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Nutritional quality of leaf detritus altered by elevated atmospheric CO_2: effects on development of mosquito larvae

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SUMMARY

1. *Populus tremuloides* leaf litter was produced under elevated (ELEV = 720 ppm) and ambient (AMB = 360 ppm) atmospheric CO_2 conditions. Leaf chemical quality was significantly altered by CO_2 enrichment. ELEV leaves had significantly higher concentrations of phenolic compounds and lignins, and higher C : N ratios than AMB.

2. Leaf litter was incubated in a headwater stream for 14 days to become colonised by microorganisms; aquatic bacterial productivity was significantly lower on ELEV than on AMB leaf litter. Colonised leaves were fed to four species of detritivorous mosquito larvae to assess their survivorship and development rates.

3. Larval mortality was 2.2 times higher for *Aedes albopictus* fed ELEV litter when compared with AMB. Although mortality of *A. triseriatus*, *A. aegypti* and *Armigeres subalbatus* was not affected by treatment, larval development rate was delayed by 78, 25 and 27%, respectively, when fed ELEV litter.

4. Increased mosquito mortality and/or delayed larval development rates are more likely to have negative implications for food web structure and productivity in ecosystems where immature stages of mosquitoes are an important food source of predators.

Keywords: atmospheric CO_2, C : N, leaf detritus, mosquito larvae, phenolic compounds

Introduction

Atmospheric carbon dioxide levels are presently accumulating at their highest rate (16% over the last 40 years) and global concentrations are expected to double from the present concentration of about 360 ppm, within the next 50–75 years (Keeling & Whorf, 1999). Direct effects of CO_2 enrichment on terrestrial plants include higher photosynthetic and growth rates and subsequent alteration of the chemical composition of the leaves (e.g. Strain & Bazaaz, 1983; Wetzel & Grace, 1983; Curtis *et al*., 1996). Higher carbon fixation rates typically result in the production of additional carbohydrates and secondary compounds including phenolic compounds, lignin and condensed tannins (Lambers, 1993). Increased carbohydrates, along with a general reduction of N (Williams *et al*., 1986; Curtis, Drake & Whigham, 1989; Norby *et al*., 1992), can result in increased C : N ratios of leaf tissues. Such changes in leaf chemical quality typically result in increased consumption rates (compensatory consumption) and reduced food assimilation efficiencies, which ultimately translates into reduced growth and survivorship by leaf feeding terrestrial insects (e.g. Lindroth, 1996a,b; and review by Bezemer & Jones, 1998).

Plant detritus from terrestrial floodplain and littoral sources constitutes up to 99% of the organic material

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that fuels biotic metabolism in most headwater streams (e.g. Minshall, 1967; Fisher & Likens, 1973) and many lake ecosystems (Wetzel, 1995, 2001). Aquatic microbial and detritivore utilisation of terrestrially derived leaf litter is highly dependent on the concentrations of leaf nitrogen and carbon-based secondary compounds of the detritus. In general, leaf species high in nitrogen (e.g. alder) decompose quickly when compared with leaves of species such as oak and magnolia that are lower in N and high in secondary compounds (e.g. Peterson & Cummins, 1974). If the nutritional quality of leaf litter grown under elevated CO_2 conditions decreases, the colonisation and utilisation of the leaf litter by aquatic microorganisms should be affected.

Mosquito larvae typically inhabit still waters including wetlands, ponds, backwater pools of streams, rivers and floodplains and tree holes where, with the exception of some predatory species, they generally consume plant detritus particles and associated bacteria (Walker, Olds & Merritt, 1988; Walker *et al.*, 1991; Merritt, Dadd & Walker, 1992). Mosquitoes are ubiquitous insects that occur in wet habitats from the tropics to the tundra. Their prevalence in some ecosystems makes them important because their large population sizes and multiple cohorts throughout the growing season render larval mosquitoes a significant food resource for aquatic macroinvertebrates, fish and amphibians. Mosquito adults also provide food to avian insects, birds and bats.

In this study, trembling aspen (*Populus tremuloides* Michaux) leaf litter was produced under ambient (AMB = 360 ppm) and elevated (ELEV = 720 ppm) atmospheric CO_2 conditions and the chemical composition of both groups of leaves was determined. Leaf litter was microbially colonised in a stream for 14 days, ground into fine particles and bacterial productivity was measured. The ground leaf litter was fed to four species of detritivorous mosquito larvae where subsequent differences in larval survivorship and development rates were assessed. Our specific hypotheses were: (1) leaf litter produced under ELEV CO_2 conditions would have lower nutritional quality (i.e. higher C : N, total phenolic compounds and lignin, and lower bacterial productivity) than control leaves and (2) utilisation of the leaf litter by larval mosquitoes would result in higher mortality and slower development rates.

Methods

Production of aspen litter in ELEV atmospheric carbon dioxide

In order to determine the effect of ELEV concentrations of atmospheric CO_2 on leaf litter phytochemistry, *P. tremuloides* trees were grown under both ELEV (720 ppm; ELEV treatment) and AMB (360 ppm; AMB treatment) atmospheric CO_2 conditions at the University of Michigan Biological Station (UMBS) in northern lower Michigan (45°34′N, 84°40′W). *Populus tremuloides* was chosen because it is the most abundant tree species in Michigan (Schmidt, Spencer & Bertsch, 1993), accounting for a significant contribution (22%) of the litter entering the East Branch of the Maple River, a third order stream near UMBS (45°32′N, 84°45′W; Tuchman, unpublished data). Clear plastic open-top chambers ($0.7 \times 0.7 \times 2$ m; Curtis & Teeri, 1992) were placed over 16 cloned 4-year-old saplings of *P. tremuloides* planted in open bottom root boxes containing a premixed soil homogenate of 80% native Rubicon sand amended with 20% locally derived Kalkaska series topsoil to provide minimal nutrients. CO_2 partial pressure was elevated in eight of the 16 experimental chambers via manually adjusted flowmeters that dispensed 100% CO_2 into chamber input blower fans allowing for equal diffusion of CO_2 throughout the chamber (Curtis & Teeri, 1992). Chamber gas concentrations were monitored continuously in eight ELEV chambers and one AMB chamber by an infrared gas analyzer (LiCor Inc. model LI-6252; Lincoln, NE, USA) that logged data into a personal computer.

Trees were treated with CO_2 enrichment from May until leaf senescence in November 1998. During the treatment period, all aspens were watered twice weekly or more often if needed. Throughout autumnal leaf abscission, leaves were collected on a daily basis, air dried and stored in airtight containers for both chemical analyses and use in microbial and detritivore experimental trials.

Leaf litter chemical analyses

Phytochemical differences between AMB and ELEV leaf litter were determined for senesced abscised leaves and senesced leaves that were incubated in the East Branch of the Maple River for 14 days. The incubated leaves incorporated chemical changes as a

result of leaching and microbial colonisation providing leaf litter in a form appropriate as food for mosquitoes. The following parameters were measured on all leaves: per cent carbon and nitrogen measured on a Carlo-Erba Elemental Analyzer (Milan, Italy), lignin concentrations using the thioglycolic acid method (Dean, 1997) and total phenolics following the Folin–Denis assay (Swain & Goldstein, 1964).

Mosquito responses to ELEV and AMB-grown leaf litter

To study the indirect effects of leaf litter from plants grown in ELEV atmospheric CO_2 on mosquito larval survivorship and development rates, laboratory feeding experiments were conducted with four species of mosquitoes: *Aedes albopictus* (Skuse), *A. triseriatus* (Say), *A. aegypti* (Linneaus) and *Armigeres subalbatus* (Coquillett). Mosquitoes were selected as the aquatic detritivore because they are ecologically significant components of food webs of many ecosystems, their short life cycles are conducive to studying development from egg to pupae, they can be readily acquired in the egg stage and the eggs hatch simultaneously, permitting analyses of the development rates of a large cohort of individuals. These four species were selected because they are common aquatic detritivores, have been used in previous leaf litter studies, and are either common in Michigan streams, lakes, and wetlands, or are exotic, as in the case of *A. subalbatus*. *Armigeres subalbatus* is a Thailand mosquito and was selected to test the potential universality of mosquito responses to CO_2-altered leaf litter quality.

Mosquito experiments were conducted in the laboratory at room temperature. Ten larval chambers (plastic bins 30 × 20 × 12 cm) were filled with 2.0 L sterile filtered (0.2 μm) lake water and fresh water was added daily to compensate for evaporative losses and maintain constant volume. Mosquito eggs were acquired from the mosquito cultures of E.D. Walker at Michigan State University and from the insectarium of F. Collins and P.R. Grimstad at the University of Notre Dame. Eggs were hatched by submersing in deoxygenated water and first instar larvae began to appear within 60 min for all species. Equal numbers (between 85 and 100 depending on availability of viable eggs for each species) of first instar larvae were transferred to each chamber to produce low densities of 0.05–0.0425 organisms mL^{-1} to prevent growth inhibition from excretory accumulation within chambers (Dye, 1982).

As mosquito larvae graze actively on the bacteria that colonise fine-particulate organic matter (FPOM; <1.0 mm) detrital particles, 100 g of both ELEV and AMB-grown leaves were placed into 10 large bags (1.4 cm mesh size) and incubated in the East Branch of the Maple River in a 10 cm s^{-1} current for 14 days to become microbially colonised for use as food in the mosquito-feeding experiments. Ten additional mesh bags containing ELEV or AMB leaf litter were colonised for 14 days in the East Branch of the Maple River, then harvested and ground into FPOM for analysis of productivity of the colonised bacteria. Leaves were removed from the stream, placed in a Ziplock® bag (Racine, WI, USA) with stream water, placed in a cooler and immediately returned to the laboratory. After gently rinsing with stream water to remove macroinvertebrates, silt and FPOM, leaves were ground into FPOM particles using a Braun® micro food processor (Boston, MA, USA). A 0.5 g wet wt aliquot of colonised FPOM was placed into 10 mL sterile filtered (0.2 μm) stream water in sterile culture tubes, sonicated on ice for 30 s to remove bacteria from the leaf particle surfaces (Thomaz & Wetzel, 1995), and size fraction-filtered to remove leaf particles and retain bacterial cells. The remaining bacteria were incubated with 10 μL of 99.9 Ci $mmol\ L^{-1}$ ^{3}H-leucine for 1 h at stream temperature (15 °C). Bacterial productivity was estimated as the rate of ^{3}H-leucine uptake and incorporation into intracellular protein (Kirchman, 1993).

To each mosquito feeding chamber, 1000 mg of finely ground microbially colonised leaf litter was added to produce five replicates per treatment (five AMB and five ELEV), which provided each individual mosquito a ration level of 10.0–11.8 mg food, a quantity about 60 times greater than the average mass of fourth instar larvae (0.175 mg).

Larval development time was estimated as the mean number of days between hatching and pupation and larval survivorship as the proportion of individuals surviving to the pupal stage.

Statistical analyses

Differences between AMB and ELEV leaf chemistry (C : N ratios, lignin and total phenolic compounds) within senesced and microbially colonised leaves were

analysed using independent one-tailed *t*-tests where the null hypothesis tested was ELEV ≤ AMB (Systat 8). Two-tailed *t*-tests were used to measure differences in mosquito development rates and survivorship.

Results

Leaf litter chemistry and bacterial colonisation

The chemistry of *P. tremuloides* litter was significantly altered by growth in ELEV levels of atmospheric CO_2. Carbon-to-nitrogen ratios, total phenolic compounds and lignin concentrations were all significantly higher in ELEV senesced leaves than in AMB leaves (*t*-tests; $P < 0.05$, Table 1). Two weeks of leaching and microbial colonisation of leaf litter in the East Branch of the Maple River removed nearly all of the soluble phenolic compounds, half of the lignins and to a lesser degree lowered C : N in both AMB and ELEV leaves (Table 1). After 14 days in the stream, ELEV litter remained significantly higher in C : N and lignin content than AMB (*t*-tests; $P < 0.05$), but treatment differences in phenolic compounds were not conserved (retained) (*t*-test; $P > 0.05$; Table 1). Leaf litter that was incubated in the East Branch of the Maple River for 14 days also demonstrated differential colonisation by bacteria. Bacterial productivity was significantly lower on ELEV than on AMB leaf litter (*t*-tests; $P < 0.05$, Table 1).

Mosquito larval development on chemically altered leaf litter

Survival of *A. albopictus* larvae from first instar to pupation was significantly higher (2.2-fold) when grown on AMB than ELEV litter (*t*-test; $P < 0.01$; Fig. 1). *Aedes triseriatus*, *A. aegypti* and *A. subalbatus* larvae demonstrated no significant treatment effects for larval survival (*t*-test; $P > 0.05$; Fig. 1).

Larval development rate, measured as the mean number of days required to reach the pupal stage from hatched eggs, was significantly delayed in the ELEV treatment for three of the four species tested (Fig. 2). Development rates were 77.6% longer for ELEV *A. triseriatus* (AMB = 26.3 days, ELEV = 46.5 days; $P = 0.037$), 25% longer for *A. aegypti* (AMB = 37.1 days, ELEV = 48.1 days; $P = 0.00004$) and 26.5% longer for *A. subalbatus* (AMB = 32.8 days,

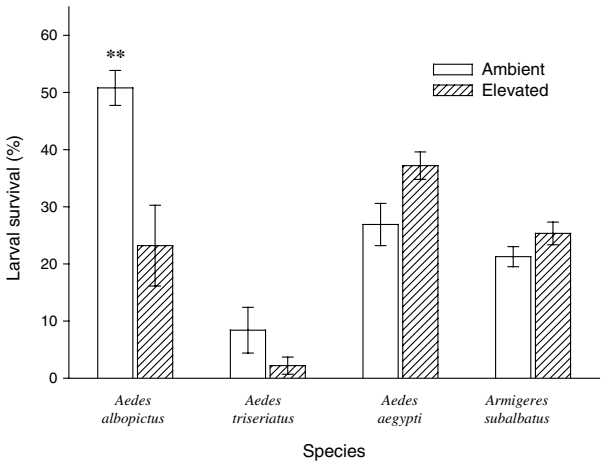

Fig. 1 Per cent survival of four species of mosquitoes from first instar larvae to the pupal stage when reared on *Populus tremuloides* leaf litter grown under ambient (360 ppm) and elevated (720 ppm) atmospheric CO_2 conditions. Values are expressed as mean ± 1 SE.

Table 1 Chemistry and microbial productivity estimates of *Populus tremuloides* leaf litter grown under ambient (360 ppm) or elevated (720 ppm) CO_2 conditions. Chemistry measurements are reported for senesced leaves and senesced leaves that were chemically leached and microbially colonised in the East Branch of the Maple River for 14 days (colonised). Bacterial productivity is reported for colonised leaves. Values reported as mean ($n = 5$ for lignin, $n = 12$ for C : N and total phenolic compounds, $n = 5$ for bacterial productivity) ±1 SE

Leaf condition	Analysis	360 ppm CO_2	720 ppm CO_2
Senesced	Lignin (mg g leaf dry mass^{-1})	55.7 ± 1.72	64.8 ± 2.44
	C : N	28.1 ± 1.03	56.1 ± 1.82
	% phenolics	3.42 ± 0.20	5.75 ± 0.28
Colonised	Lignin (mg g leaf dry mass^{-1})	24.5 ± 0.68	29.1 ± 0.71
	C : N	22.5 ± 0.89	42.1 ± 0.85
	% phenolics	0.49 ± 0.02	0.54 ± 0.02
Colonised	Bacterial productivity (CPM mg bacterial C^{-1})	96 ± 21	38 ± 11

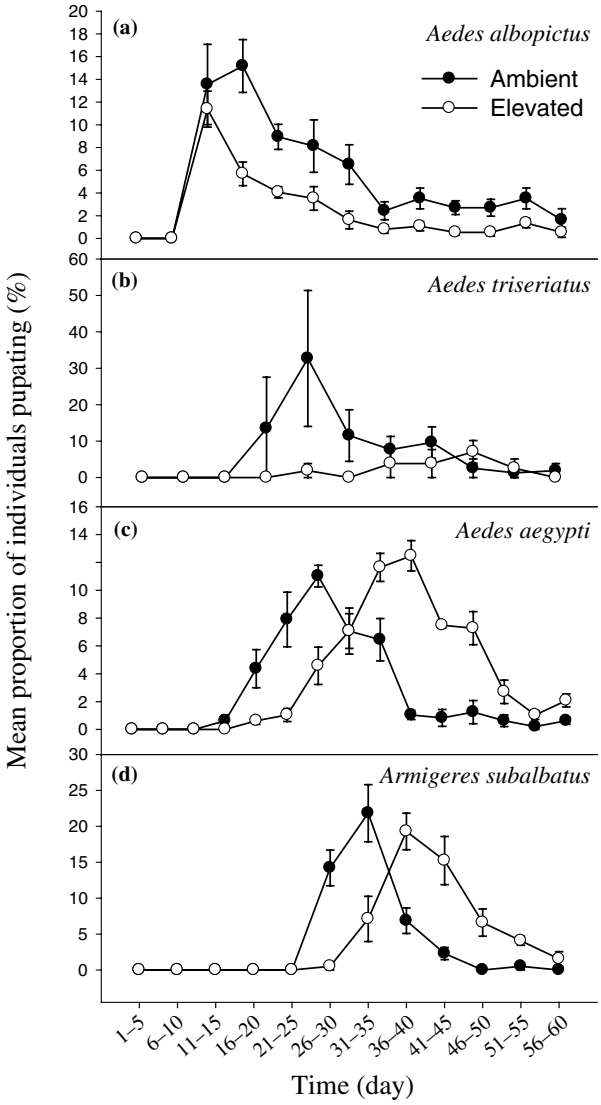

Fig. 2 Development rate of four species of mosquitoes from first instar larvae to the pupal stage when reared on *Populus tremuloides* leaf litter grown under ambient (360 ppm) and elevated (720 ppm) atmospheric CO_2 conditions. Values are expressed as the mean proportion of individuals pupating within a given 5-day increment (±1 SE) over the span of time required for >95% of the individuals to reach the pupal stage (ca. 60 days).

days, ELEV = 41.5 days; $P = 0.00003$) than their AMB counterparts (Fig. 2b–d).

Discussion

This study showed that increased atmospheric CO_2 leads to decreased nutritional quality of leaf litter from *P. tremuloides*. This reduction negatively affected bacterial productivity as well as survivorship and development times of certain detritus-feeding mosquito larvae. A substantial body of literature exists addressing the effects of food quality and quantity on the growth and development of detritivorous mosquitoes. For example, Fish & Carpenter (1982) demonstrated that rapidly decaying sugar maple litter supported greater biomass of tree-hole mosquito larvae than more refractory beech and black oak litters. Similarly, Lounibos, Nishimura & Escher (1993) demonstrated faster larval development in *A. triseriatus* when reared on flowers of oak trees versus oak leaf litter, a difference, which presumably was driven by differences in nutritional quality.

In the present study, increases in leaf lignin coupled with decreases in leaf nitrogen induced by ELEV CO_2 and subsequent lower bacterial productivity were probably responsible for decreases in survivorship and/or development rate of the four species of mosquitoes investigated. Not only were lignin and C : N ratios higher in senesced leaf litter that was grown under ELEV CO_2, but they were also higher for litter that was leached and microbially colonised in a stream for 2 weeks. These types of growth responses to natural differences among tree species in leaf litter nutritional quality have been well documented for aquatic decomposers and detritivores (e.g. Peterson & Cummins, 1974; Webster & Benfield, 1986; Stout, 1989; Ostrofsky, 1997). Typical 'low quality' plant species such as oak and conifers are relatively high in polyphenolic compounds including lignin and tannins, while species that exhibit lower concentrations of secondary compounds and relatively higher nitrogen contents tend to be more rapidly utilised by decomposing bacteria and detritivores (see review by Stout, 1989).

Detritus nutritional quality has a direct impact on the productivity of the microbial community that colonises its surfaces, which in turn defines its quality as a food resource to mosquitoes. Most mosquitoes are detritivores that browse on FPOM and the microorganisms associated with FPOM, leaf litter and other plant detritus (Ameen & Iversen, 1978) as well as filtering suspended bacteria from within the water column (Livdahl, 1982; Walker & Merritt, 1988). As bacteria associated with detritus improve the food quality of detritus for aquatic insects, Ward & Cummins (1979) categorised

nutritional quality of different detrital sources by the densities of their associated microbial communities. In that study, nutritional quality as measured by microbial mass on detritus was positively related to growth rates of larvae of the chironomid *Paratendipes albimanus*. Similarly, *P. tremuloides* leaves that were grown under CO_2 enrichment and incubated in a stream for 2–4 weeks demonstrated significantly lower (>50%) bacterial biomass-specific productivity (this study and Rier *et al.*, 2002) and subsequent utilisation of the leaves by tipulid crane fly larvae resulted in greatly reduced growth (Tuchman *et al.*, 2002). The combined effects of lower chemical nutritional value and lower biomass and productivity of bacteria colonising leaf litter produced a negative impact on aquatic macroinvertebrate detritivores in the present study and others (see reviews by Anderson & Sedell, 1979; Cummins & Klug, 1979).

Other studies that have examined the effects of ELEV CO_2 grown leaf detritus on mosquito detritivores have reported contrasting results. For example, Kaufman *et al.* (1995) and Strand *et al.* (1999) report that growth responses of microorganisms and *A. triseriatus* larvae to oak and birch leaf litter produced under ELEV CO_2 atmospheres were not related to CO_2 treatment effects.

Differences between this study and earlier ones may be largely a result of species-specific responses to leaf senescence. During leaf senescence, up to 50% of the soluble carbon and to a much lesser extent, nitrogen is resorbed back into the stem and roots of the tree prior to abscission (Chapin, Schulze & Mooney, 1990), decreasing the 'food quality' of the leaf litter for heterotrophic organisms. This resorption typically translates to a further increase in leaf C : N for senesced leaves that were produced under enriched CO_2 environments. However, this expected scenario is not always the rule (see review by O'Neill & Norby, 1996). Some studies demonstrate that the chemical differences observed between live-green AMB and ELEV CO_2-grown plants is not conserved after senescence (Hirschel, Korner & Arnone, 1997), while others clearly demonstrate that senescence exacerbates the difference in quality between AMB and ELEV CO_2 leaves as with *Fraxinus excelsior*, *Betula pubescens*, *Acer pseudoplantanus*, *Picea sitchensis* (Cotrufo, Ineson & Rowland, 1994) and *Scirpus olneyi* (Ball & Drake, 1997).

Ecological implications of ELEV CO_2 on mosquito populations

As the nutritional quality of the detritus of many species of plants may be altered by global increases in atmospheric carbon dioxide, the indirect impacts of an ELEV CO_2 atmosphere on mosquito larval survivorship and development time could potentially be great. Mosquitoes achieve high abundances in aquatic ecosystems globally. CO_2-induced effects on their survivorship and development time have ecological significance, especially in boreal and tundra habitats where mosquitoes are important members of aquatic and terrestrial food webs, and the growing season is brief. Longer larval development times could result in fewer cohorts of mosquitoes in these subarctic climates, reducing food availability to both aquatic and terrestrial mosquito predators.

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