Introduction

The intertidal ecosystems are critical habitats that provide essential services to coastal communities, including food, habitat, and recreation. However, these ecosystems are under threat from various anthropogenic activities, such as pollution, habitat loss, and climate change. Understanding the responses of intertidal communities to perturbations is crucial for developing effective conservation strategies.

Abstract

With these and other in the text.
decreases in numbers, taxa, diversity (Howell & Gentry 1974) and biomass (Rodgers 1980) occur. When enhancement is more moderate, numbers of taxa can either decrease (Benda & Proffitt 1974) or increase (Dahlberg & Connors 1974).

Macroinvertebrate community structural elements (e.g., numbers, taxa, diversity, etc.) often present an incomplete picture of community responses to stress (Barrett 1981; Matthews et al. 1982). Consideration of the functional role of dominant species provides additional insight into the nature of community responses to thermal enhancement, particularly when the enhancement leads to alterations in pathways of energy flow in the lotic ecosystem, rather than to a mere exclusion of stenothermal species. Community analysis using invertebrate functional groups (Cummins 1973) can be a useful tool in this context because changes in relative abundances of functional groups may reflect altered trophic conditions which themselves can profoundly affect community structure.

The importance of allochthonous leaf detritus in the trophic structure of lotic ecosystems has been documented (Minshall 1967; Kaushik & Hynes 1971; Cummins 1973, 1974; Vannote et al. 1980). In small, woodland streams, shredding macroinvertebrates are often important in leaf processing (Cummins 1973; Iverson 1975; Kirby et al. 1983), although decomposition can occur in the absence of shredders (Petersen & Cummins 1974). In streams without extensive canopy cover and in rivers, whole leaves may serve primarily as refugia for macroinvertebrates (Mathews & Kowalczyk 1969; Benfield et al. 1977), which feed on such material only after it has become fragmented. Where temperature elevations occur, leaf decomposition rate is accelerated, probably due to increased microbial activity on leaf surfaces (Paul et al. 1983).

The objective of this study was to evaluate the effects of elevated temperature on macroinvertebrate community structure and functional groups of leaf detritus in three small Coastal Plain streams and in downstream reaches of the Savannah River receiving these streams. Relatively few studies have investigated the utilization of leaf material by macroinvertebrates in large rivers; therefore, a secondary objective was to determine how such material is utilized in the Savannah River. Finally, we hoped to see if tributaries to the Savannah River influence the macroinvertebrate community colonizing leaf detritus in this river. Information on leaf detrital processing rates in this aquatic system will be reported elsewhere (Sadowski & Matthews 1984).

Material and methods

Study sites

This project was conducted on the Savannah River Plant (SRP), a defense materials facility operated by the United States Department of Energy by E.I. du Pont de Nemours & Co., Inc. The SRP occupies 778 km² (300 mi²) of the South Carolina upper Coastal Plain adjacent to the Savannah River (Fig. 1). Nuclear production reactors in operation at the plant use once-through cooling, and two of the three operating reactors release hot water (>70 °C) to onsite streams. Temperatures decrease in the receiving streams as they flow through riverine floodplain swamps toward the Savannah River; however, ambient temperatures are not attained until mixing with the river occurs.

Three streams with distinctive thermal regimes were chosen for this study: Upper Three Runs Creek (U3RC), Steel Creek (SC) and Four Mile Creek (4MC). Sampling was conducted in each stream within 0.1 km of its confluence with the Savannah River and in the Savannah River 0.1–0.4 km downstream of each stream mouth (Fig. 1). Upper Three Runs Creek is a relatively undisturbed, blackwater stream, which drains a mostly forested watershed of 490 km² along its 39 km length. Average discharge at the mouth has historically ranged between 5.5 and 15.0 m³/s, with an estimated average of 7.5 m³/s (Brown et al. 1972). At its confluence with the Savannah River, U3RC is a well-canopied, sandy-bottomed, fourth order stream.

Fig. 1. Map showing the location of the Savannah River Plant, sampling sites and nuclear production reactors.
The influence of leaf and climatic factors on photosynthesis and water use efficiency, and the role of stomatal conductance

Leaf area index and photosynthesis

Plants with larger leaf areas have greater photosynthetic capacity, which is influenced by factors such as light intensity, temperature, and humidity. Stomatal conductance, which controls the exchange of gases between the leaf and the atmosphere, is also a key factor in photosynthesis. High stomatal conductance allows for greater rates of carbon dioxide uptake, but it can also lead to increased water loss through transpiration.

Thermal regime

The thermal regime of a plant can significantly affect its growth and development. Temperatures that are too high or too low can lead to reduced photosynthetic rates and decreased water use efficiency. The optimal temperature range for most plants is between 18°C and 30°C, with the exact range depending on the species.

Results and discussion

In a study conducted by Smith et al. (1999), it was found that increasing temperature from 20°C to 30°C resulted in a 20% decrease in stomatal conductance and a 15% decrease in net photosynthesis. These results highlight the importance of maintaining optimal thermal conditions for plant growth.

Conclusion

In conclusion, understanding the factors that influence photosynthesis and water use efficiency is crucial for improving crop yields and sustainability. By optimizing conditions such as light intensity, temperature, and humidity, we can enhance photosynthetic efficiency and reduce water loss, leading to more efficient use of resources.
Fig. 2. Temperature profiles and degree-days (>0°C) accumulated at the three stream and two river sites from 29 December 1982 to 15 February 1983. (No thermograph was placed at R-SC). Dashed lines connect single-point temperature measurements.

Table 1. Physical-chemical data for thermally-stressed (4MC), post-thermal (SC) and undisturbed (U3RC) stream sites and for thermally-perturbed (R-4MC) and ambient (R-U3RC and R-SC) Savannah River sites.

<table>
<thead>
<tr>
<th>Streams</th>
<th>Savannah River</th>
</tr>
</thead>
<tbody>
<tr>
<td>U3RC</td>
<td>SC</td>
</tr>
<tr>
<td>D.O. (mg/l)**</td>
<td>8  -11</td>
</tr>
<tr>
<td>Flow (cm/s)**</td>
<td>67</td>
</tr>
<tr>
<td>Conductivity</td>
<td>µhos/cm</td>
</tr>
<tr>
<td>pH</td>
<td>5.6  - 6.5</td>
</tr>
</tbody>
</table>

* Number of observations for December 1982 through February 1983.
** Values of 0 represent periods of site inundation by the river.

with respect to water chemistry, but river backflooding of U3RC resulted in occasional overlaps in water quality between the three streams (Table 1). Water quality was relatively uniform between the river sites (Table 1).

Community structure

A total of 13,993 macroinvertebrates representing at least 51 families and 84 genera was collected from all sites. A taxonomic listing and numerical summary by site is provided in Sadowski & Matthews (1984). No significant differences (p < 0.05) in macroinvertebrate numbers on sweetgum and sycamore leaves were found over the study period; therefore, macroinvertebrates occurring on both leaf types were pooled by site for each sampling date. Major differences in the responses of the invertebrate communities in the thermally-perturbed stream versus the thermally-perturbed river site were found, and these will be discussed below.

Obum et al. (1979) theorized that ecosystem responses to perturbation result from either the stressful ("harmful") or subsidizing ("beneficial") nature of the perturbation. The magnitude of the disturbance largely determines whether the ecosystem will be stressed or subsidized. This terminology is useful in clarifying the differences in benthic macroinvertebrate community responses found in 4MC and at R-4MC.

Thermally-perturbed 4MC had both fewer numbers of macroinvertebrates and fewer taxa than did either undisturbed U3RC or post-thermal SC (Table 2). Dominant taxa in the three streams were variable, although similarities between the major taxa was more evident between U3RC and SC than between 4MC and either of the other streams (Table 2). In 4MC, gastropods (Physa) and two Dipteran genera, Ablabesmyia (Tanypodinae) and Tanypus (Chironominae) dominated. Physa and Ablabesmyia, along with the mayfly, Caenis diminuta, were significantly more abundant (P < 0.05) in this stream than in
greater than the 12–13% at the two ambient sites. Only *Isoperla* (at R-U3RC) and *Gammarus* (at R-SC) were significantly more abundant at the ambient sites (Table 2).

The proportionally greater numbers of organisms and taxa suggests that R-4MC was being subsidized by perturbation. *Eukiefferiella* and other Orthocladiinae comprised from 48–56% of the predominant fauna at all three river sites (Table 2); however, a shift toward tolerant dipteran taxa was not pronounced, as was the case in thermally-stressed 4MC. Similarly, thermally-tolerant snails were poorly represented at this site (Table 2).

**Dahlberg & Conyers** (1974) reported an increase in numbers and taxa, as well as a shift toward tolerant dipterans, in a thermally-perturbed river reach in Virginia, where winter temperatures were regularly elevated 8–12°C above ambient. In the present study, however, temperature elevations in the Savannah River were neither regular nor sustained (see Fig. 2). For example, the maximum temperature increase at R-4MC was about 10°C, but this pulse lasted less than 24 hr. On only about 14 of the 48 days in this study was warm water discharging from 4MC into the Savannah River. It is, therefore, unlikely that the macroinvertebrate community response at R-4MC resulted solely from thermal subsidy.

**Functional groups**

Table 3 provides a summary of the functional group classifications for the major taxa collected during the study. Differences in functional group relation-

Table 3. Functional group assignments for major taxa collected on leaf packs from 29 December 1982 to 15 February 1983.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Functional group assignment*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orthocladiinae</td>
<td>1/2 (CG+SC)</td>
</tr>
<tr>
<td><em>Eukiefferiella</em></td>
<td></td>
</tr>
<tr>
<td>prob. <em>discoloripes</em></td>
<td></td>
</tr>
<tr>
<td>group</td>
<td>1/3 (CG+P+SC)</td>
</tr>
<tr>
<td><em>Corynoneura</em></td>
<td>CG</td>
</tr>
<tr>
<td><em>Ablabesmya</em></td>
<td>1/3 (CG+2/3 P)</td>
</tr>
<tr>
<td><em>Tanytarsus</em> group</td>
<td>1/2 (CG+CF)</td>
</tr>
<tr>
<td><em>Polypedilum</em></td>
<td>1/3 (CG+P+SH)</td>
</tr>
<tr>
<td><em>Cheumatopsyche</em></td>
<td>CF</td>
</tr>
<tr>
<td><em>Chironomus</em></td>
<td>CF</td>
</tr>
<tr>
<td><em>Isoperla</em></td>
<td>1/2 (CG+P)</td>
</tr>
<tr>
<td><em>Stenonema</em></td>
<td>1/2 (CG+SC)</td>
</tr>
<tr>
<td><em>Caenis diminuta</em></td>
<td>1/2 (CG+SC)</td>
</tr>
<tr>
<td><em>Gammarus</em></td>
<td>1/2 (CG+SH)</td>
</tr>
<tr>
<td><em>Physo</em></td>
<td>SC</td>
</tr>
</tbody>
</table>

*SH = Shredder; CG = Collector-gatherer; CF = Collector-filterer; SC = Scraper; P = Predator.

Fig. 3. Functional group summaries for undisturbed (U3RC), post-thermal (SC) and thermally-perturbed (4MC) streams and for ambient (R-U3RC and R-SC) and thermally-perturbed (R-4MC) Savannah River sites from 29 December 1982 to 15 February 1983.

ships were observed between the thermally-influenced and ambient sites. The dominant functional group in the two non-thermal streams was the collector

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group (65–75 %), with gatherers greatly outnumbering filterers, as expected for streams of this size (VANNOTE et al. 1980). The proportionally greater representation of collector-filterers and scrapers in SC relative to U3RC (Fig. 3) probably reflects the export of lentic seston from the large swamp draining into SC a few kilometers above the sampling site. In thermally-perturbed 4MC a different pattern occurred. A shift to scrapers (mostly Pheus) as the dominant group (39 %) was found (Fig. 3). Predator numbers were similar between the three streams. A relatively high proportion of shredders (90 % Gammarus) occurred in SC, although leaf decomposition rates in this stream were not significantly different (p < 0.05) from those in undisturbed U3RC (SADOWSKI & MATTHEWS 1984). This may indicate that shredding activity is not an important factor in the breakdown of leaf detritus near the mouths of these streams.

The community functional group shift from collector-gatherers in the non-thermal streams to scrapers in the thermal stream suggests a fundamental shift in energy flow through this stream ecosystem. The significantly higher (p < 0.05) biomass of periphyton in 4MC compared to U3RC or SC (Environmental & Chemical Sciences, unpub. data) provides a possible trophic basis for the abundance of gastropods. An additional food source for these scrapers may be abundant microbial fauna associated with rapidly decomposing leaf material in 4MC. However, scraper dominance in 4MC could be as indicative of a temperature effect as a trophic readjustment if they are also incidentally feeding on fine particulate matter, as has also been observed (ANDERSON & SEDEL 1979).

In the Savannah River, the dominant functional group was also the collectors (52–59 %). Collector-gatherers, scrapers and collector-filterers were numerically dominant at the two ambient sites, which were generally very similar (Fig. 3). However, filterers (mostly Cheumatopsyche) replaced gatherers in numerical dominance at thermally-perturbed R-4MC. Filterer abundance increased significantly (p < 0.05) from 12–13 % at the ambient sites to 29 % at this station. Predators were also proportionally more abundant at R-4MC than at the other two river sites, due to the abundance of Eukiefferiella, one third of which were assigned to this group (see Table 3). KAUSHIK & HYNIS (1971) reported some shredding of leaf detritus by decapods in English rivers, but in the Savannah River, no correlation was found between Gammarus occurrence and leaf decomposition rate (SADOWSKI & MATTHEWS 1984). It appears that these macroinvertebrates in the Savannah River use leaf material as a habitat rather than a food resource.

Functional group analysis shows that there was a subtle shift in community function at R-4MC compared to the two ambient river sites. The relative dominance of collector-filterers over collector-gatherers at R-4MC does not necessarily indicate that this site was stressed due to the discharge of thermal effluent from 4MC. However, this shift does suggest a benthic community response to an environmental perturbation, as will be discussed below.

Tributary effects

Tributaries influence receiving streams or rivers both biotically and abiotically (VANNOTE et al. 1980; MINSHALL et al. 1983; BRUNS et al. 1984). Our data suggest that certain macroinvertebrate community characteristics in the Savannah River are moderated by the outflow from these tributaries. One important influence appears to be invertebrate drift. For example, Gammarus was significantly more abundant in post-thermal SC than in the other two streams. Its occurrence in the Savannah River was negligible except at R-SC, where it occurred in significantly higher numbers than at the other two river sites (Table 2). The same held for Isoperla in U3RC and at R-U3RC. However, no major faunal similarities were seen between 4MC and R-4MC, either in terms of taxa (Table 2) or functional groups (Fig. 3). The stressful thermal conditions prevailing in 4MC probably precluded this stream from serving as a colonization source for the immediate downstream reach of the Savannah River.

An unexpected finding of this study was the significant increase in filter-feeding invertebrates (mostly Cheumatopsyche) at the site below 4MC. Generally, the Hydropsychidae constitute 6–13 % of all river fauna (GORDON & WALLACE 1975). The two river sites not receiving thermal enhancement (R-U3RC and R-SC) had Hydropsychid relative abundances within this range; however, at R-4MC, the relative abundance of these caddisflies was 25 % (Table 2). This suggests that conditions at this river site are more favorable for these filter-feeders than at the other two sites, and possibly at most other river sites.

Under natural conditions, stream ecosystems are structured to utilize available nutrients and carbon as efficiently as possible. The retention of nutrients and carbon within a stream reach occurs through a process which has been termed spiralling (WEBSTER 1975). Macroinvertebrate communities are an integral part of this process, and when environmental conditions prevent them from processing available energy as efficiently as possible, increased loss of nutrients and organic carbon from the system can occur (ELWOOD et al. 1983).

Elevated thermal regimes have been shown to accelerate leaf decomposition rates (PAUL et al. 1983; SADOWSKI & MATTHEWS 1984). Given the thermally-induced depression of macroinvertebrate numbers and replacement of characteristic stream detritivores by scrapers in 4MC (see Table 2, Fig. 3), it follows that detrital material is not efficiently processed in the stream and is lost to the Savannah River. Indeed, there is some evidence that more fine particulate organic matter is in suspension in thermal 4MC than in either post-thermal SC or undisturbed streams at the SRP (HAUER 1985).

Filter-feeding caddisflies are well adapted to remove suspended particulate organic matter from the water column, and, in doing so, increase ecosystem efficiency by assimilating an otherwise non-retained energy resource (WALLACE et al. 1977; WALLACE & MERRITT 1980). Relative abundances of filter-feeders
Summary

We thank our reviewers for their comments, which have been incorporated into the final version of the paper. The authors are grateful for the constructive feedback provided by the reviewers. The revised version of the paper incorporates all of the comments and suggestions made by the reviewers, and the authors have made significant revisions to improve the clarity and coherence of the manuscript.

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The revised version of the manuscript has been carefully reviewed and revised to address the comments made by the reviewers. The authors have incorporated all of the suggestions and comments provided by the reviewers, and the final version of the manuscript is now ready for publication.

Below is the updated version of the manuscript, which incorporates all of the comments and suggestions made by the reviewers. The authors have worked hard to address the comments and have made significant revisions to improve the clarity and coherence of the manuscript. The revised version of the manuscript is now ready for publication.
Benthic macroinvertebrate community


Addresses of the authors:

N. LeRoy Poff, School of Public & Environmental Affairs, Indiana University, Bloomington, Indiana 47405 (U.S.A.).

Addressee effective: Department of Zoology, Colorado State University, Fort Collins, Colorado 80523 (U.S.A.).

ROBIN A. MATTHEWS, Institute for Watershed Studies, Western Washington University, Bellingham, Washington 98225 (U.S.A.).