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Influence of riparian alteration on canopy coverage and macrophyte abundance in Southeastern USA blackwater streams

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Abstract

Two tributary streams (Fourmile branch and Pen branch) located on the US Department of Energy's Savannah river site in west-central South Carolina, USA received thermal discharges from nuclear production reactors for over 30 years. Effluent releases produced stream water temperatures of over 50°C and stream flows of ten times above their base level. Consequently, existing plant and animal communities within the stream channels were killed and riparian zones largely destroyed. We compared canopy coverage and macrophyte abundance in these disturbed streams after 7-13 years of ambient flows and compared them to two similar, undisturbed streams. We also examined the effects of a more recent woody canopy removal associated with a restoration effort in 'treated' sections of Pen branch. We collected data in Spring and Fall from May 1995 through May 1997. A gradient in canopy cover existed, ranging from a fully open herbaceous canopy in the treated sections of Pen branch, through a moderately closed canopy of herbaceous plants, shrubs, and willows in the post-thermal 'control' streams, to a nearly closed hardwood tree canopy in the undisturbed streams. Even though Fourmile branch had 3 more years of growth, Pen branch had a more closed upper canopy. Total aquatic macrophyte abundance was negatively related to canopy cover producing nearly the reverse gradient among streams as did the canopy cover. However, control sections of Pen branch had a more closed canopy than Fourmile branch, but total macrophyte abundance was higher in Pen branch. This can be attributed to the presence of submergent macrophytes in Pen branch that were absent in Fourmile branch. Different structural types of macrophytes varied in their degree of limitation by canopy coverage and in their seasonal patterns of growth. Stream habitats remain severely altered due to destruction of the riparian vegetation by past thermal effluents. The full range of effects of the alteration of canopy coverage and the resultant macrophyte abundances on these streams should be the focus of future analyses.

Keywords: Riparian; Disturbance; Macrophytes; Canopy; Stream; Thermal effluents; Savannah river

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1. Introduction

The type of canopy over a stream, and the degree of its closure, largely influences the amount of incident light reaching the stream's surface (Madsen and Adams, 1989). A common response to an open stream canopy is an inflated abundance of autotrophs including periphyton (Murphy et al., 1981; Robinson and Rushforth, 1987; Hill et al., 1995), macro-algae (Sheath et al., 1986) and aquatic macrophytes (Madsen and Adams, 1989; Everitt and Burkholder, 1991). Availability of incident light as influenced by the riparian canopy coverage can be the primary factor influencing macrophyte abundance in a stream (Canfield and Hoyer, 1988; Madsen and Adams, 1989). Shade provided by riparian trees has inhibited macrophyte abundance sufficiently in some streams to warrant the recommendation of replanting riparian trees as the most effective control of macrophytes in lotic systems (Dawson, 1978; Madsen and Adams, 1989; Bunn et al., 1998). Consequently, degree of canopy openness can influence the balance of autotrophic versus heterotrophic energy sources within a stream (Minshall, 1978; Vannote et al., 1980) and alteration of the canopy may severely alter the energy pathways of a lotic system. The extent of influence that the riparian canopy has on a stream's energetic base is evident by the subsequent increase in abundance of consumers including macroinvertebrates (Murphy et al., 1981; Hawkins et al., 1982; Behmer and Hawkins, 1986), and fishes (Murphy et al., 1981; Hawkins et al., 1983; Platts and Nelson, 1989).

The prevalence of alterations of stream and river riparian canopies by industrial activities, forestry practices, agriculture, or urban development and the wide-ranging influences that riparian zones (Karr and Schlosser, 1978; Naiman et al., 1993) and aquatic macrophytes (Gregg and Rose, 1982; Sand-Jensen et al., 1989) have on streams, necessitates a thorough understanding of the interactions among human disturbance, canopy coverage and macrophyte abundance. Assessments of different types of disturbances and in different types of aquatic habitats are needed. The objectives of the current analyses were to: (1) compare canopy coverage among streams that have riparian vegetation in different successional stages (herbaceous, shrub-willow, mature hardwood) due to different disturbance histories; (2) examine the effects of canopy alteration on total macrophyte coverage and the distinctive responses of different structural types of macrophytes; and (3) examine temporal variability in canopy and macrophyte coverages over a 25-month period.

2. Methods

2.1. Study site

Our study area, located on the US Department of Energy's Savannah river site along the southwestern border of South Carolina, included reaches of four tributaries in the Savannah river drainage (Table 1). The streams are moderate-gradient blackwater streams with typically sandy substrates. Two of these tributaries, Fourmile branch (FMB) and Pen branch (PB) received thermal effluents from nuclear production reactors for three decades. During effluent release water temperatures reached to over 50°C and flow discharges above ten times ambient volumes (Wike et al., 1994). Consequently, existing plant and animal communities within the stream channels were killed and riparian zones largely destroyed. Effluent release has since ceased, and at the beginning of our study, stream and riparian communities had been recovering for 10 and 7 years, respectively.

We also used reaches of two relatively undisturbed streams (Table I) to establish baseline data for comparison to the disturbed systems. FMB and PB are third order streams 12.3 and 14.4 km in length (Newman, 1986). The undisturbed streams bracket this size range with Upper three runs (UTR) considerably larger (fifth order, approximately 33.8 km long) and Meyers branch (MB) smaller (third order, 11 km long). Upper three runs and MB are the most comparable undisturbed streams available.

Reaches of FMB, UTR, and PB cross two alluvial terraces of the Savannah river. Streams crossing these terraces have braided stream channels, typically one main channel (often two in UTR) and several smaller channels (one to more than five). Channel widths, depths, velocities, and degree of isolation vary greatly, developing a highly complex habitat (e.g. water velocities can vary from negligible to 45 cm/s). The MB study area lies just above the upper alluvial terrace and is only braided in a section that is in a delta below an old beaver pond.

The canopy of some sections of PB have been removed as part of the restoration efforts (Nelson et al., 2000); this will be referred to as the treated section of PB (Table 1). First, we will compare the undisturbed and disturbed streams, and then use the untreated section of PB and FMB as 'controls' for comparison to the treated sections of PB.

2.2. Data collection

Our study areas are divided into a hierarchical classification of stream-treatments, sections, sites, and transects. Within each of the five stream-treatments (treated PB, control PB, control FMB, undisturbed UTR, and undisturbed MB), the stream corridor was divided into sections (Table 1) to be used as replicate sampling areas within a stream-treatment. Because of the complex braided nature of the stream reaches, within each section, we selected three to seven stream channels (sites) averaging 20 m in length that were representative of the channel types present in a given section (Table 1). A section is characterized by the data collected from sites within a section, thus an assumption of our analyses is that our sites are representative of that section. Within a site, data were collected from five permanent transects that were established perpendicularly across the stream at 0, 25, 50, 75, and 100% the length of each site. We collected data from our sites during five sampling periods, Spring (May-June) and Fall (October-November) from Spring 1995 through Spring 1997 (Table 1). The Fall sample was missed in UTR in 1995 due to high water levels.

We defined 'upper canopy' as vegetation above the water's surface that shades the stream channel. 'Dominant upper canopy' type was classified as grass, other herbaceous vegetation, shrub, small tree (< 20 cm diameter), or large tree (> 20 cm diameter). 'Surface canopy' we defined as vegetation in contact with the water's surface that provides shade to the water column below. 'Dominant surface canopy' classifications included overhanging grass, other herbaceous vegetation,

Table 1
Sampling design [a]

Thermally disturbed						Undisturbed		
Control			Treated					
Stream	Sections	Number of sites	Stream	Sections	Number of sites	Stream	Sections	Number of sites
Pen branch	C	5	Pen branch	B	5	Upper three runs	A	4
	E	4		D	7		B	5
							C	3
Fourmile branch	A	3				Meyers branch	B	4
	B	4						

[a] Four streams were examined, two previously disturbed by past releases of thermal effluents and two with ambient thermal history, A portion of one thermally disturbed stream, Pen Branch, was treated with herbicide, burned and replanted with trees. Within each stream-treatment, the stream corridor was divided into sections to be used as replicate sampling areas. Each section was characterized by collecting data from multiple sites which in turn were characterized by data collected from five permanent transects within each site

shrubs, and small trees, but floating and emergent aquatic macrophytes were the dominant categories. We employed a modification of the canopy visual estimate method of shade measurement (Canfield and Hoyer, 1988; Madsen and Adams, 1989). The linear distances across each transect that were covered by each of the two types of canopy were measured and the proportion of the stream width below the canopy calculated. Even though the photosynthetically active radiation (PAR) incident upon the stream may vary at a given level of canopy closure due to differences in density and orientation, open canopy sites have been associated with higher PAR measures than more shaded sites (De Nicola et al., 1992).

We categorized aquatic macrophytes into three structural types, emergent, floating, and submergent. Submergent macrophytes were rooted in the stream bottom and the entire plant occurred below the water's surface. *Egeria densa* (waterweed) was the dominant submergent macrophyte that we observed. Floating macrophytes were rooted in the bottom of the stream channel or in the bank and the plant bodies floated, keeping significant portions of the plant above the surface of the water. *Polygonum* sp. (smartweed) was the dominant floating macrophyte. Emergent macrophytes are rooted in the bottom and stand erectly out of the water directly above their roots. *Polygonum* and grasses (Poaceae) were the dominant emergent macrophytes.

Because of the logistical constraints of collecting data from a large number of sites and concerns of the potential impacts of repeatedly sampling the same sites, spatial coverage of macrophytes was used because it is reasonably rapid, relatively non-destructive, and allows a quantification of abundance (Wright et al., 1981; Ham et al., 1982; Madsen and Adams, 1989; Everitt and Burkholder, 199 1). Presence/absence of macrophytes and structural type was recorded for point measures across each transect; point measures were taken at 0.5 and 1 m from each bank and then at l-m intervals in between. The proportion of the total number of points across each transect with macrophytes present was used to calculate the percent coverage across that transect. A site mean was calculated by averaging the coverages of the five transects.

2.3. Statistical analyses

Proportional measures were arcsine transformed (Sokal and Rohlf, 1981; Zar, 1984) prior to parametric analyses. Based on normality plots of the transformed data and normality plots and histograms of residuals from the ANOVAs, transformation improved the data normality and homoscedacity. Because we have three samples for the Spring collection period, these samples will be primarily used for spatial comparisons. We used a nested, split plot ANOVA with the three Spring samples to compare canopy and macrophyte coverages among stream-treatments. Nesting sections within stream-treatments tested variation among sections within a stream-treatment. Time and an interaction term of time and stream-treatment were included. Differences among stream-treatment could then be judged with the influence of time, and variation within a stream-treatment removed. We used the non-transformed raw data in all graphical presentations to make biological significance easier to interpret. A box and whisker plot of the raw data was used to illustrate the differences in the distribution of data points of select variables among stream-treatments. We followed each ANOVA with a Tukey pairwise comparison to determine specifically which stream-treatments differed. Because we conducted six ANOVAs, one for each variable (Tables 2 and 3), we used a Bonferonni adjustment for interpreting the *P* values. Although proportional coverage of the canopy and macrophytes were somewhat a function of stream width, particularly in wider channels, stream width was not driving the observed differences between stream-treatments. Inclusion of stream width and the interaction of stream width and stream-treatment into the above ANOVA model did not modify its results.

Within a stream-treatment, we conducted a repeated measures ANOVA to determine if coverages differed among the five sampling periods. Post hoc orthogonal contrasts compared seasons (Spring versus Fall) and tested for a linear trend in time across the five periods. We used a" Spearman rank correlation coefficient (r_{ranks}) to examine relationships among variables within a season,

Table 2
Comparison of canopy and macrophyte coverages among stream-treatments[a]

	Upper canopy	Surface canopy	Total macrophytes	Floating	Emergent	Submergent
r^2	0.87	0.71	0.89	0.84	0.56	0.71
Stream-treatment	<0.001	<0.001	<0.001	10.001	<0.001	<0.001
Collection	0.057	0.012	0.129	0.016	0.493	0.820
Collection × stream-treatment	0.701	0.001	0.017	0.002	0.768	0.868
Section (stream-treatment)	0.721	0.930	0.070	0.375	0.338	0.969

[a] ANOVA model tested for differences among stream-treatments with the influence of collection, stream-treatment/collection interaction and variation among sections within a stream-treatment accounted for. Nesting section within stream treatment also assessed variation among sections within a stream treatment. For each ANOVA, the r^2 and P values are presented.

Table 3
Temporal patterns of canopy and macrophyte coverage for each of the stream-treatments[a]

	Treated PB ***P***	Control FMC ***P***	Control PB ***P***	Undisturbed UTR ***P***
Upper canopy				
Collection	<0.001	0.001	0.022	0.512
Season	<0.001	0.263	0.086	0.123
Linear	0.427	0.009	0.193	–
Surface canopy				
Collection	<0.001	<0.001	0.011	0.006
Season	<0.001	0.005	0.040	0.016
Linear	0.003	0.089	0.776	–
Macrophytes				
Collection	<0.001	<0.001	0.158	0.007
Season	0.008	0.001	0.420	0.004
Linear	0.007	0.242	0.333	
Floating				
Collection	<0.001	<0.001	0.007	0.011
Season	<0.001	<0.001	0.045	0.015
Linear	0.003	0.331	0.784	
Emergent				
Collection	<0.001	0.360	0.001	0.043
Season	0.018	0.099	0.009	0.385
Linear	0.076	0.974	0.320	
Submergent				
Collection	0.002	No var.	<0.001	No var.
Season	0.002	No var.	<0.001	No var.
Linear	0.085	No var.	0.065	No var.

[a] For each type of coverage in each stream treatment, a repeated measures ANOVA tests for differences among the five collection periods. Orthogonal poiynomial contrasts tested for variation between seasons and then for a continuous linear increase or decrease from the first to last collection. Meyers branch did not vary enough to run the tests, so was omitted from the table.

because repeated measures occur within a season (non-independent observations). Additionally, conservative levels of significance should be used. The correlation analyses examined the relationship among the variables by comparing measures from sites without regard to stream-treatment or section, unless specifically comparing sites within a stream-treatment.

3. Results

3.1. Relationships among variables

Upper canopy coverage strongly reduced the amount of surface canopy coverage beneath it, as evident by a strong negative correlation in each, the Spring and Fall collections ($r_{ranks} < -0.81$, $n = 132$ and 76, $P < 0.001$). Surface canopy decreased linearly as upper canopy increased in all three Spring collections ($r^2 = 0.73, 0.68, 0.70$; $P < 0.001$). Because surface canopy is largely composed of aquatic macrophytes, macrophyte coverage and surface canopy are highly correlated (Spring $r_{ranks} = 0.87$; Fall $r_{ranks} = 0.91$). Floating macrophyte abundance had a particularly high correlation with surface canopy ($r_{ranks} > 0.92$, $n =$ 132 and 76) in each the Spring and Fall collections, indicating the prominence of floating macrophytes in the surface canopy. Thus, floating macrophyte abundance had a similar negative correlation with the upper canopy in the collection from both seasons ($r_{ranks} < -0.82$, $n = 132$ and 76, $P < 0.001$). Emergent macrophytes showed a weaker relationship with upper canopy ($r_{ranks} = -0.67$ and -0.60) with only 30–62% of the variation (increasing over time) explained by the linear regressions ($P < 0.001$). Only a weak relationship existed between submergent macrophyte coverage and upper canopy, which was significant in the Spring, but not the Fall collections ($r_{ranks} =$ 0.56, 0.28); during each Spring collection, < 33% of the variation was accounted for in the linear regressions ($P < 0.003$). Total macrophyte coverage was negatively correlated with upper canopy (Spring $r_{ranks} = -0.80$; Fall $r_{ranks} =$ 0.85) and decreased linearly as upper canopy increased in all three Spring collections ($r^2 = 0.64, 0.67, 0.72$; $P < 0.001$).

3.2. Spatial variation

The amount of upper and surface canopy did not differ among sections within a stream-treatment ($P > 0.70$; Table 2). Similarly the three structural types of macrophytes (floating, emergent, and submergent) varied little among sections within a stream-treatment ($P > 0.30$; Table 2). Only total macrophyte coverage varied enough among stream-treatment sections to even be near significantly different ($P = 0.070$) (Table 2).

With the influence of timing of collection and among section variation accounted for, canopy cover significantly differed among the stream-treatments (Table 2). An environmental gradient ranging from an open to closed upper canopy existed among the treated, control, and undisturbed stream-treatments (Fig. IA). The pairwise comparison indicated that the two undisturbed streams (both of which had nearly 100% coverage) did not differ from each other ($P = 0.774$), but differed from the two control streams and treated PB ($P < 0.001$). Within the thermally disturbed streams, the control sections of FMB had less canopy coverage than the control sections of PB, and treated PB had the lowest coverage (Fig. 1A).

Surface canopy varied greatly among stream-treatments ($P < 0.001$). The pairwise comparison indicated that the surface canopy did not differ between the two undisturbed streams or between the two control streams ($P = 1.000$). The negative relationship between surface canopy and the upper canopy produced the reverse environmental gradient among the stream-treatments, with treated PB higher than the control streams which were in turn higher than the undisturbed streams where surface canopy was nearly absent ($P < 0.001$) (Fig. 1B). As expected given their correlation with surface canopy, coverage of floating and emergent macrophytes differed among stream-treatments (Table 2), and based on the pairwise comparison both had the same spatial pattern as surface canopy ($P < 0.008$ or $P > 0.850$). However, the ANOVA for emergent macrophyte coverage explained a relatively smaller proportion of variation than did those for surface canopy and floating macrophytes as indicated by the r^2 values (Table 2).

Similar to the other macrophyte types, submergent macrophyte abundance varied greatly among stream-treatments. However, submergent macrophytes were unique in being prevalent in PB, but nearly absent (< 2% coverage) in control FMB, undisturbed UTR, and undisturbed MB. Consequently the pairwise comparison indicated that the latter three stream-treatments did not differ from each other ($P > 0.70$), but all three differed from the two PB stream-treatments ($P < 0.001$). Submergent coverage in treated PB was similar to that of control PB ($P = 0.094$; mean = 30.6 and 37.9; S.E. = 3.32 and 2.96). In contrast to the above correlation analyses that contained all stream-treatments, within PB where submergent macrophytes were abundant, submergent

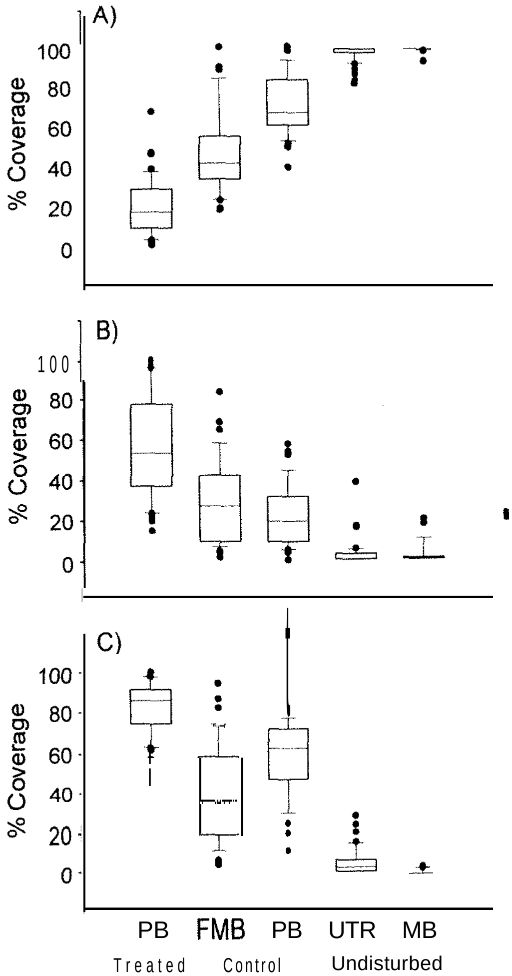

Fig. 1. Box and whisker plot of the (A) upper canopy, (B) surface canopy, and (C) total macrophytes for each of the stream-treatments. The horizontal line within each box represents the median; the surrounding box encompasses the second and third quartiles. The outer ends of the lower and upper whiskers mark the 10th and 90th percentiles. respectively. The black circles represent outlying points.

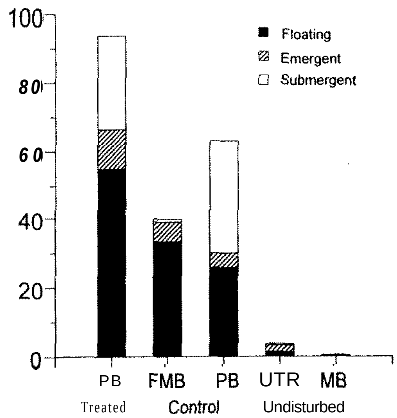

Fig. 2. Mean percent surface coverage of floating, emergent and submergent macrophyte coverage in each of the stream-treatments.

macrophyte coverage was not correlated with upper canopy coverage in either treatment (control or treated) of either season (Spring or Fall) (r_{ranks} = -0.13, -0.17, 0.15, 0.06, n = 27, 18, 36, 24). In control PB, submergent macrophytes also were not correlated with surface canopy in either season (r_{ranks} = − 0.07 and 0.22, n = 27 and 18). However, in treated PB where surface canopy coverage was most extreme, submergent macrophyte coverage was negatively correlated with surface canopy coverage in both seasons (r_{ranks} = − 0.57 and − 0.64, n = 36 and 24). Also of interest, within control PB, submergent macrophytes were positively related to total macrophyte coverage in both seasons (r_{ranks} = 0.78 and 0.60, n = 27 and 18), but not in treated PB (r_{ranks} = 0.17 and − 0.16, n = 36 and 24). This indicates the relative difference of the contribution of submergent macrophytes to total macrophyte coverage in the two stream-treatments (Fig. 2).

Total macrophyte coverage did not differ between the two undisturbed streams ($P = 0.510$) (Fig. 1C). Even though some structural types of macrophytes above did not differ between some pairs of stream-treatments, when combined into total macrophyte coverage, all other pairs of stream-treatments differed ($P < 0.001$). The lower macrophyte coverage in control FMB than control PB (Fig. 1C) is largely explained by the lack of submergent macrophytes in FMB and their high abundance in the treated and control PB (Fig. 2). Simultaneously, floating and emergent macrophytes were similar in coverage in the two control streams.

Canopy coverage of sites within the thermally disturbed streams varied more widely than did those in the undisturbed systems (Fig. 1A). Within the control stream-treatments, in addition to the upper canopy being more closed in control PB than in control FMB, the upper canopy varied over a narrower range (Fig. 1A). Canopy coverage in treated PB was the least variable of the disturbed streams due to the recent canopy removal. In response to the more varied canopy coverages in the disturbed systems, coverage of surface canopy and macrophytes also varied more widely among sites (Fig. 1B and C).

3.3. Temporal vuriation

Upper canopy did not differ among collection dates for the almost completely closed canopy of the undisturbed streams (Table 3). The closed upper canopy of MB did not vary enough to complete the repeated measures ANOVA. Not only did the extent of canopy coverage differ between the two control streams as indicated above, but the temporal patterns also differed. The upper canopy of control PB changed very little among the five collections ($P = 0.022$) and showed no sign of closing in as indicated by absence of a linear relationship ($P = 0.193$). In contrast, the upper canopy of control FMB significantly closed during the study as evident by the significant difference among collections, lack of seasonal variation, and a significant linear relationship ($P = 0.009$). Canopy coverage in FMB began at 39% in Spring 1995, had increased to 45% in Spring 1996, and to 60% in Spring 1997. Based on a Bonferroni adjustment however, the linear response may be considered statistically marginal. The upper canopy of treated PB differed among collections in a seasonal pattern (Table 3), likely due to the predominance of herbaceous plants in the upper canopy following woody canopy removal. Peak canopy coverage occurred in Fall that was at the end of the summer growing season for herbaceous vegetation.

Surface canopy, composed of herbaceous plants, varied more than the upper canopy. The MB sites, nearly void of aquatic plants, did not vary over time in surface canopy, total macrophytes, or any structural type of macrophytes. The other four stream-treatments had at least a weak seasonal pattern of surface canopy coverage with peak coverages highest in the Fall samples; treated PB and control FMB were highly significant (Table 3). Treated PB was the only stream-treatment in which the surface canopy linear contrast was significant (Table 3) indicating that surface canopy closed in over the course of our study.

As expected given the composition of surface canopy, floating macrophytes also peaked in abundance in the Fall (Fig. 3A–C). When considering only floating macrophytes, the linear increase in time is still significant in treated PB, but in no other stream-treatments. Floating macrophytes in control FMB is an example of seasonal variation of abundance being more extreme in some years. Average floating macrophyte coverage in FMB in Fall 95 (68%, S.E. = 5.4) was much higher than any of the other collections between Spring 1995 througli Spring 1997 (mean = 15, 26, 34, 23%; S.E. = 3.7, 7.7, 8.9, 5.8).

Variation of emergent macrophyte coverage seemed more constrained. Emergent coverage differed in a seasonal pattern in the control PB ($P = 0.009$) and possibly treated PB ($P = 0.018$) stream-treatments (Table 3). In contrast to floating macrophytes, peak abundance of emergent macrophytes occurred in the Spring collections. Emergent coverage did not differ temporally in the other stream-treatments (Table 3).

As indicated above in the spatial comparisons, only PB had appreciable coverages of submergent macrophytes, thus only the two PB treatments contained enough submergent macrophytes to have sufficient variation to run the repeated measures ANOVA (Table 3). Submergent macrophytes varied in a seasonal pattern in both the treated and control PB stream-treatments ($P = 0.002$ and $P < 0.001$), with peak abundance occurring in the Spring samples (Fig. 3A and B). In both of these stream-treatments submergent macrophyte growth did not significantly decrease over time ($P = 0.085$ and 0.065; Fig. 3A and B).

Total aquatic macrophyte coverage differed among collections in a seasonal pattern in treated PB, control FMB, and undisturbed UTR. Floating macrophytes were driving the seasonal pattern of total macrophyte growth as peak abundance in these stream-treatments occurred in the Fall samples (Fig. 3A–C). Only one of the stream-treatments, treated PB, increased over time (Table 3). In contrast, total macrophyte coverage of control PB did not significantly vary over time (P = 0.158). This lack of seasonal variation is due to the difference in the season of peak abundance of the structural types of macrophytes (Fig. 3B). A decrease in coverage of submergent macrophytes in the Fall is offset by an increase in abundance of floating macrophytes; the opposite pattern occurs in the Spring.

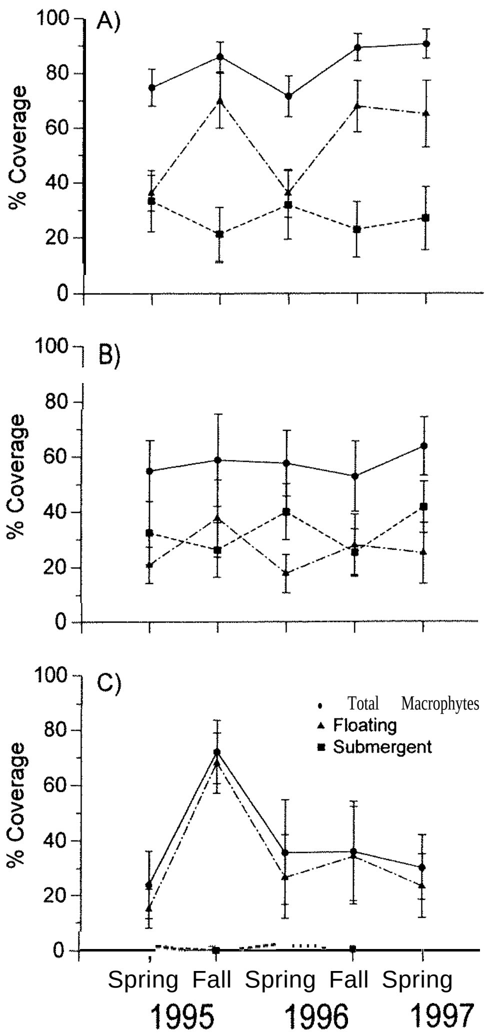

Fig. 3. Temporal variation in mean percent surface coverage of the submergent, floating, and total macrophytes in (A) control Pen branch; (B) treated Pen branch, and (C) control Fourmile branch. Data are not continuous, but lines to allow better visual comparison of the data connect the points.

4. Discussion

Upper canopy coverage of the thermally disturbed streams remains much lower than that in the undisturbed streams after IO-13 years post-disturbance. Despite having 3 more years of growth, FMB had a lower average canopy coverage than the control sections of PB. Canopy coverage over stream channels was more variable on the FMB stream corridor than in the control sections of PB. We have quantified an environmental gradient of canopy closure associated with different types of riparian vegetation. Treated sites of PB with a herbaceous canopy were the most open, shrub willow canopies of the thermally disturbed control sites were intermediate, and the undisturbed sites with hardwood canopies were the most closed. Based on the linear increase of the upper canopy coverage in FMB over the short duration of this study, the canopies of the thermally disturbed sites are still closing in. Thus, the recent nature of the disturbance is partly responsible for the observed differences. However, the type of riparian vegetation present and availability of seed source for further succession may limit the maximum level of canopy coverage that can develop in a system. The maximum level of coverage that will ever be provided by the willow canopy of the disturbed streams may still be much less than that of the hardwood trees. Anecdotal observations of extent of canopy closure of Steel creek (another local stream that received thermal effluents), indicate that even with 17 years more growth, the shrub/willow canopy may not approach the closure of a hardwood forest (pers. obs., DEF and SDW).

Collection of data on macrophyte coverage from sections of stream along this gradient of low to high amounts of canopy coverage provided an ideal situation to examine the influences of canopy coverage on macrophyte abundance in some coastal plain streams of the Southeastern US. Similar to previous studies (Canfield and Hoyer, 1988; Madsen and Adams, 1989) increased shading by riparian vegetation had a severe limiting effect on macrophyte abundance. The herbaceous canopies of the treated PB sections allowed the greatest aquatic macrophyte abundance. The willow-shrub canopies of the control streams allowed an intermediate coverage of macrophytes. The upper canopy coverages of the disturbed streams were relatively near or below the 50% coverage suggested to be necessary to greatly increase macrophyte abundances in Florida streams (Canfield and Hoyer, 1988). Macrophyte coverage was depressed to less than 4% coverage under the hardwood canopies of the undisturbed streams. A discrepancy in the relationship occurred as macrophyte abundance in FMB was lower than that in control PB, even though it has a more open canopy (but see discussion of submergent macrophytes below).

Degree of upper canopy coverage influenced the abundance of the three structural types of macrophytes differently. This difference may be due in part to the location where the different structural types of plants grow. Based on the correlation analyses and the variation explained by the ANOVA, emergent macrophyte coverage was not as strongly related to upper canopy as total macrophyte coverage in general. Water velocity, depth and substrate can also influence macrophyte distributions (Westlake, 1975; Madsen and Adams, 1989). Consequently, in addition to the influence of shading by the riparian canopy, emergent macrophyte abundance was likely restrained by water depth, bottom slope from the bank, and latitudinal patterns of water velocity. Future analyses of these systems should take these factors into account.

Of the three types of macrophytes, the abundance of floating macrophytes had the strongest relationship with upper canopy coverage. Floating macrophytes although still generally rooted in the bank or shallow water, so to some degree restricted — may extend further into the channel. Gradual growth of macrophyte beds can modify their habitat and improve conditions for additional growth by reducing local water velocities (Minckley, 1963; Madsen and Adams, 1989). Thus, floating macrophytes may not have been as restricted by stream geomorphology and velocity patterns as emergent macrophytes. However, since floating macrophytes were still likely, at least to some degree, restricted to near the bank where they may be more susceptible to shading by even a partial upper canopy.

Of the three types of macrophytes, submergent macrophytes were most weakly related to upper canopy. The nearly 60% decrease in canopy coverage in treated PB versus control PB increased abundance of floating and emergent macrophytes, but not that of submergent macrophytes. If different, submergent coverage was actually lower in treated PB. Submergent macrophytes were not restricted to the shoreline, thus grew in the center of the stream where they are less susceptible to shading. The similarity of abundance between these control and treated sections of PB may reflect the inability of the partially closed shrub/willow canopy of the control to extend out to the submergent beds located away from the bank. The filling of this niche by submergent macrophytes in PB and their concurrent absence in FMB also explains the higher abundance of total macrophytes in PB than FMB.

Plant morphology and growth patterns also can influence competition among macrophytes. As depth and velocity allow, floating plants or those with floating leaves can dominate a community by inhibiting light to submergent plants below by structural shading or sedimentation (Minckley, 1963; Westlake, 1975). The negative correlation between surface canopy and submergent abundance in treated PB where the surface canopy was most developed may also indicate the limiting of submergent abundance by surface canopy as opposed to the upper canopy. Such active competitive displacement is known to occur between aquatic macrophyte species (Ham et al., 1982; Everitt and Burkholder, 1991). Low overhanging vegetation (Davies-Colley and Payne, 1998) and floating and emergent macrophytes may provide additional shade to a stream. We have avoided some of this underestimation of light reduction by measuring and analyzing the effects of the surface canopy in addition to that of the upper canopy.

Floating and submergent macrophytes showed a strong seasonal change in abundances, with floating macrophytes peaking in abundance in the Fall and submergent macrophytes in Spring. Similar seasonal cycles and inverse growth patterns have been observed between macrophyte species (Ham et al., 1982). Seasonal changes in the types of aquatic macrophytes present could have important effects on the stream by influencing water flow patterns (both vertical and horizontal), sedimentation rates, and structural habitat availability to aquatic organisms.

5. Conclusions

A gradient in upper canopy coverage existed among the stream-treatments. Increased shading by riparian vegetation decreased macrophyte abundance. As shown in other geographic areas (Canfield and Hoyer, 1988), light availability as controlled by riparian vegetation is a major limiting factor of macrophyte abundance in moderate gradient coastal plain streams of the Southeastern United States. The degree of influence of canopy differed among structural types of macrophytes. Future analyses are necessary to determine what factors (e.g. depth, water velocity, bottom slope, distance to bank, and latitudinal position on the stream corridor) explain the rest of the variation in their abundances. Floating macrophytes were most strongly influenced by riparian shading-followed by emergent and submergent. However, extreme amounts of surface canopy (floating and emergent macrophytes) can also limit submergent macrophyte abundance.

Invasion of the submergent macrophyte *Egeria densa* has greatly inflated macrophyte abundance in PB. Because disturbed sites are prone to invasion by exotic species, restorations that document the re-establishment of habitat and communities provide an opportunity to examine the effects of non-native species (Montalvo et al., 1997) such as ***Egcriu*** on the system. Clearly, the invasion of ***Egeria*** has inflated macrophyte abundance in PB, but future analyses should characterize its influence on flow regimes, geomorphology, and stream fauna. Restoration efforts, such as the canopy manipulation conducted on the treated sections of PB, provide a unique opportunity for large-scale experimentation to test ecological hypotheses (Palmer et al., 1997). Moreover, the restoration efforts in PB have provided a large-scale experiment of the effects of stream canopy removal. Characteristics of the disturbed systems that are thought to be impaired by the canopy alteration of past effluent releases should be further evaluated. Future opportunities include testing whether fauna of these streams will naturally return if the original habitat structure of these streams (or something similar) is restored. The current analyses indicate that returning the hardwood canopy to these streams will help return the natural habitat structure. Future studies and analyses should quantify the success of the current restoration efforts and examine the responses of the stream fauna.

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