Annls Limnol. 31 (2) 1995 : 105-118

Colonization by Chironomidae (Insecta, Diptera) on three distinct leaf substrates in an Appalachian mountain stream

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Keywords : Chironomidae, colonization, leaves, shredders, *Brillia flavifrons,* gathering-collectors, substrate quality.

Patterns of leaf colonization by Chironomidae were compared on three leaf substrates differing in rate of processing and palatability for detritivores. Each leaf species was colonized by a similar number of taxa, with Orthocladiinae and Tanytarsini comprising the dominant groups. However, the chironomid assemblage, categorized by functional feeding groups, differed greatly between the three leaf types. Black cherry leaves supported a much higher proportion of shredders (e.g. *Brillia flavifrons*) than either red maple or American beech packs. In contrast, beech and maple leaf packs were colonized by distinctly higher proportions of gathering-collectors (e.g. *Corynoneura* spp., *Parametriocnemus* sp., *Stilocladius* spp., *Constempellina* spp., *Micropsectra* spp.). Overall, the cherry packs supported a significantly higher shredder and gathering-collector biomass per g leaf pack than either the maple or beech leaves. We conclude that (1) shredders were preferentially associated with cherry leaf packs due to its higher palatability compared to the maple and beech leaves, and (2) similar colonization patterns exhibited by gathering-collectors on all three leaf species were the result of a supply of similar-quality fine detritus.

Colonisation par les Chironomidae (Insecta, Diptera) de trois types de substrats foliaires dans une rivière des Appalaches

Mots clés : Chironomidea, colonisation, feuilles, déchiqueteurs, *Brillia flavifrons,* collecteurs rassembleurs, qualité de substrats.

Des modes de colonisation par les Chironomidae sont comparés sur trois types de sachets de feuilles différents dans leur taux de décomposition et dans leur facilité de dilacération pour les détritivores. Chaque type foliaire était colonisé par un nombre semblable de taxa, dont les Orthocladiinae et les Tanytarsini constituaient les groupes dominants. Cependant, l'association des chironomidés, séparée en groupes nutritifs fonctionnels, diffère grandement selon les 3 types de feuilles. Les feuilles de cerisier supportent une plus grande proportion de déchiqueteurs (p. ex. *Brillia flavifrons*) que les feuilles d'érable rouge ou de hêtre américain. Au contraire, les sachets de feuilles d'érable et de hêtre sont colonisés par des proportions plus élevées de collecteurs rassembleurs (p. ex. *Corynoneura* spp., *Parametriocnemus* sp., *Stilocladius* spp., *Constempellina* spp., *Micropsectra* spp.). Au total, les sachets de feuilles de cerisier tolèrent une biomasse par g. de feuille significativement plus élevée de déchiqueteurs et de collecteurs que les feuilles d'érable ou de hêtre. Nous concluons que (1) les déchiqueteurs sont préférentiellement associés avec les accumulations de feuilles de cerisier à cause de leur meilleure facilité de dilacération comparativement aux feuilles d'érable et de hêtre, et (2) des modes de colonisation semblables chez les collecteurs rassembleurs pour les 3 espèces de feuilles sont le résultat d'un apport en fins détritus de qualité semblable.

1. Introduction

Riparian leaf litter provides the primary energy source to forested headwater streams (e.g. Fisher & Likens 1973). This coupling of forest and stream ecosystems, combined with the in-stream conditioning, processing, and conversion of leaf litter into progressively smaller detrital particles (Boling et al. 1975), yields important food resources for benthic macroinvertebrates (Cummins et al. 1966, Coffman et al. 1971). Chironomid larvae are often one of the most numerically-abundant macroinvertebrate groups associated with leaf detritus (e.g. Benfield et al. 1977, Reice 1980). However, despite a large proportion of lotic genera in this family currently

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Article available at http://www.limnology-journal.org or http://dx.doi.org/10.1051/limn/1995007

classified as shredders or gathering-collectors (approximately 70 %, Merritt & Cummins 1984), little research has been aimed at elucidating the role of individual chironomid taxa mediating leaf processing in lotic systems (e.g. Stout & Taft 1985).

Not surprisingly, of the numerous studies examining the macroinvertebrate fauna associated with decaying leaf litter (Table 1), very few have analyzed the chironomid assemblage taxonomically in detail to permit fine-scale partitioning of higher taxa (i.e., genera, species groups, or species) into functional feeding groups. In this paper we provide a preliminary evaluation of leaf detritus utilization by chironomid larvae. Specifically, our purpose was threedold : (1) to compare the functional group assemblage, particularly shredders and gathering-collectors, of Chironomidae colonizing three distinct leaf substrates ; (2) to compare the colonization patterns exhibited by chironomid shredders and gathering-collectors on each leaf substrate ; and (3) compare the extent to which chironomid shredders colonize leaf substrates relative to their non-chironomid counterparts.

2. Study site

This study was conducted during 1992-1993 in Powdermill Run, a 3rd order, brook-trout stream situated in the Appalachian Plateau Province of eastern North America. The stream originates at an elevation of approximately 800 m and flows nearly 8 km northwest into Loyalhanna Creek, draining a 25 km^2 watershed in the Laurel Mountains, Westmoreland County, Pennsylvania. The study section

Table 1. A review of leaf litter processing studies which have analyzed the chironomid assemblage that colonized leaf packs at various levels of taxonomic resolution.

Tableau 1. Références bibliographiques des études concernant la transformation des litières de feuilles qui ont analysé les associations de chironomidés qui colonisent les sachets de feuilles à différents niveaux de détermination taxonomique.

Taxonomic resolution	References
Family	Hart and Howmiller (1975)
	Benfield et al. (1977)
	Reice (1978)
	Blackbum & Petr (1979)
	Reice (1980)
	Short & Ward (1980)
	Brown & Ricker (1982)
	Richard & Moreau (1982)
	Cowan et al. (1983)
	Mutch et al. (1983)
	Rounick & Winterbourn (1983)
	Mutch & Davies (1984)
	Benfield & Webster (1985)
	Kimmel et al. (1985)
	King et al. (1987)
	Chergui & Pattee (1988)
	Imbert & Pozo (1989)
	Mayack et al. (1989)
	Short & Smith (1989)
	Stout & Coburn (1989)
	Beiser et al. (1991)
	Chergui & Pattee (1993)
	Gessner & Dobson (1993)
	Griffith & Perry (1993)
	Basaguren & Pozo (1994)
	McArthur et al. (1994)
	Maloney & Lamberti (1995)
Family & subfamily	Pidgeon & Cairns (1981)
	Dudgeon (1983)
	Cuffney & Wallace (1987)
	Tuchman & King (1993)
Subfamily & tribe	Smith (1986)
	Chauvet et al. (1993)
	Gazzera et al. (1993)
Subfamily & genus	Garden & Davies (1988)
Genus	Short et al. (1980)
	Scheiring (1993)
	Smith & Lake (1993)
Tribe & species	Davis & Winterbourn (1977)
Genus & species	Petersen & Cummins (1974)
	Burton & Ulrich (1994)
Species	Stout & Taft (1985)
	Bunn (1988)
Genus, species group & species	Grubbs & Cummins (1994)
	present study

of Powdermill Run is completely contained within the Powdermill Nature Reserve of the Carnegie Museum of Natural History (Pittsburgh). Within this reach, the stream is moderate-gradient (3,8 %) and flows through a northern hardwood - mixed mesophytic forest. Common riparian flora along the study reach include, in order of decreasing abundance, tulip poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.)), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), red maple (*A. rubrum* L.), witch hazel (*Hamamelis virginiana* L.), northern red oak (*Quercus rubra* L.), white ash (*Fraxinus americana* L.) and black cherry (*Prunus serotina* Ehrh).

Within the study reach, approximately 90 % of the stream channel consists of riffle segments. Pools and backwater eddies are limited by areas inundated by large debris dams and/or boulders. Stream sediments are dominated by cobbles, and to a lesser extent, gravel and pebbles. In-stream nutrient content is low (PO_4 < 0,01 mg/l, NO_3 = 0,46 mg/l) and pH varies annually between 6,4 and 7,2.

3. Materials and methods

Colonization patterns of macroinvertebrates on three leaf substrates were analyzed using the leaf pack method (Merritt et al. 1979). Black cherry, red maple and American beech were chosen to represent leaf substrates that differ significantly with regard to nutritional quality for stream invertebrates (Cummins & Klug 1979) and rate of processing (Petersen & Cummins 1974). Black cherry, red maple and American beech leaves are typical representatives of fast, medium, and slow processing categories, respectively (Petersen & Cummins 1974).

Freshly-abcissed leaves were collected from the forest floor, oven-dried at 60°C for 48 h, and constructed into leaf packs (3 g cherry, beech ; 5 g maple). At least 50 leaf packs of each species were tethered to bricks and placed in riffle segments of Powdermill Run (Table 2). After 24 or 48 h five randomly chosen leaf packs of each species were sampled to provide initial post-leach data. Four to thirteen leaf packs of each species were randomly sampled at intervals of 100-200 degree-days until no leaf material remained. A 250 μm sieve was placed downstream of each sampled pack to catch associated macroinvertebrates and detrital particles that may have been dislodged while removing the leaf pack from the stream bottom. Samples were put in individual plastic bags, placed on ice, and returned to the laboratory. Ambient stream temperature was monitored with Taylor® maximum-minimum thermometers. Degree-days were computed by multiplying the number of days elapsed between each reading and the mean of the maximum and minimum temperatures.

In the laboratory, leaf packs were carefully rinsed free of macroinvertebrates, associated detritus, and inorganic particles. Leaf packs were oven-dried at 60°C to constant mass and weighed to the nearest 0.01 g to determine dry mass. Macroinvertebrates were sorted under a dissecting microscope and identified to the lowest taxonomic unit possible. Every chironomid larva was slide-mounted in Andre's solution. After identification, total body length was measured to the nearest 0.1 mm using the BioQuant™ measuring system. Body length was converted to biomass using length-dry mass regression equations (INVERTICALC, Cummins & Wilzbach, South Florida Water Management District). All macroinvertebrate taxa were categorized into functional feeding groups according to Merritt & Cummins (1984) and Coffman (University of Pittsburgh, Personal Communication).

The Kruskal-Wallis Test was used to compare densities of shredders and gathering-collectors between leaf species (BMDP 1990). Because specific *aposteriori* comparisons were unplanned when leaf packs were placed in-stream, pair-wise comparisons were corrected for experiment-wide error (Day & Quinn 1989). This was done independently for chironomid larvae and non-chironomids. Densities were analyzed as mg dry mass (shredders or gathering-collectors) per g leaf pack. We chose not to examine densities per leaf pack, as suggested by Boulton & Boon (1991), since leaf sizes were mismatched. Maple leaves are considerably larger than either cherry or beech, and may have introduced bias due to differences in leaf shape.

4. Results

4.1. Chironomid assemblage

A total of 3 970 chironomid larvae were slide-mounted and identified, comprising 55 distinct

Table 2. Summary of leaf pack sampling regime. Processing coefficients were calculated with a linear regression model with degree-days as the independant variable (Grubbs & Cummins 1994a). All regressions $r^2 \geqslant 0.90$ $p < 0.0001$.

Tableau 2. Récapitulatif des dates de collections des sachets de feuilles. Les coefficients de transformation ont été calculés à l'aide d'un modèle de régression linéaire avec les degrés-jours comme variable indépendante (Grubbs & Cummins 1994a). Toutes régressions $r^2 \geqslant 0.90$, $p <$ à 0.0001.

Leaf species	Black cherry			Red maple			American beech		
Leaf packs									
Placed in-stream	3 Nov			18 Oct			10 Oct		
Study duration (days)	160			180			336		
Number sampled	46			40			66		
Collection dates, accumulated degree-days, and % dry mass remaining	5 Nov	0	100	19 Oct	0	100	12 Oct	0	100
	24 Nov	152	92	31 Oct	84	87	26 Oct	116	95
	17 Dec	230	74	14 Nov	179	84	9 Nov	211	95
	13 Jan	386	55	3 Dec	303	70	11 Dec	383	93
	19 Feb	485	37	7 Jan	460	47	23 Jan	597	70
	25 Mar	626	22	13 Feb	589	42	19 Mar	771	68
	14 Apr	778	11	28 Mar	755	16	24 Apr	1049	66
				17 Apr	914	12	13 May	1281	70
							12 June	1616	53
							10 July	2038	44
							18 Aug	2675	25
							13 Sept	3103	12
Leaf pack processing									
Processing coefficient (± 95% C.I.)	0.124 (± 0.007)			0.102 (± 0.010)			0.027 (± 0.002)		
% dry mass loss per degree-day	0.12			0.10			0.03		

taxa (Table 3). Across all leaf species, chironomid shredders and gathering-collectors comprised an important component of the total shredder and gathering-collector fauna with increased conditioning time (Fig. 1). Chironomid gathering-collectors were generally more abundant than chironomid shredders. Chironomid gathering-collector biomass also comprised a much higher proportion of total gathering-collector biomass than chironomid shredders as a proportion of total shredder biomass.

Each leaf species supported a near-identical taxon richness. Red maple and American beech leaf packs were both colonized by 40 distinct taxa, followed closely by 39 taxa on the black cherry leaves. Orthocladiinae and Tanytarsini taxa dominated the chironomid fauna both in taxa richness and abundance on all three leaf species (Table 3). The Orthocladiinae was the predominate component of the chironomid assemblage during autumn and winter (Fig. 2). Conservely, Tanytarsini increased in relative abundance during spring and replaced the Orthocladiinae as the dominant leaf-colonizing taxa by early summer. Both the Chironomini and Tanypodinae were a steady, yet minor component of the chironomid fauna throughout the year.

Approximately 90 % of the total abundance was accounted for by 11 genera (*Brillia flavifrons* (Johannsen), *Corynoneura* spp., *Eukiefferiella* spp., *Parametriocnemus* sp., *Rheocricotopus* spp., *Stilocladius* spp., *Tvetenia bavarica* group, *Constempellina* spp., *Micropsectra* spp., *Stempellina* sp. and *Tanytarsus* spp). Tanypodinae (primarily *Thienemannimyia* group) and Chironomini (mostly *Polypedilum* spp.) were less abundant, contributing

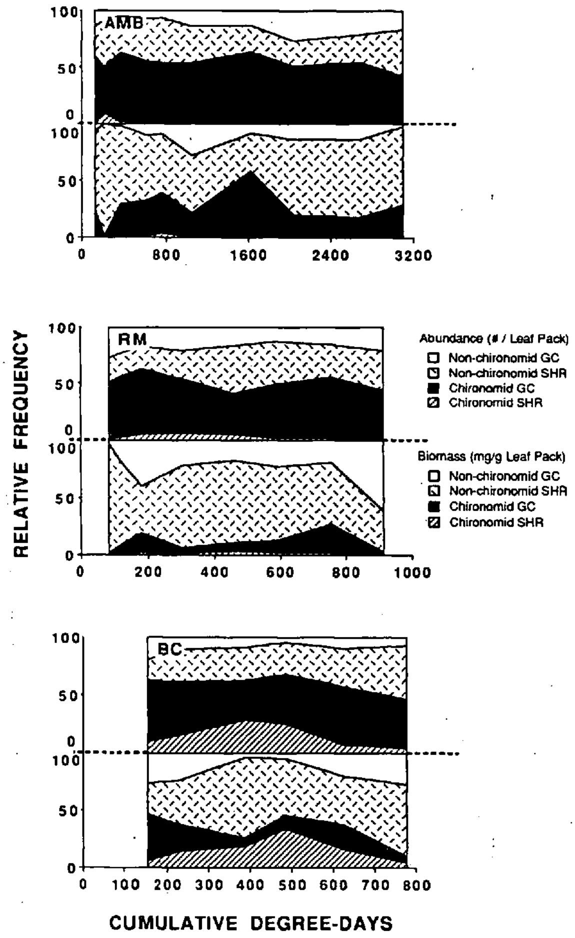

Fig. 1. Relative proportions (abundance and biomass) of chironomid shredders and gathering-collectors as a function of total shredders and gathering-collectors on three distinct leaf species in Powdermill Run. The left-hand border of each area graph corresponds to the second collection date as indicated in Table 2. BC = black cherry. RM = red maple, AMB = American beech, GC = gathering-collectors, SHR = shredders.

Fig. 1. Proportions relatives (abondance et biomasse) de chironomidés déchiqueteurs et collecteurs rassembleurs par rapport à l'ensemble des déchiqueteurs et collecteurs rassembleurs sur trois espèces différentes de feuilles dans la rivière Powdermill. La bande blanche à gauche de chaque courbe correspond au nombre de degré-jours cumulés à la date du deuxième relevé (cf. tableau 2). BC = cerisier, RM = érable rouge, AMB = hêtre américain, GC = collecteurs rassembleurs, SHR = déchiqueteurs.

3 % and 2 %, respectively. Diamesinae (*Diamesa* sp.) accounted for only 0,4 % of total abundance.

The chironomid functional assemblage differed markedly among the three leaf types. Expressed as biomass or abundance per leaf pack, the cherry leaves supported a much higher proportion of shredders (*Brillia flavifrons, Chaetocladius* spp.) than either the maple or beech packs (Fig. 3). Chironomid shredders contributed 15,3 % to total shredder biomass on the cherry leaf packs, compared with 1,8 % on maple and 0,6 % on beech. In contrast, the beech and maple leaf packs were colonized by distinctly higher proportions of gathering-collectors (e.g., *Eukiefferiella* spp., *Parametriocnemus* sp., *Tanytarsus* spp., *Tvetenia bavarica* group sp.) than the cherry packs. Overall, the cherry packs supported a significantly higher shredder and gathering-collector biomass per g leaf pack than either maple or beech (Table 4).

Shredders colonized the cherry leaf packs to a much greater extent than either the maple or beech packs. Shredder biomass per g cherry leaf pack slowly increased with time (or degree-days) until it peaked with approximately 40 % leaf mass remaining. This trend was only weakly mirrored on the maple packs and not seen at all on the beech packs (Fig. 4a).

Gathering-collectors exhibited a similar colonization pattern on each leaf species (Fig. 4b). The predominant group initially colonizing leaf packs, gathering-collectors began to accumulate by the first sampling date (approximately 100 degree-days, or 90 % leaf mass remaining), increasing in abundance steadily throughout the study with the cherry packs supporting the highest biomass per g leaf pack. Biomass of gathering-collectors slightly decreased only during the last sampling periods, corresponding to roughly 20 % mass remaining for each leaf species (Fig. 4b).

4.2. Non-chironomid shredders and gathering-collectors

Tallaperla maria (Needham & Smith) was easily the most abundant non-midge shredder colonizing each leaf species. In addition, *Allocapnia* spp., *Amphinemura* spp., *Lepidostoma* spp., *Leuctra* spp., *Paracapnia angulata* Hanson, *Pteronarcys proteus* Newman and *Taeniopteryx maura* (Pictet) were also common shredders found on each leaf

Table 3. Taxonomic composition of Chironomidae colonizing leaf packs in Powdermill Run. Abundance and biomass are summed across leaf packs by leaf species. Unless stated otherwive, species designations as sp.1, sp.2 and sp.3 do not refer to previous designations of other authors. FFG = functional feeding group, FC = filtering collector, GC = gathering collector, PR = predator, SCR = scraper, SHR = shredder, WG = wood gouger. Entries into the biomass 'mg' and '%' columns as 0.0 indicate < 0.1 mg and < 0.1 %, respectively.

Tableau 3. Composition taxonomique des Chironomidae colonisant les sachets de feuilles dans la rivière Powdermill. Abondance et biomasse sont totalisées par sachet de chaque espèce de feuilles. Sauf indication contraire, les espèces désignées sp1, sp2 et sp3 ne se rapportent pas à des désignations antérieures d'autres auteurs. FFG = groupe nutritif fonctionnel, FC = collecteur filtreur, GC = collecteur rassembleur, PR = prédateur, SCR = racleur, SHR = déchiqueteur, WG = mineur de bois. Les notations 0.0 dans les colonnes biomasse « mg » et % indiquent respectivement < 0.1 mg et < 0.1 %.

	Black Cherry				Red Maple				American Beech				
	Abundance		Biomass		Abundance		Biomass		Abundance		Biomass		
Taxa	No.	%	mg	%	No.	%	mg	%	No.	%	mg	%	FFG
Tanypodinae													
Krenopelopia sp.	1	0.1	0.0	0.0									PR
Larsia sp.									1	0.1	0.0	0.0	PR
Nilotanypus fimbricatus (Walker)									11	0.6	0.3	0.4	PR
Trissopelopia sp.									1	0.1	0.0	0.0	PR
Thienemannimyia group sp.	4	0.4	0.1	0.1	46	4.6	0.8	2.3	48	2.5	2.2	3.3	PR
Tanypodinae sp. (small)					2	0.2	0.0	0.0	6	0.3	0.0	0.0	PR
Diamesinae													
Diamesa sp.	9	0.9	1.5	1.8	3	0.3	0.0	0.1	3	0.2	0.1	0.1	GC
Orthocladiinae													
Brillia flavifrons (Johannsen)	210	20.2	43.5	51.3	47	4.7	4.7	14.1	26	1.3	2.2	3.4	SHR
Chaetocladius sp.1	27	2.6	5.4	6.4	1	0.1	0.0	0.0					SHR
Chaetocladius sp.2	6	0.6	0.7	0.8									SHR
Chaetocladius sp.3					1	0.1	0.1	0.2					SHR
undet. genus nr. *Chaetocladius*	6	0.6	0.5	0.6									SHR
Heleniella sp.	3	0.3	0.2	0.2	6	0.6	0.4	1.3					GC
Corynoneura sp.1	7	0.7	0.1	0.1	20	2.0	0.2	0.6	32	1.7	0.3	0.5	GC
Corynoneura sp.2	17	1.6	0.3	0.3	49	4.9	0.6	1.7	97	5.0	1.0	1.5	GC
Cricotopus tremulus group sp.									5	0.3	0.2	0.3	GC
Cricotopus / Orthocladius sp.									14	0.7	0.2	0.4	GC
Diplocladius sp.	1	0.1	0.0	0.0									GC
Eukiefferiella brehmi group sp.	8	0.8	0.3	0.3	10	1.0	0.3	0.8	101	5.2	2.6	4.0	GC
Eukiefferiella claripennis group sp.1	36	3.5	2.9	3.5	8	0.8	0.5	1.6	67	3.5	3.7	5.6	GC
Eukiefferiella claripennis group sp.2	5	0.5	0.0	0.1	5	0.5	0.1	0.3	28	1.4	0.5	0.8	GC
Eukiefferiella claripennis group sp.3	10	1.0	0.3	0.3	5	0.5	0.1	0.2	31	1.6	1.0	1.5	GC
Eukiefferiella gracei group sp.	12	1.2	0.6	0.7	6	0.6	0.1	0.4	15	0.8	0.4	0.5	GC
Krenosmittia sp.	1	0.1	0.0	0.0					6	0.3	0.1	0.2	GC
Limnophyes sp.	7	0.7	0.2	0.3	1	0.1	0.0	0.1	1	0.1	0.0	0.1	GC
Orthocladius (Euorthocladius) sp.									1	0.1	0.0	0.0	GC
Orthocladius (Orthocladius) sp.					4	0.4	0.0	0.1	3	0.2	0.0	0.0	GC
Parachaetocladius sp.					2	0.2	0.8	2.4	2	0.1	0.2	0.2	GC
Paracricotopus sp.	1	0.1	0.0	0.0					1	0.1	0.0	0.1	GC
Parametriocnemus sp.	113	10.9	13.9	16.3	152	15.2	10.1	30.2	409	21.2	24.9	37.9	GC
Paraphaenocladius sp.	3	0.3	0.0	0.0	3	0.3	0.1	0.2	1	0.1	0.0	0.1	GC
Pseudorthocladius sp.	3	0.3	0.1	0.1	1	0.1	0.0	0.1	2	0.1	0.1	0.2	GC
Pseudosmittia sp.	1	0.1	0.0	0.0									GC
Psilometriocnemus sp.					1	0.1	0.0	0.0					GC
Rheocricotopus sp.1	63	6.1	1.8	2.1	52	5.2	1.4	4.1	20	1.0	0.3	0.5	GC
Rheocricotopus sp.2	18	1.7	0.5	0.6	6	0.6	0.1	0.4	7	0.4	0.1	0.2	GC
Rheosmittia sp.					1	0.1	0.0	0.0					GC

Smittia sp.					1	0.1	0.0	0.0					GC
Stilocladius clinopecten Sæther	40	3.8	0.6	0.8	161	16.1	3.8	11.4	45	2.3	1.1	1.7	GC
Stilocladius sp.1	10	1.0	0.2	0.2	18	1.8	0.6	1.8	18	0.9	0.7	1.0	GC
Stilocladius sp. (small)					5	0.5	0.0	0.1					GC
Thienemanniella sp.	5	0.5	0.1	0.1	12	1.2	0.2	0.6	69	3.6	0.8	1.1	GC
Tvetenia bavarica group sp.	168	16.2	7.8	9.2	116	11.6	5.2	15.4	143	7.4	4.9	7.4	GC
Orthocladiinae sp. (small)	4	0.4	0.0	0.0	17	1.7	0.1	0.2	12	0.6	0.1	0.1	GC
Chironominae													
Chironomini													
Polypedilum aviceps Townes									19	1.0	1.6	2.4	GC
Polypedilum convictum (Walker)									2	0.1	0.0	0.0	GC
Polypedilum fallax (Johannsen)	1	0.1	0.0	0.0	1	0.1	0.0	0.0					WG
Polypedilum sp.1	9	0.9	0.2	0.2	3	0.3	0.0	0.1	8	0.4	0.1	0.2	GC
Polypedilum sp.2	1	0.1	0.0	0.0									GC
Polypedilum sp. (small)									3	0.2	0.0	0.0	GC
Chironomini sp. (small)	2	0.2	0.0	0.0	3	0.3	0.0	0.0					GC
Tanytarsini													
Cladotanytarsus vanderwulpi group sp.					1	0.1	0.0	0.0					GC
Constempellina sp.	166	16.0	1.2	1.4	73	7.3	0.4	1.1	85	4.4	0.8	1.2	GC
Micropsectra sp.1					8	0.8	0.0	0.1	7	0.4	0.3	0.5	GC
Micropsectra sp.2	6	0.6	0.1	0.1	6	0.6	0.1	0.3	11	0.6	0.2	0.3	GC
Micropsectra sp.3	19	1.8	1.2	1.4	27	2.7	1.5	4.5	241	12.5	8.3	12.7	GC
Micropsectra sp. (small)	8	0.8	0.0	0.0	1	0.1	0.0	0.0	23	1.2	0.1	0.2	GC
Micropsectra / Tanytarsus sp. (small)					3	0.3	0.0	0.1	1	0.1	0.0	0.0	GC
Rheotanytarsus sp.	1	0.1	0.0	0.0	3	0.3	0.0	0.1	15	0.8	0.2	0.4	FC
Tanytarsus sp.1	8	0.8	0.0	0.0	47	4.7	0.2	0.5	55	2.8	0.2	0.4	GC
Tanytarsus sp.2	7	0.7	0.1	0.1	3	0.3	0.0	0.1	206	10.7	5.5	8.3	GC
Tanytarsus sp. (small)					1	0.1	0.0	0.0					GC
Stempellina sp.3 (Oliver et al. 1978)					4	0.4	0.1	0.2					GC
Stempellinella sp.	13	1.3	0.2	0.2	52	5.2	0.6	1.8	30	1.6	0.3	0.5	GC
Total	1040		84.9		998		33.4		1932		65.6		

type. No individual non-chironomid shredder taxon was strongly associated with any particular leaf species. However, the colonization pattern exhibited by chironomid shredders on cherry leaves nearly mirrored the pattern exhibited by non-chironomid shredders (Fig. 5). Unlike chironomid shredders, cherry only supported significantly more non-midge biomass than beech, but not maple (Table 4).

Following the same trend as chironomids, non-midge gatherers (e.g. *Baetis* sp., *Eurylophella* sp., *Ephemerella* sp.) were the dominant group initially colonizing leaves. Both cherry and maple were colonized by significantly more gathering-collector biomass than beech (Table 4).

5. Discussion

Overall, black cherry appeared to be a strongly-preferred leaf substrate for chironomid detritivores. The fast-processed leaf material supported significantly more chironomid shredder and gathering-collector biomass than either beech or maple. Non-chironomid shredder and gathering-collector biomass was only significantly higher on the cherry versus beech leaves.

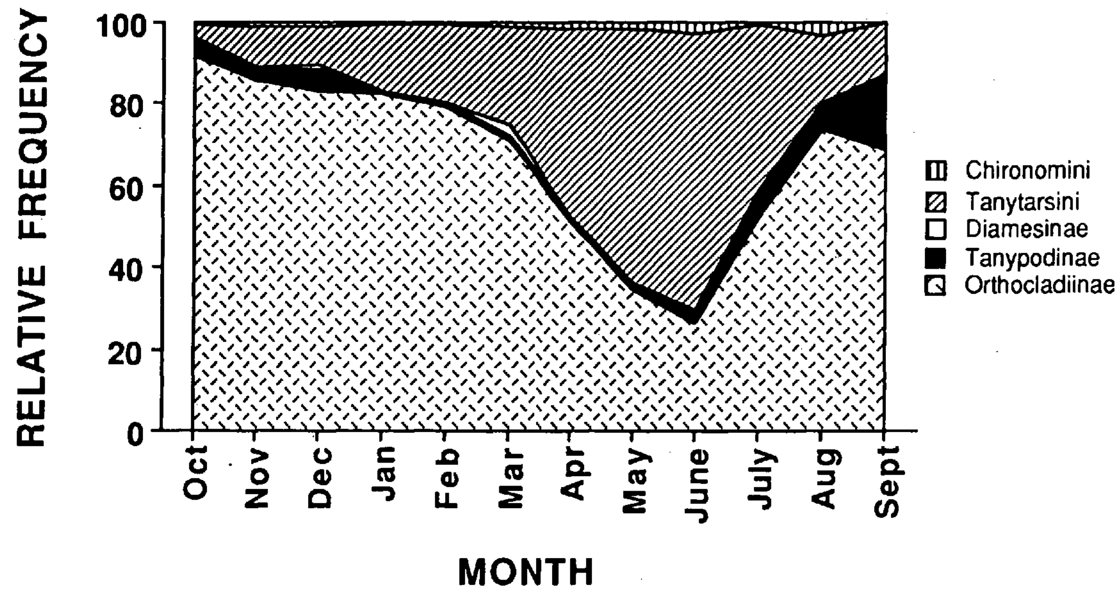

Fig. 2. Temporal changes in relative frequencies of subfamilies and tribes of leaf-colonizing chironomid larvae, summed across all three leaf species, in Powdermill Run.

Fig. 2. Evolution saisonnière de l'abondance relative des sous-familles et tribus de larves de chironomidés colonisant des feuilles, évaluée pour les trois espèces de feuilles, dans la rivière Powdermill.

Table 4. Summary of *aposteriori* pair-wise comparisons of biomass densities of shredders and gathering-collectors colonizing individual leaf species. Overall p-value refers to associated probability with the Kruskal-Wallis test. BC = black cherry, RM = red maple, AMB = American beech.

Tableau 4. Récapitulatif des comparaisons simultanées a posteriori de la biomasse « des densités » de déchiqueteurs et collecteurs rassembleurs colonisant chaque espèce de feuilles. La valeur globale de p se rapporte au test de probabilité associé de Krustal-Wallis. BC = cerisier, RM = érable rouge, AMB = hêtre américain.

		Shredders				Gathering-Collectors		
Chironomidae		Overall: $p < 0.001$				Overall: $p < 0.001$		
		BC	RM	AMB		BC	RM	AMB
	BC	-	< 0.001	< 0.001	BC	-	< 0.001	0.001
	RM		-	N.S.	RM		-	N.S.
	AMB			-	AMB			-
Non-Chironomidae		Overall: $p = 0.047$				Overall: $p < 0.001$		
		BC	RM	AMB		BC	RM	AMB
	BC	-	N.S.	0.013	BC	-	N.S.	< 0.001
	RM		-	N.S.	RM		-	< 0.001
	AMB			-	AMB			-

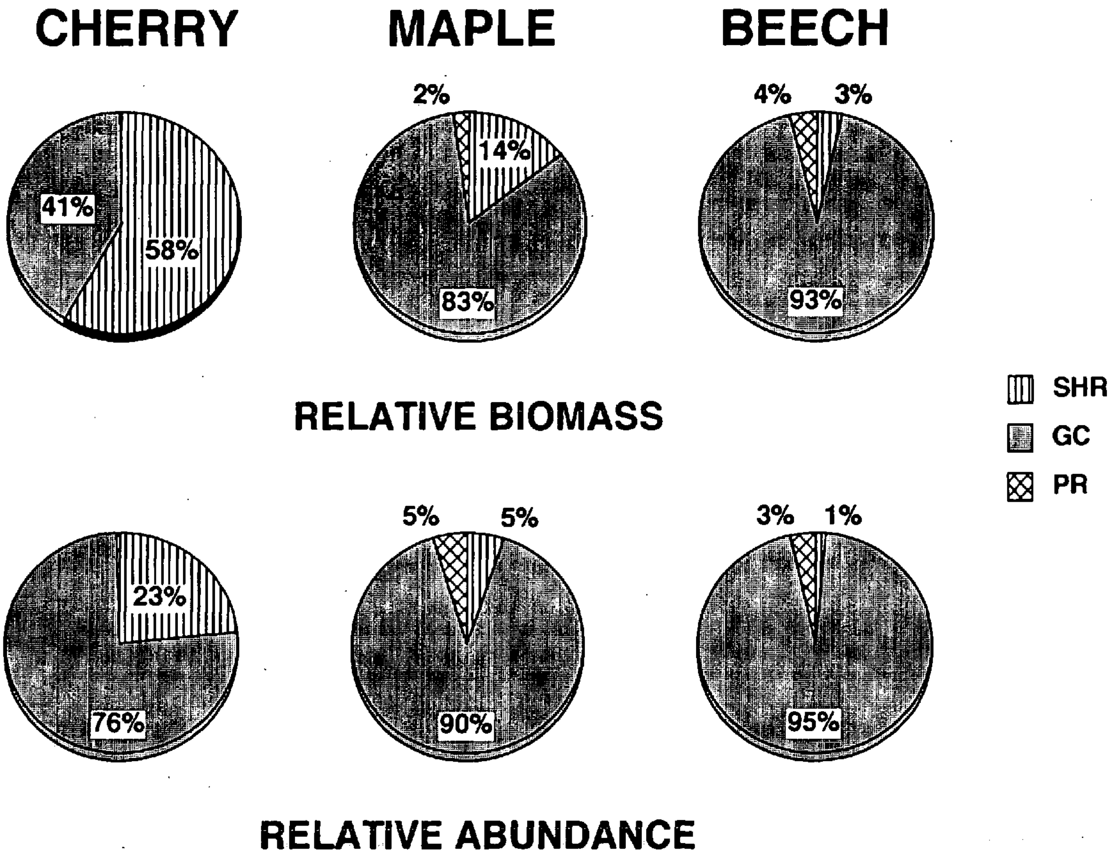

Fig. 3. Relative biomass (dry mass per leaf pack) and relative abundance (number per leaf pack) of chironomid functional feeding groups colonizing black cherry, red maple, and American beech leaves in Powdermill Run. Since filtering-collectors were excluded from each pie graph as they never exceeded 1.0 % on any leaf species and predators comprised < 1.0 % on the black cherry packs, the total of percent sums do not always equal 100 %. SHR = shredders, GC = gathering-collectors, PR = predators.

Fig. 3. Biomasse relative (poids sec par sachet de feuilles) et abondance relative (nombre par sachet) des groupes fonctionnels de chironomidés colonisant les feuilles de cerisier, d'érable rouge et de hêtre américain dans la rivière Powdermill. Puisque sont exclus de chaque graphique les collecteurs filtreurs qui n'excèdent jamais 1.0 % sur chaque espèce de feuille et que les prédateurs sont < 1.0 % sur les sachets de cerisier, le total des sommes n'atteint pas toujours 100 %. SHR = déchiqueteurs, GC = collecteurs rassembleurs, PR = prédateurs.

The colonization patterns exhibited by chironomid shredders and chironomid gathering-collectors suggest two explanations. In conjuction with the greater shredder biomass on cherry leaves, this suggests that chironomid shredders preferred black cherry as a leaf substrate (i.e. food source) to maple and beech. The peak in shredder biomass on the cherry leaf packs with approximately 40 % leaf mass remaining occurred near the 50 % processed point observed in other studies that analyzed an entire shredder guild (e.g. Cummins et al. 1989). However, the lack of response (i.e. biomass accumulation) of shredders on the maple and beech packs, with increased conditioning time, was surprising since shredders are known to feed on microbially-conditioned leaf substrates rather than on specific leaf taxa (e.g. Bärlocher & Kendrick 1973, Arsuffi & Suberkropp 1985). The data further suggests that because of textural and biochemical differences some leaf types (e.g. red maple, American beech)

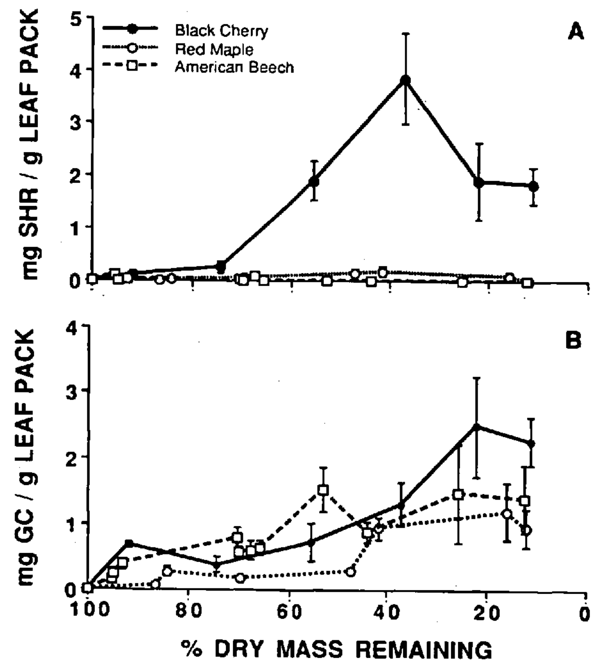

Fig. 4. Colonization patterns of (A) chironomid shredders and (B) chironomid gathering-collectors during processing of black cherry, red maple, and American beech leaves in Powdermill Run. Each point represents mean ± 1 S.E. SHR = shredders, GC = gathering-collectors.

Fig. 4. Modes de colonisation des chironomidés déchiqueteurs (A) et collecteurs rassembleurs (B) au cours de la décomposition des feuilles de cerisier, érable rouge et hêtre américain dans la rivière Powdermill. Chaque point représente la valeur moyenne ± 1 S.E. SHR = déchiqueteurs, GC = collecteurs rassembleurs.

may never become palatable equivalents to high quality litter for chironomid shredders (e.g. *Brillia flavifrons*). Hence, chironomid shredders may contribute to the breakdown of fast-processed leaf detritus, but provide little influence to medium-or slow-processed leaves.

Second, the similar colonization pattern exhibited by gathering-collectors on all three leaf species implies that a continuous source of fine detritus was accumulating on leaf surfaces, either produced within individual leaf packs or captured as seston. This partially supports Richardson (1992), who demonstrated initially that densities of early-instar *Zapada* nymphs (gathering-collectors) were significantly greater on alder versus artificial leaf packs.

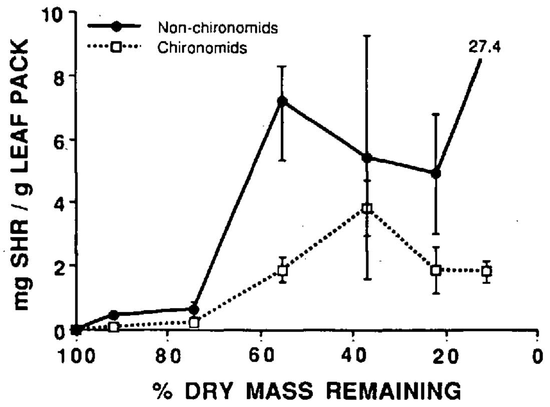

Fig. 5. Chironomid and non-chironomid shredder colonization of black cherry leaves in Powdermill Run. The high biomass value may represent an artifact of the reduced leaf pack mass (mean = 0.27 g). Each point represents mean ± 1 S.E.

Fig. 5. Colonisation des feuilles de cerisier par les déchiqueteurs chironomidés et non-chiromidés dans la rivière Powdermill. La valeur élevée de biomasse peut représenter un artéfact de la masse réduite des sachets de feuilles (moyenne = 0,27 g). Chaque point représente la valeur moyenne ± 1 S.E.

Yet when densities of *Zapada* were scaled for fine detrital mass the influence of leaf quality was subsequently unimportant. In this study cherry leaves supported significantly more gathering-collector biomass than either maple of beech. This suggests that black cherry leaves are either better traps of seston or that leaf quality was important in producing higher amounts, or better quality, of fine detritus. Fine detritus produced from decaying leaf litter has been shown to be of higher nutritional quality than the original detrital source (Suberkropp & Klug 1980, Ward 1984). The inherent nature of cherry leaves to disintegrate during decay, rather than skeletonize or fragment (Grubbs & Cummins 1994b), may provide the direct source of fine detritus.

Alternatively, despite differences in leaf quality, a direct comparison between beech and either maple or cherry colonization by chironomid shredders is difficult because of the relative absence of *Brillia flavifrons* during summer. Beech was the only leaf-pack material remaining from early May through September, since both maple and cherry leaves were completely processed by mid-April. However, in a previous study examining summer processing of cherry leaves in Powdermill Run, Grubbs &

Cummins (1994b) found the density of *B. flavifrons* was 15 times higher than that colonizing beech packs in this study during a comparable summer period (July-September). In contrast, the relative dominance of particular chironomid taxa on beech, relative to maple or cherry leaves, can probably be attributed to life history phenology and not suggested differences in food quality. *Eukiefferiella brehmi* group sp., *Micropsecta* sp. 3 and *Tanytarsus* sp.2 (all gathering-collectors) were only present in appreciable densities during late spring and summer (Table 5). This suggests that each of the above chironomid species was associated with decaying beech leaves because the slow-processed material was the only remaining colonizable leaf substrate during this period.

However, it appears unlikely that life cycle phenology produced discrepancies in colonization patterns of any macroinvertebrate taxa between cherry and maple leaves. Since black cherry trees shed a majority of their leaves at a later date than red maple (Grubbs, unpubl. data), the cherry packs were placed in-stream 16 d after the maple packs. Cherry and maple attained highest shredder biomass (cherry : 19 Feb, maple : 13 Feb) and highest gathering-collector biomass (cherry : 25 Mar, maple : 28 Mar) per g leaf pack on approximately the same calendar dates, corresponding with similar degree of mass loss for cherry (37 %, 22 %) and maple (42 %, 16 %) and thus effectively normalizing the difference in processing dynamics between species.

Although the mounting and identification of chironomid larvae can be a difficult and time-consuming task, good taxonomic keys to larval chironomid genera exist on both a regional (e.g. Epler 1992) and continent basis (Wiederholm 1983, Coffman & Ferrington 1984). However, caution should be applied when categorizing chironomid larvae into functional groups until more autecological studies on individual taxa are performed (Underwood & Petraitis 1993). With few exceptions (e.g. Coffman et al. 1971, Stout & Taft 1985) the trophic ecology of the abundant detritus-feeding chironomid taxa that colonized our leaf packs have been little investigated. In addition, special concern must be given when lumping all larvae into the large categories such as 'Chironomidae', subfamilies (except Tanypodinae) or tribes (sensu Berg 1995). For example, Orthocladiinae larvae are typically classified as gathering-collectors. However, in this study shredders (*Brillia flavifrons, Chaetocladius* spp.) comprised 62 % of orthoclad biomass on cherry leaves compared to 16 % on maple and 0.5 % on beech. Nonetheless, functional groups provides a highly useful framework for analyzing patterns or making predictions in ecological studies.

Clearly there is a need for more population - and community - level investigations focusing on the role of individual chironomid taxa and functional groups (i.e. shredder and gathering-collector) involved in the processing of terrestrially-derived organic detritus. For example, a multi-level investigation integrating (1) preference and growth/assimilation experiments of individual food items (Arsuffi & Suberkropp 1986), and (2) gut content and stable isotope analysis ($^{13}C/^{12}C$ ratios - Rau 1980, Rounick et al. 1982) in resolving sources of nutrition would be a promising approach for combining behavioral and physiological aspects of trophic ecology.

Table 5. Dominance patterns, calculated as mean number of larvae per leaf pack, of chironomids relative to differences in food quality or life history strategy. BC = black cherry, RM = red maple, AMB = American beech.

Tableau 5. Exemples de chironomidae dominants, calculés en nombre moyen de larves par sachet de feuilles, par rapport à des différences de la qualité de nourriture ou du type de cycle vital. BC = cerisier, RM = érable rouge, AMB = hêtre américain.

			Leaf species	
Mechanism	Taxon	BC	RM	AMB
Food quality :	*Brillia flavifrons*	5.1	1.3	0.4
	Chaetocladius spp.	1.0	0.1	0.0
Life history :	*Eukiefferiella brehmi* group sp.	0.2	0.3	1.6
	Micropsectra sp.3	0.5	0.8	3.9
	Tanytarsus sp.2	0.2	0.1	3.3

Specifically, gut content analysis, if corrected for calorific content of individual food items (Coffman et al. 1971), and isotope analysis places emphasis on the relative importance of different food resources that are utilized for tissue growth and not simply examining what items are present in the digestive tract.

Acknowledgement

We are grateful to Dr. Joseph Merritt, Director of the Powdermill Run Nature Reserve, for kindly providing housing and laboratory facilities. We wish to thank Brigitte Vanden Eeden for assisting in leaf pack construction, and John Lamb and Ethan Hill for sorting leaf pack samples.

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