Disturbance and Recovery of an Algal Assemblage Following Flooding in an Oklahoma Stream

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ABSTRACT: Algae at 170 fixed sites on the bed of an Oklahoma stream were monitored 1 day before, 4 days after, and 24-26 days after a large flood. Before the flood, 81% of the sampled sites had macroscopically detectable algae. Four days after the flood, algae were macroscopically detected on only 26% of sampled sites. The proportion of sites retaining algae after the flood increased with sediment size, but did not differ between pool and riffle habitats. *Rhizoclonium* and *Spirogyra,* filamentous green algae that predominated before the flood, decreased fourfold and 20-fold in frequency of occurrence, respectively. Tumbling experiments indicated that intrinsic differences in resistance to abrasion contributed to the significant differences in impact of the flood on these two algae. After the 24-26 day recovery period, algae were detected on 66% of the sites. *Spirogyra* replaced *Rhizoclonium* on 39% of the sites in pools where *Rhizoclonium* had dominated 4 days after the flood. *Spirogyra* did not replace *Rhizoclonium* at riffle sites, and *Rhizoclonium* did not replace *Spirogyra* at any site. Replacement of *Rhizoclonium* by *Spirogyra* in pools but not in riffles restored distribution patterns of these two algae before the flood.

INTRODUCTION

Floods are important agents of natural disturbance in streams (Starrett, 1951; Hoopes, 1974; Bilby, 1977; Siegfried and Knight, 1977; Tett *et al.*, 1978; Kimmerer and Allen, 1982; Fisher *et al.*, 1982; Hemphill and Cooper, 1983; Fisher, 1983). During floods, scour and the redistribution of sediment can drastically affect attached algae (Douglas, 1958; Tett *et al.*, 1978; Fisher *et al.*, 1982). Stream algae may survive a flood if they are intrinsically resistant to scouring or if they grow in protected areas in the stream channel. Floras that develop during initial recovery periods will be influenced by relative growth rates of survivors and by colonization rates of algae from outside sources (Stevenson, 1983). If stream discharge remains relatively stable after a flood, biotic interactions, such as grazing, have increasing influence on algal distributions with time (Fisher, 1983; Power and Matthews, 1983; Power *et al.*, 1985).

Warm-water streams subject to periodic flooding provide opportunities to study responses of natural communities to disturbances that vary in frequency, timing and severity (Fisher *et al.*, 1982; Fisher, 1983). Responses of stream algae to these disturbances are of particular interest, because algae are important as primary producers and as a food base in many streams (*e.g.,* Minshall, 1978; Siegfried and Knight, 1977; Power, 1983; Busch and Fisher, 1981). Here we document damage and recovery of algae in Brier Creek, a small stream in S-central Oklahoma, following disturbance by a large flood.

STUDY SITE DESCRIPTION

Brier Creek is a clear-flowing stream in Marshall Co., S-central Oklahoma (33°0′N, 97°2′W), with a base flow discharge of 0.1-0.2 m^3sec^{-1} for much of the year. Pools are typically shallow (<80 cm) and partially isolated by shallow riffles, many of which have minimum thalweg depths of only 2-3 cm. Although upper reaches of Brier

Creek may dry completely by late summer, the 1-km study reach described here remains free-flowing in all but very dry years. The stream channel is incised 2-3 m into sandstone bedrock and Cretaceous deposits of marine limestone. Trees, predominantly oak *(Quercus* spp.), hickory *(Carya* spp.), hackberry *(Celtis* sp.), rough-leafed dogwood *(Cornis drummondi)* and sycamore *(Platanus occidentalis)*, line the stream banks, but channel widths (9-12 m) greatly exceed stream width (2-5 m) at base flow, so most pools are relatively unshaded.

Brier Creek water is moderately hard (1.28-6.00 meq/L as $CaCO_3$), consistently low in soluble reactive phosphorus (3 ug/L), and slightly alkaline (*p*H 7.6-8.7 for water in the main channel). Specific conductance (260-560 uS/cm) and alkalinity are strongly related, indicating that the bicarbonate-carbonate buffer system dominates ionic activity in this creek. NH_4^+ s undetectable (< 0.5 ug/L); concentrations of nitrate and nitrite are unknown, but are probably not limiting for algae because the Brier Creek watershed is largely pastureland stocked with cattle. Water temperatures during June 1983 ranged from 23-36C.

Attached and floating filamentous green algae *(Rhizoclonium* sp. and *Spirogyra* sp.) dominate Brier Creek for most of the year (Power and Matthews, 1983; Power *et al.*, 1985). Phytoplankton is sparse. Attached diatoms (*Synedra* sp., *Navicula* sp., *Fragilaria* sp., *Achnanthes* sp., *Cymbella* sp. and *Gomphonema* sp.) and bluegreen algae (primarily *Oscillatoria* sp.) are locally common and almost ubiquitous as understories beneath the filamentous green algae. From June through October, *Chara zeylanica* occurs in locally dense stands on sandy or muddy substrates in quiet water. At times, *Rhizoclonium* and *Chara* are encrusted with epiphytic diatoms.

METHODS

Algae in seven sequential pools and eight adjacent riffles of a 0.6-km reach of Brier Creek were sampled along cross-stream transects. Three transects were placed across each pool at downstream, middle and upstream positions, and two were placed across each riffle near upstream and downstream ends. Each transect was located by stretching a meter tape between two permanent markers in the stream bank. Because successive measurements of total transect widths varied by only 1-2 cm, we assume our error in relocating sites on the stream bed under the transects was ≤ 4 cm.

At five intervals along each transect (usually 0.5 or 1.0 m apart), we noted depth and substrate and sampled algae. Substrate was described according to a modified Wentworth scale (Hynes, 1970). We initially distinguished six substrate types: mud (organic-rich, not gritty); sand (mineral particles ≤ 2-mm diam); pebbles (2-64 mm); cobbles (65-256 mm); boulders (> 256 mm); and bedrock (fixed rock formations). Substrates above the water level were classified as "dry" regardless of sediment type over them. Boulder and mud substrates were rare before and after the flood (each was represented at only two of 170 sampling sites) and were combined for some analyses with bedrock and sand substrates, respectively.

Dominant and subdominant algae were determined visually at each site. When necessary, algae were identified to genus in the laboratory. We recorded algal condition (scored from 1 = senescent to 3 = fresh) and density (scored from 1 = sparse, 3 = 100% cover) and noted whether algae were attached to the substrate. At each site we also measured the height (or length, if algae were unattached) of typical algal strands (those visually estimated to represent the average). For a sample representing dominant types of algae in Brier Creek during this study, algal height was positively correlated with biomass (ash-free dry weight/cm²) (r = 0.91; n = 23, p < 0.001).

A preflood census was completed on 13 June 1983. The largest flood of the year crested 3.45 m above base flow at ca. 0620 on 14 June 1983. Shortly before 0620, water rose rapidly; stage height increased visibly as an observer (W. J. Matthews) monitored a staff gauge installed in a stream pool. Many large logs and even whole trees were swept downstream. Peak discharge for the flood was computed to be 49.2 m³,

based on cross-sectional area of the channel where crest height was recorded and from direct observations of the velocity of debris on the water surface. (Average velocity was computed as 0.8 surface velocity.) By 1030 on 14 June, the muddy flow had subsided to 0.71 m above base flow. Stream discharge then was estimated to be 0.65 m³ by interpolation, using assumptions of hydraulic geometry (Dunne and Leopold, 1978). We carried out a postflood census on 18 June, when the stream was once again running clear and the water level had subsided enough to allow sampling. A third census was made on 8-10 July 1983 to document the extent of algal recovery 3 weeks after the flood.

To evaluate the relative resistance of various algae to abrasion, we simulated scouring flood conditions by tumbling cobbles in a cement mixer. Algae-covered cobbles from Brier Creek, 48-120 mm median diam, were tumbled individually or in groups in about 20 liters of water at 48 rpm. Before and periodically during tumbling, algal cover was quantified using a clear plastic overlay on which 30 dots were randomly positioned. Algae under each dot were noted, as were "skins" (thin, tightly adhering layers dominated by *Oscillatoria*) and "bare" rock, categories that increased as algal overstories were rubbed off. The overlay was held in the same position for repeated scorings of cobbles, so that site-specific changes could be followed.

For the following analyses, proportions were subjected to arc sin transformations (Steel and Torrie, 1960; Sokal and Rohlf, 1981) before statistical tests of differences were applied.

RESULTS

COMPARISONS OF PREFLOOD AND POSTFLOOD CONDITIONS (13 AND 18 JUNE 1983)

Despite devastating scour in the stream channel, we recovered markers necessary to relocate 34 of the 37 crossstream transects: 18 in pools and 16 in riffles. Comparisons of 170 sites along these transects showed major changes in physical substrates and algae. Because only 5 days elapsed between preflood and postflood sampling, we assume that these changes were caused by the flood.

Changes in substrate. — Overall, only 38% of the sampled sites in our study reach had the same dominant substrate before and after the flood (Table 1). This proportion was slightly higher in pools (44%) than in riffles (31%) ($P < 0.10$ from a two-tailed t-test). Sites left dry by channel path changes are considered altered as habitat for algae even if they retained original substrates. The proportion of sites with unaltered substrate increased with particle size. For sites that initially had mud, sand, pebble, cobble and boulder-bedrock substrates, the proportions of unchanged sites were 0.00, 0.24, 0.18, 0.36, and 0.71, respectively ($r_s = 0.90$; $P < 0.05$). The flood scoured finer sediments out of the channel. Proportions of submersed sites with pebble-sized or finer substrates decreased from 48 to 29% in pools, and from 49 to 28% in riffles ($P < 0.01$ and $P < 0.02$, respectively, from two-tailed t-tests).

Changes in algae. — Before the flood, filamentous green algae (*Spirogyra* sp. and *Rhizoclonium* sp.) covered most substrates, dominating at 76% of the riffle sites and at 88% of the pool sites (Table 2). *Spirogyra* was significantly more abundant in pools than in riffles and was more common than *Rhizoclonium*. The reverse was true in riffles, where *Rhizoclonium* dominated (Table 2, $P < 0.001$ from two-tailed t-tests for all four comparisons). On substrates where *Rhizoclonium* dominated, it was on average taller than *Spirogyra*, but appeared in poorer condition (Table 3). At many sites, a tall overstory of slightly frayed, epiphyte-covered *Rhizoclonium* lay over short, thick turfs of fresh *Spirogyra*. *Spirogyra* appeared to be in similar stages of development in riffles and pools, for filament height and condition were similar in both habitats (Table 3). *Rhizoclonium* condition was similar in pools and riffles as well, and this alga was slightly, but not significantly, shorter in riffles.

Rhizoclonium was the dominant alga on sites that ranged in depth from 0-76 cm, while *Spirogyra* dominated on sites with depths ranging from 0-136 cm (the deepest site sampled). Algal heights (y) for both species were weakly related to water depth (x): for

TABLE 1. – Transition matrices for substrates in pools (upper) and riffles (lower), determined from pre- and postflood sampling on 13 and 18 June 1983, respectively. Numbers are total sampled sites where a given substrate type dominated

	Dry	Mud	Sand	Pebbles	Cobbles	Bedrock	Total	Proportion
Pools				18 June (postflood)				
Dry	0	0	0	0	0	0	0	0.00
Mud	0	0	1	0	0	0	1	0.01
Sand	1	0	4	2	3	7	17	0.19
Pebbles	2	0	6	5	4	8	25	0.28
Cobbles	0	0	2	1	4	5	12	0.13
Bedrock	2	1	1	2	2	27	35	0.39
Total	5	1	14	10	13	47	90	
Proportion	0.05	0.01	0.16	0.11	0.14	0.52		1.00
Riffles				18 June (postflood)				
Dry	1	0	0	3	0	1	5	0.06
Mud	0	0	0	0	0	0	0	0.00
Sand	0	0	0	0	0	0	0	0.00
Pebbles	8	0	4	6	8	11	37	0.46
Cobbles	5	0	0	4	8	4	21	0.26
Bedrock	5	0	0	0	2	10	17	0.21
Total	19	0	4	13	18	26	80	
Proportion	0.24	0.00	0.05	0.16	0.22	0.33		0.99

Spirogyra, y = − 0.02x + 3.23, n = 87, r² = 0.06 (P < 0.05); for *Rhizoclonium*, y = 0.22 x + 3.15, n = 60, r² = 0.19 (P < 0.001).

Before the flood, *Chara zeylanica* was the dominant algae at 2% of the sites. Diatoms and bluegreen algae (mostly *Oscillatoria* sp.) were common under and among filamentous green algae, but were dominant as a thin "skin" in only one site in a riffle (Table 4).

Massive amounts of algae were lost from the study reach of Brier Creek due to the flood. *Chara* was completely eliminated from sampled sites, and the occurrence of *Spirogyra* and *Rhizoclonium* dropped from 47 and 36% of the 170 sampled sites to 2 and 9%, respectively (P < 0.001 from two-tailed t-tests for both comparisons). *Rhizoclonium* survivorship (at 15 of 61 sampled sites = 15%) was significantly higher than that of *Spirogyra* (4/79 = 5% of sampled sites) (P < 0.001 from a two-tailed t-test). In most areas of the stream, the formerly lush stands of filamentous green algae remained only as thin fringes or tufts on the edges and corners of cobbles, boulders and bedrock. The proportion of sites that were bare or covered with a thin algal skin increased from 12% to 59% (P < 0.001 from a two-tailed t-test) (Table 4).

Diatoms and bluegreen algae were not dominant at any sampling site before the

TABLE 2. — Composition of attached algae in riffles and pools before (13 June) and after a flood (18 June). Numbers are proportions of sampled sites where a given algal type dominated

Algae	Riffles (n = 80)		Pools (n = 9)	
	Preflood	Postflood	Preflood	Postflood
Rhizoclonium	0.54	0.09	0.20	0.09
Spirogyra	0.22	0.00	0.68	0.04
Bluegreens	0.00	0.04	0.00	0.06
Diatoms	0.00	0.14	0.00	0.04
Chara	0.03	0.00	0.01	0.00
Skin	0.01	0.01	0.00	0.01
Detritus	0.00	0.00	0.02	0.04
Bare	0.15	0.49	0.09	0.66
Dry	0.05	0.22	0.00	0.06

TABLE 3. — Average height and condition of algae in pools and riffles before the flood (13 June 1983)

Algae		Algal height (cm)		Condition score[a]	
		Pools	Riffles	Pools	Riffle
Spirogyra	x̄	2.58	2.17	2.29	2.49
	SE	0.18	0.30	---	---
	n	81	37	81	37
Rhizoclonium	x̄	7.90[b]	4.65	1.31[c]	1.14
	SE	1.54	0.79	---	---
	n	35	48	35	48

[a]1 = senescent, 3 = fresh
[b]*Rhizoclonium* height greater than *Spirogyra* height in pools and riffles (P < 0.01 and P < 0.001, respectively, from two-tailed t-tests)
[c]*Spirogyra* condition appears better than *Rhizoclonium* condition in both pools and riffles (P < 0.001, median test, Siegel, 1956, p. 111)

TABLE 4. — Transition matrices for algae in pools (upper) and riffles (lower) before (13 June) and after (18 June) a flood. Numbers are total sampled sites where a given algal type dominated

	Rhizoclonium	Spirogyra	Bluegreen	Diatom	Chara	Skin	Detritus	Bare	Dry	Total	Proportion
Pools					18 June (postflood)						
Rhizoclonium	0	0	1	2	0	1	1	12	1	18	0.20
Spirogyra	6	4	4	2	0	0	2	40	3	61	0.68
Bluegreen	0	0	0	0	0	0	0	0	0	0	0.00
Diatom	0	0	0	0	0	0	0	0	0	0	0.00
Chara	0	0	0	0	0	0	0	1	0	1	0.01
Skin	0	0	0	0	0	0	0	0	0	0	0.00
Detritus	0	0	0	0	0	0	0	2	0	2	0.02
Bare	2	0	0	0	0	0	1	4	1	8	0.09
Dry	0	0	0	0	0	0	0	0	0	0	0.00
Total	8	4	5	4	0	1	4	59	5	90	
Proportion	0.09	0.04	0.06	0.04	0.00	0.01	0.04	0.66	0.06		1.00
Riffles					18 June (postflood)						
Rhizoclonium	5	0	3	5	0	2	0	21	7	43	0.54
Spirogyra	2	0	0	6	0	0	0	8	2	18	0.23
Bluegreen	0	0	0	0	0	0	0	0	0	0	0.00
Diatom	0	0	0	0	0	0	0	0	0	0	0.00
Chara	0	0	0	0	0	0	0	2	0	2	0.03
Skin	0	0	0	0	0	0	0	1	0	1	0.01
Detritus	0	0	0	0	0	0	0	0	0	0	0.00
Bare	0	0	0	0	0	0	0	4	8	12	0.15
Dry	0	0	0	0	0	0	0	3	1	4	0.05
Total	7	0	3	11	0	2	0	39	18	80	
Proportion	0.09	0.00	0.04	0.14	0.00	0.03	0.00	0.49	0.22		1.01

(Row groups labeled "13 June (preflood)" for both Pools and Riffles sections.)

flood. Afterwards, bluegreens dominated at 5/90 sites in pools and 3/80 sites in riffles; diatoms dominated at 4/90 pool sites and at 11/80 riffle sites (Table 4). Increases in proportions of both types of algae were significant (P < 0.02 and P < 0.001 for bluegreens in riffles and pools, respectively; P < 0.001 and P < 0.02 for diatoms in riffles and pools, respectively, from two-tailed t-tests). After the flood, bluegreens (mainly *Oscillatoria* sp.) were conspicuous on many boulders and large cobbles, where they appeared as turquoise-colored skins studded with bubbles. The photosynthetic activity of these former understories appeared intense following their 'release' from filamentous green algal overstories.

Persistence of particular algae in the study site after a flood could be affected by its position in the stream channel or by intrinsic resistance of the alga to abrasion. When 15 cobbles with 100% *Rhizoclonium* cover and 15 with 100% *Spirogyra* cover were tumbled together for 2 min at 48 rpm in a "flood simulator" (concrete mixer), generic differences in resistance of the algae to scouring were apparent. Of the original 30 points scored before tumbling on each cobble, *Rhizoclonium* cobbles had on average 12.4 (± 1.6; SE) sites that retained *Rhizoclonium*; significantly fewer [1.5 (± 0.6; SE)] sites on *Spirogyra* cobbles retained *Spirogyra* (P < 0.001 Mann-Whitney U test).

No differences in the relative vulnerability of pool and riffle habitats to scouring were detected. In pools, 5% of the sampled sites retained their original flora, while 8% retained original flora in riffles (P > 0.20, one-tailed t-test). Similarly, so few postflood sampling sites retained filamentous green algae that differences in its persistence on different types of substrate could not be detected. There was, however, a substrate-dependent difference in the proportion of sites that retained any algae (filamentous greens or diatom/bluegreen understories) compared with those that were bare after the flood (Table 5), with greater algal retention on bedrock-boulder substrates. Substrate stability increased with particle size: bedrock slabs were not moved by the flood, although some boulders > 256 mm median diam were moved.

To further examine relationships between substrate stability and algal persistence, we classified sites that had algae before the flood into two groups: those in which substrate type was changed, and those that were unchanged. For this analysis only, we considered the substrate to have changed if neither the dominant nor the subdominant substrate noted before the flood was present as the dominant on 18 June. This definition was adopted to increase the probability that substrate types reported as changed were actually different particles, rather than resident substrates whose relative abundances had been altered. In this analysis, we found no relationship between substrate change and the retention of algae; the proportion of changed and unchanged sites retaining algae was 0.39 (n = 59) and 0.27 (n = 59), n = 70, respectively ($\chi^2 = 3.04$, df = 1, ns). Processes that would obscure or weaken this relationship include replacement of old substrates by new substrates of the same type, severe scouring of substrates *in situ*, and "rafting" of algae on displaced particles. Evidence of the last two processes was apparent in Brier Creek after the flood. New channels several centimeters deep were carved into the surfaces of fixed sandstone bedrock in some areas. Pebbles and cobbles 3-12 cm median diam (many bearing tufts of *Spirogyra* or *Rhizoclonium* and showing obvious signs of abrasion) were strewn on the formerly sand-covered bottoms of pools. We visually estimated that one pool contained 3-6 such transported stones per m². These "rafts" may have been important in the postflood recolonization of stream pools by algae.

RECOVERY PERIOD (18 JUNE TO 8-10 JULY 1983)

No floods occurred from 18 June to 10 July, although a brief rain did increase the stage height a few cm on one occasion. During this recovery phase, substrates at more sites remained unchanged in pools (67%), in riffles (45%) and in the reach as a whole (59%) than from 13 June to 18 June (p < 0.05, p < 0.001, and p < 0.001, respectively, from one-tailed t-tests). Substrate changes that occurred during this period were primarily due to movements of fine sediments (pebble-size and smaller), some of which

sloughed from bank-side deposits. Redistribution of fine sediment within the stream channel covered or exposed coarser substrates. A number of transects in riffles prior to the flood fell within pools after the flood because of channel changes. Reclassification of these transect sites results in an increase in the number of pool sites and a decrease of riffle sites (Table 6).

The period of relative physical stability in the stream allowed us to examine changes in the algal flora as recovery on scoured areas. During the 20 to 22d after the first postflood survey, the number of sites with *Spirogyra* and *Rhizoclonium* both increased, but

TABLE 5. — Proportion of pool and riffle sampling sites retaining algae at sites where substrate type was unaltered by the flood[a]

	Substrate type			
	Mud, sand	Pebbles	Cobbles	Boulders, bedrock
Proportion of sites retaining algae	0.00	0.17	0.32	0.60
Number of sites	10	48	28	43

[a]$\chi^2 = 25.28$; df = 3, P < 0.001

TABLE 6. — Transition matrices for substrates in pools[a] (upper) and riffles for sampling dates 4 days and 3 weeks after a flood (18 June and 8-10 July, respectively). Numbers are total sampled sites where substrate type dominated

Pools				8-10 July			
Substrate	dry	mud	sand	pebs	cobs	b'rock	Total
Dry	1	0	0	0	0	0	1
Mud	0	0	0	0	0	1	1
Sand	1	0	6	3	1	1	12
Pebbles	1	0	1	4	2	2	10
Cobbles	0	0	0	2	6	5	13
Bedrock	2	0	3	9	1	55	70
Total	5	0	10	18	10	64	107

(18 June, left column labels)

Riffles				8-10 July			
Substrate	dry	mud	sand	pebs	cobs	b'rock	Total
Dry	2	0	0	2	2	0	6
Mud	0	0	0	0	0	0	0
Sand	0	0	0	1	0	0	1
Pebbles	1	0	0	9	3	1	14
Cobbles	1	0	0	7	7	5	20
Bedrock	4	0	0	6	1	10	21
Total	8	0	0	25	13	16	62

(18 June, left column labels)

[a]Channel changes caused 17 sites located in riffles before the flood to fall in pools afterwards.

Spirogyra increased more than *Rhizoclonium*. In the reach as a whole *Spirogyra* increased from 3% to 39% of sampled sites (P < 0.001, one-tailed t-test), while *Rhizoclonium* increased from only 14% to 15% of sampled sites (P > 0.20). *Rhizoclonium* increased more in riffles (from 8% to 26% of sampled sites; P < 0.01, one-tailed t-test), but actually decreased in pools (from 17% to 9% of sampled sites; P < 0.20, one-tailed t-test). *Spirogyra* replaced *Rhizoclonium* on 7 of 18 sites where it had initially occurred in pools after the flood (Table 7). *Rhizoclonium* never replaced *Spirogyra* in pools, and no overgrowths of either filamentous green alga by the other occurred in riffles during this period (Table 7).

Substrates covered by bluegreen algae in pools declined from 5% to 2% of sampled sites because of overgrowth by *Rhizoclonium* (two sites) and *Spirogyra* (one site). The proportion of sites with detritus, presumably derived from organic matter transported by the flood, increased from 6% to 21% in pools, and from 0% to 7% in riffles caused by deposition as the flow receded.

DISCUSSION

Disturbance of streams by floods is a common and conspicuous phenomenon (Siegfried and Knight, 1977; Cummins, 1977; Fisher *et al.*, 1982; Fisher, 1983). The effects of flood disturbances on streams depend on flood frequency and magnitude and on antecedent conditions (Wolman and Miller, 1960; Cummins *et al.*, 1983). Frequent floods can truncate algal successional sequences, thereby favoring either tightly attached, resistant forms or those with recolonization and growth rates high enough to accumulate biomass between floods. In this study, for example, extensive mats of *Spirogyra* recovered within weeks after the flood. *Chara*, however, took months to recover (A. J. Stewart, pers. observ.), suggesting that if scouring occurred frequently, this alga would be unable to persist in Brier Creek.

Flood magnitudes determine the nature of their effects on stream organisms. During small floods, sand and mud entering and moving within the channel can smother adnate algae but may promote growth of algae such as *Chara*. Inputs and mixing during small floods may also increase nutrient availability. Blooms of filamentous green algae followed small floods in Brier Creek (Power *et al.*, 1985). Large floods like that of June 1983, on the other hand, severely erode the stream bed and may have long-term consequences to algal assemblages if they move major channel features, such as gravel bars, or if they reduce densities of stream fauna that affect algae. For example, when large floods coincide with spawning periods of stream fishes, year classes can be severely reduced or eliminated (Starrett, 1951; Pflieger, 1975).

The effect of a flood of particular magnitude on stream biota depends on a number of antecedent conditions, including the amounts and types of sediment and detritus in storage in the channel, and the growth stage, species composition and spatial distributions of biota (Cummins *et al.*, 1983). A flood occurring when sand and pebbles are in low supply may have less effect on biota than a flood of the same magnitude occurring when fine sediments are available for transport and scouring. Large organic debris that stabilizes sediment mitigates the scouring effects of floods (Keller and Swanson, 1979).

Developmental state apparently influenced the ability of *Spirogyra* in Brier Creek to resist scour. Several weeks before the June flood, we rubbed a bare patch on a flat bedrock substrate. Much of the short, fresh turf of *Spirogyra* that regrew in this patch remained after the flood, while similar adjacent bedrock substrate, which had supported a turf of longer, more senescent *Spirogyra* filaments just before the flood, was scoured to bare rock.

Species differences among algae also strongly affect their ability to resist shearing forces associated with high flow. *Oscillatoria* in Brier Creek was resistant to scour by virtue of its nearly endolithic growth habit under filamentous green algal overstories. *Oscillatoria* was an important component of a turquoise-colored "algal skin" that persisted on cobbles, boulders and bedrock in the stream and on cobbles during tumbling experiments, after filamentous green algal overstories had been abraded off.

TABLE 7. — Transition matrices for algae in Brier Creek pools and riffles 18 June to 8-10 July 1983

Pools

8-10 July (postflood)

	Rhizoclonium	Spirogyra	Bluegreen	Diatom	Chara	Skin	Detritus	Bare	Dry	Total	Proportion
Rhizoclonium	5	7	0	2	0	0	3	1	0	18	0.17
Spirogyra	0	4	0	0	0	0	1	0	0	5	0.05
Bluegreen	2	1	0	1	0	0	1	0	0	5	0.05
Diatom	0	6	0	1	0	0	1	0	0	8	0.07
Chara	0	0	0	0	0	0	0	0	0	0	0.00
Skin	0	0	0	0	0	0	0	0	0	0	0.00
Detritus	2	2	2	0	0	0	0	0	0	6	0.06
Bare	3	31	0	6	0	0	16	4	4	64	0.60
Dry	0	0	0	0	0	0	0	0	1	1	0.01
Total	12	51	2	10	0	0	22	5	5	107	
Proportion	0.09	0.48	0.02	0.11	0.00	0.00	0.20	0.05	0.05		1.00

(18 June rows at left)

Riffles

8-10 July (postflood)

	Rhizoclonium	Spirogyra	Bluegreen	Diatom	Chara	Skin	Detritus	Bare	Dry	Total	Proportion
Rhizoclonium	2	0	0	1	0	0	0	2	0	5	0.08
Spirogyra	0	0	0	0	0	0	0	0	0	0	0.08
Bluegreen	0	0	0	0	0	0	0	0	0	0	0.00
Diatom	3	2	0	1	0	0	1	1	0	8	0.13
Chara	0	0	0	0	0	0	0	0	0	0	0.00
Skin	1	1	0	0	0	1	0	2	0	4	0.06
Detritus	0	0	0	0	0	0	0	0	0	0	0.00
Bare	9	12	0	4	0	1	2	9	3	40	0.64
Dry	1	0	0	0	0	0	1	1	2	5	0.08
Total	16	15	0	6	0	1	4	15	5	62	
Proportion	0.26	0.24	0.00	0.10	0.00	0.01	0.06	0.24	0.08		0.99

(18 June rows at left)

Spirogyra and Rhizoclonium differ markedly in their ability to cling to substrates. Rhizoclonium has specialized basal attachment cells that anchor filaments firmly to stony substrates (Round, 1973), while Spirogyra is "usually unbranched and free-floating, but sometimes attached by lateral or terminal hapteroid outgrowths" (Silva, 1982, p. 158). The latter method of attachment is weak compared to that of Rhizoclonium, as evidenced by the relative resistance of the two algae during tumbling experiments. Developmental differences did not account for these differences, because cobbles with short fresh turfs of Spirogyra were selected for tumbling experiments.

Before the June 1983 flood, Rhizoclonium was the most common alga on riffle substrates, while Spirogyra dominated in pools (Table 2). After the flood, Rhizoclonium persisted on more sites than Spirogyra in both habitats. On all 170 sampling sites in pools and riffles, Rhizoclonium occurrence decreased fourfold after the flood, while Spirogyra occurrence decreased by a factor of 20. The pool-riffle segregation of these two algae and their differential abilities to survive flood conditions, may result from differences in their methods of attachment. Differential resistance to scouring caused by attachment differences have been reported for lotic macrophytes (Elodea vs. Potamogeton; Bilby, 1977) and riparian mosses (Conocephalum vs. Fissidens; Kimmerer and Allen, 1982).

Despite dominance of Rhizoclonium 4 days after the flood, Spirogyra surpassed it in frequency of sites occupied only 3 weeks later. Spirogyra accumulated especially rapidly in pools, where it replaced Rhizoclonium on 39% of the sites where Rhizoclonium had been dominant 4 days after the flood. In the weeks following the flood, dense mats of unattached Spirogyra accumulated over attached Rhizoclonium. These floating mats shaded the rock-bound algae and may have reduced their growth rates. The growth rate advantage of Spirogyra over Rhizoclonium during periods of low flow may be further enhanced by the tendency for Rhizoclonium, but not Spirogyra, to become heavily overgrown by epiphytic diatoms. Epiphytes can shade their hosts, deprive them of nutrients, and sometimes physically damage cell walls, leaving host algae open to fungal or bacterial attack (Sand-Jensen, 1977; Eminson and Phillips, 1978; Stevenson and Stoermer, 1982). In Brier Creek, preliminary studies show that epiphytes also increase preference for Rhizoclonium by the dominant grazer, the minnow Campostoma anomalum. Floods that wash epiphytes off Rhizoclonium and displace floating mats of Spirogyra could periodically enhance the growth and abundance of Rhizoclonium.

Disturbance, sometimes attended by compensatory mortality of competitive dominants, has been shown to promote coexistence of sessile species in intertidal and terrestrial forest communities (Dayton, 1971, 1984; Connell, 1978; Sousa, 1979a, 1979b, 1984; Paine and Levin, 1981; Paine, 1984). Discharge changes have been reported to disrupt competitive monopolies and increase space held by subordinate species of benthic insects in California (Hemphill and Cooper, 1983), and Montana (McAuliffe, 1984) streams. We have no direct evidence that Rhizoclonium and Spirogyra compete in Brier Creek, but high-standing crops (at low flow, some pools can be nearly filled with these filamentous green algae) and evidence of nutrient limitation (Stewart, 1987) suggest that, in the absence of flooding, competition between these two abundant, co-occurring algae is likely. In this context, characteristics that are advantageous for Spirogyra at low flow (e.g., tenuous attachment, high growth rates as floating mats) render this alga more vulnerable than Rhizoclonium to washout during high flow.

Sousa (1984, p. 356) has defined disturbance as, "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established." Bare space on Brier Creek substrates is created not only during floods, but after prolonged periods of low flow when algal mats senesce, and pieces break off and are buoyed to the water surface by gas bubbles (Power et al., 1985). In Brier Creek, as in many natural communities (Sousa, 1984), the lack of environmental fluctuations as well as their occurrence can disturb organisms, and the response to a particular disturbance regime depends on characteristics peculiar to individual target species.

LITERATURE CITED

BILBY, R. 1977. Effects of a spate on the macrophyte vegetation of a stream pool. *Hydrobiologia,* **56**:109-112.

BUSCH, D. E. AND S. G. FISHER. 1981. Metabolism of a desert stream. *Freshwater Biol.,* **11**:301-307.

CONNELL, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science,* **199**:1302-1310.

CUMMINS, K. W. 1977. From headwater streams to rivers. *Am. Biol. Teach.,* **39**:305-312.

————, J. R. SEDELL, F. J. SWANSON, G. W. MINSHALL, S. G. FISHER, C. E. CUSHING, R. C. PETERSEN AND R. L. VANNOTE. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation, p. 299-353. *In:* J. R. Barnes and G. W. Minshall (eds.). Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

DAYTON, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.,* **41**:351-389.

————. Processes structuring some marine communities: are they general? p. 181-197. *In:* D. R. Strong, Jr., D. Simberloff, L. G. Abele and A. B. Thistle (eds). Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, N.J.

DOUGLAS, B. 1958. The ecology of the attached diatoms and other algae in a small stony stream. *J. Ecol.* **46**:295-322.

DUNNE, T. AND L. B. LEOPOLD. 1978. Water in environmental planning. W. H. Freeman and Co., San Francisco, Calif. 818 p.

EMINSON, D. AND G. PHILLIPS. 1978. A laboratory experiment to examine the effects of nutrient enrichment on macrophyte and epiphyte growth. *Int. Verh. Limnol.,* **20**:82-87.

FISHER, S. G. 1983. Succession in streams, p. 7-27. *In:* J. R. Barnes and G. W. Minshall (eds.). Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

————, L. J. Gray, N. B. Grimm and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecol. Monogr.,* **52**:93-110.

HEMPHILL. N. AND S. D. COOPER. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia,* **58**:378-382.

HOOPES, R. L. 1974. Flooding, as a result of hurricane Agnes, and its effect on a macrobenthic community in an infertile headwater stream in central Pennsylvania. *Limnol. Oceanogr.,* **19**:853-857.

HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto. 555 p.

KELLER, E. A. AND F. J. SWANSON. 1979. Effects of large organic material on channel form and fluvial processes. *Earth Surf. Proc.,* **4**:361-383.

KIMMERER, R. W. AND T. F. H. ALLEN. 1982. The role of disturbance in pattern of a riparian bryophyte community. *Am. Midl. Nat.,* **107**:370-383.

McAULIFFE, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology,* **65**:894-908.

MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. *BioScience,* **28**:767-771.

PAINE, R. T. 1984. Ecological determinism in the competition for space. *Ecology,* **65**:1339-1348.

———— AND S. A. LEVIN. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.,* **51**:145-178.

PFLIEGER, W. L. 1975. Reproduction and survival of the smallmouth bass in Courtois Creek, p. 231-239. *In:* H. Clepper (ed.). Black bass biology and management. Sport Fishing Institute, Washington, D.C.

POWER, M. E. 1983. Grazing responses of tropical freshwater fishes to different scales of varia-
    tion in their food. *Environ. Biol. Fishes*, **9**:103-115.
_____ AND W. J. MATTHEWS. 1983. Algae-grazing minnows (*Campostoma anomalum*), piscivor-
    ous bass *(Micropterus* spp.) and the distribution of attached algae in a small prairie-
    margin stream. *Oecologia*, **60**:328-332.
_____, _____ AND A. J. STEWART, 1985. Grazing minnows, piscivorous bass and stream al-
    gae: dynamics of a strong interaction. *Ecology*, **66**:1448-1456.
ROUND, F. E. 1973. The biology of the algae. Edward Arnold, London. 278 p.
SAND-JENSEN, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.*, **3**:55-63.
SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Co., New
    York. 312 p.
SIEGFRIED, C. A. AND A. W. KNIGHT. 1977. The effects of washout in a Sierra foothill stream.
    Am. Midl. Nat., **98**:200-207.
SILVA, P. C. 1982. Chlorophyceae, p. 133-61. *In*: S. P. Parker (ed.). Synopsis and classification
    of living organisms, Vol. 1. McGraw-Hill, New York.
SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry — The principles and practices of statistics in bi-
    ological research. W. H. Freeman and Co., San Francisco, Calif. 859 p.
SOUSA, W. P. 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium main-
    tenance of species diversity. *Ecology*, **60**:1225-1239.
_____. 1979b. Experimental investigations of disturbance and ecological succession in a
    rocky intertidal algal community. *Ecol. Monogr.*, **49**:227-254.
_____. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable pat-
    terns of succession. *Ecology*, **65**:1918-1935.
STARRETT, W. C. 1951. Some factors affecting the abundance of minnows in the Des Moines
    River, Iowa. *Ibid.*, **32**:13-27.
STEEL, R. G. D. AND J. H. TORRIE. 1960. Principles and procedures of statistics with special
    reference to the biological sciences. McGraw-Hill Book Co., New York. 481 p.
STEVENSON, R. J. 1983. Effects of current and conditions simulating autogenically changing
    microhabitats on benthic diatom immigration. *Ecology*, **64**:1514-1524.
_____ AND E. F. STOERMER. 1982. Seasonal abundance patterns of diatoms on *Cladophora* in
    Lake Huron. *J. Great Lakes Res.*, **8**:169-183.
STEWART, A. J. 1987. Response of stream algae to grazing minnows and nutrients: a field test
    for interactions. Oecologia. In press.
TETT, P., C. GALLEGOS, M. G. KELLY, G. M. HORNBERGER AND B. G. COSBY. 1978. Relation-
    ships among substrate, flow, and benthic microalgal pigment density in the Mechums
    River, Virginia. *Limnol. Oceanogr.*, **23**:785-797.
WOLMAN, M. G. AND J. P. MILLER. 1960. Magnitude and frequency of forces in geomorphic
    processes. *J. Geol.*, **68**:54-74.