

## Diet and growth of a leaf-shredding caddisfly in southern Appalachian streams of contrasting disturbance history

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Received 1 August 1996; in revised form 7 January 1997; accepted 13 February 1997

**Key words:** stream, disturbance, caddisfly, shredder, diet, growth

### Abstract

Diet and growth of leaf-shredding caddisfly larvae, *Pycnopsyche* spp., were examined in streams draining a reference catchment and a 16-year-old clear-cut (disturbed) catchment at Coweeta Hydrologic Laboratory in southwestern North Carolina, USA. The objective was to explain why shredder production is higher in the disturbed streams despite the larvae having less food (i.e., leaves) available. We predicted larvae would grow faster on fast-decaying leaf material representative of the disturbed streams. Larvae consumed mostly leaf detritus in three streams draining each catchment over three seasons (fall, winter, and spring), which showed larvae did not consume higher quality foods (e.g., algae and animal material) in disturbed streams. When fed 2-month-old conditioned black birch (*Betula lenta* L.) (a fast-decaying leaf species) and white oak (*Quercus alba* L.) (a slow-decaying leaf species) leaves in the laboratory, larvae grew significantly faster on the birch leaves. However, when larvae were fed the same leaf types after 3-months conditioning, larvae grew significantly faster on oak leaves. A field growth experiment conducted for 42 d using mixed-species leaf diets representative of each catchment and initially conditioned for 2 months found that *Pycnopsyche* grew significantly better on the diet representative of the reference catchment. The 'reference diet' contained more oak leaves which apparently became a more acceptable food as the experiment proceeded. High shredder production in the disturbed streams could not be explained by high *Pycnopsyche* growth rates on fast-decaying leaves. Instead, larvae grew better on leaves that were apparently conditioned optimally regardless of conditioning rate.

### Introduction

Most forested headwater stream ecosystems rely on allochthonous organic inputs (tree leaves) as a primary energy source (e.g., Fisher & Likens, 1973). Forest disturbances such as logging can profoundly affect these streams by altering the quantity and quality of leaf inputs through a change from mature to early-successional tree species (Webster et al., 1990). In addition, a decrease in large woody debris inputs after logging results in a decline in the number of debris dams (Hedin et al., 1988; Webster et al., 1990) that, in turn, reduces retention of coarse particulate organic matter (CPOM), e.g., leaves and sticks (Webster et al., 1994).

Long-term effects of logging on streams have important implications for leaf-shredding macroinvertebrates (shredders). Leaves from early-successional trees are often fast decaying (fast) species (Webster et al., 1983; Benfield et al., 1991), which are rapidly colonized and conditioned by microbes. Fast leaves are preferred by many shredders (Wallace et al., 1970; Kaushik & Hynes, 1971; Mackay & Kalff, 1973; Golladay et al., 1983), but quickly disappear due to rapid decay (Webster & Benfield, 1986) and the lower number of retention structures in streams affected by logging. Stout et al. (1993) compared shredder production in three streams draining an 11-year-old clear-cut catchment (disturbed) and three streams draining a >60 year-old undisturbed catchment (reference) at Coweeta Hydrologic Laboratory. They found

that shredders were significantly more productive in the disturbed streams despite significantly more total leaf material being present in reference streams. The higher secondary production was, in part, attributed to significantly higher standing stocks of fast leaf material early in the year in disturbed streams.

We conducted experiments with larvae of the leaf-shredding caddisfly, *Pycnopsyche* spp., to test whether observed differences in leaf quantity and quality between the two catchments studied by Stout et al. (1993) affected shredder energetics. Stout et al. (1993) found that *Pycnopsyche* biomass was positively correlated with the abundance of fast leaf material and concluded that faster growth rates on fast leaf material may explain why shredders were more productive in disturbed streams. Furthermore, larval populations in disturbed streams may have been more productive because they consumed higher quality alternative food resources (e.g., algae or animal material) during part of the year when leaves were scarce.

The objective of this study was to investigate the role of diet in the energetics of *Pycnopsyche* larvae inhabiting streams in two catchments of contrasting disturbance history. First, gut contents were analyzed during three seasons to determine larval food sources in the field. Second, laboratory experiments were performed in a controlled environment to investigate larval growth rates on different leaf species that had been conditioned in-stream for various periods of time. Finally, a field experiment was conducted to examine larval growth on mixed-species leaf diets representative of each catchment. We predicted that *Pycnopsyche* larvae would grow faster on the fast leaf material representative of disturbed streams.

## Materials and methods

### Study organism

*Pycnopsyche* (Trichoptera:Limnephilidae) is a genus of caddisfly, whose case-building larvae are present in streams of the temperate deciduous forests of eastern North America (Ross, 1963). *Pycnopsyche* larvae are found predominantly in depositional areas associated with allochthonous organic matter. Larvae typically consume CPOM and are considered to be in the shredder functional feeding group (Cummins, 1973). Some species also eat leaves and periphyton (Cummins, 1964; Williams & Williams, 1982).

Table 1. Selected catchment parameters. \* Stream temperature data for 1 September 1992–31 August 1993 supplied by U.S. Forest Service.

Parameter	Disturbed	Reference
Basin area (ha)	59.5	61.1
Main tributary length (m)	1225	1125
Gradient (m/m)	0.19	0.15
Mean annual discharge (l/s)	17.7	19.0
Maximum elevation (m)	1060	996
Minimum elevation (m)	724	708
Basin orientation	S	N
Disturbance history	logged in 1977	undisturbed for >60 yr
Stream temperature (°C)*		
Mean	12.3	12.0
Minimum	4.0	2.0
Maximum	17.5	19.5
Total degree-days	4469	4355

Stout (1990) found *Pycnopsyche* larvae in reference and disturbed streams at Coweeta and considered them to be representative of two cohorts of a single species, *P. gentilis* (McLachlan), based on larval morphology and case construction. Because more than one species of *Pycnopsyche* often is found in some streams (e.g., Mackay & Kalf, 1973), we collected adults in the field and reared larvae to pupae and adults in the lab to confirm that only one species was present. Adults and pupae were identified using the keys of Betten (1950) and Wojtowicz (1982), and two species, *P. gentilis* and *P. flavata* (Banks), were found to be present in the two catchments. Both species occupy similar habitats, construct very similar cases, and are difficult to separate as early instar larvae (Wojtowicz, 1982). Consequently, we were unable to positively identify which species was used in our larval growth experiments. However, we suspect that we used only *P. gentilis* as the experiments were done in mid-winter (January–February) with approximately third-instars, and *P. gentilis* typically does not reach fifth instar until March, whereas *P. flavata* typically reaches fifth instar by December–January (Wojtowicz, 1982).

### Site description

The research was conducted at Coweeta Hydrologic Laboratory, Macon Co., North Carolina, USA. Coweeta is a US Forest Service experimental forest in the southern Appalachian Mountains and serves as a Long-Term Ecological Research site. The two catchments

are similar in size, elevation, gradient, main tributary length, discharge, and stream temperature, but differ in aspect (Table 1). The reference catchment (Catchment 14), drained by Hugh White Creek, has been undisturbed since selective logging before 1930 and the chestnut blight in the 1930s. Dominant vegetation includes white and red oak (*Quercus alba* L. and *Q. rubra* L.), hickory (*Carya glabra* (Mill.) Sweet), red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), yellow poplar (*Liriodendron tulipifera* L.), and beech (*Fagus grandifolia* Ehrh.). The disturbed catchment (Catchment 7), drained by Big Hurricane Branch, was clear-cut and cable-logged in 1976–77. Overstorey vegetation includes black locust (*Robinia pseudoacacia* L.), yellow poplar, black birch, dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* (Nutt.) Nees), white oak, and red oak. Understorey vegetation includes blackberry (*Rubus* spp.), grape (*Vitis* spp.), greenbrier (*Smilax* spp.), and various herbs. Dense growths of rhododendron (*Rhododendron maximum* L.) overhang the stream channels in much of both catchments.

#### Gut content analysis

Gut contents of 6–15 larvae collected from each of three tributaries in each catchment in September 1992 (autumn), January 1993 (winter), and April 1993 (spring) were analyzed. A total of 83 and 81 larvae from reference and disturbed streams, respectively, were studied. Larvae were frozen soon after collection to preserve gut contents, which were subsequently dissected from larvae, mixed thoroughly, filtered onto gridded filters, and cleared with immersion oil (Cummins, 1973). Gut contents were quantified by counting all particles along four transects on each filter using a compound microscope at 100 $\times$ . Particles were classified into three categories: leaf detritus, wood, and autotrophic material. Mean percent composition of each food type in the guts of larvae from each tributary on each date were calculated and used for statistical comparisons ( $n = 6$  tributaries for each date). Percent composition of each food type was arcsine transformed (Zar, 1984), and comparisons made between dates and catchments using 2-way ANOVA (SAS, 1989). Significant differences among dates of larval collection were tested with the Student-Newman-Keuls (SNK) multiple comparison method.

#### Laboratory growth experiments

We conducted two growth experiments in the laboratory, using two leaf species as food, to test whether *Pycnopsycha* larvae grew better on fast- or slow-decaying leaves. Black birch (a fast species) and white oak (a slow species) were collected at Coweeta in autumn after leaf abscission, air-dried, and placed in large-mesh bags (mesh size: ca. 5 mm). These leaves were microbially conditioned for 3 (Experiment I) and 2 months (Experiment II) in Hugh White Creek. Leaf softness was measured on 25 leaves of each species with a penetrometer (Feeny, 1970; Suberkropp & Klug, 1981). Leaf disks (ca. 2.5 cm dia) were punched from leaves and served as food in the experimental trials.

We collected similar-sized larvae (approx. instar III) from one tributary in each catchment in 1992–93 (Experiment I), but only from the disturbed catchment in 1993–94 (Experiment II). Only disturbed-catchment larvae were used for Experiment II because larval growth was not significantly different between catchments in Experiment I (see Results). Larvae were brought to the laboratory, placed individually into separate plastic dishes (80 mm  $\times$  95 mm  $\times$  95 mm) containing filtered, aerated stream water, and held in an unlit environmental chamber at 10 °C. For Experiment I, 10 larvae from each catchment were randomly assigned to fast and slow leaf diets, whereas in Experiment II 20 larvae from the disturbed catchment were assigned to each diet. Two chambers containing each leaf diet but without larvae served as controls. Larvae were blotted dry and weighed at the beginning of the experiment and provided 3–8 pre-weighed leaf disks every 3–8 days. Uneaten leaf material was removed, blotted dry, and weighed. Feces were collected by filtration each time food material was removed. Both experiments ran for 30 d. At the end of each experiment, the larvae were blotted dry, weighed, dried at 55 °C, and reweighed. Cases also were weighed to account for leaf material added to the case or lost due to consumption by larvae.

Ecological efficiencies were calculated for each larva using the following indices (after Waldbauer, 1968): relative growth rate (RGR), instantaneous growth rate (IGR), consumption index (CI), assimilation efficiency (AE), gross growth efficiency (GGE), and net growth efficiency (NGE). These indices were calculated as follows:

$$\text{RGR} = \frac{(G/T)}{\bar{W}}, \quad (1)$$

where  $G$  = larval dry weight growth,  $T$  = time in days, and  $\bar{W}$  = mean larval dry weight;

$$\text{IGR} = \frac{\ln(W_2) - \ln(W_1)}{T}, \quad (2)$$

where  $W_1$  = initial larval dry weight and  $W_2$  = final larval dry weight;

$$\text{CI} = \frac{(I/T)}{\bar{W}}, \quad (3)$$

where  $I$  = ingested leaf dry weight;

$$\text{AE} = \frac{(I - E)}{I} \times 100, \quad (4)$$

where  $E$  = egested leaf dry weight;

$$\text{GGE} = \frac{(W_2 - W_1)}{I} \times 100; \quad (5)$$

and

$$\text{NGE} = \frac{(W_2 - W_1)}{(I - E)} \times 100. \quad (6)$$

Blotted wet weights were converted to dry weights using wet weight:dry weight ratios developed for larvae and each leaf species. AE, GGE, and NGE were arc-sine transformed for statistical analysis. Differences in indices between diets were tested by ANCOVA, using initial larval weight as the covariate because smaller larvae tend to grow faster than larger larvae (e.g., Iversen, 1979; Perry et al., 1987). In cases where the slopes between larval preweight vs. diet or catchment were not parallel, we used a General Linear Model (GLM) instead of ANCOVA. Leaf softness was compared between leaf species with a Student's  $t$ -test.

#### *Field growth experiment*

Six (41 cm × 28 cm × 15 cm) plastic experimental chambers were placed in each of the three disturbed and three undisturbed streams and secured to the bottom with stakes. Only ca. 0.1 m of the container was underwater due to shallow stream depth. Rectangular holes cut in the long sides of each container and covered with 0.9-mm mesh plastic screen served to maintain water flow and prevent the escape of larvae. Similar-sized larvae from each stream were collected 1–2 d prior to stocking the chambers and weighed in groups of 15. On 25 January 1993, groups of 15 larvae were placed in chambers and set in their 'home' streams. Larval density in the chambers was in the range of

natural density in disturbed and reference streams during winter (Stout et al., 1993). Half the chambers in each stream were provided with mixed-leaf diets in amounts that were representative of disturbed streams (disturbed diet) and half were provided with leaves in amounts that were representative of reference streams (reference diet) in January based on data from Stout et al. (1993). Although the reference diet contained three times more leaf material than the disturbed diet, the reference diet was dominated by slow-decaying white oak and rhododendron leaves compared with the disturbed diet (80% of reference diet vs 60% of disturbed diet). Fast-decaying black birch and red maple leaves made up the rest of each diet. Leaves that had been conditioned in large-mesh bags (mesh size: ca. 5 mm) in Hugh White Creek for 2 mo were weighed in the field and added to the chambers. One chamber of each diet type without *Pycnopsyche* was placed in one stream of each catchment as a control. After 41 d, larvae from each chamber were removed, weighed wet as a group, dried, and reweighed.

RGR and IGR were calculated on an individual larva basis for each container by dividing by the number of larvae remaining in each container to correct for larval mortality during the experiment. In addition to calculating RGR and IGR on a daily basis, we calculated RGR on a temperature (degree-day) basis because the streams differed slightly in temperature. Wet weights were converted to dry weights using wet weight:dry weight ratios developed for larvae. Mean growth rates calculated for each diet type in each tributary were used for statistical comparisons. Differences in RGR, RGR on a degree-day basis, and IGR between diets and larval 'home' catchments were tested with ANCOVA using initial larval weight as the covariate. Larval survivorship was compared between diets and catchment using 2-way ANOVA.

## **Results**

### *Gut content analysis*

Analyses of gut contents indicated that larvae consumed leaf detritus almost exclusively (Table 2). Wood was the second most common food type and autotrophic material was found occasionally. Larvae from reference streams had significantly more leaf detritus (ANOVA,  $p < 0.05$ ) and less wood in their guts than larvae from disturbed streams. Larvae collected in spring had significantly less leaf detritus and signif-

Table 2. Percent composition (mean [SE]) of each food type in larval guts  $n$  = total number of larvae analyzed per catchment in each season.

	Disturbed catchment (%)	Reference catchment (%)
<b>Fall</b>		
$n$	29	27
Leaf detritus	95.9 (2.7)	100.0 (0)
Wood	3.3 (2.5)	0
Autotrophic material	0.9 (0.3)	0
<b>Winter</b>		
$n$	27	27
Leaf detritus	97.1 (0.7)	99.4 (0.6)
Wood	2.9 (0.8)	0.6 (0.6)
Autotrophic material	0.1 (0.1)	0 (0)
<b>Spring</b>		
$n$	27	27
Leaf detritus	86.3 (3.6)	92.5 (4.9)
Wood	9.7 (3.8)	4.7 (4.3)
Autotrophic material	4.0 (2.7)	2.8 (0.8)

icantly more autotrophic material (ANOVA followed by SNK,  $p < 0.05$ ) than larvae collected in autumn and winter. Although these differences were apparent, larval *Pycnopsyche* diets were dominated by leaf detritus in both catchments and in all seasons.

#### Laboratory growth experiments

Fast-decaying birch leaves were significantly softer than slow-decaying oak leaves in both experiments ( $t$ -test, Experiment I:  $p < 0.05$ ; Experiment II:  $p < 0.001$ ). Mean ( $\pm$  1 SE) penetrometer weights for birch leaves were 149.0 ( $\pm$  13.8) g and 146.5 ( $\pm$  14.5) g in Experiments I and II, respectively, whereas the mean weights for oak leaves in the experiments were 195.8 ( $\pm$  13.5) g and 225.4 ( $\pm$  11.9) g, respectively.

*Pycnopsyche* larvae consumed the softer birch leaves faster than the tougher oak leaves (Table 3, GLM,  $p < 0.01$ ; Table 4, ANCOVA,  $p < 0.001$ ). However, larvae did not always grow better on the birch diet. Instead, larval growth efficiencies on each diet varied depending on the amount of time the leaves were conditioned. RGR and IGR were lower for larvae eating birch than oak leaves in Experiment I after 3-months conditioning (Table 3) but higher in Experiment II after 2-months conditioning (Table 4). These differences in growth rates were significant in both experiments

(ANCOVA,  $p < 0.001$ ). Similarly, GGE and NGE were lower for birch in Experiment I (Table 3) but higher in Experiment II (Table 4), and both of these differences were statistically significant (ANCOVA,  $p < 0.001$ ). Larvae assimilated oak leaves slightly more than birch in Experiment I (Table 3, GLM,  $p > 0.05$ ) and significantly more in Experiment II (Table 4, ANCOVA,  $p < 0.001$ ). Disks of each leaf type in control chambers without larvae present did not differ between initial and final weights. No significant differences were observed between larvae collected from different catchments for any growth variable (Table 3). Finally, *Pycnopsyche* survivorship was high on both diets in Experiment I (Table 3). In Experiment II, 60% of larvae fed the oak diet died before the experiment was completed; none of the larvae fed birch leaves died (Table 4).

#### Field growth experiment

Despite there being proportionally more fast-decaying leaves (birch and maple) in the disturbed diet, larval growth rates were higher on the reference diet than on the disturbed diet on both a day and degree-day basis (ANCOVA,  $p < 0.05$ , Table 5). Larval growth rates were not significantly different between larvae located in different catchments (ANCOVA,  $p > 0.05$ ) even though the disturbed streams were slightly warmer than the reference streams. On average, disturbed streams accumulated 62 degree days more than reference streams, but this difference was not significant ( $t$ -test,  $p > 0.05$ ). No significant differences in mortality were found between larvae fed the two diets or located in the two catchments (ANOVA,  $p > 0.05$ ), and larvae survived well on both mixed-species diets (Table 5).

## Discussion

#### Gut content analysis

During autumn, winter, and spring guts of *Pycnopsyche* larvae in the disturbed streams contained mostly leaf detritus, indicating that the differences in shredder production found by Stout et al. (1993) can not be explained by a shift from leaves to more nutritious foods such as algae or animal material. Furthermore, even though little leaf material was present in the disturbed streams during spring, larvae did not shift to wood as an alternate food resource. Roeding & Smock (1989) found wood was an important component of the diet of two other species of *Pycnopsyche* in a

Table 3. Larval survivorship and growth variables (mean [SE]) for Experiment I (asterisks indicate significant differences between diets and catchments where larvae were collected for relative growth rate (RGR), instantaneous growth rate (IGR), gross growth efficiency (GGE), and net growth efficiency (NGE), ANCOVA,  $**p < 0.001$ ; consumption index (CI) and assimilation efficiency (AE) were compared with GLM,  $*p < 0.01$ ).

	No. and (%) of larvae surviving	RGR (mg/g/d)	IGR (d <sup>-1</sup> )	CI (g/g/d)	AE (%)	GGE (%)	NGE (%)
Diet							
Birch	20 (100)	16.8 (1.9)**	0.0174 (0.0021)**	1.40 (0.09)*	27.7 (3.0)	1.1 (0.1)**	4.5 (0.5)**
White oak	19 (95)	22.0 (1.7)	0.0233 (0.0020)	1.03 (0.06)	29.0 (2.1)	2.1 (0.1)	8.1 (0.8)
Catchment							
Disturbed	20 (100)	18.4 (1.8)	0.0192 (0.0020)	1.18 (0.07)	26.3 (1.3)	1.6 (0.1)	6.0 (0.5)
Reference	19 (95)	20.3 (2.0)	0.0214 (0.0023)	1.27 (0.11)	30.5 (3.5)	1.6 (0.2)	6.5 (1.0)

Table 4. Larval survivorship and growth variables (mean [SE]) in Experiment II for disturbed catchment larvae only (asterisks indicate significant differences between diets for growth variables, ANCOVA,  $*p < 0.001$ ).

	No. and (%) of larvae surviving	RGR (mg/g/d)	IGR (d <sup>-1</sup> )	CI (g/g/d)	AE (%)	GGE (%)	NGE (%)
Diet							
Birch	20 (100)	29.0 (1.6)*	0.0313 (0.0019)*	1.47 (0.04)*	35.2 (1.9)*	2.0 (0.1)*	6.0 (0.4)*
White oak	8 (40)	8.3 (2.6)	0.0084 (0.0027)	0.89 (0.08)	59.6 (2.8)	1.0 (0.3)	1.8 (0.5)

low-gradient Piedmont stream during spring when leaf biomass was low. Even though less leaf material was present in the disturbed Coweeta streams in spring, *Pycnopsyche* was still consuming mostly leaf detritus indicating that a major shift in larval diet did not occur. As hypothesized by Webster & Waide (1982) and Cummins et al. (1989), slow-decaying leaves like rhododendron appear to be important to the stability of shredder diets in spring and summer when fast-decaying leaves are absent.

#### Lab growth experiments

Fast-decaying birch leaves were significantly softer than slow-decaying oak leaves after 2 and 3 months of conditioning in streams and larvae always consumed the birch leaves faster than the oak. Larvae also consumed the softer 3-month-old oak leaves faster than the tougher 2-month-old oak leaves. These findings support previous suggestions that leaf softness helps to increase ingestion rates for caddisflies (Mackay & Kalff, 1973; Herbst, 1982; Rounick & Winterbourn, 1983; Arsuffi & Suberkropp, 1986). In contrast, lar-

val growth was not always fastest on the softer, fast-decaying birch leaves. Whereas larvae grew faster when eating 2-month-old birch leaves in Experiment II, they grew faster on the tougher 3-month-old oak leaves in Experiment I. Thus, larval growth rates appeared to be more dependent on how long leaves were conditioned rather than leaf toughness or whether leaves were fast or slow. These laboratory growth results did not completely support our prediction that shredders are more productive in the disturbed than in the reference streams because they can grow faster when consuming the more prevalent fast leaf biomass in disturbed streams. Instead, larvae only grew faster on fast leaves when the conditioning time was short and grew better on slow leaves when the conditioning time was long.

Taken together, our consumption and growth results do not support the findings of Iversen (1974) and Anderson & Cummins (1979) that shredders can compensate for low growth rates by increasing ingestion rates, i.e., *Pycnopsyche* did not always ingest more of the lower-quality diet. Smock & MacGregor (1988) also did not observe compensatory consumption of

Table 5. Larval survivorship and growth variables (mean [SE]) for field experiment. Means were based on three streams in each catchment containing both diet types (asterisks indicate significant differences for growth variables between diets and the catchments where larvae were located, ANCOVA, \* $p < 0.05$ ).

	No. and (%) of larvae surviving	RGR (mg/g/d)	RGR (mg/g/degree-day)	IGR ( $d^{-1}$ )
Diet				
Disturbed	12.0 (80.0)	24.3 (1.4)*	3.0 (0.3)*	0.0270 (0.0018)
Reference	14.5 (96.7)	28.1 (1.1)	3.4 (0.2)	0.0325 (0.0017)
Catchment				
Disturbed	13.9 (92.7)	25.6 (1.6)	2.8 (0.2)	0.0288 (0.0022)
Reference	12.5 (83.3)	26.9 (1.3)	3.6 (0.1)	0.0306 (0.0019)

lower quality red oak leaves compared to higher quality American chestnut and pignut hickory leaves by either *Pycnopsyche luculenta* (Betten) or the crane fly, *Tipula abdominalis* (Say).

Whereas assimilation efficiencies did not help explain differences in growth in either experiment, gross and net growth efficiencies were useful. Assimilation efficiencies were not significantly different in Experiment I, and in Experiment II they were higher for larvae feeding on the white oak diet despite the high mortality and low growth observed for this diet. Similar poor relationships between food quality and assimilation efficiencies were reported by Golladay et al. (1983) for a leaf-shredding stonefly. In contrast, higher growth rates in both experiments were accompanied by more efficient conversion of ingested and assimilated leaf material to growth (GGE and NGE, respectively). Iversen (1974) and Arsuffi & Suberkropp (1986) also found that differences in leaf-shredding caddisfly growth rates on different diets could be explained by the efficiency of converting ingested leaf material to growth.

In summary, larval growth responses (i.e., RGR, IGR, GGE, and NGE) to birch and oak leaf diets in the laboratory appeared to depend on how long the leaves were conditioned rather than whether leaves were fast or slow. After two months in the stream, fast birch leaves were better food resources for *Pycnopsyche* larvae than slow oak leaves, but after three months birch seemed to decline in food quality and oak appeared to become a better food resource. This apparent switching in food quality is consistent with the model proposed by Boling et al. (1975) that fast leaves become more rapidly 'fully-conditioned' than slow leaves and therefore fast leaves are better food resources for shredders sooner. However, this 'fully-conditioned' stage is tem-

porary and is followed by a 'post-conditioned' stage in which microbial activity decreases and the leaves presumably become less palatable to shredders. Because of this apparent overriding importance of leaf conditioning time over overall decay rate, these growth results did not completely explain the higher shredder production in the disturbed streams.

#### Field growth experiment

Many studies have reported that insect feeding and growth are affected by temperature (e.g., Cummins et al., 1973; Sweeney & Vannote, 1986; Sweeney et al., 1986; Perry et al., 1987) and the interaction between temperature and food quality (Anderson & Cummins, 1979; Cargill et al., 1985; Sweeney & Vannote, 1986; Sweeney et al., 1986). Whereas all of our laboratory growth experiments were conducted at 10 °C, the field experiment tested how differences in diet between the two catchments might affect larval growth under natural thermal regimes. Although the disturbed streams were slightly warmer than the reference streams during the field experiment, this difference did not appear to greatly affect larvae. Larvae were provided mixed-species leaf diets representative of the disturbed and reference streams. The disturbed diet contained proportionally more fast-decaying birch and maple leaves and fewer slow-decaying oak and rhododendron leaves than the reference diet. Larvae were predicted to grow faster on the disturbed stream diet. However, larval growth did not respond as predicted, as larvae grew faster on the reference diet.

We hypothesize that larvae grew faster on the reference diet because the leaves continued to be conditioned over the course of the experiment, which would presumably alter the quality of the leaves as a food

resource. Larvae were initially provided leaves that had been conditioned for 2 months, but these leaves were further conditioned over the 42 d experiment. Our laboratory growth experiments indicated that birch leaves apparently changed from a relatively good diet after 2 months of conditioning to a lower quality diet after 3 months of conditioning, and that oak leaves changed in the opposite direction. Consequently, the greater amounts of oak leaves present in the reference diet compared with the disturbed diet could have provided *Pycnopsyche* larvae with a better food resource as the field experiment progressed. This result once again may indicate that the amount of time leaves are conditioned seems to have a greater impact on shredder growth than the overall decay rate of the leaves.

## Conclusion

Fast-conditioning leaves have been predicted to be better foods than slow-conditioning leaves if compared at the same time and at the same temperature (Petersen & Cummins, 1974; Cummins & Klug, 1979; Maltby, 1992). However, knowing only whether a leaf is conditioned at a fast or slow rate was not a good predictor of larval growth in this study. Instead, larvae grew better on leaves that were apparently optimally conditioned regardless of their overall conditioning rate. This conclusion mirrors the observation by Cummins et al. (1989) that shredders do not prefer litter from a particular plant species, but rather prefer appropriately conditioned litter regardless of species. This conclusion also agrees with that of Bärlocher (1985) who stated that once the peak in acceptability of a leaf species is reached, any additional conditioning lessens the attractiveness of the leaf to shredders. Considering the importance of leaf conditioning to shredders, more detailed study of the conditioning process is needed. Perhaps studying possible differences in the conditioning process between disturbed and reference streams at Coweeta will help explain the differences in production between these streams.

## Acknowledgments

We thank the Virginia Tech Stream Team (Terry Ehrman, Mary Schaeffer, Jennifer Tank, Patricia Turner, and Alan Yeakley) for assistance and discussions about this study. In addition, Jimmy Blakeney, Patricia Greiner, Derek Hodges, and Robin Hutchens provided

much assistance in the field and the lab. Dr J. R. Voshell gave many constructive comments throughout this project. Dr Oliver Flint (Department of Entomology, Smithsonian Institution, Museum of Natural History) verified *Pycnopsyche* pupal and adult identifications. Stream temperature data and logistical support was provided by the Coweeta Hydrologic Laboratory, US Forest Service. This work was supported in part by the National Science Foundation-Long-Term Ecological Research Program (BSR #9011661) to EFB and JRW, Sigma Xi, Virginia Academy of Science, VPI & SU Graduate Student Assembly, and VPI & SU Department of Biology to JJH.

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