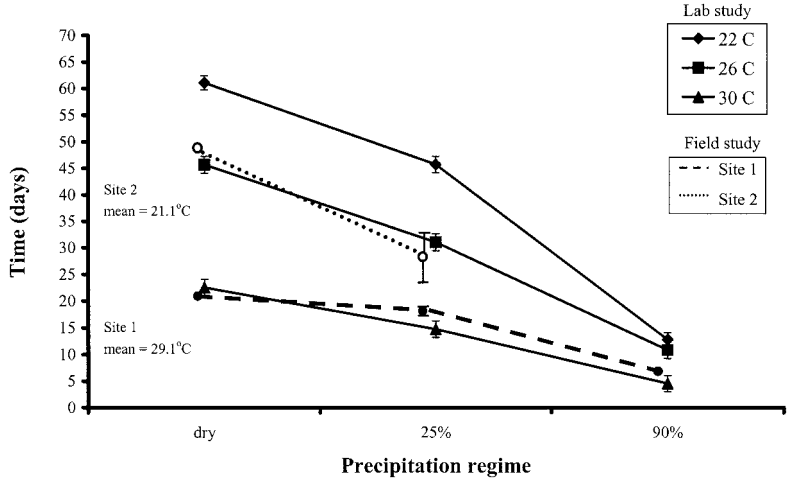

Fig. 5. Least squares means ± SE mean interval of time (d) between water additions for containers in the lab experiment and mean time for tires to decrease to ≤90%, ≤25%, and dry for field sites 1 and 2. No estimate was calculable to 90% at site 2 because no tires had volumes >90%. Points lacking error bars indicate standard errors that were too small to appear on the graph.

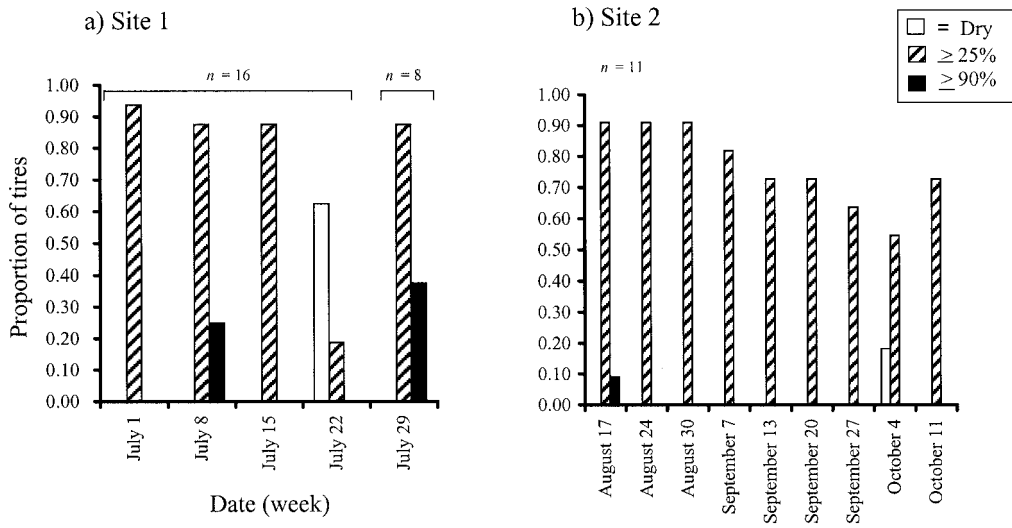

Fig. 6. Proportions of tires at sites 1 and 2 that have tire water volumes ≥90%, ≥25%, and dry.

yielded shorter development time for the first cohort (Fig. 3), and both higher average adult mortality and eclosion rates, with mortality rate making the larger contribution to this temperature effect (Fig. 2a). Therefore, in this experiment, temperature effects on adult mortality appear to be the most important factor producing temperature-dependent differences in numbers of adults.

These temperature-dependent differences in adult populations were also dependent on the precipitation regime. At 26 and 30°C, the drying treatment severely reduced adult production (Fig. 1). High temperature and drying were both associated with greater per capita mortality rate (Fig. 2). Smaller population sizes at high temperatures and drying regimes may result from increased desiccation of adults and thus higher mortality (Fig. 2) (Reeves et al. 1994, Mogi et al. 1996), rapid depletion of the pulse of resource added at the beginning, and by negative effects of habitat drying on resource quality (Aspbury and Juliano 1998). These precipitation effects on adult production are absent at 22°C (Fig. 1).

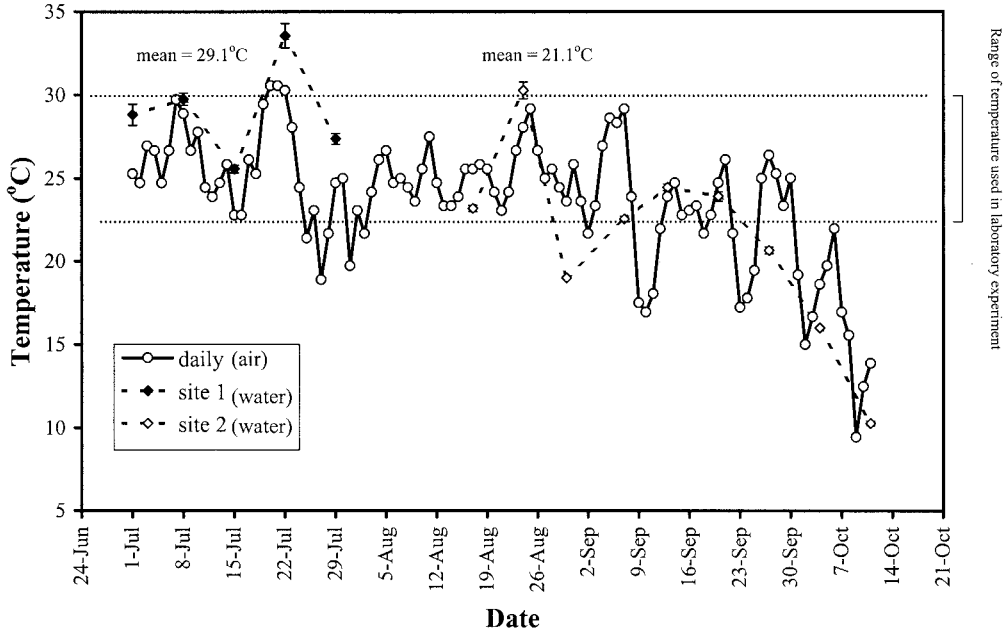

Fig. 7. Mean daily ambient air temperatures and weekly water temperatures for sites 1 and 2. Mean water temperatures for sites 1 and 2 were determined over the entire monitoring period. For sites 1 and 2, points lacking error bars indicate standard errors that were too small to appear on the graph.

The absence of a significant regression of cumulative number of adults versus cumulative water volume added demonstrates that differences in production of adults are not simply the result of more cumulative water added producing more adults. Rather, the pattern of precipitation (i.e., 90%, 25%, and dry regimes) is a key determinant of production of adults. In this experiment, it appears that variation in precipitation input has little effect on the size of the adult population unless there is complete drying of the aquatic habitats.

Previous studies have shown that habitat drying has a variety of negative effects on container dwelling mosquitoes (Bradshaw and Holzapfel 1988; Sota and Mogi 1992a, 1992b; Juliano and Stoffregen 1994; Mogi et al. 1996; Aspbury and Juliano 1998). In this experiment, we expected that drying regimes coupled with high temperatures would greatly increase egg mortality due to desiccation (Sota and Mogi 1992a, 1992b). Although we did find an increase in egg mortality with increasing temperature, we failed to detect differences in egg mortality among precipitation regimes. Drying also caused considerable mortality of larvae and pupae. On occasion we did observe older larvae (III and IV) surviving a 5-d dry period at 22°C and 26°C, presumably in damp leaf detritus. Such survival was never observed at 30°C, suggesting that high temperatures enhanced the mortality effect of habitat drying. Also, in this experiment, although adult size decreased with increasing temperature, we found no evidence that adults in more variable precipitation regimes (i.e., 25% and dry) were smaller compared with adults in less variable precipitation regimes (i.e., 90%) (Fig. 4), as would be expected if low water volumes enhanced crowding and competition. On the contrary, in the most variable precipitation regime (i.e., dry), adults were significantly larger than those in the 90% regime. Thus, the principal detrimental effect of habitat drying seems to be direct mortality of the aquatic stages.

Our field results suggest that temperature treatments used in the laboratory experiment closely parallel mean water and air temperatures in and around tires during the active season in the vicinity of East St. Louis (Fig. 7). Single measurements of water temperature may not accurately describe the daily thermoperiods, nevertheless, the water and mean air temperatures are similar (Fig. 7). Also, field results indicate that precipitation regimes like those used in the laboratory experiment occur in the midwest, and that most tire water volumes fluctuate between 25% and 90% of their maximum volume (Fig. 6). The amount of time for tires to dry at site 2 in autumn was nearly twice that of site 1 in summer and the mean water temperature at site 2 was much lower due to differences in season (Fig. 5). Although the sample period for site 2 was over twice as long as that for site 1, cumulative precipitation was similar for the two sites (site 1 = 112.0 mm, site 2 = 108.5 mm). This result suggests, as observed in the laboratory experiment (Fig. 5), that differences in temperature are the primary reason for the different drying times. Conditions in the field were quite variable, in part because the initial water volumes were variable. Nonetheless, drying times in the field were within the range produced in the laboratory experiment.

Results from these studies may provide a basis for understanding current and future distribution of *A. albopictus* in North America. Prior results suggest that a temperature of ≈26°C alone is likely to enhance the performance and spread of *A. albopictus* in North America by increasing intrinsic rates of increase of adult populations (Alto and Juliano, 2001). In the present experiment, greater temperature coupled with 25 or 90% fluctuation regimes increased overall production of adults (Fig. 1). However, high temperatures in combination with drying regimes produced strong detrimental effects on adult production (Fig. 1). Therefore, populations of *A. albopictus* in warmer temperate regions with greater probability of summer drought (e.g., southern United States, Bradshaw and Holzapfel 1984) are likely to have greater production of adults as long as container habitats do not dry completely. Increasing frequency of habitat drying would be expected to cause lower production of adults. In contrast, populations in cooler, wetter temperate regions (e.g., northern United States) are likely to have somewhat lower production of adults, with the variability of precipitation contributing relatively less to variation in production of adults.

Climate change in North America is likely to alter the distribution of *A. albopictus.* Because resolution of general circulation models (GCM's) diminishes at smaller scales, it is difficult to make quantitative predictions of the effects of climate change on local precipitation patterns (IPCC 1995), resulting in uncertainty about how *A. albopictus* will be affected. If some of the broad-scale predictions of GCM's are borne out (e.g., increased average temperature and frequency of summer droughts), we may expect that more arid climates will become relatively more common and perhaps limit the spread of *A. albopictus.* Predicted climate changes are also likely to cause a northward shift in the current distribution of *A. albopictus* (Nawrocki and Hawley 1987) by decreasing winter mortality (Pumpuni et al. 1992, Focks et al. 1994, Hanson and Craig 1995) due to a decrease in the number of winter days with extremely low temperatures. Our data suggested that warmer summer temperatures, if precipitation remains dependable, will also contribute to the northern expansion of *A. albopictus.* Although our study provides some information on how abiotic factors may influence the performance and distribution of *A. albopictus*, it is likely that biotic factors will also play an important role in shaping *A. albopictus* distribution. Species interactions are likely to be altered by climate change (Ives and Gilchrist 1993) rendering prediction of range expansion complex. Experiments incorporating both biotic and abiotic factors are needed to provide more accurate predictions of the ultimate distribution of *A. albopictus* in North America.

Acknowledgments

We thank R. L. deFreese, and K. Rodriguez for help in daily maintenance of the experiment, B. K. Stannis for measuring egg mortality, J. Angel (Illinois State Climatologist office) for providing daily temperature and precipitation for field sites, J. Toppins (East Side Health District Vector Mosquito Control and Tire Removal program) for aid in locating field sites, and L. P. Lounibos, W. A. Riddle, and D. W. Whitman for helpful comments on the manuscript. This research was supported by grants from the National Institutes of Health (R15-AI-39700–01 and R01-AI-44793–01), Illinois State University office of Research, and the Beta Lambda Chapter of the Phi Sigma Biological Honor Society.

References Cited

Alto, B. W., and S. A. Juliano. 2001. Temperature effects on the dynamics of *Aedes albopictus* (Diptera: Culicidae) populations in the laboratory. J. Med. Entomol. (in press).

Aspbury, A. S., and S. A. Juliano. 1998. Negative effects of habitat drying and prior exploitation on the detritus resource in an ephemeral aquatic habitat. Oecologia (Berl.) 115: 137–148.

Bradshaw, W. E., and C. M. Holzapfel. 1984. Seasonal development of tree-hole mosquitoes (Diptera: Culicidae) and chaoborids in relation to weather and predation. J. Med. Entomol. 21: 366–378.

Bradshaw, W. E., and C. M. Holzapfel. 1988. Drought and the organization of tree-hole mosquito communities. Oecologia 74: 507–514.

Daugherty, M. P., B. W. Alto, and S. A. Juliano. 2000. Invertebrate carcasses as a resource for competing *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae). J. Med. Entomol. 37: 364–372.

Day, J. F., A. M. Ramsey, and J. Zhang. 1990. Environmentally mediated seasonal variation in mosquito body size. Environ. Entomol. 19: 469–473.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. Wiley, New York.

Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. Am. Nat. 138: 1067–1091.

Focks, D. A., S. B. Linda, G. B. Craig, W. A. Hawley, and C. P. Pumpuni. 1994. *Aedes albopictus* (Diptera: Culicidae): a statistical model of the role of temperature, photoperiod, and geography in the induction of egg diapause. J. Med. Entomol. 31: 278–286.

Glantz, S. A., and B. K. Slinker. 1990. Primer of applied regression and analysis of variance. McGraw-Hill, New York.

Hanson, S. M., and G. B. Craig, Jr. 1995. Relationship between cold hardiness and supercooling point in *Aedes albopictus* eggs. J. Am. Mosq. Control Assoc. 11: 35–38.

Hawley, W. A. 1985. The effect of larval density on adult longevity of a mosquito, *Aedes sierrensis:* epidemiological consequences. J. Anim. Ecol. 54: 955–964.

Hawley, W. A. 1988. The biology of *Aedes albopictus.* J. Am. Mosq. Control Assoc. (Suppl. 1) 4: 1–39.

Hawley, W. A., P. Reiter, R. S. Copeland, C. B. Pumpuni, and G. B. Craig, Jr. 1987. *Aedes albopictus* in North America: probable introduction in used tires from Northern Asia. Science 236: 1114–1115.

Ho, B. C., K. L. Chan, and Y. C. Chan. 1971. *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) in Singapore city 3. Population Fluctuations Bull. W.H.O. 44: 635–641.

(IPCC) Intergovernmental Panel on Climate Change. 1995. Climate change 1995, The science of climate change: Contribution of Working Group I to the second assessment report of the Intergovernmental Panel of Climate Change. Cambridge University Press, Cambridge, UK.

Ives, A. R., and G. Gilchrist. 1993. Climate change and ecological interactions, pp. 120–146. *In* P. J. Kareiva, J. G. Kingsolver, and R. Huey [eds.], Biotic interactions and global change. Sinauer, Sunderland, MA.

Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? Ecology 79: 255–268.

Juliano, S. A., L. J. Hechtel, and J. R. Waters. 1993. Behavior and risk of predation in larval tree hole mosquitoes: effects of hunger and population history of predation. Oikos 68: 229–241.

Juliano, S. A., and T. L. Stoffregen. 1994. Effects of habitat drying on size at and time to metamorphosis in the tree hole mosquito *Aedes triseriatus.* Oecologia (Berl.) 97: 369–376.

Kitching, R. L. 1971. An ecological study of water-filled treeholes and their position in the woodland ecosystem. J. Anim. Ecol. 40: 281–302.

Lawton, J. H. 1995. The response of insects to environmental change, pp. 4–22. *In* R. Harrington and N.E. Stork [eds.], Insects in a changing environment: 17th Symposium of the Royal Entomological Society, 7–10 September 1993. The Royal Entomological Society, London, UK.

Livdahl, T. L., and M. S. Willey. 1991. Prospects for invasion: competition between *Aedes albopictus* and native *Aedes triseriatus.* Science 253: 189–191.

Lord, C. C. 1998. Density dependence in larval *Aedes albopictus* (Diptera: Culicidae). J. Med. Entomol. 35: 825–829.

Lounibos, L. P. 1981. Habitat segregation among African treehole mosquitoes. Ecol. Entomol. 6: 129–154.

Lounibos, L. P. 1985. Interactions influencing production of treehole mosquitoes in south Florida, pp. 65–78. *In* L. P. Lounibos, J. R. Rey, and J. H. Frank [eds.], Ecology of mosquitoes: proceedings of a workshop. Florida Medical Entomology Laboratory, Vero Beach, FL.

Mitchell, J.F.B., T. C. Johns, J. M. Gregory, and S.F.B. Tett. 1995. Climate response to increasing levels of greenhouse gases and sulphate aerosols. Nature (Lond.) 376: 501–504.

Mogi, M., I. Miyagi, K. Abadi, and Syafruddin. 1996. Inter- and intraspecific variation in resistance to desiccation by adult *Aedes* (*Stegomyia*) spp. (Diptera: Culicidae) from Indonesia. J. Med. Entomol. 33: 53–57.

Nasci, R. S. 1986. Relationship between adult mosquito (Diptera: Culicidae) body size and parity in field populations. Environ. Entomol. 15: 874–876.

Nawrocki, S. J., and W. A. Hawley. 1987. Estimation of the northern limits of distribution of *Aedes albopictus* in North America. J. Am. Mosq. Control Assoc. 3: 314–317.

Novak, R. J., and D. A. Shroyer. 1978. Eggs of *Aedes triseriatus* and *A. hendersoni:* a method to stimulate optimal hatch. Mosq. News 38: 515–521.

Packer, M. J., and P. S. Corbet. 1989. Size variation and reproductive success of female *Aedes punctor* (Diptera: Culicidae). Ecol. Entomol. 14: 297–309.

Pumpuni, C. B., J. Knepler, and G. B. Craig, Jr. 1992. Influence of temperature and larval nutrition on the diapause inducing photoperiod of *Aedes albopictus.* J. Am. Mosq. Control Assoc. 8: 223–227.

Reeves, W. C., J. L. Hardy, W. K. Reisen, and M. M. Milby. 1994. Potential effect of global warming on mosquito-borne arboviruses. J. Med. Entomol. 31: 323–332.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Rueda, L. M., K. J. Patel, R. C. Axtell, and R. E. Stinner. 1990. Temperature-dependent development and survival rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera: Culicidae). J. Med. Entomol. 27: 892–898.

SAS Institute. 1989. SAS/STAT user's guide, version 6, SAS Institute, Cary, NC.

Scheiner, S. M. 1993. Multiple response variables and multispecies interactions, pp. 94–112. *In* S. M. Scheiner and J. Gurevitch, [eds.], Design and analysis of ecological experiments. Chapman & Hall, New York.

Sota, T., and M. Mogi. 1992a. Survival time and resistance to desiccation of diapause and non-diapause eggs of temperate *Aedes* (*Stegomyia*) mosquitoes. Entomol. Exp. Appl. 63: 155–161.

Sota, T., and M. Mogi. 1992b. Interspecific variation in desiccation survival time of *Aedes* (*Stegomyia*) mosquito eggs is correlated with habitat and egg size. Oecologia (Berl.) 90: 353–358.

Sulaiman, S., and J. Jeffery. 1986. The ecology of *Aedes albopictus* (Skuse) (Diptera: Culicidae) in a rubber estate in Malaysia. Bull. Entomol. Res. 76: 553–557.

Sutherst, R. W., G. F. Maywald, and D. B. Skarrat. 1995. Predicting insect distributions in a changed climate, pp. 60–88. *In* R. Harrington and N. E. Stork [eds.], Insects in a Changing Environment: 17th Symposium of the Royal Entomological Society 7–10 September 1993. The Royal Entomological Society, London, UK.

Teng, H. J., and C. S. Apperson. 2000. Development and survival of immature *Aedes albopictus* and *Aedes triseriatus* (Diptera: Culicidae) in the laboratory: Effects of density, food, and competition in response to temperature. J. Med. Entomol. 37: 40–52.

Trpis M., W. O., Haufe, and J. A. Shemanchuk. 1973. Embryonic development of *Aedes (O.) sticticus* (Diptera: Culicidae) in relation to different constant temperatures. Can. Entomol. 105: 43–50.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures, pp. 113–137. *In* S.M. Scheiner and J. Gurevitch, [eds.], Design and analysis of ecological experiments. Chapman & Hall, New York.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annu. Rev. Ecol. Syst. 17: 567–594.

Received for publication 16 October 2000; accepted 16 April 2001.