EFFECTS OF ELEVATED CO_2 AND SHADE ON THE DECOMPOSITION OF SENESCED TREE FOLIAGE: IMPACTS ON MICROBIAL ACTIVITY

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Abstract: We examined microbial respiration and carbon/nitrogen content of decomposing leaf material in microcosms used for growth studies of the treehole mosquito, *Aedes triseriatus*. Leaf material originated from birch and oak trees exposed to conditions of shade/sun and elevated/ambient levels of CO_2. Microbial respiration as measured by CO_2 production was generally greatest on birch leaves grown under shaded conditions, however, ANOVA indicated possible light X CO_2 interactions. There were also strong interactions between species of leaf and CO_2 levels, but oak leaves grown under elevated CO_2 supported significantly higher microbial respiration rates than oak leaves grown in an ambient CO_2 atmosphere. Birch leaves grown under elevated CO_2 also generally supported higher rates of microbial respiration. However, light effects were much more pronounced and birch leaves grown under full sun and elevated CO_2 conditions supported relatively low microbial respiration. Microbial respiration varied inversely with leaf carbon:nitrogen ratio and directly with nitrogen content across treatments, however, initial carbon and nitrogen content of leaf material was not a consistent predictor of microbial respiration. In general, mosquito production paralleled microbial respiration, suggesting a tight link between the two trophic levels. These data indicate that interactions between available light and CO_2 on parent plant material could have variable, species-dependent effects on microorganisms and secondary consumers in aquatic, detritus-based systems.

INTRODUCTION

Most investigations of the potential effects of elevated atmospheric CO_2 levels on ecosystems have been directed toward plant growth in terrestrial environments. Repercussions from atmospheric perturbations, however, will also be seen in the indirect effects on other trophic levels (Field et al. 1992). The majority of vascular plant production ultimately enters the detrital pool in both terrestrial and aquatic systems, yet little is known about how atmospheric CO_2 changes might affect organisms involved in processing of detritus. Presumably, biochemical characteristics of litter produced under elevated CO_2 will be the key factors in detritus decomposition and a knowledge thereof should allow predictions of what may happen to detritus processing as atmospheric CO_2 concentrations increase (Mooney et al. 1991, Field et al. 1992, Meyer and Pulliam 1991). This assumption has not been consistently met, however (e.g. Norby et al. 1986), and there is a conspicuous lack of investigation of this question in aquatic systems that depend upon terrestrial leaf litter as a major carbon source (Carpenter et al. 1992).

Larvae of most mosquitoes are detritivores in aquatic environments and many species are thought to be dependent upon terrestrial plant litter and associated decomposer microorganisms for nutrition. One such species in North

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America is the treehole mosquito *Aedes triseriatus*. Previous studies have suggested that *Ae. triseriatus* growth and development are directly related to the quantity and quality of plant material available to larvae (Carpenter 1983, Fish and Carpenter 1982, Walker and Merritt 1988, Walker et al. 1991). Although not well-documented at present, larvae are presumed to feed mainly on microorganisms that metabolize senescent leaf material in the treehole habitat (Fish and Carpenter 1982). Therefore, factors that affect the abundance, activity, and/or composition of microbial communities in the habitat would be expected to influence mosquito production.

In this study, we investigated the effects of parent-plant growth conditions on the microbial respiration associated with the decomposition of senescent leaf material in simulated larval *Ae. triseriatus* habitats. Overall microbial respiration was significantly affected by leaf species, light conditions, and CO_2 levels. These results were related to leaf carbon and nitrogen content, and linked to mosquito growth and development.

METHODS

Experimental treatments and conditions

Senescent leaf material was obtained from one-year-old seedlings of paper birch (*Betula papyrifera* Marsh) and red oak (*Quercus rubra* L.) after growth under light and CO_2 conditions described by Kubiske and Pregitzer (1995). The conditions were either full sun (sun) or 26 percent of full sun (shade), and ambient CO_2 levels (350 ppm) or approximately twice ambient levels (714 ppm). These treatments were administered via open top chambers.

Microcosms were set up in parallel to those described by Strand et al. (this volume). 600 mg of dry leaf material was added to 300 ml of a weak solution containing inorganic nutrients (Na_2HPO_4, Na_2SO_4, KNO_3) and a microbial inoculum from natural treeholes. Nitrate (152 μM), sulfate (68 μM), and phosphate (33 μM) ion concentrations in the solution were within ranges found in stemflow and treeholes (Walker et al. 1991, Carpenter 1982a). Leaf material was incubated in the microcosm solution for one week at room temperature (23 - 25°C) prior to the first sampling. Mosquito larvae were added to half of the microcosms in the same proportion (one larva per 50 mg dry wt. leaf material) used by Strand et al. (this volume).

Microbial respiration and elemental analyses

On days 0 (coinciding with addition of larvae), 3, and 10, two subsamples of approximately 100 mg each of leaf material were removed, weighed, and placed into 38 ml serum vials. Serum vials were then capped and the headspace was sampled at approximately six hours (exact times recorded and used for rate calculations) after incubation at room temperature (24 - 25°C). Preliminary studies had shown CO_2 production from leaf material was linear for up to 18 hours under these conditions. Headspace gas was analyzed for CO_2 content with a Beckman® (#865, Beckman Instruments, Inc., Fullerton, CA) Infrared Analyzer. Remaining leaf material was dried, weighed, and analyzed for total carbon (C) and nitrogen (N) content with a Carlo Erba Nitrogen Analyzer® (#1500, Series 2, Carlo Erba, Milan, Italy).

Statistics

There was insufficient material for a complete leaf X light X CO_2 factorial ANOVA (no leaves from the oak shade treatment). Consequently, birch sun and birch shade treatments were analyzed as a two-way, repeated measures, fully factorial ANOVA (©Systat, Inc.). The birch sun and oak sun data were analyzed in another two-way, repeated measures ANOVA. Data were transformed as necessary with log or square root functions to reduce variance heteroscedasticty as determined with Bartlett's test (Sokal and Rolhf 1969, ©Systat, Inc.). Initial analyses revealed no significant effects of larvae within any treatment or on any leaf parameter measured. Consequently, replicates from microcosms with and without larvae were combined within treatments for all analyses. Relationships between microbial respiration and leaf percent nitrogen, percent carbon, and carbon:nitrogen ratio (C/N) were analyzed with Pearson correlation and standard regression techniques. Relationships between grand means of total adult mosquito biomass (from Strand et al., this volume) and grand means of microbial respiration (averaged across all sampling dates), initial (prior to water addition) senescent leaf percent N, percent C, and C/N were similarly analyzed.

RESULTS AND DISCUSSION

Microbial respiration

Microbial respiration as indicated by CO_2 production rate varied greatly with time, leaf species, light, and CO_2 treatment (Fig. 1, Tables 1 and 2). Leaf X CO_2 comparisons (Table 1) showed significant interaction between all main factors, reflecting the more pronounced effect of growth-condition CO_2 levels on senescent oak leaf decomposition vs. birch leaf decomposition. Additionally, differences between treatments were less distinguishable as decay progressed. In contrast, the light X CO_2 comparison of birch leaves showed significant increases in microbial respiration rates on leaves from the shaded treatment and fewer interactions with other factors (Table 2). There was no evidence of a direct CO_2 effect in the birch-only comparison, however, significant interaction of light with time and CO_2 suggests elevated CO_2 history may have influenced microbial respiration during a portion of the decay process. As in the leaf X CO_2 comparison, differences between treatments became attenuated over time.

The convergence of respiration values on day 10 in both comparisons indicates that differences in leaf chemistry due to growth conditions were in the relatively labile fraction. This fraction would be utilized more readily in earlier stages of decomposition and remaining leaf material of all types would be similar in its refractory nature. Although mass loss was not determined in this study, decay curves for different deciduous leaves in aquatic and terrestrial habitats typically show the most pronounced divergence early in the process (Willoughby, 1974, Jensen 1974, Carpenter 1982b, Aber et al. 1990). Additionally, the overall decline of respiration rates with time may reflect depletion of initial inorganic nutrient sources that would normally be replenished by stemflow (Carpenter 1982a, Walker et al. 1991).

Carbon and nitrogen content

Nitrogen (N) content and carbon:nitrogen (C/N) ratios of leaf material also varied considerably with time and treatment (Figs. 2 and 3, Tables 2 - 6). Nitrogen concentration in birch leaf material generally increased with time (Figure 2, Table 4), however, this trend was not obvious in the oak leaf material during the sampling period (Figure 2). An increase in N content during decay is characteristic of most litter and is presumably due to microbial immobilization and humification (Willoughby, 1974, Suberkropp et al. 1976, Melillo et al. 1982). Percent leaf N was significantly lower in decomposing oak than birch, but this was dependent upon growth-condition CO_2 level (Table 3). However, there was no overall main effect of plant growth-condition CO_2 on N content.

In general, C/N ratios in the leaf material reflected trends in nitrogen content; C/N declined with time as nitrogen increased and the trend was most obvious in the birch treatments. In contrast to percent N, however, analysis of C/N ratios showed significant light and CO_2 main effects (Tables 5 and 6). These main effects must be cautiously interpreted along with significant interaction terms, however, results from ANOVA of C/N ratios more closely parallel those found for microbial respiration (compare Tables 1 and 2 with 5 and 6). This suggests that carbon content and/or quality, not nitrogen content or quality, during decay was most affected by parent-plant treatment conditions and that carbon sources in the leaf material influenced microbial respiration more directly.

Relationships between microbial respiration, leaf carbon:nitrogen content, and adult mosquito biomass

That the relationship between microbial respiration, and carbon and nitrogen content is complex is illustrated in Figure 4. Microbial respiration varied directly with percent N, but inversely with percent C and C/N ratio. Although correlations are all significant, only 5 - 8 percent of the variance can be explained by any factor. This would further suggest that other factors, including carbon quality of the leaf material, may have the strongest overall influence on microbial respiration. Carbon quality, for example, has been shown to be the major limiting factor for microbial decomposer activity in many terrestrial systems (e.g. Collins et al. 1990, Melillo et al. 1982).

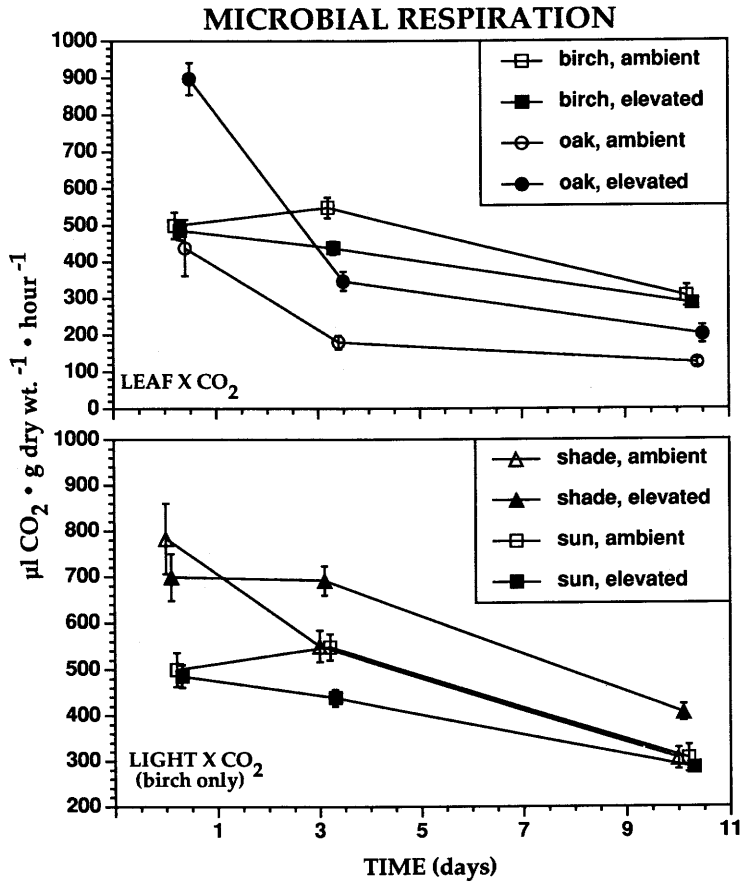

Figure 1. Microbial respiration on decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Values are mean ± S.E. n = 6 in all cases. Initial values (day 0) correspond to addition of larvae in parallel microcosms.

Table 1. Repeated measures ANOVA results comparing microbial respiration on decomposing, senescent birch and oak leaf material grown under ambient and elevated CO_2 levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
LEAF	68930.641	1	68930.641	5.962	0.024
CO_2	156967.476	1	156967.476	13.576	0.001
LEAF*CO_2	359770.118	1	359770.118	31.116	0.000
ERROR	231246.895	20	11562.345		
WITHIN SUBJECTS					
TIME	1490252.429	2	745126.214	111.552	0.000
TIME*LEAF	538468.305	2	269234.153	40.307	0.000
TIME*CO_2	152280.638	2	76140.319	11.399	0.000
TIME*LEAF*CO_2	107048.693	2	53524.346	8.013	0.001
ERROR	267184.288	40	6679.607		

Table 2. Repeated measures ANOVA results comparing microbial respiration on decomposing, senescent birch leaf material grown under ambient and elevated CO_2 levels, and two light levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
CO_2	98.467	1	98.467	0.007	0.934
LIGHT	381763.220	1	381763.220	26.881	0.000
CO_2*LIGHT	45612.067	1	45612.067	3.212	0.088
ERROR	284043.486	20	14202.174		
WITHIN SUBJECTS					
TIME	1134588.130	2	567294.065	73.464	0.000
TIME*CO_2	25508.008	2	12754.004	1.652	0.205
TIME*LIGHT	109450.810	2	54725.405	7.087	0.002
TIME*CO_2*LIGHT	78295.658	2	39147.829	5.070	0.011
ERROR	308880.754	40	7722.019		

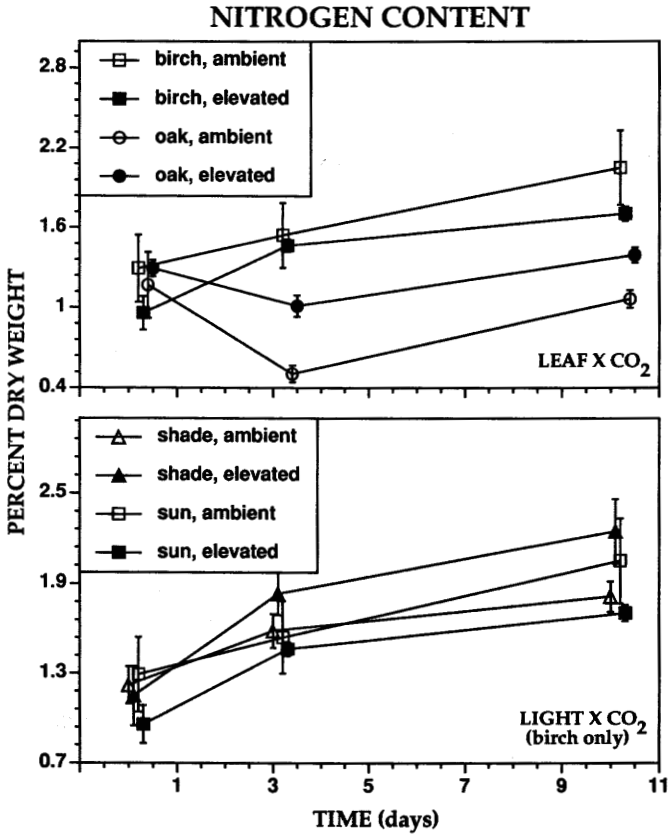

Figure 2. Nitrogen content of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Values are mean ± S.E. n = 6 in all cases. Initial values (day 0) correspond to addition of larvae in parallel microcosms.

Table 3. Repeated measures ANOVA results comparing nitrogen concentration of decomposing, senescent birch and oak leaf material grown under ambient and elevated CO_2 levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
LEAF	2.171	1	2.171	15.372	0.001
CO_2	0.307	1	0.307	2.173	0.156
LEAF*CO_2	1.278	1	1.278	9.053	0.007
ERROR	2.824	20	0.141		
WITHIN SUBJECTS					
TIME	2.011	2	1.005	19.280	0.000
TIME*LEAF	2.171	2	1.085	20.813	0.000
TIME*CO_2	0.514	2	0.257	4.929	0.012
TIME*LEAF*CO_2	0.071	2	0.036	0.681	0.512
ERROR	2.086	40	0.052		

Table 4. Repeated measures ANOVA results comparing nitrogen concentration of decomposing, senescent birch leaf material grown under ambient and elevated CO_2 levels, and two light levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
CO_2	0.003	1	0.003	0.064	0.803
LIGHT	0.062	1	0.062	1.375	0.255
CO_2*LIGHT	0.109	1	0.109	2.404	0.137
ERROR	0.908	20	0.045		
WITHIN SUBJECTS					
TIME	1.341	2	0.670	33.714	0.000
TIME*CO_2	0.064	2	0.032	1.611	0.212
TIME*LIGHT	0.008	2	0.004	0.212	0.810
TIME*CO_2*LIGHT	0.024	2	0.012	0.596	0.556
ERROR	0.795	40	0.020		

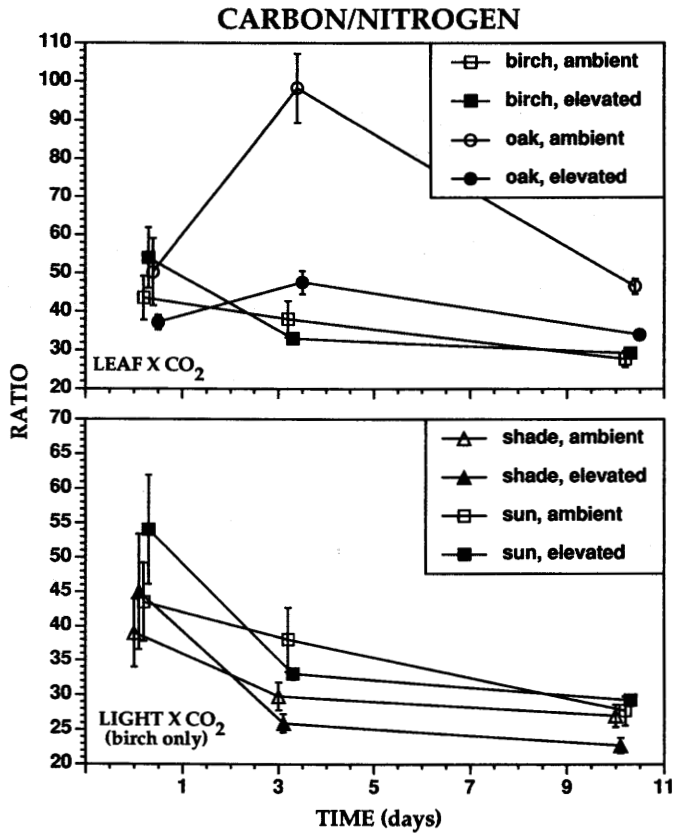

Figure 3. Carbon:nitrogen ratios (percent carbon/percent nitrogen) of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Values are mean ± S.E. n = 6 in all cases. Initial values (day 0) correspond to addition of larvae in parallel microcosms.

Table 5. Repeated measures ANOVA results comparing carbon:nitrogen ratio of decomposing, senescent birch and oak leaf material grown under ambient and elevated CO_2 levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
LEAF	1.731	1	1.731	14.287	0.001
CO_2	0.558	1	0.558	4.605	0.044
LEAF*CO_2	1.141	1	1.141	9.415	0.006
ERROR	2.423	20	0.121		
WITHIN SUBJECTS					
TIME	1.802	2	0.901	17.551	0.000
TIME*LEAF	1.919	2	0.959	18.691	0.000
TIME*CO_2	0.565	2	0.283	5.504	0.008
TIME*LEAF*CO_2	0.064	2	0.032	0.625	0.540
ERROR	2.053	40	0.051		

Table 6. Repeated measures ANOVA results comparing carbon:nitrogen ratio of decomposing, senescent birch leaf material grown under ambient and elevated CO_2 levels, and two light levels (see text).

SOURCE	SS	DF	MS	F	P
BETWEEN SUBJECTS					
CO_2	0.001	1	0.001	0.006	0.938
LIGHT	0.528	1	0.528	4.361	0.050
CO_2*LIGHT	0.086	1	0.086	0.712	0.409
ERROR	2.422	20	0.121		
WITHIN SUBJECTS					
TIME	3.028	2	1.514	27.720	0.000
TIME*CO_2	0.237	2	0.118	2.169	0.128
TIME*LIGHT	0.037	2	0.018	0.337	0.716
TIME*CO_2*LIGHT	0.037	2	0.019	0.340	0.714
ERROR	2.184	40	0.055		

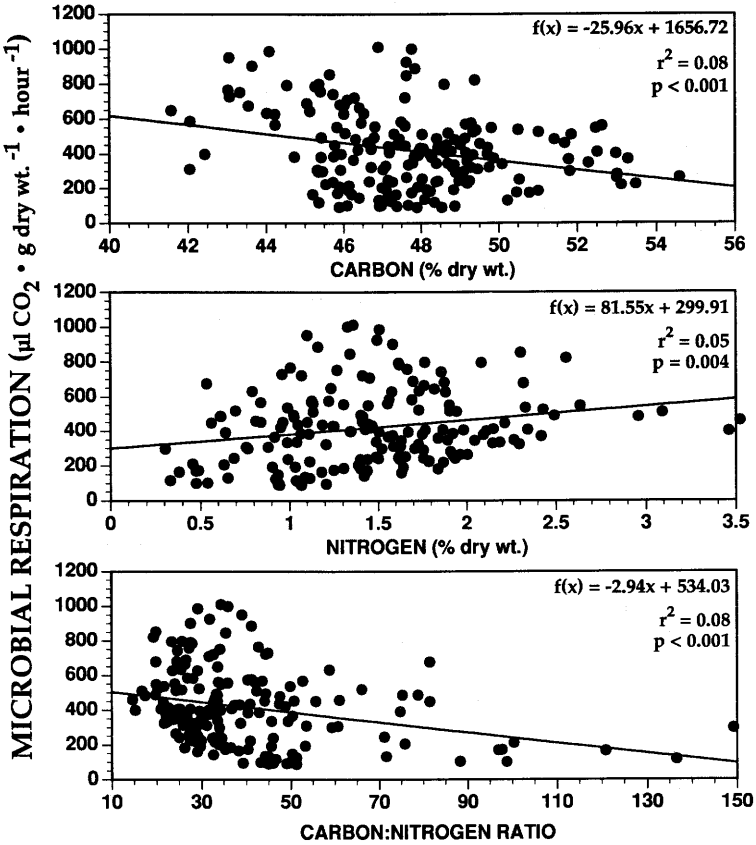

Figure 4. Correlation between microbial respiration and percent carbon, percent nitrogen, and carbon:nitrogen ratios of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Data from all leaf types and all three sampling dates are illustrated in each panel.

The initial carbon and nitrogen content of the senescent leaf material (Table 7) is likely to be a poor predictor of microbial respiration during decay or of adult mosquito biomass produced (Table 8). Only the relationship between initial percent N and mosquito adult biomass produced was significant, although the analysis also suggested a possible relationship between initial percent N and microbial respiration (Table 8). The negative relationships between percent N and mosquito biomass, and between percent N and microbial respiration are surprising in that nitrogen content of leaf detritus often is positively correlated with decomposition rates and detrivore growth in aquatic systems (Anderson and Sedell 1979 and references therein). These data must be viewed cautiously, however, since correlations based upon grand means simply reflect the relationships of general trends in the data set. Nevertheless, in contrast to earlier studies (see Park 1975, Jensen 1974) initial leaf N and C/N were not broad indicators of microbial respiration or detrital processing potential in these microcosms. Elevated CO_2 is generally thought to decrease overall percent N and increase C/N in terrestrial leaf litter; resulting in lower decomposition rates (Mooney et al. 1991, Field et al. 1992). However, excess carbon content of leaf litter from CO_2-enhanced parent plants is mostly in the form of sugars and starches, not lignin (Mooney et al. 1991). Therefore, decomposition rates of the litter could conceivably be increased provided other nutrients (e.g., N) are in adequate supply from external sources. It has been recognized more recently that percent N and C/N in detritus may be inadequate predictors of decomposition since other factors such as lignin content have a more pronounced influence on decay processes in aquatic habitats (Gessner and Chautier 1994, Boulton and Boon 1991, Stout 1989, Polunin 1984, Suberkropp et al. 1976). This further underscores the need to investigate specific carbon sources in treehole systems.

Table 7. Initial (before water addition and incubation) nitrogen (N), carbon (C), and carbon:nitrogen ratios (C/N) of senescent leaf material in *Ae triseriatus* microcosms. Values are mean ± S.E. of subsamples from pooled and homogenized material. n = 4 in all cases. BSHA = birch, shade, ambient CO_2; BSHE = birch, shade, elevated CO_2; BSA = birch, sun, ambient CO_2; BSE = birch, sun, elevated CO_2; OSA = oak, sun, ambient CO_2; OSE = oak, sun, elevated CO_2.

Treatment	N (% dry wt.)	C (% dry wt.)	C/N
BSHA	1.25 ± 0.05	32.86 ± 1.12	26.41 ± 0.80
BSHE	1.09 ± 0.02	44.67 ± 0.08	41.00 ± 0.81
BSA	1.27 ± 0.03	48.78 ± 0.10	38.63 ± 1.03
BSE	1.70 ± 0.03	47.70 ± 0.14	28.09 ± 0.47
OSA	1.56 ± 0.06	47.13 ± 0.11	30.56 ± 1.24
OSE	1.49 ± 0.02	46.88 ± 0.12	31.47 ± 0.33

Table 8. Pearson correlation analysis of initial (before water addition and incubation) carbon (C) and nitrogen (N) content of senescent leaf material vs. grand means of microbial respiration and total adult mosquito biomass. n = 6 in all cases.

Leaf content vs.	Pearson Correlation			
	Microbial Respiration		Mosquito Biomass	
	Coeff.	p value	Coeff.	p value
% N	-0.780	0.067	-0.842	0.038
% C	-0.381	0.456	-0.729	0.103
C:N	0.474	0.343	0.688	0.211

Although leaf biochemical characters that may influence microbial respiration and decay processes are complex and incompletely-addressed in this study, microbial respiration appears to be a good predictor of larval *Ae. triseriatus* production in the microcosms. Figure 5 illustrates the relationship between grand means of adult mosquito biomass and microbial respiration. Such a relationship has been shown for other detritivore/microbe systems (e.g. Ward and Cummins 1979), but this study represents the first such evidence for larval mosquitoes. The positive relationship supports our contention that mosquito larvae in treehole habitats are limited by microbial biomass and/or respiration. The results also reinforce the idea of a tight link between trophic levels in the system and that microorganisms are the key intermediates. Higher microbial respiration measurements have been associated with higher microbial biomass in detritus (Ward and Cummins, 1979). Since observations indicate that *Ae triseriatus* larvae feed directly upon leaf surface-associated microorganisms (Fish and Carpenter 1982, Walker and Merritt 1991, Kaufman unpub. obs.), the higher biomass of emerging adults in some treatments is potentially attributable to a higher biomass of microbes. Alternatively, higher microbial respiration may be acting to release more leaf material for larval consumption. Since we presently have no data on microbial turnover rates or microbial biomass/vs. leaf material contributions to larval growth, additional experimentation will be required to address the details of the linkage. Further examination of this linkage will allow more detailed predictions of the effects of atmospheric changes on small, aquatic, detritus-based systems.

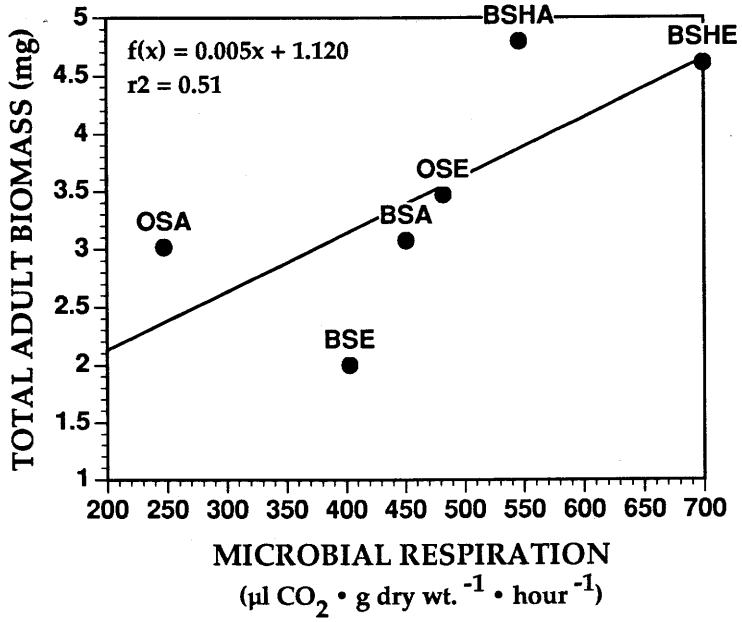

Figure 5. Correlation between mean total mosquito biomass and mean respiration values of decomposing, senescent leaf material in *Ae. triseriatus* microcosms. Mean respiration values are the average of mean respiration rates over the three sampling dates. Treatments are indicated as BSHA = birch, shade, ambient CO_2; BSHE = birch, shade, elevated CO_2, BSA = birch, sun, ambient CO_2, BSE = birch, sun, elevated CO_2; OSA = oak, sun, ambient CO_2; OSE = oak, sun, elevated CO_2.

SUMMARY AND CONCLUSIONS

Microbial respiration on decaying leaves in *Ae. triseriatus* microcosms was affected by leaf species and CO_2 conditions during growth of the parent plant. However, both of the effects changed significantly with time. Microbial respiration on oak was enhanced by growth-condition elevated CO_2 while birch leaves showed the opposite trend.

Microbial respiration on decomposing senescent birch leaves was affected most by parent-plant light conditions and this effect was more pronounced in earlier stages. Leaves from plants grown in shade supported higher levels of

respiration than those produced in full sun. Elevated CO_2 conditions during parent-plant growth enhanced microbial respiration on decomposing, senescent leaves only when the leaves originated from plants grown under shaded conditions.

Nitrogen content and carbon-nitrogen ratios, both of which are known to be altered by microbial biomass and respiration, were significantly correlated with microbial respiration. Senescent leaf material with higher nitrogen content had lower C/N values and higher microbial respiration. Carbon content or quality, however, appeared to have a more direct influence on microbial respiration.

Initial values for percent nitrogen and carbon-nitrogen ratios in the senescent leaf material were not good indicators of either microbial respiration or mosquito production. This warrants further investigation, however, it also points out that over simplistic models of decomposition may not adequately predict the flow of carbon and nitrogen in plant material through decomposer and detritivore communities.

Adult mosquito production was directly and positively related to microbial respiration, suggesting a tight trophic link between mosquito larvae and decomposer microorganisms. Effects of elevated CO_2 and light on senescent leaf material will likely have complex repercussions for detritivores in aquatic systems and will depend upon the microbial mediation of the detritus-detritivore interactions.

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