

Herbs and grasses as an allochthonous resource in open-canopy headwater streams

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SUMMARY

1. The organic matter dynamics of streams dominated by herbs and grass on their banks are poorly understood, despite the fact that such streams are common worldwide. Further, herbs and grasses can provide large quantities of detritus to stream food webs, and particularly small streams can be heavily shaded by overhanging vegetation, perhaps limiting in-stream primary production.
2. We quantified the standing crop of edge vegetation and associated macroinvertebrate communities along three headwater streams with herbaceous and grass riparian vegetation on agricultural land in the Piedmont of Maryland, U.S.A., measured the decomposition of four common species of herbs and grasses using experimental leaf packs, and removed edge vegetation experimentally to determine the effect of shading on benthic algal production.
3. Large standing crops of plant material (average range: 68–276 g ash-free dry mass per m⁻²), composed largely of monocotyledons, were found at all three study streams. These values are similar to those for coarse particulate organic matter in deciduous forested streams in the eastern U.S.A. In addition, diverse assemblages of shredding macroinvertebrates were observed at all three study sites.
4. Decomposition of the herbs was faster than that of the grasses, and both decomposed faster than most deciduous tree leaf litter. The decomposition rates of the herbs and grasses were significantly related to leaf quality as measured by leaf nitrogen content. Macroinvertebrate shredders colonized all experimental leaf packs, and the colonization of the herbs was faster than that of the grasses.
5. The accrual of chlorophyll-*a* after the removal of shading vegetation was faster than that measured prior to removal as well as that in an unmanipulated control reach.
6. Given that the standing crop of organic matter in streams with herbs and grass along their banks was similar to that in forested streams, that the organic matter was rich in nitrogen and used by detritivores, and riparian shading limited algal growth, we suggest that herbaceous and grass plant material may be an important allochthonous food resource in such systems.

Keywords: agriculture, headwater stream, herbaceous vegetation, macroinvertebrate, organic matter decomposition

Introduction

Deforestation has well-known impacts on stream ecosystems (Gregory *et al.*, 1991; Sweeney, 1993; Allan, 2004). The removal of shade obviously increa-

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ses solar radiation to the streambed and increases algal production and water temperature (Hetrick *et al.*, 1998a; Bourque & Pomeroy, 2001). These changes, in turn, affect invertebrate communities (Hetrick *et al.*, 1998b; Kelly, Bothwell & Schindler, 2003), and recent work by Sweeney *et al.* (2004) suggests that deforestation may profoundly affect organic matter processing and nitrogen uptake by the streambed. Open-canopy streams with bank vegetation dominated by herbs and grasses are now very common in suburban and agricultural landscapes throughout the world. Understanding the ecosystem function, particularly the organic matter dynamics, of such streams is important given that many formerly agricultural streams, along with their riparian corridors of herbaceous vegetation, may persist as the dominant source of undeveloped land in rapidly urbanizing regions (Moore & Palmer, 2005).

Research on the ecological roles of herbs and grasses growing along open-canopy streams has been limited largely to describing the ability of the vegetation to mitigate the effects of agricultural land use (Montgomery, 1997; Lyons, Trimble & Paine, 2000). The decomposition dynamics of herbs and grasses and their availability to stream consumers are sparsely studied (but see Mackay, Zak & Whitford, 1992; Young, Huryn & Townsend, 1994) compared with those of deciduous tree leaf litter (Webster & Benfield, 1986; Ostrofsky, 1997). In fact, studies of treeless streams have suggested that algae are the dominant basal resource of stream food webs (Delong & Brusven, 1998). Work by Moore & Palmer (2005) in mid-Atlantic Piedmont streams, however, has shown that the diversity and abundance of invertebrates, including detritivores, can be extremely high in headwater streams with riparian vegetation dominated by herbaceous plants.

Throughout and following the growing season along open-canopy headwater streams, we have observed both living and dead herbs and grasses slumping over into the active stream channel while

still remaining rooted on the bank. We hypothesized that this plant material, though still attached to the banks, may provide a substantial source of organic matter to small streams. Further, because many of these open-canopy headwater streams have narrow channels (<1 m), we also hypothesized that the herbs and grasses on the stream edge may provide a low-level 'canopy' that reduces light penetration and limits algal growth.

In this paper, we evaluate the hypotheses that herbs and grasses growing along treeless streams within agricultural catchments provide an important allochthonous source of organic matter to the stream food web and limit primary production by shading. To do this, we first quantified the standing crop of slumped riparian herbaceous vegetation and their associated macroinvertebrate communities in three, open-canopy headwater streams in Maryland, U.S.A. Secondly, we studied the decomposition of four common riparian herbs and grasses. Finally, by removing vegetation from the stream banks, we examined the effect of shading on benthic algal growth.

Methods

Study sites

The study was conducted in three headwater streams with riparian vegetation dominated by herbs and grasses in the Piedmont physiographic province of Maryland, U.S.A. (Table 1). Cattail Creek (CC) (39.322°N, 77.067°W), a tributary of the Hawlings River, drains a 3.37-km² catchment that is dominated by arable (row-crop) and pasture agricultural land use (61%). Reddy Branch (RB) (39.182°N, 77.067°W), also a tributary of the Hawlings River, drains a 5.15-km² catchment substantially under agriculture (56%) and forest (32%). Folly Quarter Creek (FQC) (39.253°N, 76.929°W), a tributary of the Middle Patuxent River, drains a 0.98-km² catchment that is largely composed of arable agriculture (81%) with some forest (17%).

Site	Catchment size (km ²)	Mean width (m)	Mean depth (m)	Mean bank height (m)	Mean baseflow discharge (L s ⁻¹)
CC	3.37	0.83	0.18	0.78	4.16
RB	5.15	1.16	0.20	0.62	14.57
FQC	0.98	0.61	0.19	0.51	3.32

Table 1 Characteristics of stream study sites

CC, Cattail Creek; RB, Reddy Branch; FQC, Folly Quarter Creek.

All three streams have at least a 3-m wide riparian strip composed entirely of herbaceous forbs and grasses (no tree cover).

The standing crop of edge vegetation and the fauna associated with it

The edge vegetation along a 75-m reach within each site was sampled between the 22 October and the 6 November 2001. The open-end frame of a large 0.25-m² Surber sampler (150- μ m mesh size) was randomly placed over the stream but abutting an 0.5-m length of the edge. All vegetation inside the frame (including both overhanging and submerged plant material that was rooted on the bank) was clipped and collected in plastic bags. Vegetation consisted of both detritus and live plant material (at time of collection, 2 : 1 ratio of detritus : live vegetation, unpublished data). A total of eight replicate samples per reach was collected. Vegetation in each sample was sorted in the laboratory and identified to the lowest taxonomic level possible, generally genus. Vegetation was dried at 60 °C for at least 3 days, weighed and then ashed at 550 °C for 1 h to determine ash-free dry mass (AFDM) of plant material per metre stream length. We assumed that, in addition to the submerged material, all rooted vegetation overhanging the edge would also become in-stream detrital material. We doubled our initial estimates taken from one side of the stream to account for inputs from both banks. We then divided that number by average stream width for each site to determine g AFDM m⁻², so that our reported results were comparable with those of other studies that measured inputs and standing crops of detritus on an areal basis.

We were also interested in the stream macroinvertebrates associated with the submerged fraction of vegetation. Prior to drying clipped vegetation, all macroinvertebrates from each sample were washed out and stored in 70% ethanol. They were then identified to lowest practical taxonomic level and assigned to functional feeding groups (Merritt & Cummins, 1996; Thorp & Covich, 2001).

Decomposition experiment

Four herbs and grasses that dominated the study sites and many other open-canopy streams were collected from local streambanks in September 2001. Two of the

species were dicotyledons and included the native *Impatiens capensis* Meerb. (Jewelweed) and the invasive exotic, *Polygonum perfoliatum* L. (Tearthumb). The other two species were monocotyledons and also included one native species, *Panicum dichotomiflorum* Michx. (Spreading witchgrass) and one invasive exotic species, *Microstegium vimineum* Trin. (Asian stiltgrass). For each species, fresh cut leaves and stems were wet-weighed and placed into seven replicate mesh-bag packs. A regression of wet mass to AFDM was developed for each species and used to determine initial AFDM of leaf packs (range: 0.36–1.41 g). Dried samples of each species were also analysed for C : H : N content (Research Environmental Analysis Laboratory, University of Maryland).

On 15 September 2001 (day 0), all mesh-bag leaf packs were attached to the bottom of a 10-m reach of Folly Quarter Creek (discharge, 4.58 L s⁻¹) with tent stakes and cable ties such that packs were suspended in the flow. Packs were arranged in seven groups of four, with one pack from each species per group. Leaf pack groups were collected from the most downstream to upstream positions on days 2, 9, 16, 23, 30, 37 and 44. Packs were collected underwater in a Ziplock® bag (S.C. Johnson & Son, Racine, WI, U.S.A.) and placed on ice. In the laboratory, bag contents were rinsed through a 500 μ m sieve and the leaf pack and mesh bag were thoroughly rinsed to collect macroinvertebrates and remaining leaf contents. Leaf contents were placed in pre-weighed tins, dried for 24 h at 60 °C and combusted at 550 °C for 1 h to determine AFDM (g) remaining. Macroinvertebrates were stored in 70% ethanol, identified to lowest practical taxonomic level and assigned to functional feeding groups (Merritt & Cummins, 1996; Thorp & Covich, 2001).

Data analysis

We determined the decomposition rate (k) of each species using the exponential decay model, $W_t = W_0 e^{-kt}$, where W_0 is the initial mass, W_t is the mass remaining after time t and k is the decomposition rate (Petersen & Cummins, 1974; Webster & Benfield, 1986). To estimate a decomposition rate for each species, we used an ANCOVA to analyse $\ln(W_t - W_0)$ as a function of day, species and the interaction between day and species (Proc Mixed, SAS v. 8.2; SAS Institute Inc., Cary, NC, U.S.A.). Initial dry mass was fixed, so

no intercept was fitted for the decay models. Residuals were examined to ensure the assumptions of normality and homogeneity of variance were met. We used an ANCOVA to make pairwise comparisons between the decomposition rates of each leaf species, i.e. to test for differences among the slopes of the regression lines for each species (day \times species interaction; Littell *et al.*, 2006). We adjusted for multiple comparisons using the Bonferroni correction. We then used simple linear regression to analyse decomposition rate k as a function of leaf quality (% N) (Proc Reg, SAS v. 8.2; SAS Institute Inc.). Similar to the calculation and analysis of leaf decomposition rates, we used an ANCOVA to calculate shredder colonization rates and then compare colonization rates among the four leaf species treatments.

Benthic algal growth

In July 2002, two 25-m reaches (upstream, downstream) were established at Folly Quarter Creek, separated by a 50-m length of channel. No side tributaries entered the stream within the entire study length, and we measured no significant differences among the up- and downstream reaches in water chemistry, ambient light input, channel width, depth or flow throughout the study period. On 18 July 2002, we deployed unglazed ceramic tile sets in three transects (upstream, mid-stream, downstream) across the width of the stream in the upstream and downstream reaches. Each tile set consisted of 12, 5.29-cm² individual tiles connected to one another in a 3 \times 4 rectangular array. Tile sets were staked to the streambed in a consecutive line across the width of the stream (two–five sets/transect depending on stream width) and were oriented perpendicular to the flow. On 31 July 2002 (13 days later), we collected all tile sets from the three transects in each reach. On 1 August 2002, we trimmed the herbaceous vegetation growing along the stream edge of the downstream reach to a width of 1-m on each side. Vegetation clippings were carefully removed by hand to avoid leaf litter inputs to the stream. The clipped treatment was maintained by hand-trimming every 2 weeks. On 14 September 2002, we re-deployed three tile transects in both the unclipped upstream reach and the downstream clipped reach as above. Tiles were collected on 28 September 2002 (14 days later).

Following removal from the stream, tile sets were immediately wrapped in aluminium foil to prevent degradation of chlorophyll (chl)-*a* due to ambient light, placed on ice and returned to the laboratory for processing. Six individual tiles from each component set comprising each transect were processed for chl-*a*. To dislodge algae, tiles were submerged in a shallow bath of distilled water and scrubbed with a stiff-bristled brush under low-light conditions. This water, as well as that used to rinse the brush and aluminium foil, were filtered through a 0.70 μ m Whatman[®] GF/F filter (Whatman, Brentford, Middlesex, U.K.). Chl-*a* for each tile set in each transect was extracted by placing filters in 15-mL 90% ethanol for at least 48 h. Concentrations of chl-*a* were determined with a spectrophotometer (Steinman & Lamberti, 1996), substituting the absorption coefficient for ethanol extraction derived from Nusch (1980). Chl-*a* values for each set were standardized by tile area and by day to determine accrual rate (mg m⁻² day⁻¹).

Data analysis

We calculated mean chl-*a* accrual rate for each transect in up- and downstream reaches, before and after vegetation removal. We used a two-factor ANOVA (Proc Mixed, SAS v.8.2), weighting transect means by the number of tile sets in each transect, to determine differences in chl-*a* accrual rates between up- and downstream reaches before and after vegetation removal (Smith, 2002). Recognizing the design limitations, because we did not replicate the control and vegetation removal reaches across a sample of stream sites (Hurlbert, 1984), we cannot unequivocally infer that any differences between our reaches are because of the experimental treatment.

Results

The standing crop of edge vegetation and the fauna associated with it

The standing crop of overhanging and submerged vegetation along the banks of Cattail Creek averaged 276.4 g AFDM m⁻² (SE, 81.8; n , 8) (Table 2). Grasses (Poaceae) dominated the bank vegetation, comprising 93.7% of the total biomass. Identification of grasses and other monocotyledons to species was difficult, as many of the plants lacked flowers. Dicotyledons at

Table 2 Biomass per m² of overhanging and submerged edge vegetation found at three open-canopy study streams

Site	Monocot (g AFDM m ⁻²)		Dicot (g AFDM m ⁻²)		Total (g AFDM m ⁻²)	
	Mean (SE)	Median	Mean (SE)	Median	Mean (SE)	Median
CC	259.0 (83.7)	193.9	17.4 (6.8)	11.8	276.4 (81.8)	213.7
RB	203.9 (50.9)	177.3	10.3 (3.5)	6.7	214.2 (51.0)	178.0
FQC	49.9 (20.3)	18.8	17.8 (13.9)	4.5	67.7 (20.2)	40.3

Mean \pm 1 SE and median are presented for monocotyledons, dicotyledons and total g AFDM m⁻² at three sites ($n = 8$ samples per site).

AFDM, ash-free dry mass; CC, Cattail Creek; RB, Reddy Branch; FQC, Folly Quarter Creek.

Cattail Creek included smartweed (*Polygonum* L. sp.: Polygonaceae), goldenrod (*Solidago* L. sp.: Compositae) and other members of the Compositae. Reddy Branch averaged 214.2 g AFDM m⁻² (SE, 51.0; n , 8), where monocotyledons similarly dominated the edge vegetation (95.2%) and included rice cutgrass (*Leersia oryzoides* L.: Poaceae), rush (*Juncus* L. sp.: Juncaceae) and sedge (*Carex* L. sp.: Cyperaceae). Dicotyledons identified at Reddy Branch also included smartweed (*Polygonum* L. sp.: Polygonaceae) and goldenrod (*Solidago* L. sp.: Compositae) as well as jewelweed (*I. capensis* Meerb.: Balsaminaceae). While Folly Quarter Creek had a much smaller average total crop of edge vegetation than the other two sites, 67.7 g AFDM m⁻² (SE, 20.2; n , 8), dicotyledons and specifically jewelweed (*I. capensis*), comprised a much larger portion of the crop (26.3%). The dominant monocotyledon at this site was the invasive reed canary grass (*Phalaris arundinacea* L.: Poaceae).

Average macroinvertebrate density ranged from 7.4 individuals g⁻¹ AFDM edge vegetation at Reddy Branch to 63.7 individuals g⁻¹ at Folly Quarter Creek (Table 3). Ephemeroptera (mostly Leptophlebiidae and Heptageniidae) and Diptera (mostly Chironomidae) were the two dominant taxa at Cattail Creek and Reddy Branch, whereas Diptera (again mostly Chironomidae), Amphipoda (Hyalellidae, Crangonyctidae) and Isopoda (Asellidae) dominated the macroinvertebrate assemblage at Folly Quarter Creek. With respect to functional feeding groups, collector-gatherers made up the largest proportion of individuals across all sites (CC: 74.3%, RB: 34.7%, FQC: 64.6%) (Table 4). Shredders were second numerically (CC: 10.0%, RB: 29.7%, FQC: 19.8%), followed by predaceous invertebrates (CC: 9.3%, RB: 14.3%, FQC: 14.2%). Each stream site had a diverse assemblage of shredder macroinvertebrates, and Plecoptera (Cap-

Table 3 Average density (\pm 1 SE) of macroinvertebrate taxa collected in vegetation from edge samples at three open-canopy streams

Taxon	Site		
	CC	RB	FQC
Insects			
Ephemeroptera	6.7 (5.1)	3.1 (1.9)	0.1 (0.1)
Odonata	0.2 (0.1)	0.1 (0.1)	0.6 (0.2)
Hemiptera	0	<0.1 (<0.1)	0.2 (0.1)
Plecoptera	0.3 (0.2)	0.7 (0.3)	0.2 (0.1)
Megaloptera	0	<0.1 (<0.1)	<0.1 (<0.1)
Trichoptera	1.6 (0.9)	0.9 (0.6)	0.8 (0.2)
Lepidoptera	0	<0.1 (<0.1)	0.1 (0.1)
Coleoptera	2.9 (2.3)	0.4 (0.3)	2.2 (0.7)
Diptera	4.0 (2.0)	1.2 (0.8)	49.7 (16.1)
Non-insects			
Isopoda	0	0	4.8 (3.0)
Amphipoda	0	0.2 (0.2)	5.0 (2.8)
Nematomorpha	0	0.1 (0.1)	0.1 (0.1)
Oligochaeta	<0.1 (<0.1)	0.7 (0.4)	0.1 (0.1)
Total	15.7 (10.3)	7.4 (4.1)	63.7 (18.8)

Density is reported as number of individuals g⁻¹ AFDM of herbaceous vegetation collected from the stream edge ($n = 8$ samples per site).

CC, Cattail Creek; RB, Reddy Branch; FQC, Folly Quarter Creek.

niidae, Leuctridae), Trichoptera (Limnephilidae, Phryganeidae) and Diptera (Tipulidae) were numerous at all sites. Folly Quarter Creek was the only site where crustaceans, Isopoda (Asellidae) and Amphipoda (Crangonyctidae, Hyalellidae) dominated the shredder community numerically.

Decomposition experiment

The exponential decay model explained well the decomposition of herbs and grasses (Fig. 1). All curves were highly significant ($P < 0.0001$) and had

Functional feeding group	Site					
	CC		RB		FQC	
	Density	%	Density	%	Density	%
Collector-gatherer	12.6 (8.8)	74.3	4.1 (2.8)	34.7	46.3 (15.0)	64.6
Collector-filterer	0.5 (0.4)	4.1	0.1 (0.1)	4.1	0.2 (0.1)	1.3
Shredder	1.4 (0.8)	10.0	1.7 (0.8)	29.7	10.8 (5.8)	19.8
Scraper	0.1 (<0.1)	1.0	0.3 (0.2)	8.4	0	0
Predator	1.0 (0.6)	9.3	0.4 (0.2)	14.3	6.1 (1.7)	14.2
Deposit feeder	<0.1 (<0.1)	1.3	0.7 (0.4)	8.7	0.1 (0.1)	0.1

CC, Cattail Creek; RB, Reddy Branch; FQC, Folly Quarter Creek.

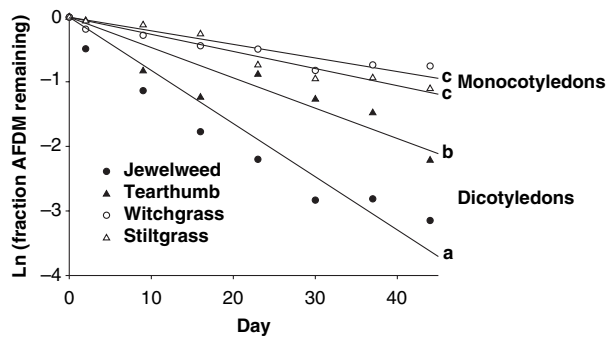


Fig. 1 The natural logarithm of the fraction of initial ash-free dry mass (AFDM) remaining for each plant species over the course of the decomposition experiment (44 days), where the slope of each line represents the decomposition rate k . All slopes are significantly different from 0 ($P < 0.05$), and different letters indicate significantly different decomposition rates ($P < 0.05$) for each plant species.

r^2 values ≥ 0.95 . There was a significant effect of species on the leaf decomposition rate, k (ANCOVA, day \times species, $F_{3,24} = 54.20$, $P < 0.0001$). Jewelweed (k , 0.082 day^{-1}) decomposed fastest, followed by tearthumb (k , 0.047 day^{-1}), stiltgrass (k , 0.027 day^{-1}) and witchgrass (k , 0.021 day^{-1}) (Table 5). The decom-

Table 4 Average density (number g^{-1} AFDM vegetation ± 1 SE) and per cent contribution to total (%) for each macroinvertebrate functional feeding group collected in vegetation from edge vegetation samples ($n = 8$ samples per site)

position rates of witchgrass and stiltgrass were not significantly different ($P = 0.32$).

Leaf quality, as measured by nitrogen content, varied among the four plant species. Jewelweed had the highest leaf nitrogen content followed by tearthumb, stiltgrass and witchgrass, respectively (Table 5). A regression of decomposition rate as a function of nitrogen content suggests that decomposition rate was significantly related to leaf quality ($P = 0.013$; r^2 , 0.97) (Fig. 2).

Shredding macroinvertebrates including *Caecidotea communis* Cole & Minkley (Isopoda: Asellidae), *Hyal-ella* S.I. Smith sp. (Amphipoda: Hyalellidae), *Crangonyx* Bate sp. (Amphipoda: Crangonyctidae) and tipulid fly larva (Diptera: Tipulidae) colonized experimental leaf packs linearly over time. As with leaf decomposition, there was a significant effect of leaf species on shredder colonization rate (ANCOVA, day \times species, $F_{3,13.6} = 24.70$, $P < 0.0001$). Similarly, the rate of colonization mirrored decomposition rate, whereby shredders colonized jewelweed fastest (4.9 shredders g^{-1} AFDM remaining day^{-1}), followed by tearthumb (2.0 shredders g^{-1} day^{-1}), stiltgrass (0.8 shredders g^{-1} day^{-1}) and witchgrass (0.6 shred-

Species	k (day^{-1}) (SE)	r^2	% C	% N	C : N	Colonization rate (individuals g^{-1} AFDM remaining day^{-1}) (SE)
Jewelweed	0.082 (0.004) a	0.97	46.59	4.02	11.59	4.9 (0.7) a
Tearthumb	0.047 (0.004) b	0.95	46.43	2.87	16.18	2.0 (0.2) b
Witchgrass	0.021 (0.004) c	0.95	43.77	1.77	24.73	0.6 (0.2) c
Stiltgrass	0.027 (0.004) c	0.98	47.30	2.33	20.30	0.8 (0.1) c

Decomposition rates k (± 1 SE) and shredder colonization rates (± 1 SE) were estimated using ANCOVA and are all significantly different from 0 ($P < 0.0001$). Different letters indicate significantly different ($P < 0.05$) decomposition and shredder colonization rates determined using multiple comparisons tests with the Bonferroni correction.

Table 5 Results from decomposition experiment using four common species of herbs and grasses found at study sites

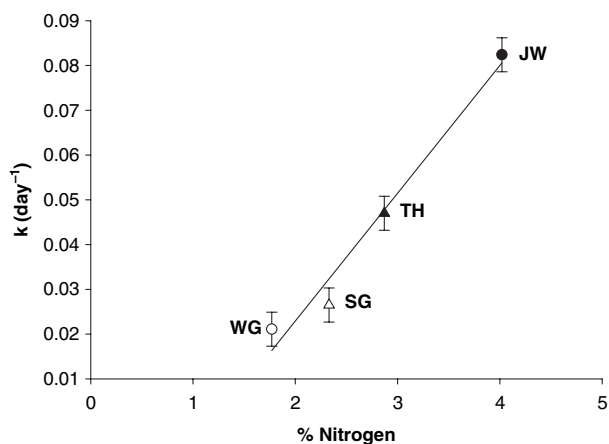


Fig. 2 Linear regression showing a positive relationship between decomposition rate (k) and leaf nitrogen content ($P = 0.013$, $r^2 = 0.97$). Symbols as in Fig. 1. Error bars represent ± 1 SE calculated from ANCOVA.

ders $\text{g}^{-1} \text{day}^{-1}$) (Table 5; Fig. 3). The shredder colonization rates of witchgrass and stiltgrass did not significantly differ ($P = 0.13$).

Benthic algae

Chlorophyll- a accumulation rate was much greater in the downstream reach ($1.61 \pm 0.14 \text{ mg m}^{-2} \text{ day}^{-1}$) of Folly Quarter Creek after vegetation was removed than in the same reach before clipping and in the upstream control reach either before or after the

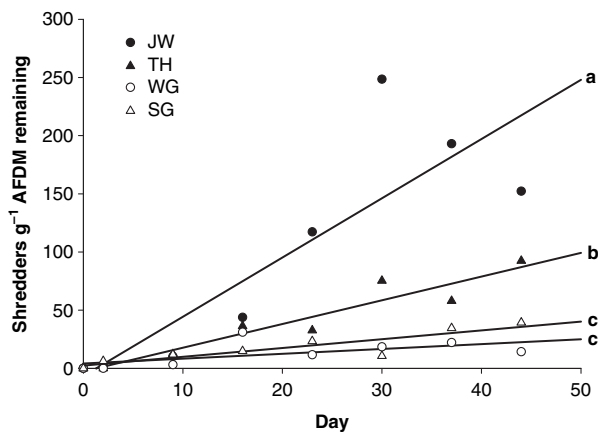


Fig. 3 Colonization of shredders (individuals g^{-1} AFDM remaining) over the course of the decomposition experiment (44 days). Symbols as in Fig. 1. All slopes (representing the colonization rate) are significantly different from 0 ($P < 0.05$), and different letters indicate significantly different shredder colonization rates ($P < 0.05$) for each plant species.

manipulation (ANOVA, reach \times time, $F_{1,8} = 29.75$, $P = 0.0006$). Chl- a accrued at similar mean rates in the upstream control reach during both time periods (before, $0.02 \pm 0.12 \text{ mg m}^{-2} \text{ day}^{-1}$; after, $0.02 \pm 0.14 \text{ mg m}^{-2} \text{ day}^{-1}$) and in the downstream treatment reach prior to clipping ($0.03 \pm 0.17 \text{ mg m}^{-2} \text{ day}^{-1}$).

Discussion

Large standing crops of plant material (average range: $68\text{--}276 \text{ g AFDM m}^{-2}$), composed largely of monocotyledons, were found submerged or overhanging the edges of all three of these open-canopy, agricultural streams. This was composed of submerged live and detrital plant material, as well as overhanging vegetation that would eventually slump into the stream. Leaves and stems of herbs and grasses slump into the stream while still rooted on the bank and therefore remain in place, unlike leaves and small wood from deciduous trees that are often transported downstream from the site of input. Thus, we found it useful to compare our measurements to published estimates of both standing stock of coarse particulate organic matter (CPOM) (g AFDM m^{-2}) collected locally within stream reaches, as well as yearly inputs of leaf litter ($\text{g AFDM m}^{-2} \text{ year}^{-1}$). Estimates of herbaceous plant and grass material at our study sites were similar to standing stocks of CPOM reported for streams nearby draining deciduous forest but slightly less than their yearly litterfall estimates. For example, a CPOM standing crop of $118 \text{ g AFDM m}^{-2}$ and litterfall of $313 \text{ g AFDM m}^{-2} \text{ year}^{-1}$ was reported for White Clay Creek (Pennsylvania) (Minshall *et al.*, 1983; Newbold *et al.*, 1997), and $175 \text{ g AFDM m}^{-2}$ standing crop CPOM and $459 \text{ g AFDM m}^{-2} \text{ year}^{-1}$ litterfall for the West Fork of Walker Branch (Tennessee) (Mulholland *et al.*, 1985; Mulholland, 1997).

Only a few previous studies have examined organic matter in open canopy streams, and they emphasized algal production as the primary source of organic matter (Matthews, 1988; Campbell *et al.*, 1992; Delong & Brusven, 1994). These studies reported smaller quantities of CPOM and generally lower litter inputs than in our study. For example, in treeless reaches of Kings Creek, a tallgrass prairie stream in Kansas, the standing crop of non-woody coarse benthic organic matter (which included grasses, aquatic macrophytes, moss and algae) ranged from 38 to 43 g AFDM m^{-2} ,

while direct and lateral litterfall ranged from 118 to 128.1 g AFDM m⁻² year⁻¹ (Gurtz *et al.*, 1988; Gray, 1997; Stagliano & Whiles, 2002). Similarly, in three agriculturally impacted streams in southern Illinois, Stone *et al.* (2005) reported mean estimates of non-woody coarse benthic organic matter (which included grass, leaves and corn residues) ranging from 20.9 to 49.2 g AFDM m⁻². In the herbaceous plant-lined reaches of Lapwai Creek in northern Idaho, mean input of non-woody organic matter ranged between 1.33 and 112.42 g AFDM m⁻² year⁻¹ (DeLong & Brusven, 1994). In montane tussock grassland streams in New Zealand, Scarsbrook & Townsend (1994) reported amounts of CPOM generally <12 g AFDM m⁻².

The larger quantity of herbaceous and grass organic matter we report may reflect significant differences in the land-water interface between ecoregions. Downstream of their source, prairie streams are typically incised and riparian plants do not necessarily intersect the stream edge nor do they block light to the channel (Whiles, pers. comm). Inputs of herbaceous material in prairie streams occur seasonally after senescence by being blown in or by overland flow during rainstorms (Matthews, 1988; Stagliano & Whiles, 2002). In the braided stream channels of New Zealand tussock grasslands, senesced grasses enter the streams following floods (Scarsbrook & Townsend, 1994). In contrast, herbaceous vegetation and grasses at our study sites grow so densely along the edges that they slump into the stream while still rooted on the bank. Additionally, evidence from the vegetation removal experiment suggests that edge vegetation can shade narrow stream channels and limit primary production.

Consistent with the large standing crops of herbaceous organic matter in our open-canopy streams, we found a diverse macroinvertebrate shredder assemblage living in the submerged vegetation, including representatives of orders sensitive to poor water quality, the Plecoptera (stoneflies) and Trichoptera (caddisflies). These results suggest that herbaceous riparian vegetation may be an important allochthonous energy resource to small streams in non-forested catchments and contrast directly with observations from other studies of agriculturally impacted streams that found very few shredding invertebrates associated with CPOM (Stone *et al.*, 2005; Hagen, Webster & Benfield, 2006). In addition, shredders appeared to respond to differences in leaf nutritional quality in the decomposition experiment; the highest shredder den-

sities and fastest colonization rates occurred on the two dicotyledons (jewelweed and tearthumb) with the fastest decomposition rates and the highest nitrogen contents. The other two plant species, spreading witchgrass and Asian stiltgrass, had lower leaf quality than the dicotyledons (C : N ratios of the monocotyledons were almost twice as high) and, like other grasses, probably had a high silica content (Lanning & Eleuterius, 1987), contributing to their lower rates of decomposition and colonization by shredders.

An interesting finding was that all the rates of decomposition reported here are generally much higher than published rates for tree leaf litter (Webster & Benfield, 1986), aquatic macrophytes and other grasses (e.g. tussock grass in New Zealand; Young *et al.*, 1994; Niyogi, Simon & Townsend, 2003). In addition, the herbs and grasses we studied have higher per cent leaf nitrogen than has been reported for common eastern U.S.A. deciduous tree species (Ostrowsky, 1997) (Fig. 4). One reason for this difference is that most studies of decomposition have used autumn-shed leaf litter, collected after the trees have re-absorbed nutrients. We measured decomposition of fresh leaves and grass, however, because green plant material frequently slumps into the stream at our field sites. Additionally, high nutrient concentrations, as regularly observed in agricultural streams, may also lead to increased leaf decomposition rates via increased shredder (Robinson & Gessner, 2000) and microbial activity (Suberkropp, 1998).

Today, forested catchments continue to be extensively converted to agricultural and residential land use, such that 'classic' forested headwater streams, where much of our understanding of stream organic matter and food web dynamics were developed (Hynes, 1975; Vannote *et al.*, 1980; Wallace *et al.*, 1997), are becoming less and less common (Meyer & Wallace, 2001; Meyer *et al.*, 2003). Indeed in many regions, urbanization pressures are so great that agricultural catchments with headwater streams with banks dominated by herbs and grasses are viewed as the primary form of undeveloped land, and land preservation programmes have even been implemented to promote their conservation (Moore & Palmer, 2005). Thus, understanding the organic matter dynamics in open-canopy headwater streams is particularly critical.

While other studies have suggested that small reductions in forest cover reduce terrestrial-aquatic

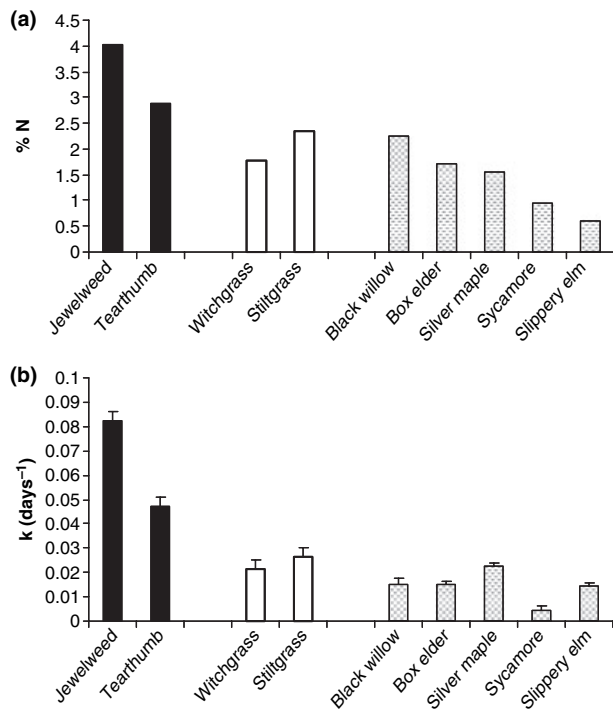


Fig. 4 (a) The leaf nitrogen content and (b) the decomposition rate, $k \pm 1$ SE (day^{-1}), of herbs and grasses used in this study compared with published values (Ostrofsky, 1997; Swan & Palmer, 2004) for common deciduous riparian trees in the eastern Piedmont, U.S.A.: black willow (*Salix nigra* Marshall), box elder (*Acer negundo* L.), silver maple (*Acer saccharinum* L.), sycamore (*Platanus occidentalis* L.) and slippery elm (*Ulmus rubra* Muhl.) Dark bars represent herbaceous dicotyledons, open bars represent grasses and hatched bars represent deciduous riparian tree species.

linkages because of a decline in deciduous tree leaf litter inputs (England & Rosemond, 2004), the results of our study suggest that inputs from herbs and grasses growing along small open-canopy streams may actually promote a significant terrestrial-aquatic linkage. First, the standing crops of herbs and grasses slumping into the agricultural streams were similar in magnitude to the standing crops and inputs of deciduous leaf litter in other eastern U.S. forested streams. Secondly, because these herbs and grasses were rich in nitrogen, their leaf material probably provides a high-quality resource. Thirdly, the high rates of decomposition and shredder colonization strongly point to the ability of stream macroinvertebrates and microbes to readily use herbaceous plant and grass material. Finally, the results of the vegetation removal experiment suggest that algal production, typically considered the primary source of organic matter in

open-canopy streams, may actually be limited by shading from the dense riparian herbs and grasses. Thus, given a suite of results that point to a terrestrial-aquatic linkage between headwater streams and the herbaceous and grass vegetation growing along their banks, we encourage future research to determine how the organic matter provided by these plants makes its way to higher trophic levels.

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