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EFFECTS OF ELEVATED ATMOSPHERIC CO_2 ON WATER CHEMISTRY AND MOSQUITO (DIPTERA: CULICIDAE) GROWTH UNDER COMPETITIVE CONDITIONS IN CONTAINER HABITATS

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ABSTRACT

We investigated the direct and indirect effects of elevated atmospheric CO_2 on freshwater container habitats and their larval mosquito occupants. We predicted that a doubling of atmospheric CO_2 would (1) alter the chemical properties of water in this system, (2) slow degradation of leaf litter, and (3) decrease larval growth of *Aedes albopictus* (Skuse) mosquitoes raised on that litter under competitive conditions. Effects of elevated CO_2 on water quality parameters were not detected, but the presence of leaf litter significantly reduced pH and dissolved oxygen relative to water-filled containers without litter. Degradation rates of oak leaf litter from plants grown under elevated CO_2 atmospheres did not differ from breakdown rates of litter from ambient CO_2 conditions. Litter from plants grown in an elevated CO_2 atmospheres did not influence mosquito population growth, but mosquito production decreased significantly with increasing larval density. Differences among mosquito density treatments influenced survivorship most strongly among male *Ae. albopictus* and time to emergence most strongly among females, suggesting fundamental sex-determined differences in response to competition. Results of this and other studies indicate that direct and indirect effects of doubled atmospheric CO_2 are minimal in artificial containers with freshwater.

Key Words: global change, freshwater, *Aedes albopictus*, larval competition, population growth parameters

RESUMEN

Nosotros investigamos los efectos directos e indirectos de niveles elevados de CO_2 atmósferico en medio ambiente de recipientes de agua fresca y con larvas de mosquitos. Nosotros predecimos que al doblar la cantidad de CO_2 de atmósfera resultaria: (1) en alterar las caracteristicas químicas del agua en este sistema, (2) en retrasar la degradación de la hojarasca, y (3) disminuir el crecimiento de las larvas de mosquitos *Aedes albopictus* (Skuse) criadas en la hojarasca bajo condiciones de competencia. Efectos de un nivel elevado de CO_2 sobre los parametros de la calidad de agua no fueron detectados, pero la presencia de la hojarasca redujo significativamente el pH y oxigeno disuelto en relación con los recipientes llenados con agua sin hojarasca. La tasa de degradación de la hojarasca de roble en plantas sembradas bajo niveles elevados de CO_2 atmósferico no fue diferente de la tasa de degradación de la hojarasca bajo condiciones de CO_2 ambiental. La hojarasca de plantas sembradas en una atmósfera elevada de CO_2 no tuvo una influencia sobre el crecimiento de la población de mosquitos, pero la producción de mosquitos bajo significativamente al aumentar de la densidad de las larvas. Las diferencias entre los tratamientos de densidad de mosquitos tuvo una influencia mas marcada sobre la sobrevivencia entre los machos de *Ae. albopictus* y con respecto al tiempo de emergir fue mas marcado entre las hembras, esto sugiere que hay diferencias fundamentales determinadas por el sexo en respuesta a la competición. Resultados de este y otros estudios indican que los efectos directos e indirectos al doblar el CO_2 atmosférico son minimos en recipientes artificiales de agua fresca.

Atmospheric carbon dioxide concentrations are anticipated to double by the end of this century (Houghton et al. 1995). Increased CO_2 is expected to have a variety of direct and indirect effects on ecosystem processes, mediated primarily by changes in plant productivity and distribution (reviewed by Bazzaz 1990; Idso & Idso 1994; Drake et al. 1997). Whereas these effects are becoming increasingly predictable for terrestrial communities (but see Navas 1998), less attention has been paid to potential effects of elevated atmospheric CO_2 on aquatic systems.

The chemical properties of water are influenced in part by the composition of the overlying atmosphere. Most freshwater habitats are net sources of CO_2 (Wetzel 2001) and are unlikely to be greatly affected by elevated atmospheric CO_2 concentrations. However, marine environments (e.g., Hein & Sand-Jensen 1997) and carbon-limited freshwater ecosystems (e.g., oligotrophic

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lakes; Schindler et al. 1972) are potential sinks for atmospheric CO_2. Changes in the concentration of atmospheric CO_2 may directly affect water quality parameters, particularly pH, in these systems. Ultimately, direct effects of increased atmospheric CO_2 on pH and other parameters are related to physicochemical properties that vary regionally and among systems.

Indirect effects of elevated atmospheric CO_2 on freshwater habitats primarily stem from changes in the quality of terrestrial leaf litter, which serves as a resource base for aquatic detritivores (e.g., Egglishaw 1964; Cummins & Klug 1979). Elevated atmospheric CO_2 generally reduces the nutritional quality of living leaf material for terrestrial herbivores through reductions in N concentration resulting in increased C/N ratios. This increased relative carbon content affects leaf structural properties and may further the production of carbon-based secondary metabolites such as phenolics (e.g., Lindroth et al. 1993; Drake et al. 1997; Stiling et al. 1999, 2003). Differences in nutritional quality of naturally abscised terrestrial leaf litter resulting from elevated atmospheric CO_2 are less clear. Some studies show no (or minimal) observable effects of elevated CO_2 on leaf litter (Norby & Cotrufo 1998; Strand et al. 1999; King et al. 2001), whereas others show clear differences in leaf litter quality (Cotrufo & Ineson 1996; Cotrufo et al. 1994; Cotrufo et al. 1999; Rier et al. 2002; Tuchman et al. 2003), perhaps due to differences among leaf types in nutrient resorption during senescence. Abscised leaves from plants grown in elevated CO_2 environments tend to decompose more slowly due to changes in lignin/N, C/N ratios, and N and lignin concentrations (Cotrufo et al. 1994; Cotrufo & Ineson 1996; Cotrufo et al. 1999; Frederiksen et al. 2001), and reduced bacterial activity (Frederiksen et al. 2001; Rier et al. 2002; Tuchman et al. 2003). Detritivore productivity is often related to the decomposition rate of litter in freshwater (Fish & Carpenter 1982; Yanoviak 1999), so even minor changes in litter quality may have important ecological implications. Despite several avenues by which elevated atmospheric CO_2 may effect freshwater habitats, the topic largely has been ignored.

Water-filled artificial containers (e.g., discarded tires, flower vases, etc.) present simple systems to examine effects of environmental change on ecological processes. Water in containers is especially likely to be directly influenced by atmospheric conditions because it originates as rainfall, lacks contact with soils or groundwater, and often has a large exposed surface relative to its total volume. Container water is not well buffered against pH shifts, temperature fluctuations, and other effects of atmospheric perturbations. Here we explored the direct effects of elevated atmospheric CO_2 on basic chemical properties of water in container habitats. Assuming that these systems have poor buffering capabilities, we expected a reduction in pH of the container water in the elevated CO_2 environment.

Container habitats also are good models for investigating the indirect effects of elevated atmospheric CO_2 on discrete freshwater systems. Plant detritus, typically in the form of fallen leaf litter, is the base of food webs in these settings. Food webs in containers tend to be relatively simple and frequently include mosquitoes as the dominant consumers of litter-derived nutrients. Mosquitoes generally feed by filtering particles (e.g., microbes) from the water column and browsing upon surfaces (Clements 1992). Mosquito productivity is influenced by the quality of litter inputs (Fish & Carpenter 1982; Lounibos et al. 1993; Walker et al. 1997; Strand et al. 1999; Yanoviak 1999; Daugherty & Juliano 2002), and reduced litter quality due to elevated atmospheric CO_2 is likely to negatively affect mosquito population growth parameters. Strand et al. (1999) tested this hypothesis with the eastern treehole mosquito *Ochlerotatus triseriatus* (Say), and Tuchman et al. (2003) tested it with a suite of mosquitoes that included *O. triseriatus*, *Aedes albopictus* (Skuse), *Aedes aegypti* (L.), and *Armigeres subalbatus* (Coquillett). Results from these studies showed that the negative effects of elevated CO_2 were either nonsignificant or limited to differences in development time for a few mosquito species or survivorship of *Ae. albopictus*. However, in neither of these studies were the mosquitoes reared under nutrient-limited conditions typical of such habitats. If resource quality is an important determinant of mosquito growth and survivorship, then this should be most clearly illustrated by differences in the outcome of competitive interactions (i.e., when the resource is limiting).

Here we examined the potential indirect effects of elevated atmospheric CO_2 on litter decomposition and productivity of the mosquito *Ae. albopictus* in container habitats. We chose *Ae. albopictus* because it naturally colonizes containers and it is an exotic species (Lounibos 2002) that outcompetes larvae of established species (Juliano 1998). In nature, intra- and interspecific larval competition is often strong among container mosquitoes and it may play an important role in shaping container communities (Novak et al. 1993; Juliano 1998; Teng & Apperson 2000; Lounibos et al. 2001, 2003). Limited effects of elevated CO_2 on mosquito population growth found by Strand et al. (1999) and Tuchman et al. (2003) may be partly due to the experimental set-up not being sufficiently competitive to produce differences in mosquito performance between ambient and elevated CO_2 litter treatments. Differences in mosquito growth in ambient versus elevated CO_2 litter are likely to become more pronounced as intraspecific competition is increased.

Because some changes in water quality parameters, particularly pH, influence litter decomposi-

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tion rates in freshwater (Groom & Hildrew 1989; Kok & Van der Velde 1994), we hypothesized that any direct effects of elevated atmospheric CO_2 on water quality would alter litter decomposition rates in containers. We also expected that oak litter originating from an elevated CO_2 environment would decompose more slowly in water-filled containers. Finally, we predicted that population growth correlates of *Ae. albopictus* would be depressed, and intraspecific competition more intense, when individuals are reared on elevated CO_2 litter. Adult aedine mosquitoes are sexually dimorphic, with males typically smaller than females and are the first to emerge to adulthood (Briegel & Timmermann 2001). Given that the response to competition may be sex-determined, we analyzed males and females separately.

Materials and Methods

We compared water chemistry in containers set in scrub-oak habitats at the Kennedy Space Center (KSC), Cape Canaveral, Florida (28°29'N, 80°34'W). Sixteen octagonal open-top chambers (3.6 × 2.5 m, width × ht.) were constructed from clear polyester film ('Mylar,' Melinex 071) overlying PVC frames. Eight chambers were ventilated with ambient air and 8 with CO_2 concentration artificially elevated to approximately double ambient levels (see Dijkstra et al. 2002 for additional details).

Container Water Chemistry in Elevated vs. Ambient CO_2

Black plastic cups (max. volume = 500 ml) served as our experimental units and were arranged in a split-plot design at KSC on March 18, 2003. Each cup received distilled water to the level of a small drain hole located ca. 3 cm from the top (to prevent overflow), resulting in a functional volume of approximately 350 ml. We added 1.0 ± 0.005 g oak leaves (*Quercus virginina* Mill.) and 5.0 ml of filtered (180 µm sieve) oak infusion inoculum (O'Meara et al. 1989) to half of the cups (hereafter, "litter" treatment). The litter used in this experiment consisted of freshly fallen leaves collected on the grounds of the Florida Medical Entomology Laboratory (FMEL) (27.6°N, 80.5°W). The leaves were dried at 60°C for 48 h before weighing. The remaining cups received distilled water but no leaves or inoculum ("water" treatment). All cups were individually covered with a nylon screen (0.8 mm mesh) to prevent additional litter inputs and mosquito colonization.

We placed one water treatment and one litter treatment cup in 8 replicates of each of three experimental environments spaced 5-10 m apart: elevated CO_2 chamber, ambient air chamber, or ambient air plot without a chamber (hereafter, "elevated", "ambient", and "control"), for a total $n = 48$ cups (2 treatments × 3 environments × 8 replicates). Portable meters were used to measure dissolved oxygen (DO), nitrate (NO_3), pH, and temperature of the water in each cup weekly for 9 weeks. Measurements were initiated at 0900-1000 h on each sample date. No data were collected on week 7, and equipment problems prevented pH measurements on weeks 3 and 6. All of these instances were treated as missing values in analyses. Initial (week 0) means were obtained for the litter treatments by measuring water quality parameters in 10 cups (5 litter and 5 water) in the laboratory. Final water volume was measured in each cup on week 9, and remaining litter was collected, dried, and weighed as above.

Water quality parameters (DO, nitrate, and pH) were compared between treatments and among environments with mixed model repeated-measures analysis of variance (SAS Institute 2002). This maximum-likelihood approach is preferred over general linear models for repeated measures because it permits more appropriate modeling of variance structure (von Ende 1993; Saavedra & Douglass 2002). All repeated-measures tests employed autoregressive order 1 variance structure and "block" (individual chamber or plot) within litter and environment treatments as the error subject. Satterthwaite-type degrees of freedom were obtained by the Kenward-Roger method (Kenward & Roger 1997; SAS Institute 2002). General linear models ANOVAs were used to analyze final water volume and litter mass. Normality was confirmed with Kolmogorov-Smirnov tests and normal probability plots (Sokal & Rohlf 1995; SAS Institute 2002). Nitrate values were log-transformed to reduce variance heterogeneity and DO values were corrected for water temperature. pH values were not transformed since they adequately met the assumptions. All means include ± 1 standard error and were calculated from untransformed data.

Effects of Leaves from Elevated CO_2 on Mosquito Growth and Competition

We planned to conduct mosquito productivity experiments in the field, but pilot data showed that summer water temperatures in artificial containers placed in CO_2 enclosures at KSC often exceeded 36°C, which was lethal to *Ae. albopictus* larvae reared in the lab (0.62% survivorship to emergence from 12 cups each with 40 larvae). Thus, we conducted the mosquito productivity portion of this study in growth chambers at FMEL.

On 31 March 2003 we collected oak leaf litter (a combination of *Quercus chapmanii* Sargent, *Q. myrtifolia* Willd., and *Q. geminata* Small in approximately equal proportions) from each of the 16 experimental chambers at KSC. We chose *Quercus* spp. litter because it was readily available and it is commonly found in water-filled containers occupied by mosquitoes in peninsular Florida (personal observations, BWA). The individual litter collections were pooled by treatment, providing

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25.0 g elevated CO_2 litter and 25.0 g ambient CO_2 litter. Leaves were wiped (not washed) to remove dirt and sand, and then dried at 60°C for 24 h.

Experiments were conducted in 500-ml plastic cups containing 350 ml distilled water and 1.0 ± 0.005 g elevated or ambient CO_2 litter. After the litter had soaked in the cups for 3 d, *Ae. albopictus* first instars (<24 h old) were added at densities 10, 20, 30, 40, or 50 per cup. Pilot data using similar water volumes and leaves (*Q. virginiana*) suggested these densities would provide a range of competitive conditions. Mosquitoes used in the experiment were the progeny of wild larvae collected from artificial containers near Vero Beach, FL. Each leaf litter and larval density treatment was replicated 5 times ($2 \times 5 \times 5 = 50$ cups total). Cups were individually covered with a nylon screen (0.8 mm) and housed in an incubator at a mean temperature (± SD) 25.3 ± 0.4°C, relative humidity of 78.3 ± 5.6%, and a photoperiod of 14:10 (L:D). When pupae were first detected, cups were checked daily and pupae were removed and housed in 40-ml vials with tap water until emergence. Adult emergence was recorded daily, and adults were dried at 60°C for 48 h and individually weighed on a Cahn® electrobalance. The litter remaining in a cup was dried and weighed after all mosquitoes from that cup had emerged. The experiment continued until all *Ae. albopictus* had emerged or died.

Multivariate analyses of variance (MANOVA) were used to analyze the treatment effects of leaf litter, larval density, and litter × density interaction on *Ae. albopictus* response variables (time to emergence, survivorship to emergence, and adult mass). Developmental parameters are sex-specific in many mosquito species, including *Ae. albopictus* (Juliano 1998; Teng & Apperson 2000; Bedhomme et al. 2003). Thus, we used a separate MANOVA for each sex. Raw data for males were $\log_{10}$-transformed to meet assumptions of univariate normality and homogeneous variances. For all analyses, significant effects were further analyzed by contrasts of all possible pairs of main effect multivariate means with experimentwise = 0.05 (sequential Bonferroni method; Rice 1989). Standardized canonical coefficients (SCCs) were used to determine the relative contribution of each of the response variables to significant multivariate effects as well as their relationship to each other (e.g., positive or negative; SAS Institute 2002; Scheiner 1993).

Additionally, we calculated an estimated finite rate of increase, lambda (λ'), for each leaf litter by larval density replicate. λ' synthesizes multiple population growth correlates to describe population performance (Juliano 1998). λ' was calculated as follows:

$$\lambda' = \exp(r') = \exp\left(\frac{\ln[(1/N_o)\Sigma_x A_x f(w_x)]}{D + [\Sigma_x x A_x f(w_x)/\Sigma_x A_x f(w_x)]}\right) \quad (1)$$

where λ' is an alternative form of r', a composite index of population performance described by Livdahl and Sugihara (1984) and Livdahl (1982). r' is an estimate of $r = dN/Ndt$ which describes the per capita growth rate. N_o is the initial number of females in a cohort (assumed to be 50% of introduced larvae); A_x is the number of females emerging on day x; w_x is the mean female size on day x; $f(w_x)$ is a function relating the number of eggs produced by a female to her size; and D is the time (in days) from emergence to oviposition. For *Ae. albopictus*, D is assumed to be 14 d (Livdahl & Willey 1991). We used the following size-fecundity relationships to calculate ($f(w_x)$) (Lounibos et al. 2002):

$$f(w_x) = 19.5 + (152.7*X) \quad (2)$$

where $r^2 = 0.573$.

Equation 2 was derived from two separate regressions in Lounibos et al. (2002). We assume that the regression function for *Ae. albopictus* approximates individual reproductive capacity. We analyzed effects of leaf litter origin (elevated or ambient CO_2) and larval density on *Ae. albopictus* λ' by two-way ANOVA. Significant effects were further analyzed by comparisons of pairs of main effect means with experimentwise = 0.05 (Ryan-Einot-Gabriel-Welsch multiple range test; SAS Institute 2002).

Finally, we used a *t*-test to compare the mean proportion (arcsine square root transformed) of litter mass remaining at the end of the experiment between litter treatments (all densities within a litter type pooled).

Results

Container Water Chemistry in Elevated vs. Ambient CO_2

The nitrate data set included an extreme value (22.5 mg/L) on week 6 in the water treatment cup located in the ambient environment. We determined this to be a statistical outlier for both the week 6 ambient environment data (Dixon's test, $P < 0.01$) and for the complete data set ($P < 0.005$, according to Grubbs 1969; Sokal & Rohlf 1995), and excluded it from the analysis (treated as missing data). The cause of this outlier is unknown, but excreta from a perching or passing bird is a likely possibility.

The presence or absence of leaf litter significantly affected nitrate concentrations, pH, and DO in the cups (Table 1). Mean nitrate concentrations were consistently greater in water containing leaf litter during weeks 1-9, whereas pH and DO were significantly lower in cups containing litter over the same period (Table 1; Fig. 1). All parameters varied significantly over time, and time × litter interactions were significant for pH and DO (Table 1). There was a trend for lower pH variance in cups with litter relative to cups without

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TABLE 1. REPEATED-MEASURES ANOVA FOR WATER QUALITY PARAMETERS. LITTER = LEAF LITTER PRESENT OR ABSENT; ENVIRONMENT = AMBIENT CO_2, ELEVATED CO_2, OR CONTROL ENVIRONMENTS. AR(1) = AUTOREGRESSIVE ORDER 1 COVARIANCE ESTIMATE WITH SUBJECT = BLOCK(LITTER × ENVIRONMENT). DECIMAL *DF* VALUES RESULTED FROM SATTERTHWAITE-TYPE *DF* CALCULATION.

					Covariance Parameter Estimates	
	Factor	*df*	*F*	*P*	AR(1)	Residual
Nitrate	Litter	1, 60.6	18.80	<0.0001	0.6173	0.2755
	Environment	2, 60.6	5.78	0.0051		
	Time	7, 281	48.00	<0.0001		
	Litter × Environment	2, 60.6	0.54	0.5829		
	Litter × Time	7, 281	0.80	0.5899		
	Environment × Time	14, 289	1.45	0.1277		
	Litter × Environment × Time	14, 289	1.00	0.4555		
pH	Litter	1, 45.3	6.95	0.0114	0.8373	0.4592
	Environment	2, 45.3	2.35	0.1073		
	Time	5, 203	37.69	<0.0001		
	Litter × Environment	2, 45.3	1.76	0.1830		
	Litter × Time	5, 203	4.07	0.0015		
	Environment × Time	10, 205	1.25	0.2637		
	Litter × Environment × Time	10, 205	1.02	0.4251		
DO	Litter	1, 74.9	297.20	<0.0001	0.3740	0.0053
	Environment	2, 74.9	1.65	0.1983		
	Time	7, 271	130.80	<0.0001		
	Litter × Environment	2, 74.9	0.81	0.4498		
	Litter × Time	7, 271	3.16	0.0032		
	Environment × Time	14, 285	2.35	0.0043		
	Litter × Environment × Time	14, 285	1.16	0.3083		

litter (Fig. 1b). Initial (week 0) values for water quality parameters did not differ between litter and water treatments (Nitrate: $t = 1.07$, $P = 0.32$; pH: $t = 0.03$, $P = 0.98$; DO: $t = 2.20$, $P = 0.06$; $df = 8$ for each test; Fig. 1).

Doubling the atmospheric CO_2 concentration had minimal or no effects on water quality parameters in the cups. The dissolved oxygen content and pH of container water did not differ among the three experimental environments, whereas mean nitrate concentrations were significantly lower in controls (i.e., cups located outside the environmental chambers; Table 1). For nitrate values, post-hoc univariate tests and Tukey comparisons indicate that the only significant difference between ambient and elevated CO_2 environments occurred on week 6. Nitrate was significantly lower in cups in the control environment than in either ambient or elevated (or both) on weeks 2 and 4-9 (Fig. 2). Reanalysis excluding the control environment data nullified the significant environment effect ($F_{1,41.6} = 0.76$, $P = 0.39$), but did not change the results for litter, time, or interaction effects.

The mean (± SE) volume of water remaining in cups at the end of the experiment did not differ between litter treatments, but was lower in the control environment (284 ± 5.2 ml) than in the elevated CO_2 chambers (309 ± 3.6 ml; Table 2). Average final volume in the ambient environment (297 ± 4.6) did not differ from the final volumes in the other environments. Elevated atmospheric CO_2 had no effect on litter degradation rates in the cups in the field experiment (Table 2). Mean litter mass remaining at the end of the experiment was similar among ambient (0.812 ± 0.0054 g) elevated (0.814 ± 0.0067 g) and control (0.811 ± 0.0041 g) environments.

Effects of Leaves from Elevated CO_2 on Mosquito Growth and Competition

ANOVA output for λ' of *Ae. albopictus* showed significant larval density treatment effects, but litter type and the litter type × density treatment interaction were not significant. Pairwise comparisons showed that λ' increased with decreasing larval densities when <30 larvae were present, and was significantly lower at higher larval densities, which were similar to each other (Fig. 3).

MANOVA output for males and females showed significant effects of larval density on response variables (time to emergence, survivorship to emergence, adult mass; Table 3). Leaf litter type and the litter type × density interaction did not

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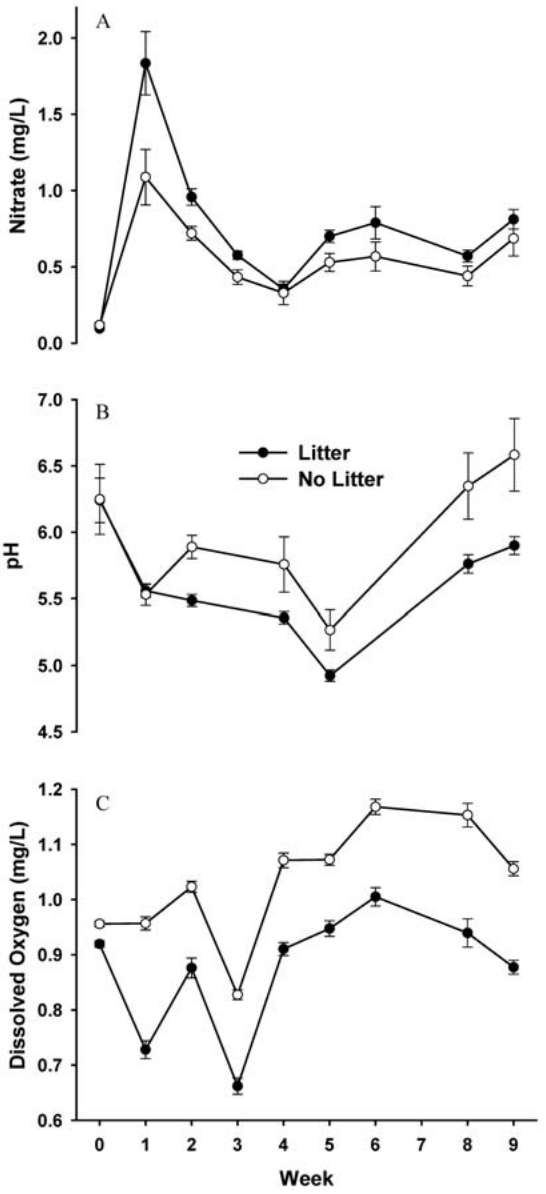


Fig. 1. Mean (± SE) nitrate concentration (A), pH (B), and DO (C) in cups containing leaf litter plus water and cups with water only. n = 16 for each mean on weeks 1-9. Week 0 means were based on n = 5 cups which were added to illustrate starting values and were not included in the repeated-measures ANOVA. One nitrate measurement (22.5 mg/L) in the water treatment on week 6 was excluded after significance testing for outliers.

significantly affect these response variables (Table 3). For males, the magnitude of the standardized canonical coefficients (SCCs) showed that survivorship contributed the most to the density effect, followed by time to emergence and mass. For females, SCCs showed that time to emergence contributed the most to the density effect followed by survivorship and mass (Table 3). For both sexes, opposite signs of the SCCs show that time to emergence was negatively related to survivorship and mass. Multivariate contrasts for the significant density effect for males and females showed consistently and significantly greater survivorship and shorter time to emergence among lower larval densities (Table 4). Overall, females had greater survivorship and longer time to emergence compared to males (Fig. 4). Similar to the main MANOVA for males, SCCs showed that survivorship contributed the most to the significant multivariate contrasts followed by time to emergence, except for two contrasts (Table 4). Likewise, for females, SCCs showed that time to emergence contributed the most to the significant multivariate contrasts followed by survivorship (Table 4).

Litter derived from an elevated CO_2 environment did not degrade more slowly than litter from an ambient CO_2 environment. The mean (± SE) proportions of elevated CO_2 (0.822 g ± 0.0074) and ambient CO_2 (0.831 g ± 0.0081) litter remaining were similar (t = 0.855, df = 48, P = 0.397).

Discussion

Contrary to our expectations, elevated atmospheric CO_2 had no direct effects on water quality in the container system. The presence or absence of leaf litter was much more important in determining the chemical characteristics of the water than was the overlying atmosphere. Although not measured, these effects are probably associated with compounds leached from the litter (leading to greater nitrate concentrations) and the metabolic activities of microorganisms colonizing the litter (resulting in lower dissolved oxygen content). The difference in pH between cups with and without litter is likely a function of both the leaf material and the microflora acting upon it. We attribute the lower pH in cups having litter to tannins and other organic acids leached from the leaf material (e.g., Stout 1989). The trend for lower variance of pH in cups with litter suggests that leached compounds, and perhaps CO_2 production by microorganisms, have a stabilizing effect on pH in this system.

Other studies investigating the productivity of mosquitoes reared on litter from elevated CO_2 environments either found no effect (Strand et al. 1999) or found differences in development time for three mosquito species and in survivorship of *Ae. albopictus* (Tuchman et al. 2003). Our results concur with those of Strand and coworkers (1999). We observed that litter derived from an elevated CO_2 atmosphere did not alter mosquito performance even under food-limited conditions.

Not all tree species respond similarly to elevated CO_2 (e.g., Cotrufo et al. 1994), and leaf litter species composition can influence mosquito pro-

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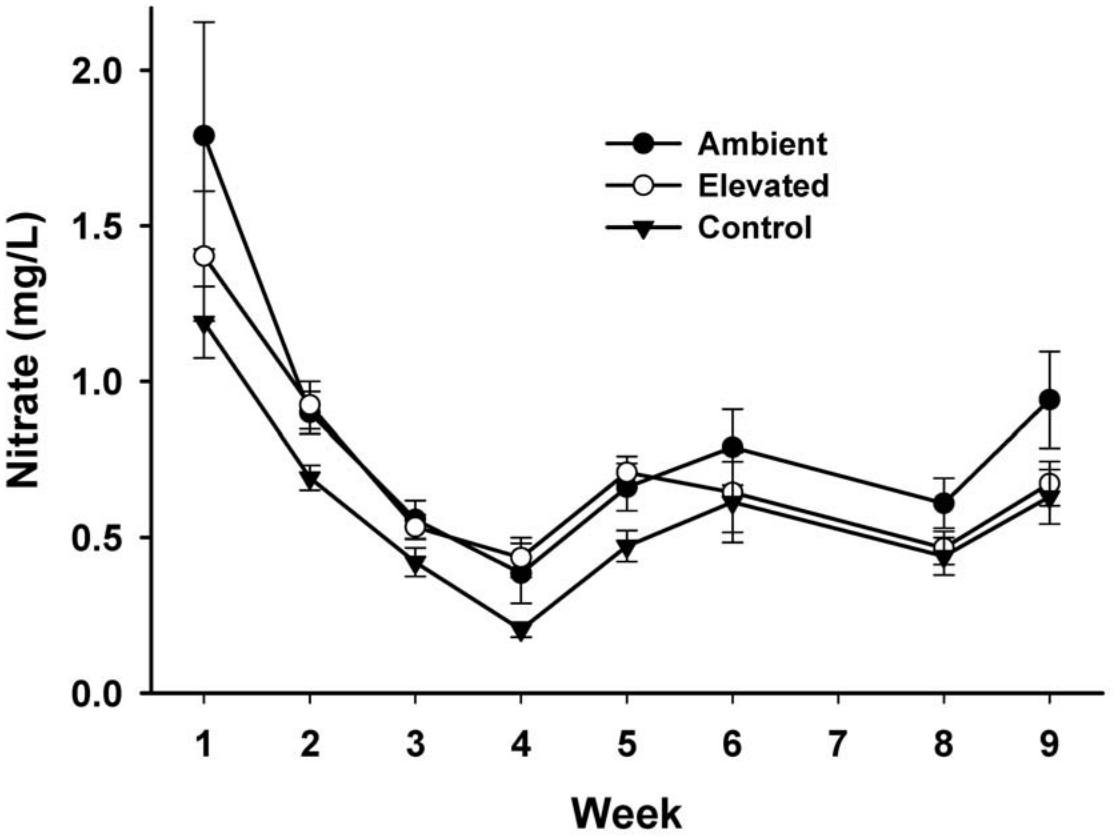


Fig. 2. Mean (± SE) nitrate concentration in cups located in different experimental environments (n = 8 for each mean). One outlier (22.5 mg/L) in the ambient environment on week 6 was excluded.

ductivity (Yanoviak 1999), thus the lack of an elevated CO_2 effect in this study may be related to the type of litter we used. Higher lignin concentration, associated with elevated CO_2 litter, slows decomposition and bacterial productivity, as shown by Tuchman et al. (2003) with *Populus tremuloides* Michaux. In the current study, data pertaining to the nutritional quality of naturally abscised oak litter in the KSC chambers is limited to *Q. myrtifolia*, which showed no difference in C concentration and only slight (nonsignificant) reductions in N concentration between litter of elevated and ambient CO_2 (Stiling et al. 2002). Also, our expectation that litter produced in an elevated CO_2 environment would degrade more slowly in this experiment was not supported. Thus, we speculate that perhaps microbial populations colonizing *Quercus* spp. litter may not have been sufficiently different among CO_2 treatments to produce differences in *Ae. albopictus* performance. *Quercus* spp. are naturally high in lignin and tannins (Stout 1989), thus CO_2 mediated differences

TABLE 2. ANOVA FOR WATER VOLUME AND DRY MASS OF LITTER REMAINING IN THE CUPS AT THE END OF THE STUDY (WEEK 9). MS = MEAN SQUARE. * = $P < 0.002$.

	Factor	*df*	MS	*F*
Volume	Litter	1	36.75	0.11
	Environment	2	2562.90	7.52*
	Litter × Environment	2	92.31	0.27
	Error	42	340.80	
Dry Mass	Environment	2	1.53×10^{-5}	0.06
	Error	21	2.43×10^{-4}	

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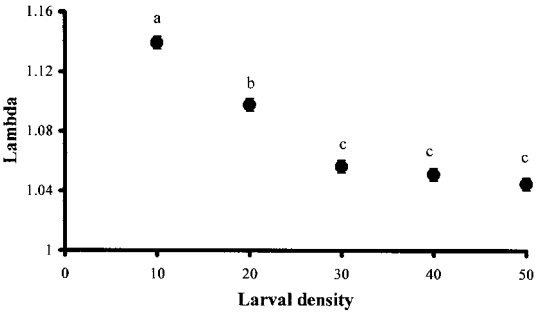


Fig. 3. Mean (± SE) estimated finite rate of population increase (λ′). Different letters indicate significant differences among *Ae. albopictus* density treatments ($F = 90.08$, $df = 4, 40$, $P < 0.0001$), but litter type and the litter type × density treatment interaction were not significant (all $F < 3.75$, $P > 0.05$).

in leaf quality may not be sufficient to affect mosquito performance.

Although other studies have shown differences in growth variables due to intraspecific larval competition (Lord 1998), as well as sex differences (Teng & Apperson 2000; Bedhomme et al. 2003), few have quantified competition-induced differences in fitness correlates between males and females. Here, we observed that differences in survivorship were the major contributors to the density effect for males, whereas differences in time to emergence were the major contributors to the density effect for females. The relationship among the response variables for each sex was asymmetrical. In particular, for females, time to emergence contributed about twice as much as survivorship to the density effect. For males, survivorship contributed approximately 20% more than emergence to the density effect.

Although males were significantly smaller than females (mean ± SE: 0.138 ± 0.006 and 0.293 ± 0.008 mg, respectively), mass contributed little to the density effect, and its contribution was nearly equal between sexes. Thus, although competition had similar global effects on both sexes (e.g., longer time to emergence, lower survivorship, lower mass), the individual life history traits affected were sex-determined, suggesting fundamental differences in male and female *Ae. albopictus* physiological responses to competition. Other mosquito studies suggest that natural selection may act differently on each sex, since female fitness is related to fecundity whereas male fitness is related to number of matings (Steinwascher 1982; Kleckner et al. 1995). For *Ae. aegypti*, Bedhomme et al. (2003) showed sex-determined effects of larval competition, consistent with the hypothesis that the effects of competition on traits most important for each sex's reproductive fitness (e.g., time to emergence for males and size for females) are minimized at the expense of other traits. However, their study did not investigate survivorship since larval mortality was very low (i.e., 1%), and so, individual life history traits were measured only in replicates where all *Ae. aegypti* survived to emergence. In the current study we did measure survivorship, and our results show the costs of competition were equally minimal for body mass of adults of both sexes, similar to other findings where resource levels were low for *Ae. albopictus* and *Ae. aegypti* (Juliano 1998). For males, the larger effect of competition on survivorship compared to time to emergence suggests that this latter trait is less sensitive to effects of competition. For females, effects of competition on time to emergence were far greater than survivorship suggesting that females may minimize larval mortality at the expense of increased time to emergence.

Results of this and other studies suggest that indirect effects of elevated atmospheric CO_2 on freshwater systems via terrestrial litter inputs are minimal. Ultimately, carbon inputs into freshwater systems may increase through increased

TABLE 3. MANOVA OUTPUT FOR EFFECTS OF LEAF LITTER TYPE (ELEVATED VS. AMBIENT), LARVAL DENSITY, AND LEAF × DENSITY INTERACTION TREATMENTS ON MALE AND FEMALE *AE. ALBOPICTUS* RESPONSE VARIABLES; TIME TO EMERGENCE, SURVIVORSHIP TO EMERGENCE, AND ADULT MASS. STANDARDIZED CANONICAL COEFFICIENTS (SCCS) SHOW THE RELATIVE CONTRIBUTION OF EACH OF THE RESPONSE VARIABLES TO SIGNIFICANT TREATMENT EFFECTS.

					First SSCs		
	Source	*df*	Pillai's Trace	*P*	Time	Survivorship	Mass
Males	Litter Type	3, 37	0.10	0.2811			
	Density	12, 117	1.16	<0.0001	-1.15	1.45	0.28
	Litter × Density	12, 117	0.27	0.4932			
Females	Litter Type	3, 38	0.13	0.1421			
	Density	12, 120	1.22	<0.0001	-2.07	1.00	0.21
	Litter × Density	12, 120	0.23	0.6086			

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TABLE 4. MULTIVARIATE PAIRWISE CONTRASTS FOR EFFECTS OF LARVAL DENSITY TREATMENTS ON MALE (*DF* = 3, 37) AND FEMALE (*DF* = 3, 38) *AE. ALBOPICTUS* RESPONSE VARIABLES; TIME TO EMERGENCE, SURVIVORSHIP TO EMERGENCE, AND ADULT MASS. STANDARDIZED CANONICAL COEFFICIENTS (SCCS) SHOW THE RELATIVE CONTRIBUTION OF EACH OF THE RESPONSE VARIABLES TO SIGNIFICANT PAIRWISE CONTRASTS. SIGNIFICANT DIFFERENCES BETWEEN PAIRWISE CONTRASTS ARE SHOWN BY ASTERISKS: * = $P < 0.05$, ** = $P < 0.001$, *** = $P < 0.0001$.

	Males				Females			
		First SCCs				First SCCs		
Comparison	Pillai's Trace	Time	Surv.	Mass	Pillai's Trace	Time	Surv.	Mass
10 vs. 20	0.30*	-0.57	1.43	0.88	0.39**	-1.43	1.25	0.66
10 vs. 30	0.65***	-0.90	1.61	0.49	0.77***	-1.97	1.10	0.12
10 vs. 40	0.84***	-0.98	1.55	0.50	0.83***	-2.05	1.03	0.21
10 vs. 50	0.87***	-1.19	1.42	0.25	0.85***	-2.00	1.04	0.35
20 vs. 30	0.36**	-1.04	1.52	0.12	0.59***	2.00	-0.83	0.26
20 vs. 40	0.72***	-1.09	1.51	0.32	0.71***	2.17	-0.81	0.04
20 vs. 50	0.80***	-1.26	1.27	0.03	0.75***	2.16	-0.89	-0.18
30 vs. 40	0.46***	-1.09	1.45	0.51	0.18			
30 vs. 50	0.64***	1.38	-1.09	0.03	0.37**	-1.68	0.69	0.83
40 vs. 50	0.26*	1.22	-0.26	0.66	0.11			

structural carbon in litter (Tuchman et al. 2003) and increased abscission rates (Stiling et al. 2002), but the consequences of this increased carbon to detritivores and other consumers are likely to be protracted and difficult to measure (e.g., Hungate et al. 1997). This poses the question: Is there any freshwater system in which indirect effects of elevated atmospheric CO_2 could be expected? We suggest that future studies addressing this topic should focus on phytotelmata (plant-held waters: Varga 1928), specifically water held in living terrestrial plants. Bromeliads, pitcher plants (e.g., *Sarracenia purpurea* L.) and *Heliconia* spp. flower bracts are excellent candidates for such an investigation because they support a variety of heterotrophic organisms and tend to interact physiologically with the water they contain (e.g., Bronstein 1986; Juniper et al. 1989; Benzing 2000). If any physiological properties or products of the plants are modified by ele-

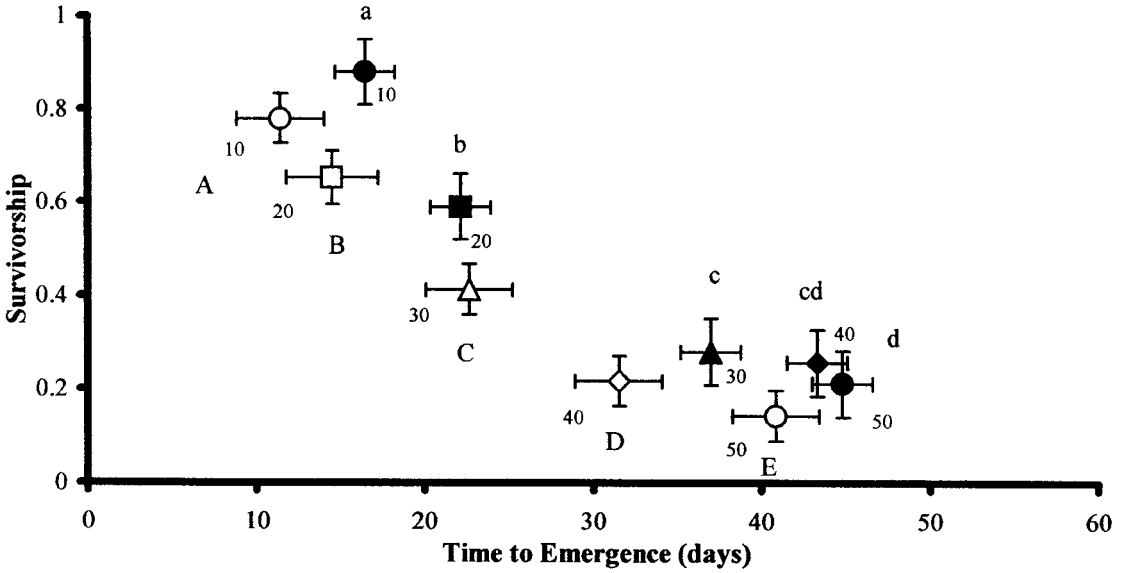


Fig. 4. Mean (± SE) survivorship and time to emergence for the significant *Ae. albopictus* density effect. Open and filled symbols show male and female bivariate means, respectively. Different lower case and capital letters indicate significant differences among means. Mass values were omitted because they contributed little to the density effect.

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vated CO_2, they should have measurable indirect effects on the resident fauna.

Apart from potential indirect effects on litter quality and physiological properties of phytotelmata, elevated atmospheric CO_2 has other broad-ranging effects, such as increased regional surface temperatures. Altered species distributions resulting from these concomitant climatic effects may be more ecologically significant than the direct or indirect effects of elevated CO_2 (Weltzin et al. 2003; Thomas et al. 2004). Many aquatic organisms reproduce and disperse outside of water, thus the potential for water to act as a physical buffer against atmospheric change is irrelevant for many species. These types of considerations need to be addressed if we are to make accurate predictions about the consequences of elevated atmospheric CO_2 on freshwater systems.

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