Freshwater Biology (2007) **52**, 1–11 doi:10.1111/j.1365-2427.2006.01657.x

Aquatic and terrestrial invertebrate drift in southern Appalachian Mountain streams: implications for trout food resources

ERIC D. ROMANISZYN,* JOHN J. HUTCHENS JR† AND J. BRUCE WALLACE*,†
*Department of Entomology, The University of Georgia, Athens, Georgia 30602-2603, U.S.A.
†Institute of Ecology, The University of Georgia, Athens, Georgia 30602, U.S.A.

SUMMARY

1. We characterised aquatic and terrestrial invertebrate drift in six south-western North Carolina streams and their implications for trout production. Streams of this region typically have low standing stock and production of trout because of low benthic productivity. However, little is known about the contribution of terrestrial invertebrates entering drift, the factors that affect these inputs (including season, diel period and riparian cover type), or the energetic contribution of drift to trout.
2. Eight sites were sampled in streams with four riparian cover types. Drift samples were collected at sunrise, midday and sunset; and in spring, early summer, late summer and autumn. The importance of drift for trout production was assessed using literature estimates of annual benthic production in the southern Appalachians, ecotrophic coefficients and food conversion efficiencies.
3. Abundance and biomass of terrestrial invertebrate inputs and drifting aquatic larvae were typically highest in spring and early summer. Aquatic larval abundances were greater than terrestrial invertebrates during these seasons and terrestrial invertebrate biomass was greater than aquatic larval biomass in the autumn. Drift rates of aquatic larval abundance and biomass were greatest at sunset. Inputs of terrestrial invertebrate biomass were greater than aquatic larvae at midday. Terrestrial invertebrate abundances were highest in streams with open canopies and streams adjacent to pasture with limited forest canopy.
4. We estimate the combination of benthic invertebrate production and terrestrial invertebrate inputs can support 3.3–18.2 g (wet weight) m^{-2} $year^{-1}$ of trout, which is generally lower than values considered productive [10.0–30.0 g (wet weight) m^{-2} $year^{-1}$].
5. Our results indicate terrestrial invertebrates can be an important energy source for trout in these streams, but trout production is still low. Any management activities that attempt to increase trout production should assess trout food resources and ensure their availability.

Keywords: aquatic invertebrates, drift, secondary production, terrestrial invertebrates, trout

Correspondence: Eric D. Romaniszyn, Haywood Waterways Association, PO Box 389, Waynesville, NC 28786, U.S.A.
E-mail: romaniszyne@yahoo.com
Present address: John J. Hutchens, Department of Biology, Coastal Carolina University, PO Box 261954, Conway, SC 29528-6054, U.S.A.

Introduction

Trout biomass and production are strongly correlated with densities of drifting invertebrates (Elliott, 1973; Wilzbach, Cummins & Hall, 1986) and drift densities are positively correlated with benthic productivity (Pearson and Kramer 1972, Benke, Parsons & Dhar,

© 2006 The Authors, Journal compilation © 2006 Blackwell Publishing Ltd

1991; Sagar & Glova, 1992). During periods of low drift, trout shift to foraging on bottom-dwelling invertebrates (Bechara, Moreau & Planas, 1992; Nakano, Miyasaka & Kuhara, 1999a). Southern Appalachian streams typically have low standing stocks of trout [i.e. <4 g (wet weight) m^{-2}; Harshbarger, 1978; Whitworth & Strange, 1983; Habera & Strange, 1993] compared with productive streams [10–30 g (wet weight) m^{-2}; Waters, 1988] because of low benthic productivity and drift densities (Coulston & Maughan, 1981; Whitworth & Strange, 1983; Cada, Loar & Slade, 1987a; Wallace, Webster & Lowe, 1992; Habera & Strange, 1993). Benthic productivity in trout streams of the southern Appalachians ranges from 5.0 to 21.0 g ash-free dry mass (AFDM) m^{-2} $year^{-1}$ (Wohl, Wallace & Meyer, 1995; Grubaugh, Wallace & Houston, 1997). Assuming trout ingest 80% of available benthic prey (Huryn, 1996) and have a food conversion efficiency of 20% (Waters, 1988), benthic communities in these streams are capable of supporting 4.4–18.6 g (wet weight) m^{-2} $year^{-1}$ (1 g AFDM = 5.55 g wet; Waters, 1988) of trout production. However, trout production estimates may be higher if they include drifting terrestrial invertebrates as prey (Waters, 1988; Huryn, 1996).

Terrestrial invertebrates can comprise a significant proportion of drift and may be an important food subsidy for salmonids (Elliott, 1973; Cada, Loar & Cox, 1987b; Nakano *et al.*, 1999a; Kawaguchi & Nakano, 2001; Allan *et al.*, 2003), particularly in unproductive streams (e.g. Ellis & Gowing, 1957). Tebo & Hassler (1963) found terrestrial invertebrates comprised 33% of annual trout diet in western North Carolina streams. However, little is known about the quantity of terrestrial invertebrates entering southern Appalachian streams or the factors that affect these inputs, which include season, diel period and riparian cover type. Trout consume greater proportions of terrestrial invertebrates during periods of low invertebrate productivity (Ellis & Gowing, 1957; Bridcutt, 2000). In late summer and early autumn, benthic invertebrate densities are reduced (Reisen & Prins, 1972; Hunt, 1975; Stoneburner & Smock, 1979) and terrestrial invertebrate drift densities are at their peaks (Cada *et al.*, 1987b; Sagar & Glova, 1992; Edwards & Huryn, 1995; Cloe & Garman, 1996). Hence, terrestrial invertebrates may be an important dietary component for trout at these times.

When examining different diel periods, inputs of terrestrial invertebrates to drift are highest at midday and sunset (Elliott, 1967; Jenkins, Feldmeth & Elliott, 1970; Elliott, 1973; Furukawa-Tanaka, 1985), whereas aquatic invertebrate drift densities are highest at night, particularly just after sunset and before sunrise (Waters, 1965; Skinner, 1985; Brittain & Eikeland, 1988; Sagar & Glova, 1992). Elliott (1973) found that trout fed primarily on drifting benthic invertebrates just after dusk, but switched to terrestrial and emerging invertebrates in daylight, particularly at midday and sunset. Nakano *et al.* (1999b) found terrestrial invertebrates comprised a larger proportion of trout diets than aquatic invertebrates at times when terrestrial invertebrates were more abundant than aquatic invertebrates in drift. This suggests trout optimise foraging by switching to prey items of greatest availability (Giroux *et al.*, 2000).

Riparian vegetation can influence benthic macroinvertebrates (Brewin & Ormerod, 1994; Wallace *et al.*, 1997; Wipfli & Musslewhite, 2004). Stream reaches with no overhanging vegetation can have greater autochthonous production and support greater aquatic invertebrate biomass and a greater food supply for trout (Hunt, 1975). The type of riparian vegetation is also known to influence terrestrial invertebrate contributions to drift (Wilzbach *et al.*, 1986; Edwards & Huryn, 1996; Wipfli, 1997; Allan *et al.*, 2003; Piccolo & Wipfli, 2003) and the composition of fish diets (Cadwallader, Eden & Hook, 1980). Wipfli (1997) found terrestrial invertebrates were important components of young salmonid diets and concluded that young growth forested areas (=coppice forest) with a dense understory may have higher inputs of terrestrial invertebrates. Dolloff (1987) found annual production of coho salmon, *Oncorhynchus kisutch* Waulbum, was greatest in stream reaches with a meadow surrounding the stream and least in streams draining forests.

The goals of this study were to characterise drift in southern Appalachian streams and to examine its implications for trout production. Our specific objectives were to determine rates of terrestrial invertebrate inputs and aquatic invertebrate drift and how they varied by season, diel period and riparian cover type. For terrestrial invertebrates, we predicted: (i) seasonal inputs would be highest in summer and autumn and lowest in spring; (ii) diel period inputs would be highest at midday and lowest at sunrise; and (iii)

riparian cover types with a greater density of overhanging riparian vegetation would provide the greatest contributions. For aquatic invertebrates, we predicted: (i) drift would be highest in spring and lowest in late summer; (ii) drift would be greatest at sunset and lowest at midday; and (iii) drift would be greatest in reaches with no riparian vegetation. We also predicted aquatic invertebrates would contribute more to drift than terrestrial invertebrates during each season, diel period and riparian cover type because they are the dominant components of stream ecosystems. We compare our results with published accounts of trout feeding behaviour and production to provide the basis for improved management efforts aimed at increasing trout production.

Methods

Study sites

This study was conducted in six south-western North Carolina streams in the vicinity of the Coweeta Hydrologic Laboratory and the Wine Spring Creek Ecosystem Management Area in the Nantahala National Forest (Macon County, North Carolina; Table 1). Eight sites were sampled in four riparian cover types. Three sites were in older secondary growth (80–100 years) forests with a rhododendron, *Rhododendron maximum* Linnaeus, understory and oaks, *Quercus* spp., beech, *Fagus grandifolia* Ehrhart, red maple, *Acer rubrum* Linnaeus, sugar maple, *A. saccharum* Marshall and yellow birch, *Betula alleghaniensis* Britton as the overstory shading the stream. One site was in a young secondary growth (30 year) forest with riparian cover of sparse understory vegetation (compared with the older secondary growth sites) and a denser overstory of the same tree species as the older forested canopy plus black locust, *Robinia pseudoacacia* Linnaeus. Two sites were bordered by old field/pasture with an open canopy, and two sites were bordered by old field/pasture with narrow (2–4 m) forested riparian cover consisting of beech, sugar maple and silver maple, *Acer saccharinum* Linnaeus, shading the stream. The open and narrow forested riparian cover sites had denser understory vegetation (grasses and shrubs) adjacent to the stream compared with forested sites.

Brown trout, *Salmo trutta* Linnaeus, rainbow trout, *Oncorhynchus mykiss* Walbaum, and mottled sculpins, *Cottus bairdi* Girard, are the dominant predatory fish in these streams. All sites are on first- to fourth-order streams with high gradients (i.e. slopes >2.0%).

Table 1 Riparian cover types at each study site. Discharge (Q), stream width, and stream sample area are means ($n = 4$; spring, early summer, late summer and autumn)

Stream	Riparian cover type	Stream order	Q ($m^3 s^{-1}$)	Width (m)	Area (m^2)
Wine Spring Creek	Older forest	2	0.10	2.5	46.5
Coweeta Creek	Older forest	4	0.65	5.8	116.0
Shope Fork Creek	Older forest	3	0.44	4.5	100.6
Shope Fork Creek	Open	3	0.44	4.7	93.9
Jones Creek	Open	4	0.57	5.4	108.3
Jones Creek	NRP	4	0.63	5.9	118.5
Allison Creek	NRP	4	0.52	5.5	109.1
Big Hurricane Branch	Coppice	1	0.09	1.5	29.2

NRP, narrow forested riparian cover.

Drift and terrestrial invertebrate contributions

We used the methods of Edwards & Huryn (1995) to measure terrestrial contributions to drift and drift rates of aquatic invertebrates. A 6-mm mesh shade cloth was placed over 20 m of the stream bed to prevent trout from drift feeding. A 1-mm mesh seine was placed at the upstream end of the study reach to block upstream drift inputs and also at the downstream end to collect drifting invertebrates. After 2 h, the net was removed, placed in a large sealable bag and taken to the laboratory for processing. All invertebrates were preserved in 7–8% formalin. Invertebrates were identified to the lowest practical taxon and as terrestrial invertebrate, emerged aquatic adult, or aquatic larvae. Terrestrial invertebrates were further categorised as winged or non-winged. Emergent adults were separated from aquatic larvae if they had fully developed wings and were not included as terrestrial invertebrate for analysis. Lengths were measured to the nearest millimetre using a stage micrometer and estimates of AFDM were calculated using published length-mass regressions (Sample *et al.*, 1993; Benke *et al.*, 1999) or equations developed in this study.

Stream sample area, discharge and stream and air temperatures were measured on each collection date (Table 1). Discharge was measured immediately below the downstream net. Samples were collected

during spring, early summer, late summer and autumn. Winter months were not sampled because trout reduce feeding and activity at this time (Hunt, 1975; Elliott, 1976). In early summer, only sunrise and sunset samples were collected, while in other seasons samples were collected at sunrise, midday and sunset. Drift was calculated in units per surface area (m^{-2}) for comparisons between aquatic larvae and terrestrial organisms. Surface area and sample time were used to estimate input rates of abundance (no. m^{-2} $time^{-1}$) and biomass (mg AFDM m^{-2} $time^{-1}$). Rates were expressed in units per day for seasonal and cover type data and units per hour for diel data.

The implications of drift and terrestrial inputs for trout food resources and production were assessed using literature estimates of annual benthic production in southern Appalachian streams (Wohl *et al.*, 1995; Grubaugh *et al.*, 1997), ecotrophic coefficients (Huryn, 1996) and food conversion efficiencies (Waters, 1988). These estimates were used to calculate potential annual trout production supported by the benthos and terrestrial invertebrates. Annual drift estimates were calculated as mean daily input rates multiplied by 365. Because winter drift samples were not obtained in this study, we used a conservative winter input rate of zero to calculate the annual drift rate.

Comparisons were made among invertebrate categories and among seasons, diel periods and riparian cover type. Input and drift rates were log10(x+1) transformed to normalise variance and compared using one-way ANOVA with Tukey pair-wise comparison tests ($P < 0.05$). Transformed data that failed the assumptions of normality were analysed using Kruskal–Wallis ANOVA on ranks. Regression analysis was used to determine the effects of discharge, stream temperature and air temperature on terrestrial invertebrate input rates and aquatic larval drift rates.

Results

Season

Terrestrial invertebrate abundance input rates in early summer were significantly greater than both spring and late summer ($P \leq 0.02$; Table 2; Fig. 1) and autumn input rates were greater than late summer ($P < 0.01$). Input rates of terrestrial invertebrate biomass in early summer were significantly greater than

Table 2 Analysis of variance output for significant comparisons of terrestrial invertebrate (TI) and aquatic larval (AQL) abundance (season and cover type = no. m^{-2} day^{-1}; diel period = no. m^{-2} h^{-1}) and biomass (season and cover type = mg AFDM m^{-2} day^{-1}; diel period = mg AFDM m^{-2} h^{-1}) inputs to drift. Comparisons were made by season, diel period and cover type.

	Test	Comparison	ANOVA result
Season	TI abundance	Early summer > spring	$P = 0.02$
		Early summer > late summer	$P < 0.01$
		Autumn > late summer	$P < 0.01$
	TI biomass	Early summer > late summer	$P < 0.01$
	AQL abundance	Spring > late summer	$P < 0.01$
		Spring > autumn	$P = 0.02$
		Early summer > late summer	$P = 0.02$
		Early summer > autumn	$P < 0.02$
	AQL biomass	Spring > late summer	$P < 0.01$
		Spring > autumn	$P < 0.01$
		Early summer > late summer	$P < 0.01$
		Early summer > autumn	$P < 0.01$
	TI versus AQL abundance	Spring: AQL > TI	$P = 0.02$
	TI versus AQL biomass	Autumn: TI > AQL	$P < 0.01$
Diel Period	AQL abundance	Sunset > sunrise	$P = 0.02$
		Sunset > midday	$P < 0.01$
	AQL biomass	Sunset > sunrise	$P < 0.01$
		Sunset > midday	$P < 0.01$
	TI versus AQL biomass	Midday: TI > AQL	$P < 0.01$
Cover Type	TI abundance	Open > older forest	$P < 0.01$
		Open > coppice	$P = 0.01$
		NRP > older forest	$P < 0.01$
		NRP > coppice	$P < 0.01$
	TI versus AQL abundance	Older forest: AQL > TI	$P < 0.03$

NRP, narrow forested riparian cover.

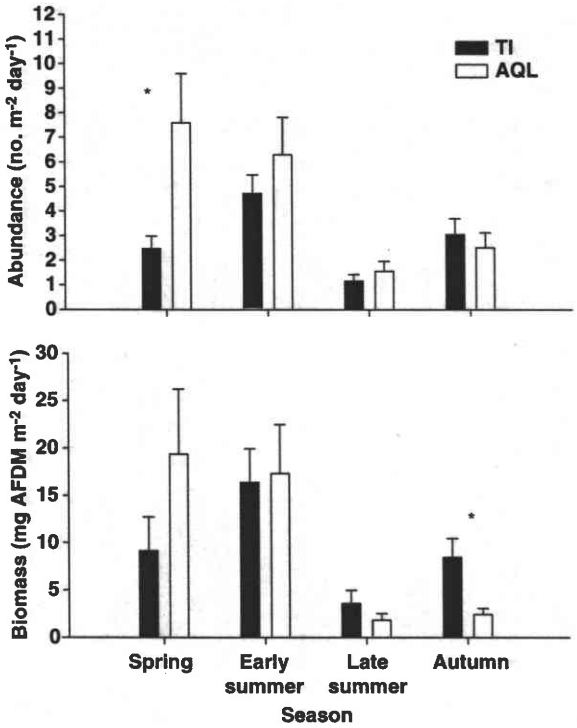

Fig. 1 Abundance and biomass of terrestrial invertebrate (TI) input rates and aquatic larval (AQL) drift rates by season for all sites (mean ± 1 SE). *TI and AQL were significantly different ($P < 0.05$; $n = 8$ per season).

late summer ($P < 0.01$). In the spring and early summer, mean aquatic larval abundance and biomass were significantly greater than late summer and autumn ($P \leq 0.02$). Abundances of aquatic larvae in spring were also significantly greater than terrestrial invertebrates ($P = 0.02$). *Epeorus* sp. (Ephemeroptera, Heptageniidae) was the most abundant invertebrate in drift during these seasons (Table 3), but emerged aquatic adults increased in late summer. Terrestrial invertebrate mean biomass was significantly greater than aquatic larvae in autumn ($P < 0.01$; Fig. 1), primarily because of the large contribution of Lepidoptera larvae and adult Orthoptera (Table 3). Lepidoptera larvae also contributed the most biomass in spring and late summer.

A positive relationship was observed between mean seasonal aquatic larval drift abundance and discharge (Table 4). Mean terrestrial invertebrate abundance and biomass were positively or negatively related to discharge, stream temperature and air temperature. However, as demonstrated by low r^2 values, very little of the variance in each relationship was explained by the independent variables.

Diel period

Mean terrestrial invertebrate abundance and biomass in drift did not differ significantly by diel period (Fig. 2). Mean aquatic larval abundance and biomass at sunset were significantly greater than sunrise and midday ($P \leq 0.02$; Table 2). Mayfly (Ephemeroptera) larvae and adults contributed the most organisms to

Table 3 Contributions of the top two contributors to drift abundance and biomass for each riparian cover type, season and diel period

	Abundance (season and cover type = no. m^{-2} day^{-1}; diel period = no. m^{-2} h^{-1})		Biomass (season and cover type = mg AFDM m^{-2} day^{-1}; diel period = mg AFDM m^{-2} h^{-1})	
	1	2	1	2
Season				
Spring	*Epeorus* sp., AQL, 2.38	Ephemerellidae, AQL, 1.75	Lepidoptera, NWT, 6.85	*Epeorus* sp., AQL, 5.21
Early Summer	*Epeorus* sp., AQL, 1.79	Ephemeroptera, AA, 1.56	*Epeorus* sp., AQL, 4.89	Coleoptera, WGT, 4.78
Late Summer	Trichoptera, AA, 0.84	Ephemeroptera, AA, 0.62	Lepidoptera, NWT, 1.24	Trichoptera, AA, 1.19
Autumn	Formicidae, NWT, 0.62	Diptera, WGT, 0.59	Lepidoptera, NWT, 2.51	Orthoptera, WGT, 2.49
Diel Period				
Sunrise	Ephemerellidae, AQL, 0.029	Brachycera, AA, 0.026	Lepidoptera, NWT, 0.132	Coleoptera, WGT, 0.053
Midday	Ephemeroptera, AA, 0.041	Diptera, WGT, 0.031	Lepidoptera, NWT, 0.228	Orthoptera, WGT, 0.113
Sunset	*Epeorus* sp., AQL, 0.115	Ephemeroptera, AA, 0.061	*Epeorus* sp., AQL, 0.272	Coleoptera, WGT, 0.131
Cover Type				
Older Forest	*Epeorus* sp., AQL, 0.59	Trichoptera, AA, 0.58	Orthoptera, WGT, 2.33	Lepidoptera, WGT, 1.36
Open	*Epeorus* sp., AQL, 2.24	Ephemeroptera, AA, 1.35	*Epeorus* sp., AQL, 5.12	Lepidoptera, NWT, 4.68
NRP	*Epeorus* sp., AQL, 0.90	Ephemeroptera, AA, 0.89	Lepidoptera, NWT, 4.68	Coleoptera, WGT, 3.65
Coppice	Peltoperlidae, AQL, 2.08	*Epeorus* sp., AQL, 1.25	Peltoperlidae, AQL, 11.49	*Epeorus* sp., AQL, 5.69

AA, aerial adult of aquatic origin; NWT, non-winged terrestrial invertebrate; WGT, winged terrestrial invertebrate; AQL, aquatic larvae; NRP, narrow forested riparian cover.

Table 4 Significant results of regression analysis between inputs of terrestrial invertebrates (TI) and drift rates of aquatic larvae (AQL) with discharge (Q), air temperature (T) and stream temperature

	Test	r^2	Slope	*P*-value
Season	AQL abundance × Q	0.13	+	0.04
	TI abundance × Q, Air T, Stream T	0.43	+, +, +	<0.02
	TI biomass × Q, Air T, Stream T	0.52	+, −, +	≤0.02
Diel Period	TI abundance × Q	0.14	+	0.02
	TI biomass × Q	0.31	+	<0.01

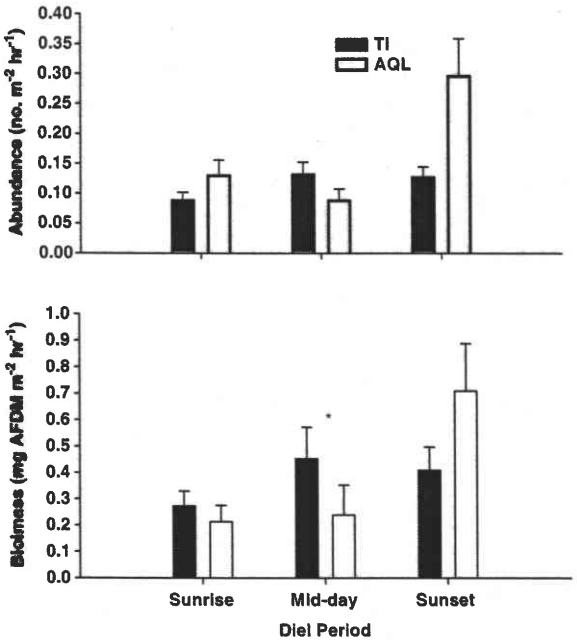

Fig. 2 Abundance and biomass of terrestrial invertebrate (TI) input rates and aquatic larval (AQL) drift rates during each diel period for all sites (mean ± 1 SE). *TI and AQL were significantly different ($P < 0.05$; sunrise, sunset, $n = 32$; midday, $n = 24$).

drift during all periods, particularly at sunset (Table 3) and *Epeorus* sp. contributed more biomass at sunset than any other organism. The only significant difference between terrestrial invertebrates and aquatic larvae was at midday when mean terrestrial invertebrate biomass was significantly greater than aquatic larvae ($P < 0.01$), possibly because of large lepidopteran larval biomass.

No relationship was found between diel aquatic larval drift rates and temperature or discharge. Positive relationships were observed between input rates

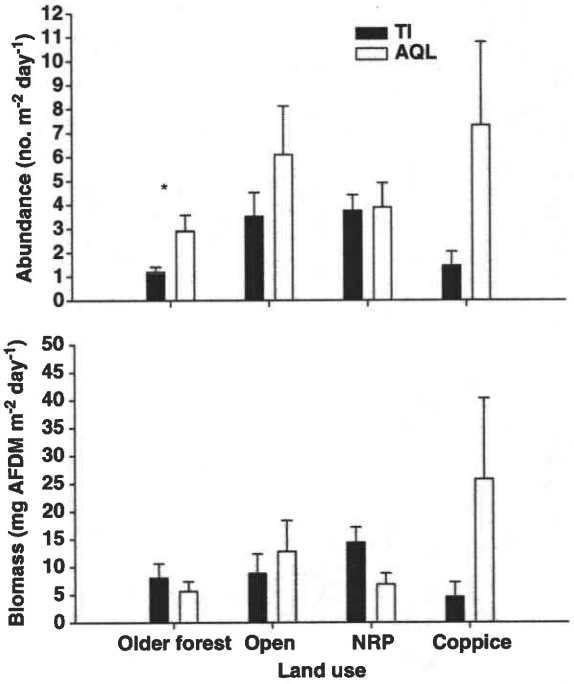

Fig. 3 Abundance and biomass of terrestrial invertebrate (TI) input rates and aquatic larval (AQL) drift rates from four riparian cover types for all sites (mean ± 1 SE). NRP, narrow forested riparian cover. *TI and AQL were significantly different ($P < 0.05$; older forest, $n = 12$; open, $n = 8$; NRP, $n = 8$; coppice, $n = 4$).

of terrestrial invertebrate abundance and biomass with discharge, although the relationships were weak (Table 4).

Cover type

Mean terrestrial invertebrate abundance from open and narrow forested riparian cover types were significantly greater than both forested cover types ($P \leq 0.01$; Table 2; Fig. 3), but there were no differences in biomass. Mean aquatic larval abundance and biomass did not differ significantly among cover types. Although aquatic larvae, particularly *Epeorus* sp., were generally the most abundant organisms collected within each cover type, the only significant difference between aquatic larvae and terrestrial invertebrate abundance input rates was in the older forest where mean aquatic larvae inputs were significantly greater than terrrestrial invertebrates ($P < 0.03$; Fig. 3). No relationships were found between terrestrial invertebrate inputs and aquatic

larval drift rates from each cover type with the independent variables.

Discussion

Season

Seasonal inputs of terrestrial invertebrates and aquatic larval drift rates generally followed our predictions. High aquatic larval drift rates in spring and early summer is typical of southern temperate streams (Stoneburner & Smock, 1979; O'Hop & Wallace, 1983; Benke *et al.*, 1991) and drift rates have been positively correlated with benthic invertebrate densities (Pearson & Kramer 1972, Benke *et al.*, 1991; Sagar & Glova, 1992; Siler, Wallace & Eggert, 2001) and emergence (Waters, 1972). It may be assumed that emerged aquatic adults are a loss of energy from the stream, but this study and others (Mason & Macdonald, 1982; Bridcut, 2000) demonstrate emerged aquatic adults can be an important potential energy source in drift (Table 3). The higher aquatic larval drift in spring and early summer may also be a result of resource limitation for benthos as litter inputs from the previous autumn become exhausted. Siler *et al.* (2001) found higher proportions of benthic organisms drifting in a treatment stream with detritus removed. However, reduced litter resources alone probably cannot explain all the increased aquatic larval drift because some important species in the drift (e.g. *Epeorus*) feed primarily on other resources (e.g. periphyton).

Aquatic organisms were expected to contribute more to drift than terrestrial invertebrates. This was true in spring when aquatic larval abundances were greater than terrestrial invertebrates. However, aquatic larval biomass was not significantly greater in spring and terrestrial invertebrates contributed greater biomass than aquatic larvae in autumn. Other studies found similar results (Chaston, 1969; Cada *et al.*, 1987b; Garman, 1991) and show that terrestrial invertebrate inputs can be similar to aquatic larvae in the drift (Mason & Macdonald, 1982; Cloe & Garman, 1996; Nakano *et al.*, 1999a).

Inputs of terrestrial invertebrates were highest in early summer and lowest in late summer, as found in other studies in temperate streams (Mason & Macdonald, 1982; O'Hop & Wallace, 1983; Garman, 1991; Cloe & Garman, 1996; Bridcut, 2000; Kawaguchi & Nakano, 2001). However, this finding differed from our prediction that the lowest inputs would occur in spring. This may be attributed to large invertebrate abundances during spring emergence, which is correlated with increases in temperature and discharge. Air temperature affects winged invertebrate activity and their input rates (Angermeir & Karr, 1983; Edwards & Huryn, 1995; Bridcut, 2000), but this study also indicated air temperature influences non-winged activity. Many studies have found that discharge and stream velocity are the two primary hydrological characteristics affecting invertebrate drift (Brittain & Eikeland, 1988). High discharge, particularly in spring and early summer, can increase aquatic larval drift by scouring the stream bottom or increasing accidental drift (Ciborowski, 1983; O'Hop & Wallace, 1983). Higher flow can increase terrestrial invertebrate inputs by increasing the wetted stream perimeter and stream surface area that terrestrial invertebrates can encounter (Edwards & Huryn, 1995), reaching new substrates and overhanging vegetation that is occupied by terrestrial invertebrates (Angermeir & Karr, 1983) and increasing bank erosion which can increase inputs of ground-dwelling invertebrates (Hunt, 1975).

Diel period

Input and drift rates also differed by the time of day samples were collected. Drift rates of aquatic larval abundance and biomass drift rates were highest around sunset as predicted and to a lesser degree at sunrise. These trends were observed by others (Reisen & Prins, 1972; Hunt, 1975; Benke *et al.*, 1991; Rader & McArthur, 1995). The lack of correlation between aquatic larval drift rates and temperature and discharge supports the observation that diel drift fluctuations are governed by behaviour, particularly to reduce predation (Waters, 1972; Allan, 1984; Peckarsky, 1996; Huhta *et al.*, 1999). Typically, inputs of terrestrial invertebrates are highest at midday (Elliott, 1967; Chaston, 1969; Jenkins *et al.*, 1970); however, we found no significant diel differences. Similarly, Edwards & Huryn (1995) found no differences between day and night terrestrial invertebrate biomass input rates. Aquatic larvae were expected to contribute more to drift than terrestrial invertebrates during all diel periods, but this study found terrestrial invertebrate contributions are similar and sometimes greater than aquatic larvae.

Cover type

Abundances of terrestrial invertebrates were influenced by cover type and agreed with our prediction. However, terrestrial invertebrate biomass inputs and aquatic larval drift rates were not influenced by cover type, as found by Bridcut (2000). Kawaguchi & Nakano (2001) generally found no differences among cover types, except during summer. Discharge also did not influence terrestrial invertebrate inputs, unlike other studies in similar cover types (Hunt, 1975; Edwards & Huryn, 1995; Wipfli, 1997). Stream reaches with higher vegetation densities closer to the stream and stream banks susceptible to erosion would be expected to have higher terrestrial invertebrate inputs. Terrestrial invertebrate inputs to drift are an accidental occurrence (Sagar & Glova, 1995; Bridcut, 2000) and have been attributed to wind and rain (Hunt, 1975). This might explain the high inputs in the open and narrow forested riparian canopies because of their increased exposure to wind and rain relative to the forested sites. An additional factor may be the dense rhododendron understory commonly found in the southern Appalachians. Input rates of terrestrial invertebrates in the forested sites were lower than other studies (Cloe & Garman, 1996; Edwards and Huryn 1996; Wipfli, 1997; Nakano *et al.*, 1999a). This may be because of the thick, leathery leaves of rhododendron, which may help protect from invertebrate herbivory.

Implications for food limitation in trout

The peak seasonal and diel input and drift rates in this study corresponded to known trends in trout feeding and production. Trout production corresponds to peak food availability and is highest in spring and early summer (Ellis & Gowing, 1957; Hunt, 1975; Elliott, 1976; Whitworth & Strange, 1983; Cada *et al.*, 1987b; Bilby & Bisson, 1992). The peak aquatic larval drift at sunset found in this study and others (see review by Brittain & Eikeland, 1988) corresponds to the most commonly observed trout feeding time (e.g. Elliott, 1973; Allan, 1981; Giroux *et al.*, 2000). Increased trout feeding at midday has been demonstrated during periods of reduced aquatic larvae in the benthos and drift, and probably involves feeding on terrestrial organisms (Elliott, 1967; Chaston, 1969; Jenkins *et al.*, 1970) such as in late summer and autumn (Edwards & Huryn, 1995). Wipfli (1997) found terrestrial invertebrates were more abundant than aquatic larvae in trout diets during the latter seasons.

Riparian cover type may influence the distribution of salmonids through inputs of terrestrial invertebrates (Kawaguchi & Nakano, 2001). According to Mundie (1969), the ideal place for terrestrial invertebrates to enter the stream as prey for trout is in a small stream with numerous eddies and abundant overhanging vegetation. Trout production is highest in logged areas and in areas where meadows or open fields surround the stream (Wilzbach *et al.*, 1986; Dolloff, 1987; Bilby & Bisson, 1992). Our study found the highest contributions of terrestrial invertebrates came from open and narrow forested riparian cover types.

To relate how terrestrial invertebrate inputs may contribute maximally to annual trout production, we assumed all terrestrially derived organisms were preyed upon by trout (Edwards & Huryn, 1995). We estimated that terrestrial invertebrates provided approximately 2.86 ± 0.42 g AFDM m^{-2} $year^{-1}$ to drift. Therefore, using a food conversion efficiency of 0.20 (Waters, 1988), terrestrial invertebrates can support 0.57 ± 0.08 g AFDM m^{-2} $year^{-1}$ of trout [=3.16 g (wet weight) m^{-2} $year^{-1}$]. When combined with estimates of trout production supported by benthic secondary production in streams of this region [5.0–21.0 g AFDM m^{-2} $year^{-1}$ of invertebrates (Wohl *et al.*, 1995; Grubaugh *et al.*, 1997) =0.8–3.4 g AFDM m^{-2} $year^{-1}$ of trout], the total available food resources can potentially support 1.4–3.9 g AFDM m^{-2} of trout annually in these study streams [=7.6–21.8 g (wet weight) m^{-2} $year^{-1}$]. However, if estimates of invertebrate predator production are accounted for [0.5–1.3 g AFDM m^{-2} $year^{-1}$ (Grubaugh *et al.*, 1997)], the trout production supported by the available food resources is reduced to 3.3–18.2 g (wet weight) m^{-2} $year^{-1}$. Productive streams typically have trout production values in the range of 10–30 g (wet weight) m^{-2} $year^{-1}$ (Waters, 1988). Therefore, this study demonstrates that some southern Appalachian streams are capable of supporting productive trout populations.

Although a large quantity of energy may be available in invertebrate drift, not all of it is used by trout. Other predators, such as sculpins, may reduce the available food base (Dahl & Greeneburg, 1996).

Also, when food items are scarce in the drift, trout are known to feed on the benthos (Tippets & Moyle, 1978; Bechara *et al.*, 1992; Nakano *et al.*, 1999a). The energy spent actively searching the benthos may reduce energy available for other uses. Finally, although terrestrial organisms can comprise a significant proportion of drift, smaller fish may not be capable of feeding on them because some terrestrial invertebrates are too large (Hunt, 1975). This may be applicable to trout of the southern Appalachians because they are frequently considered stunted (Coulston & Maughan, 1981; Whitworth & Strange, 1983).

This study demonstrated terrestrial invertebrates can contribute a significant amount of energy to available trout food resources and can potentially be important components of trout diet when aquatic productivity is low. The importance of these terrestrial inputs has implications for trout management. Much of the historical effort to increase trout production has focused on stream habitat improvements, but few have examined trout food resources. Information concerning the linkages between trout and invertebrates, and their habitats and resources should be used in fisheries management (Wallace & Webster, 1996). Any management activity that attempts to increase trout production must ensure abundant food resources are available, perhaps through methods that increase invertebrate secondary production in both the stream and riparian cover.

Riparian management has seldom been explored for managing trout populations. Although we found the highest terrestrial invertebrate inputs in riparian areas with little or no forested canopies, we do not recommend removing riparian vegetation as a means of increasing trout production. There is a risk that this could increase bank erosion, sedimentation and loss of leaf litter and woody debris inputs that support benthic populations. One technique may be to avoid managing trout populations in forested areas and focus on land already disturbed. Planting limited riparian vegetation known to support greater terrestrial invertebrate abundances may increase the terrestrial inputs from disturbed landscapes. Maintaining forest land upstream will maintain allochthonous inputs under open riparian canopies as the material flows downstream, thus supporting greater secondary benthic production in disturbed landscapes.

Acknowledgments

This research was supported by NSF grants DEB-0218001 and DEB-9632854. We thank Sue Eggert, Brent Johnson, John Nowak, Andy Willats, Emma Rosi, Ted Siler, Corey Lewis and David Banks for their help during field collections and laboratory assistance. We also thank Brent and two anonymous reviewers for comments on previous drafts of the manuscript.

References

Allan J.D. (1981) Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 184–192.

Allan J.D. (1984) The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos*, **42**, 68–76.

Allan J.D., Wipfli M.S., Caouette J.P., Prussian A. & Rodgers J. (2003) Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 309–320.

Angermeir P.L. & Karr J.W. (1983) Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes*, **9**, 117–135.

Bechara J.A., Moreau G. & Planas D. (1992) Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2093–2103.

Benke A.C., Parsons K.A. & Dhar S.M. (1991) Population and community patterns of invertebrate drift in an unregulated coastal plain river. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 811–823.

Benke A.C., Huryn A.D., Smock L.A. & Wallace J.B. (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, **18**, 308–343.

Bilby R.E. & Bisson P.A. (1992) Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old growth forested streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 540–551.

Brewin P.A. & Ormerod S.J. (1994) Macroinvertebrate drift in streams of the Nepalese Himalaya. *Freshwater Biology*, **32**, 573–583.

Bridcut E.E. (2000) A study of terrestrial and aerial macroinvertebrates on river banks and their contribution to drifting fauna and salmonid diets in a Scottish catchment. *Hydrobiologia*, **427**, 83–100.

Brittain J.E. & Eikeland T.J. (1988) Invertebrate drift – a review. *Hydrobiologia*, **166**, 77–93.

Cada G.F., Loar J.M. & Slade M.J. (1987a) Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Transactions of the American Fisheries Society*, **116**, 692–702.

Cada G.F., Loar J.M. & Cox D.K. (1987b) Food and feeding preferences of rainbow and brown trout in southern Appalachian streams. *American Midland Naturalist*, **117**, 374–385.

Cadwallader P.L., Eden A.K. & Hook R.A. (1980) Role of streamside vegetation as a food source for *Galaxis olidus* Gunther (Pisces: Galaxiidae). *Australian Journal of Marine and Freshwater Research*, **31**, 257–262.

Chaston I. (1969) A study of the exploitation of invertebrate drift by brown trout (*Salmo trutta* L.) in a Dartmoor stream. *Journal of the Fisheries Research Board of Canada*, **26**, 2165–2171.

Ciborowski J.H. (1983) Influence of current velocity, density, and detritus on drift of two mayfly species (Ephemeroptera). *Canadian Journal of Zoology*, **61**, 119–125.

Cloe W.W. & Garman G.C. (1996) The energetic importance of terrestrial arthropod inputs to three warm-water streams. *Freshwater Biology*, **36**, 105–114.

Coulston P.J. & Maughan O.E. (1981) Age and growth of trout from two lightly fished North Carolina streams. *Journal of the Elisha Mitchell Science Society,*, **97**, 191–193.

Dahl J. & Greeneburg L. (1996) Impact on stream benthic prey by benthic vs drift feeding predators: a meta-analysis. *Oikos*, **77**, 177–181.

Dolloff C.A. (1987) Seasonal population characteristics and habitat use by juvenile coho salmon in a small southeast Alaska stream. *Transactions of the American Fisheries Society*, **116**, 829–838.

Edwards E.D. & Huryn A.D. (1995) Annual contribution of terrestrial invertebrates to a New Zealand trout stream. *New Zealand Journal of Marine and Freshwater Research*, **29**, 467–477.

Edwards E.D. & Huryn A.D. (1996) Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia*, **337**, 151–159.

Elliott J.M. (1967) The food of trout (*Salmo trutta*) in a Dartmoor stream. *Journal of Applied Ecology*, **4**, 59–71.

Elliott J.M. (1973) The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *Oecologia*, **12**, 329–347.

Elliott J.M. (1976) The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *Journal of Applied Ecology*, **45**, 923–948.

Ellis R.J. & Gowing H. (1957) Relationship between food supply and condition of wild brown trout, *Salmo trutta* Linnaeus, in a Michigan Stream. *Limnology and Oceanography*, **2**, 299–308.

Furukawa-Tanaka T. (1985) The ecology of salmonid fishes in Japanese mountain streams. *Japanese Journal of Ecology*, **35**, 481–504.

Garman G.C. (1991) Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. *Environmental Biology of Fishes*, **30**, 325–331.

Giroux F., Ovidio M., Philippart J.C. & Baras E. (2000) Relationship between the drift of macroinvertebrates and the activity of brown trout in a small stream. *Journal of Fish Biology*, **56**, 1248–1257.

Grubaugh J.W., Wallace J.B. & Houston E.S. (1997) Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. *Freshwater Biology*, **37**, 581–596.

Habera J.W. & Strange R.J. (1993) Wild trout resources and management in the Southern Appalachian Mountains. *Fisheries*, **18**, 6–13.

Harshbarger T.J. (1978) Factors affecting regional trout stream productivity. In: *Southeastern Trout Resource: Ecology and Management Symposium Proceedings*, pp. 11–27. USDA, Forest Service, Southeastern Forest Experimental Station, Asheville, NC.

Huhta A., Muotka T., Juntunen A. & Yrjonen M. (1999) Behavioral interactions in stream food webs: the case of drift-feeding fish, predatory invertebrates and grazing mayflies. *Journal of Animal Ecology*, **68**, 917–927.

Hunt R.L. (1975) Food relations and behaviour of salmonid fishes. In: *Coupling of Land and Water Systems* (Ed. A.D. Hasler), pp. 137–151. Springer Verlag, New York, NY, U.S.A.

Huryn A.D. (1996) An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography*, **41**, 243–252.

Jenkins T.M., Feldmeth O.R. & Elliott G.V. (1970) Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. *Journal of the Fisheries Research Board of Canada*, **27**, 2356–2361.

Kawaguchi Y. & Nakano S. (2001) Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology*, **46**, 303–316.

Mason C.F. & Macdonald S.M. (1982) The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biology*, **12**, 305–311.

Mundie J.H. (1969) Ecological implications of the diet of juvenile coho in streams. In: *Symposium on Salmon and Trout Streams* (Ed. T.G. Northcote), pp. 135–152. University of British Columbia, Canada.

Nakano S., Miyasaka H. & Kuhara N. (1999a) Terrestrial-aquatic linkages: riparian arthropod inputs alter

trophic cascades in a stream food web. *Ecology*, **80**, 2435–2441.

Nakano S., Kawaguchi Y., Taniguchi Y., Miyasaka H., Shibata Y., Urabe H. & Kuhara N. (1999b) Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in Northern Japan. *Ecological Research*, **14**, 351–360.

O'Hop J. & Wallace J.B. (1983) Invertebrate drift, discharge, and sediment relations in a southern Appalachian headwater stream. *Hydrobiologia*, **98**, 71–84.

Peckarsky B.L. (1996) Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology*, **77**, 1888–1905.

Pearson W.D. & Kramer R.H. (1972) Drift and production of two aquatic insects in a mountain stream. *Ecological Monographs*, **42**, 365–385.

Piccolo J.J. & Wipfli M.S. (2003) Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 503–513.

Rader R.B. & McArthur J.V. (1995) The relative importance of refugia in determining the drift and habitat selection of predaceous stoneflies in a sandy-bottomed stream. *Oecologia*, **103**, 1–9.

Reisen W.K. & Prins R. (1972) Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. *Ecology*, **53**, 876–884.

Sagar P.M. & Glova G.J. (1992) Invertebrate drift in a large, braided New Zealand river. *Freshwater Biology*, **27**, 405–416.

Sagar P.M. & Glova G.J. (1995) Prey availability and diet of juvenile brown trout (*Salmo trutta*) in relation to riparian willows (*Salix* spp.) in three New Zealand streams. *New Zealand Journal of Marine and Freshwater Research*, **29**, 527–537.

Sample B.E., Cooper R.J., Greer R.D. & Whitmore R.C. (1993) Estimation of insect biomass by length and width. *American Midland Naturalist*, **129**, 234–240.

Siler E.R., Wallace J.B. & Eggert S.L. (2001) Long-term effects of resource limitation on stream invertebrate drift. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1624–1637.

Skinner W.D. (1985) Night-day drift patterns and the size of larvae of two aquatic insects. *Hydrobiologia*, **124**, 283–285.

Stoneburner D.L. & Smock L.A. (1979) Seasonal fluctuation of macroinvertebrate drift in a South Carolina Piedmont stream. *Hydrobiologia*, **63**, 49–56.

Tebo L.B. & Hassler W.W. (1963) Food of brook, brown, and rainbow trout from streams in western North Carolina. *Journal of the Elisha Mitchell Science Society*, **79**, 44–53.

Tippets W.E. & Moyle P.B. (1978) Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud River, California. *Journal of Animal Ecology*, **47**, 549–559.

Wallace J.B. & Webster J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, **41**, 115–139.

Wallace J.B., Webster J.R. & Lowe R.L. (1992) High-gradient streams of the Appalachians. In: *Biodiversity of Southeastern United States: Aquatic Communities* (Eds C.T. Hackney, S.M. Adams & W.A. Martin), pp. 133–191. John Wiley & Sons, Philadelphia, PA, U.S.A.

Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, **277**, 102–104.

Waters T.F. (1965) Interpretation of invertebrate drift in streams. *Ecology*, **46**, 327–334.

Waters T.F. (1972) The drift of stream insects. *Annual Review of Entomology*, **17**, 253–272.

Waters T.F. (1988) Fish production-benthos production relationships in trout streams. *Polskie Archiwum Hydrobiologii*, **35**, 545–561.

Whitworth W.E. & Strange R.J. (1983) Growth and production of sympatric brook and rainbow trout in an Appalachian stream. *Transactions of the American Fisheries Society*, **112**, 469–475.

Wilzbach M.A., Cummins K.W. & Hall J.D. (1986) Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology*, **67**, 898–911.

Wipfli M.S. (1997) Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1259–1269.

Wipfli M.S. & Musslewhite J. (2004) Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia*, **520**, 153–163.

Wohl D.L., Wallace J.B. & Meyer J.L. (1995) Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). *Freshwater Biology*, **34**, 447–464.

(Manuscript accepted 7 September 2006)