Effects of Elevated Atmospheric CO$_2$ on Competition Between the Mosquitoes *Aedes albopictus* and *Ae. triseriatus* via Changes in Litter Quality and Production

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ABSTRACT Elevated atmospheric CO$_2$ can alter aquatic communities via changes in allochthonous litter inputs. We tested effects of atmospheric CO$_2$ on the invasive *Aedes albopictus* (Skuse) and native *Aedes triseriatus* (Say) (Diptera: Culicidae) via changes in competition for microbial food or resource inhibition/toxicity. *Quercus alba* L. litter was produced under elevated (879 ppm) and ambient (388 ppm) atmospheric CO$_2$. Saplings grown at elevated CO$_2$ produced greater litter biomass, which decayed faster and leached more tannins than saplings at ambient CO$_2$. Competition was tested by raising larvae in different species and density combinations provisioned with elevated- or ambient-CO$_2$ litter. Species-specific performance to water conditions was tested by providing single-species larval cohorts with increasing amounts of elevated- or ambient-CO$_2$ litter, or increasing concentrations of tannic acid. Larval densities affected some fitness parameters of *Ae. albopictus* and *Ae. triseriatus*, but elevated-CO$_2$ litter did not modify the effects of competition on population growth rates or any fitness parameters. Population growth rates and survival of each species generally were affected negatively by increasing amounts of both elevated- and ambient-CO$_2$ litter from 0.252 to 2.016 g/liter, and tannic acid concentrations above 100 mg/liter were entirely lethal to both species. *Aedes albopictus* had consistently higher population growth rates than *Ae. triseriatus*. These results suggest that changes to litter production and chemistry from elevated CO$_2$ are unlikely to affect the competitive outcome between *Ae. albopictus* and *Ae. triseriatus*, but that moderate increases in litter production increase population growth rates of both species until a threshold is exceeded that results in resource inhibition and toxicity.

KEY WORDS *Aedes*, climate change, competition, freshwater, tannins

Mean concentrations of atmospheric CO$_2$ have increased from 280 to 390 ppm since the 18th century because of accelerated fossil-fuel burning and industrial processes (IPCC 2007). The Intergovernmental Panel on Climate Change (IPCC) predicts that atmospheric CO$_2$ concentrations may approach 970 ppm by 2100 (IPCC 2007). Recorded emissions from 2000 to 2005 exceeded the worst case scenario of the IPCC (A1FI) and indicated that CO$_2$ concentrations may even exceed 1,000 ppm by 2100 (Raupach et al. 2007). Increases in atmospheric CO$_2$ have been attributed to deforestation and land use change. Atmospheric CO$_2$ gradients have been observed along rural to urban transects (Ziska et al. 2003, George et al. 2007, Garcia et al. 2012), whereas point measures of CO$_2$ have exceeded 1,400 ppm near highways in at least one study (Tomoda et al. 1997).

Increasing atmospheric CO$_2$ can have substantial impacts on plant–animal interactions and the composition of ecological communities. Numerous studies have shown that exposure to elevated atmospheric CO$_2$ increases photosynthetic rates and alters phytochemistry in many species (Körner 2006, Taub and Wang 2008). Corresponding increases in plant biomass are likely to relax competitive effects among primary consumers in resource-limited systems. Elevated atmospheric CO$_2$ may also reduce nitrogen (N) concentration, increase carbon (C) concentration and C:N ratios, or both (Peñuelas and Estiarte 1998, Tuchman et al. 2003, Huttunen et al. 2009, Lindroth 2010). These phytochemical changes decrease the nutritional quality of the leaves, and may reduce the uptake efficiency and intensify resource competition in primary consumers (Bezemer and Jones 1998, Kaufman and Walker 2006). In addition, with increasing CO$_2$, foliar C may be allocated to increased carbon-based secondary metabolites, such as phenolics, tannins, and lignin (Peñuelas and Estiarte 1998, Tuchman et al. 2003, Huttunen et al. 2009). Tannins and lignin are among the most studied secondary metabolites and have been shown to reduce digestibility by pre-

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cipitating proteins and act as toxins (Hagerman et al. 1992, Murdiati et al. 1992). Numerous studies have documented the negative effects of CO_2-induced changes to mammalian and insectivorous herbivory in terrestrial systems (Martin et al. 1985, Mehansho et al. 1987, Hagerman et al. 1992). Although senesced allochthonous leaf litter is the resource basis for many aquatic habitats (Cummins and Krug 1979, Richardson 1991, Walker et al. 1991), few studies have investigated how elevated atmospheric CO_2 affects aquatic invertebrate communities, mainly because most aquatic ecosystems rarely are thought to be C limited (Tortell et al. 2000).

Water-filled artificial containers (e.g., discarded tires, flower vases) are good model systems to examine effects of environmental change on heterotrophic aquatic communities. Container communities are relatively simple and often dominated by a few co-occurring mosquito species that compete for limited food resources (e.g., Fish and Carpenter 1982, Kling et al. 2007, Leisnham et al. 2009). Mosquito larvae feed on decomposing litter and its associated microorganisms (Merritt et al. 1992). Litter quality is positively related to its decomposition rate, colonization of associated microbial communities, and mosquito development (Merritt et al. 1992, Daugherty and Juliano 2002, Murrell and Juliano 2008), whereas tannin concentrations have been shown to delay mosquito development and decrease larval survival (e.g., Mercer 1993, Sota 1993, David et al. 2001). Therefore, reduced litter quality and increased tannins because of elevated atmospheric CO_2 are likely to reduce mosquito production.

Strand et al. (1999) and Tuchman et al. (2003) tested the hypothesis that CO_2-induced changes in litter quality affect mosquito development by using single densities of *Aedes triseriatus* (Say), and *Aedes triseriatus*, *Aedes albopictus* (Skuse), *Aedes aegypti* (L.), and *Armigeres subalbatus* (Coquillett), respectively. Results from these studies showed that the negative effects of elevated CO_2 were either nonsignificant or limited to differences in development time for *Ae. triseriatus, Ae. aegypti, and Armigeres subalbatus,* and survival of *Ae. albopictus.* Alto et al. (2005) tested the same hypothesis with varying densities of *Ae. albopictus* to directly test effects of litter treatment and competition. They found that although elevated CO_2 litter did not influence *Ae. albopictus* population growth or survival, development time decreased with increasing larval density, which is consistent with other studies that have shown competition-induced decreases in mosquito fitness (e.g., Murrell and Juliano 2008, Leisnham et al. 2009, Leisnham and Juliano 2010). Numerous studies have shown that litter amount directly affects competitive effects on mosquito larvae, and increased litter input as a result of elevated CO_2 is expected to relax competition by increasing available food resources (Griswold and Lounibos 2005). However, high amounts of litter may cause resource inhibition and toxicity because of increased tannins (Mercer 1993, Sota 1993, Mercer and Anderson 1994) or microbial blooms that coat the

water surface and prevent the larvae from breathing (Yee and Juliano 2006). Species-specific tolerances to these effects may alter the composition of mosquito communities in container systems. Although there is evidence for species-specific impacts on the development and survival of mosquitoes because of elevated CO_2 and competition-induced effects on population growth rates, no studies have examined the effects of CO_2-induced changes in litter quantity and phytochemistry on community composition.

Aedes albopictus, the Asian tiger mosquito, invaded the continental United States in the mid-1980s (Juliano and Lounibos 2005). Since then, it has spread throughout the southeastern United States and has become one of the most common human-biting mosquitoes in its new range (Juliano and Lounibos 2005). *Aedes albopictus* uses natural (e.g., tree holes, plant axils) and human-made (e.g., buckets, used tires) water-holding containers where it often co-occurs and competes for food with the native congener *Ae. triseriatus* in the eastern United States. Past laboratory and field studies show that *Ae. triseriatus* is competitively inferior to *Ae. albopictus* (e.g., Livdahl and Willey 1991, Teng and Apperson 2000, Aliabadi and Juliano 2002). Despite its competitive inferiority, *Ae. triseriatus* has persisted during the spread of *Ae. albopictus* and even remains the dominant mosquito in some areas (Lounibos et al. 2001). It is possible that a superior tolerance of *Ae. triseriatus* to tannins compared with *Ae. albopictus* may foster its coexistence with *Ae. albopictus,* but this has not been tested. *Aedes albopictus* and *Ae. triseriatus* are of medical importance. *Aedes albopictus* is a competent vector for West Nile virus (family *Flaviviridae*, genus *Flavivirus*, WNV), dengue (family *Flaviviridae*, genus *Flavivirus*, DENV), eastern equine encephalitis (family *Togaviridae*, genus *Alphavirus*, EEEV), and La Crosse encephalitis (family *Bunyaviridae*, genus *Orthobunyavirus*, LACV), and *Ae. triseriatus* is the principal vector for La Crosse encephalitis (Calisher 1994, Ibañez-Bernál et al. 1997, Gerhardt et al. 2001, Turell et al. 2005). Thus, it is important to understand how global changes, such as alterations to atmospheric CO_2 from fossil-fuel burning and land use changes, affect *Aedes* communities.

The objective of this study was to determine if increased litter production and altered phytochemistry because of elevated atmospheric CO_2 would affect resource competition between *Ae. albopictus* and *Ae. triseriatus* and relative abundances of each species. Decreasing litter quality is expected to suppress microbial growth, intensify interspecific competition, and promote increased competitive dominance of the invader *Ae. albopictus* over the native *Ae. triseriatus.* In contrast, higher litter production with elevated atmospheric CO_2 is expected to increase container food resources and relax interspecific resource competition, thus fostering coexistence between *Ae. triseriatus* and *Ae. albopictus.* However, we may expect excessive litter inputs or increased foliar tannins to alter community composition because of differential toxicity tolerances of *Ae. albopictus* and *Ae. triseriatus.*

Methods and Materials

Tree Growth, Leaf Production, and Leaf Chemistry. Thirty 3-yr-old *Quercus alba* L. (white oak) saplings were grown in two identical environmental growth chambers (model no. M40, Environmental Growth Chambers, OH) with mean ($\pm$ SD) atmospheric CO_2 concentrations of 388 ± 39 ppm (ambient) and 878 ± 113 ppm (elevated) over a 6-mo growing season. Saplings were grown in 6.25-gal black plastic pots in Sun Gro Sunshine Professional Growing Mix (Sun Gro Horticulture, Bellevue, WA). These pots were sized much larger than original root volume with the goal of minimizing potting effects on plant growth and nutrient or water relations. The height and stem diameter of each sapling was measured for 15 randomly selected plants in each of the two chambers. Both chambers were set 26°C nighttime and 14°C daytime temperatures, and a photoperiod of 14:10 (L:D) h to mimic summer conditions. Commercial fertilizer (Miracle-Gro; 12–4-8, N-P-K, The Scotts Company LLC, OH) was applied weekly to each sapling over the duration of the growing season. Each sapling received a total of 2.6 g of N over the growing season (0.1 g of N per week over 26 wk). Pots were rotated systematically within each chamber weekly to account for any within-chamber environmental gradients. Because we lacked the facilities to replicate CO_2 across multiple chambers, we switched trees and CO_2 treatments between chambers 3 mo into the growing season to minimize any chamber effects. We also confirmed by multivariate analysis of variance (MANOVA) (SAS Institute 2004) that light intensity (μmol m^{-2}s^{-1}), relative humidity (percent), and temperature (°C) were consistent between the two chambers and that overall interchamber variation was almost entirely because of CO_2 with little variation because of the other factors (results not shown for brevity). This assumption often is made in analyses of treatment effects (e.g., temperature, CO_2) in chamber experiments on vegetation and insects (e.g., Rueda et al. 1990; Teng and Apperson 2000; Alto and Juliano 2001a,b; van Heerwaarden et al. 2005). Five saplings grown under elevated atmospheric CO_2 were eliminated from the study during the growing season because they exhibited visible signs of being root-bound or iron deficient. By eliminating these trees, we retained only trees that appeared to be uninhibited by potting.

Five months after being placed in the chambers, the height and stem diameter of each sapling were re-measured and the total number of leaves on three randomly selected saplings in each CO_2 treatment was counted. Ten fresh leaves were selected randomly from each sapling, measured for area by using a LI-3100C Area Meter (LI-COR Biosciences, NE), dried (>48 h at 40°C), and weighed. To estimate total leaf biomass for each sapling, mean leaf area was multiplied by the average number of leaves per tree in that treatment. Leaf senescence was induced by decreasing the temperature and daylength of both chambers in a stepwise fashion over 6 wk until all saplings were fully senesced. Leaves for each CO_2 treatment were collected, pooled, and dried (>48 h at 40°C) until analysis.

A LECO CHN-2000 instrument (Leco Corporation, MI) was used to analyze leaf chemistry for percent C and N of the pooled dry litter from all the trees, which totaled 15 ambient and 10 elevated samples.

Mosquito Competition Experiment. Microcosms consisting of 400-ml cups filled with 360 ml of deionized (DI) water were provisioned with 0.7 g of either ambient or elevated CO_2 leaf litter and inoculated with 100 μl of pond water to foster microbial colonization. All microcosms were placed in one Percival I-36VL growth chamber (Percival, Perry, IA) set at 24°C and a photoperiod of 14:10 (L:D) h to mimic summer conditions. After 4 d, one of 10 density combinations of newly hatched (<24 h) *Ae. albopictus* and *Ae. triseriatus* larvae (*Ae. albopictus: Ae. triseriatus:* 10:0, 20:0, 40:0, 10:10, 10:30, 20:20, 30:10, 0:40, 0:20, 0:10) were added to each microcosm to create a response surface design. Larvae were F_2-F_3 generation individuals of laboratory colonies synchronously hatched in a 0.3 g/liter nutrient (lacalbumin) mixture. Four replicates of each litter–density combination were intended, but because of egg availability, one extra 10:0 replicate and one less 0:10 replicate were established, thus yielding 57 microcosms with *Ae. albopictus* and 55 microcosms with *Ae. triseriatus.* Microcosms were rotated daily to control for any chamber effects and supplemented with the same amount and detritus type on days 14, 28, and 42 to mimic natural periodic inputs. Pupae were removed from the microcosms daily and placed in separate vials until eclosion. Eclosed adults were sexed and identified to species level, and had their dry mass and female wing lengths recorded.

Twelve additional microcosms of each litter treatment without mosquitoes (24 total microcosms) also were established to measure baseline water chemistry of litter treatments that were not confounded by mosquito activity. Three microcosms from each litter treatment were randomly selected and destructively sampled on days 0, 4, 7, and 21. From each microcosm, tannin–lignin concentration was measured from a 20-ml water sample by using a Hach colorimeter and TA-3 Test Kit (Hach Company, Loveland, CO). A second 20- ml sample was taken from each microcosm after homogenizing the water column, and used for serial dilution and plating on general microbiological media (Tryptone yeast extract [TYE] agar, Sigma-Aldrich Co., St. Louis, MO) determine the relative abundance of fast-growing, aerobic, heterotrophic bacteria. Samples from each microcosm were extracted by pipetting from the water column after homogenizing the water to give a standardized representation of bacteria abundance between litter treatments. Dry litter mass (>48 h at 50°C) was sieved using a 105-μm sieve and weighed to the nearest 0.1-g.

Litter Toxicity Experiment. To compare potential inhibition and toxicity effects of elevated and ambient litter on the two *Aedes* species, litter amounts were manipulated experimentally in an additional 64 microcosms. Sixteen treatment combinations were set up with four replicates of each treatment. Treatments consisted of microcosms provisioned with 0.7, 1.4, 2.8, or 5.6 g (0.252–2.016 g/liter) of leaf litter grown at

Table 1. Morphological characteristics of *Q. alba* trees grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations

Dependent variables	Ambient CO_2	Elevated CO_2	df	F	P
Leaf area (cm^2)	44.05 ± 2.10	59.58 ± 5.81	1, 23	8.39	**0.0081**
Leaf dry mass (g)	0.28 ± 0.02	0.49 ± 0.06	1, 23	15.58	**0.0006**
Number of leaves per tree	298.67 ± 70.20	365.00 ± 49.70	1, 4	0.59	0.4836
Change in height (cm)	14.65 ± 3.05	44.84 ± 7.59	1, 23	13.63	**0.0001**
Change in stem diameter (cm)	0.13 ± 0.02	0.37 ± 0.07	1, 23	10.06	**0.0037**

Values reported are means ± SE. Effects significant at experimentwise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.

either ambient or elevated CO_2 concentrations and cohorts of 10 newly hatched (<24 h) *Ae. albopictus* or *Ae. triseriatus* larvae (0.7–0.56 g per larva). Microcosms were inoculated with pond water, rotated daily, and censused for mosquito pupae in the same manner as the mosquito competition experiment. On day 10, pH and the dissolved oxygen were measured in each remaining microcosm by using a YSI Environmental pH 100 m and a YSI Environmental Dissolved Oxygen 55 m (YSI, Inc., Yellow Springs, OH). Microcosms were supplemented with the same litter amount and type on days 14, 28, and 42.

Tannic Acid Experiment. Commercial powdered tannic acid (LOT 085769, Fisher Scientific, Hampton, NH) was used to test the effects of tannic acid concentration on *Ae. albopictus* and *Ae. triseriatus.* Tannin powder was mixed into microcosms holding 360 ml of a 0.2 g/liter lactalbumin solution (LOT NO. 4292F, MP Biomedicals, LLC, Solon, OH) to create tannic acid concentrations of 0, 50, 100, 500, and 1,000 mg/liter. Ten newly hatched (<24 h) *Ae. albopictus* or *Ae. triseriatus* larvae were each added to four replicate microcosms at each concentration (20 total microcosms). Microcosms were inoculated with pond water, rotated daily, and censured for mosquitoes in exactly the same manner as the mosquito competition and toxicity experiments.

Statistical Analyses. Proportion survivorship, mean development time (days to eclosion; ♀ and ♂), and mean dry mass (♀ and ♂) were recorded for each species from each microcosm. These fitness parameters were used to estimate the finite rate of population growth for each species (λ', Juliano 1998):

$$\lambda' = \exp\left[\frac{\ln\left[(1/N_0)\sum_x A_x f(w_x)\right]}{D + \left[\sum_x x A_x f(w_x) \Big/ \sum_x A_x f(w_x)\right]}\right]$$

where N_0 is the initial number of females (assumed to be 50% per microcosm), x is the mean time to eclosion (measured in days), A_x is the mean number of females eclosing on day x, w_x is the mean body size on day x, and $f(w_x)$ is a function describing size dependent fecundity for each species, estimated from the mean wing length on day x, wx, of female mosquitoes (Livdahl and Sugihara 1984, Juliano 1998). The function for *Ae. albopictus* was $f(wx) = -121.240 + 78.02wx$, where wx is wing length (millimeters) (Lounibos et al.

2002). The function for *Ae. triseriatus* was $f(wx) =$ (one-half) $\exp[4.5801 + 0.8926(\ln wx)] - 1$ (Nannini and Juliano 1998). D is the mean days it takes for an adult mosquito to mate, bloodfeed, and oviposit, and is estimated at 14 d for *Ae. albopictus* (Lounibos et al. 2002) and 12 d for *Ae. triseriatus* (Nannini and Juliano 1998).

Linear models (PROC GLM; SAS Institute 2004) were used to test effects of CO_2 treatment, litter treatment, litter amount, time, or mosquito densities on sapling morphology and growth rate parameters, leaf chemistry, leaf decay, water chemistry, or mosquito λ' and fitness parameters. Mosquito densities, litter amount, tannin concentration, and time were all treated as continuous independent variables in analyses. To better approximate parametric assumptions of normality and homogeneity of variance, we square-root transformed bacterial abundance, $\log_{10}(x + 1)$-transformed *Ae. albopictus* λ' and *Ae. triseriatus* λ', and arcsine-square root (x + 0.5)–transformed *Ae. albopictus* and *Ae. triseriatus* survival from the mosquito competition experiment, $\log_{10}(x + 1)$-transformed λ' and arcsine-square root (x + 0.5)–transformed survival from the toxicity experiment, and arcsine square root (x + 0.5)–transformed survival from the tannic acid experiment. Some response variables still did not meet parametric assumptions despite transformation, for which we also tested for effects by using randomization models (Randomization-wrapper for SAS PROCs; Cassell 2011). Randomization models yielded the same significant effects as the parametric models, hence we report only parametric results. To compensate for a potential increase in experiment wise type I error rate because of running linear models for multiple dependent variables on the same experimental units, we used a sequential Bonferroni adjustment for tests for each model, with experimentwise $\alpha = 0.05$. However, we note that there is no consensus in the literature on whether or not to apply corrections for multiple tests or how to apply corrections (e.g., Huberty and Morris 1989, Moran 2003); thus, we report all *P* values so that the reader can interpret them as they are.

Results

Tree Growth, Leaf production, and Leaf Chemistry. Trees grown in elevated atmospheric CO_2 exhibited greater increases in height and stem diameter and higher leaf area and mass, but no difference in numbers of leaves, than trees grown in ambient atmo-

Table 2. Leaf chemistry of *Q. alba* litter grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations

Variables	Ambient CO_2	Elevated CO_2	df	F	P
Total carbon (%)	46.58 ± 0.161	47.29 ± 0.256	1, 23	6.05	0.0218
Total nitrogen (%)	1.20 ± 0.077	1.19 ± 0.070	1, 23	0.01	0.9320
C:N	40.57 ± 2.14	41.02 ± 2.68	1, 23	0.02	0.8970

Values reported are means ± SE. Effects significant at experiment-wise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.


Fig. 1. Tannin concentration (A), bacterial abundance (colony forming units, CFU/ml) (B), and percentage litter decay (C) of *Q. alba* leaf litter grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations over time. Day 0 corresponds to when mosquitoes were added. Values plotted are means ± SE. Bacterial abundance represents back-transformed values. Absence of error bars indicates that SE was smaller than symbol.

spheric CO_2 (Table 1). Leaf chemistry did not differ between elevated and ambient litter (Table 2). Water tannin concentrations and litter decay rate were higher, but bacteria abundance was lower, in microcosms provisioned with elevated-CO_2 litter than in microcosms provisioned with ambient-CO_2 litter (Table 3; Fig. 1).

Mosquito Competition Experiment. *Aedes albopictus* had higher λ' than *Ae. triseriatus* across all heterospecific and conspecific densities and with both litter treatments (Fig. 2), indicating that *Ae. albopictus* had consistently higher population growth rates. However, there was no evidence that litter treatment moderated the effects of competition on λ' or any individual fitness parameters, or that heterospecific and conspecific densities had any overall effects on λ' or survival (Table 4; Fig. 2). Heterospecific and conspecific densities decreased female *Ae. albopictus* mass, whereas conspecific density increased female *Ae. albopictus* development time and heterospecific density increased female *Ae. triseriatus* development time (Table 4; Fig. 2).

Litter Toxicity Experiment. Linear models testing the effects of litter amount, litter treatment, and species showed nonsignificant two- and three-way interactions (Table 5). Litter treatment also did not affect λ' or any individual fitness parameter (Table 5). Finite rate of population growth (λ') and survival, however, decreased as litter amount increased (Table 5; Fig. 3). *Aedes albopictus* had higher survival than *Ae. triseriatus* (Fig. 3), which had complete mortality at 5.6-g litter. Female mass was unaffected by litter amount, litter treatment, or species (Table 5). Elevated-CO_2

Table 3. Linear model results for tannin-lignin concentration (mg/liter), bacterial abundance (colony forming units, CFU/ml), and proportion litter decay over time in microcosms provisioned with 0.7 g of *Q. alba* leaf litter grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations

Source		Tannin–lignin		Bacteria		Proportion litter decay	
	df	F	P	F	P	F	P
Litter treatment	1	70.68	**<0.0001**	4.89	0.0419	11.53	**0.0029**
Day	3	6.73	**0.0038**	2.95	0.0642	189.42	**<0.0001**
Litter × day	3	2.05	0.1470	0.07	0.9758	4.39	0.0727
Error	16						

Effects significant at experimentwise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.

litter ($F_{1,57} = 4.32$, $P = 0.0422$) and increasing litter amount ($F_{1,57} = 11.22$, $P = 0.0014$) reduced water pH (Fig. 4), but there was no litter treatment × amount interaction ($F_{1,57} = 0.08$, $P = 0.7751$). Dissolved oxygen decreased with increasing litter amount ($F_{1,57} = 32.26$, $P < 0.0001$; Fig. 4) but was unaffected by litter treatment ($F_{1,57} = 0.41$, $P = 0.5221$) or the litter treatment × litter amount interaction ($F_{1,57} = 0.04$, $P = 0.8468$).

Tannic Acid Experiment. No *Ae. albopictus* or *Ae. triseriatus* survived 500 mg/liter or 1,000 mg/liter tannic acid (Fig. 5), and we removed these concentrations from analyses. *Aedes albopictus* had higher λ' and survival than *Ae. triseriatus*, but the concentration × species interaction was nonsignificant (Table 6; Fig. 5). Tannic acid concentration from 0 to 100 mg/liter had no effect on λ' or individual fitness parameters (Table 6; Fig. 5).

Discussion

This study showed that litter treatment did not moderate the effect of competition on λ' or any in-
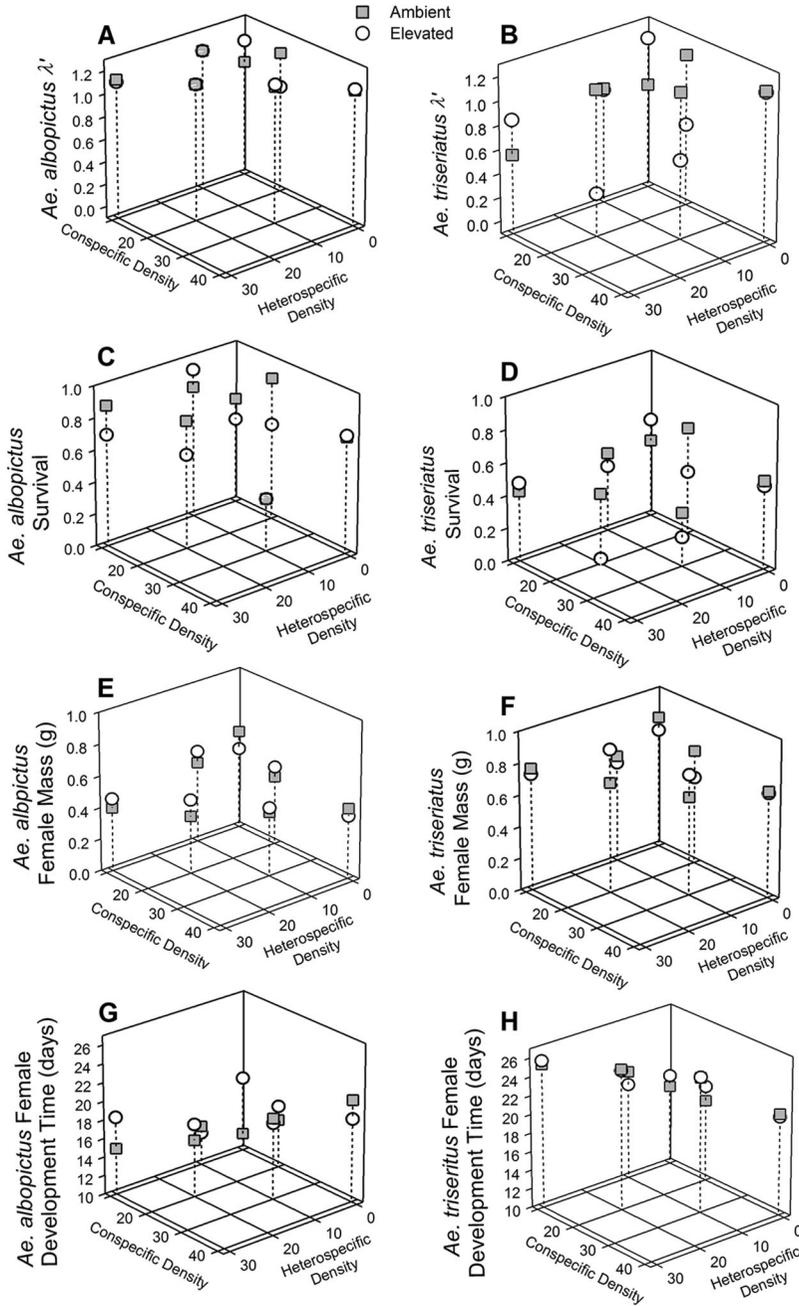
Fig. 2. Effects of heterospecific and conspecific larval densities and litter treatment on λ' (A and B), survival (C and D), female mass (E and F), and female development time (G and H) of *Ae. albopictus* and *Ae. triseriatus*. Values plotted are means. λ' and survival represent back-transformed values. Error bars are removed for clarity.

dividual fitness parameters of either *Ae. albopictus* or *Ae. triseriatus.* Our prediction of increased competition with litter grown under elevated atmospheric CO_2 is based on altered photochemistry, subsequent reduction in litter quality, and increases in toxicity. In general, litter decomposition is positively related to N, which can increase microbial (likely fungal) groups that digest leaf material (Cotrufo et al. 1995, Kaufman

and Walker 2006, Liu et al. 2009). Nitrogen is also negatively related, likely more weakly, to carbon-based secondary metabolites that may suppress microbial activity (Mercer and Anderson 1994, Schimel et al. 1996, Tuchman et al. 2003). In this study, there was no evidence of litter differences in overall C, N, or C:N. Interestingly, however, litter produced under elevated CO_2 leached higher tannin concentrations

Table 4. Linear model results testing effects of mosquito densities and litter treatment on λ' and individual fitness parameters of *Ae. albopictus* and *Ae. triseriatus* in microcosms provisioned with *Q. alba* leaf litter grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations

	λ'			Survival			Female mass			Female development time		
	df	F	P	df	F	P	df	F	P	df	F	P
Aedes albopictus												
Conspecific density	1	0.84	0.3640	1	2.35	0.1313	1	15.93	**0.0002**	1	28.83	**<0.0001**
Heterospecific density	1	2.16	0.1476	1	0.02	0.8764	1	10.33	**0.0023**	1	3.25	0.0774
Litter treatment	1	0.10	0.7511	1	0.53	0.4683	1	0.14	0.7109	1	7.56	0.0084
Conspecific × litter	1	0.22	0.6437	1	0.09	0.7592	1	0.03	0.8586	1	6.62	0.0132
Heterospecific × litter	1	1.01	0.9064	1	0.06	0.8027	1	2.66	0.1093	1	0.22	0.6448
Error	51			51			49			49		
Aedes triseriatus												
Conspecific density	1	0.34	0.5616	1	1.42	0.2396	1	1.15	0.2898	1	7.38	0.0101
Heterospecific density	1	2.09	0.1543	1	3.87	0.0548	1	0.15	0.7037	1	47.73	**<0.0001**
Litter treatment	1	0.42	0.5186	1	0.01	0.9250	1	1.55	0.2213	1	0.53	0.4716
Conspecific × litter	1	1.87	0.1774	1	0.60	0.4408	1	1.23	0.2744	1	0.38	0.4272
Heterospecific × litter	1	0.32	0.5734	1	0.26	0.6116	1	1.36	0.2506	1	0.64	0.5404
Error	49			49			36			36		

Effects significant at experimentwise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.

than ambient-CO_2 litter but had higher decomposition rates. These results suggest that increased tannins appear to be insufficient to overcome no changes in N to mediate changes in litter decomposition, microbial abundance, and effects of resource competition on *Ae. albopictus* and *Ae. triseriatus.*

Past studies on senesced *Quercus* (oak) litter also have shown no effects on phytochemistry after doubling atmospheric CO_2 concentrations over ambient concentrations (Strand et al. 1999, Alto et al. 2005). In this study, we exposed *Q. alba* to a higher mean elevated CO_2 concentration than these prior studies (878 ppm), which is expected under worst case, but increasingly likely, climate scenarios, and which may already be experienced by trees in some urban areas (Tomoda et al. 1997). Thus, the lack of change in *Q. alba* litter chemistry found in this study are consistent with what we may expect from oak responses to elevated CO_2 in nature. Effects of elevated CO_2 in senesced litter are generally less consistent among species than living leaves, probably because of species-specific variation in nutrient reabsorption during senescence. *Quercus* species are among the most common trees throughout eastern United States (Brown

and Brown 1972), common sources of senesced litter in containers (Yee and Juliano 2006), and have been used regularly in prior mosquito competition studies (Juliano 2010). However, a range of plant species can provide both senesced and living leaves to containers, indicating that future research is warranted on the effects on *Aedes* competition of different senesced and living litter species that may vary in their phytochemical responses to elevated CO_2.

In this study, *Q. alba* grown in elevated atmospheric CO_2 produced larger leaves than *Q. alba* grown in ambient CO_2. The finding in this study of higher leaf biomass with increasing CO_2 is consistent with numerous past studies showing large increases in foliar biomass with elevated CO_2 (Körner 2006, Taub and Wang 2008). Nutrients are usually limiting in container habitats (Fish and Carpenter 1982, Leisnham et al. 2009), and we may expect higher litter inputs with increasing atmospheric CO_2 to relax competitive effects on *Aedes* communities. Larval densities and litter amounts used in this study were based on natural and artificial containers surveyed in Maryland (P.T.L., unpublished data), findings from past studies that show naturally occurring resource levels in tree holes

Table 5. Linear model results testing effects of leaf litter amt, litter treatment, and mosquito species on λ' and individual fitness parameters of *Ae. albopictus* and *Ae. triseriatus* in microcosms provisioned with *Q. alba* leaf litter grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations

	λ'			Survival			Female mass			Female development time		
	df	F	P	df	F	P	df	F	P	df	F	P
Litter amount	1	19.18	**<0.0001**	1	37.71	**<0.0001**	1	0.17	0.6830	1	4.42	0.0431
Litter treatment	1	0.00	0.9521	1	5.37	0.0241	1	0.01	0.9244	1	3.52	0.0694
Mosquito species	1	6.72	0.0121	1	27.17	**<0.0001**	1	2.47	0.1257	1	7.98	0.0078
Litter amount × litter treatment	1	0.46	0.5018	1	0.55	0.4628	1	2.16	0.1510	1	0.45	0.4455
Litter amount × species	1	1.04	0.3112	1	1.20	0.2774	1	0.03	0.8664	1	0.14	0.1445
Litter treatment × species	1	0.07	0.7981	1	1.93	0.1699	1	0.68	0.4161	1	0.95	0.9456
Litter amount × litter treatment × species	1	0.15	0.7006	1	1.01	0.3197	1	1.50	0.2298	1	0.77	0.7686
Error	56			56			34			34		

Effects significant at experimentwise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.
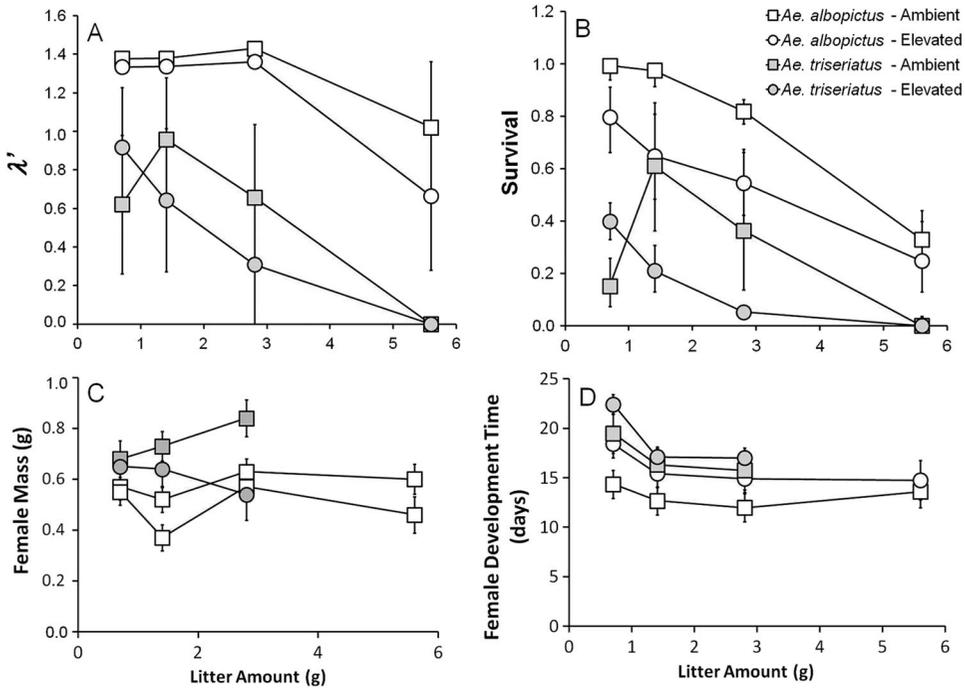
Fig. 3. Effects of *Q. alba* litter amounts grown in ambient or elevated atmospheric CO_2 on λ' (A), survival (B), female mass (C), and female development time (D) of *Ae. albopictus* and *Ae. triseriatus*. Values reported are means $\pm$ SE λ' and survival represent back-transformed values.
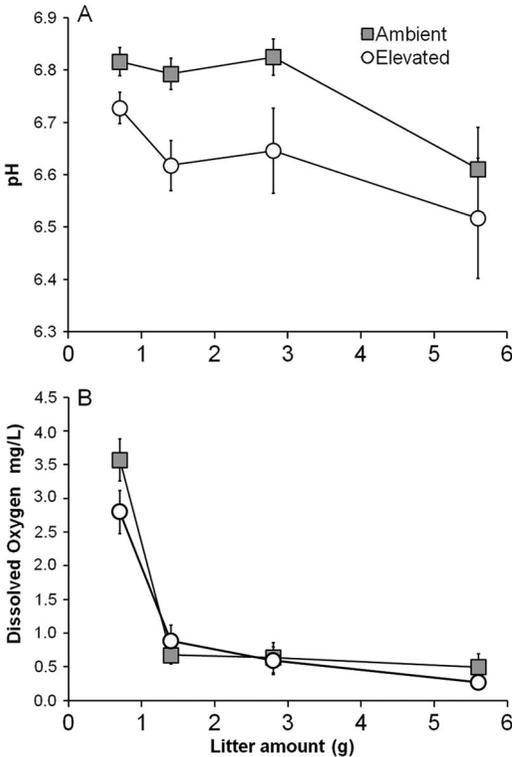

Fig. 4. Effects of *Q. alba* litter amounts grown in ambient or elevated atmospheric CO_2 on pH (A) and dissolved oxygen (B) of microcosm leachate. Values reported are means $\pm$ SE.

(Walker et al. 1991), and other competition studies that have elicited resource competition among *Aedes* (Leisnham et al. 2009). Based on the results of this study, global increases in atmospheric CO_2 may be expected to increase average production of *Q. alba* litter and available container food, and likely promote population growth among *Aedes* mosquitoes, but would not contribute to shifts in the outcome of competition between *Ae. albopictus* and *Ae. triseriatus.*

The effects of competition on female mass or development time were not strong enough to produce detectable negative effects on population growth rates, likely because they were buffered by the effects of competition on survival. Finite rate of population growth (λ') is influenced strongly by survival (Juliano 1998), a fitness parameter for which we found no significant negative effects on either *Ae. albopictus* or *Ae. triseriatus.* The observed negative effects of competition on body size and development time may enable individuals to reduce risk of death in poor conditions, and therefore may serve to buffer negative effects on survival, which is the variable most likely to determine population growth. However, our finding of consistently higher *Ae. albopictus* λ' than *Ae. triseriatus* λ' under conditions of resource competition (and toxicity) still suggests competitive asymmetry in favor of *Ae. albopictus.* Higher λ' is likely because of superior foraging ability and physiological efficiency of using harvested food to support survival and reproduction (Tilman 1982). These characters are likely to confer strong competitive ability when resources are
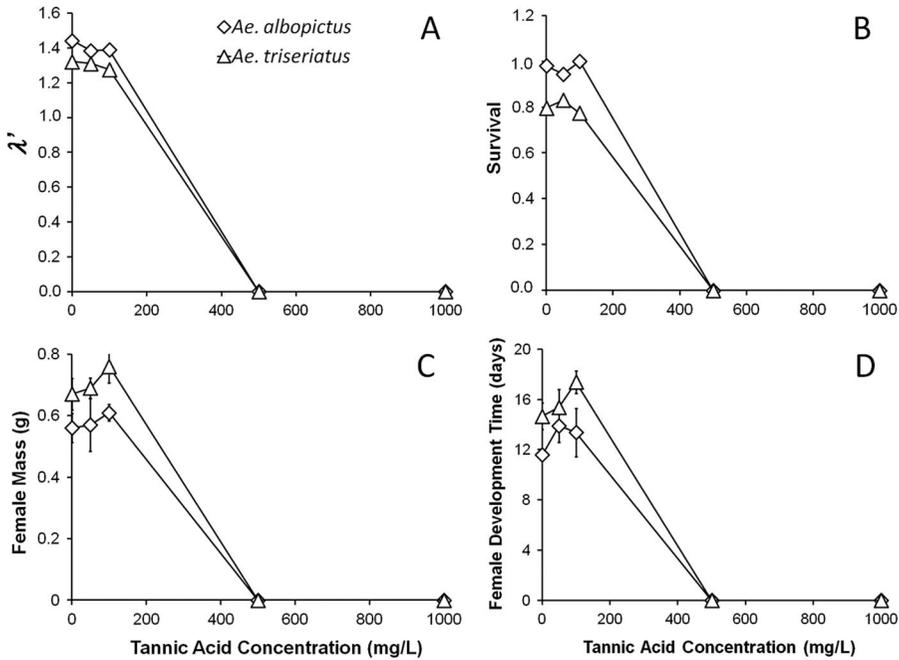
Fig. 5. Effects of tannic acid concentrations on λ' (A), survivorship (B), female mass (C), and female development time (D) of *Ae. albopictus* and *Ae. triseriatus*. Values reported are means $\pm$ SE λ' and survival represent back-transformed values. Absence of error bars indicates that SE was smaller than symbol.

scarce and, consistent with prior studies, we may expect *Ae. albopictus* to be a superior competitor in conditions of more limiting food resources (e.g., Livdahl and Willey 1991, Teng and Apperson 2000, Aliabadi and Juliano 2002).

Based on models of resource competition (Tilman 1982, Grover 1997), we expect that population growth rates should be related to resource availability as a hyperbolic function. However, although this may be true for terrestrial plant systems, resource inhibition and toxicity may be common in ephemeral aquatic habitats, such as natural and artificial containers. Negative responses of mosquito population growth to high concentrations of litter detritus have been observed in past studies (Yee and Juliano 2006; E. Murrell, Illinois State University, unpublished data). Such effects may be a result of increased tannins, microbial blooms, or both that coat the water surface and prevent the larvae

from breathing. In this study, complete mortality of *Ae. albopictus* and *Ae. triseriatus* occurred at >100 mg/liter. Tannin-lignin and total phenolic concentrations have been found to vary widely among tree holes (Sota 1993: 2.5–109.2 mg tannin–lignin/liter, Mercer and Anderson 1994: 36–268 mg total phenolics/liter), and tannic acid probably commonly approaches and sometimes exceeds 100 mg/liter in the field. Finite rate of population growth (λ') for both *Ae. albopictus* and *Ae. triseriatus* also decreased similarly with increasing litter amounts above 0.7-g litter per 360-ml water. Although litter concentrations used in this study were based on natural and artificial containers surveyed in Maryland, detritus (mainly leaf litter) concentrations in artificial containers have been found to exceed 7.0 g/liter in as little as 10 d (E. Murrell, Illinois State University, unpublished data), and may accumulate as rapidly as 0.11 g/d in tree holes (Yee et al. 2007). These

Table 6. Linear model results testing effects of tannic acid concentrations from 0 to 100 mg/liter on λ' and individual fitness parameters of *Ae. albopictus* and *Ae. triseriatus* in microcosms provisioned with *Q. alba* leaf litter grown under ambient (388 ± 39 ppm) or elevated (878 ± 113 ppm) atmospheric CO_2 concentrations

	df	λ'		Survival		Female mass		Female development time	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Tannic acid concentration	1	5.58	0.0284	0.32	0.8653	2.50	0.1295	2.26	0.0564
Species	1	15.77	**0.0008**	10.04	0.0217	1.71	0.2052	3.36	0.0374
Tannic acid × species	1	0.02	0.8800	0.13	0.9752	0.17	0.6880	0.14	0.6149
Error	20								

Effects significant at experimentwise $\alpha = 0.05$ (sequential Bonferroni) are shown in bold.

results indicate that resource inhibition and toxicity effects may be common in some container habitats, and that these effects are likely to become more pronounced in systems that experience increasing atmospheric CO_2 because of greater litter production. In this study, *Ae. albopictus* had a consistently higher λ' than *Ae. triseriatus* when provisioned with either elevated-CO_2 or ambient-CO_2 litter and across all litter amounts, which indicates no evidence that the coexistence of the native tree hole mosquito with *Ae. albopictus* is facilitated by an increased tolerance to tannins. Sota et al. (1993) showed that *Ae. albopictus* was more tolerant to commercial tannic acid and higher litter concentrations than the common tree hole breeding *Aedes riversi* Bohart and Ingram. Although *Ae. albopictus* is known to use artificial containers in urban areas rather than tree holes in forested sites, there is no evidence that it is more vulnerable to tannin concentrations. This result is likely because leaf litter also constitutes the main source of detritus in artificial containers in urban environments. It is possible that litter may even constitute a higher proportion of detritus in urban containers because of lower inputs of dead terrestrial invertebrate carcasses (Daugherty et al. 2000).

This is the first study to test the effects of altered phytochemistry and increased resource production because of elevated atmospheric CO_2 on the population performances of co-occurring mosquitoes and on the invasion success and ecological impacts of an exotic species. We found minimal evidence that litter grown under elevated CO_2 will affect competition among *Ae. albopictus* and *Ae. triseriatus*, but that increases in the amount and inputs of senescent leaf biomass may increase population growth rates of both species, as long as tannin concentrations remain under concentrations. However, effects of elevated CO_2 on primary consumers are likely to vary depending on specific plant species and consumer communities involved. For ephemeral container communities, which are likely to be particularly sensitive to changes in litter quality and inputs, elevated CO_2 may variably alter competitive interactions and community composition among systems. This variable effect has the potential to facilitate species coexistence or displacement in some systems, and thus merits further investigations on a greater range of plant and mosquito species.

Acknowledgments

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