

Effects of riparian willow trees (*Salix fragilis*) on macroinvertebrate densities in two small Central Otago, New Zealand, streams

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Abstract The effects of an introduced willow tree species (*Salix fragilis*) on the densities of macroinvertebrates were examined in two Central Otago, New Zealand, streams during 1991. Significantly lower invertebrate densities and biomass were observed in willow-lined sections of the streams than in nearby open sections in summer, autumn, and winter. This result was observed in riffles and pools, for most dominant species and nearly all functional feeding groups. The effect was not associated with differences in the amount of fine particulate organic matter (< 1 mm), stone surface organic layer biomass, or chlorophyll *a* concentration, which were similar at open and willow-shaded sites. Amounts of coarse particulate organic matter (> 5 mm) were significantly higher in willow-shaded riffles, but this did not result in increased abundance or biomass of shredders. Willow trees reduced incident stream illumination by as much as 80%, but did not appear to influence water chemistry between open and willow-shaded sites. The decreased invertebrate densities probably result from a decrease in average substrate size and/or a lowering of food production through shading effects.

Keywords Riparian willows; *Salix fragilis*; macroinvertebrates; streams; invertebrate foods; substrate

INTRODUCTION

Since their introduction into New Zealand by European settlers, willows (in particular *Salix fragilis*) have been widely used in river training and protection of stop banks against flood damage. Their spread has been further aided by the tendency for twigs and broken branches to take root and form separate trees. Willows are now the dominant riparian vegetation along the banks of many New Zealand rivers and streams (Glova & Sagar 1990). According to a 1962 survey the total area of willows in New Zealand is about 41000 ha, making them the second most common exotic tree species (Van Kraayenoord 1974).

Willows can affect aquatic macroinvertebrate communities in a number of ways. They may increase abundance of stream invertebrates through the input of leaves, which are a potential food source (Cummins 1974), or through enhancing primary production by increased plant nutrient levels from leaf leachates. Alternatively, in some areas willow trees have become so dense that they reduce water velocity. This effect can result in increased sedimentation and smaller average substratum size (Young 1980), which has been associated with reduced invertebrate abundance (Minshall 1984). Another potentially detrimental effect on invertebrates is a decrease in the illuminance of the stream, which may decrease primary production and hence reduce the rate at which food becomes available for secondary production (Keithan & Lowe 1985; Boston & Hill 1991).

In this study we examined the effects of a high density of willow (*S. fragilis*) trees on the abundance and biomass of macroinvertebrates in two Central Otago streams. Samples were taken in summer, when shading of the streams was expected to be greatest, in autumn during leaf fall, and in

winter when shading by willow trees would be least. We also determined the effects of willows on chlorophyll *a* concentrations of periphyton, fine and coarse particulate organic material, and on the light regime and plant nutrient concentrations.

METHODS

Study sites

The streams examined in this study were Styx Creek (45°26'S, 169°57'E) and Heeney Creek (45°23'S, 170°13'E). These streams are approximately 3–5 m wide and have a dense canopy of *S. fragilis* 5 to 10 m high on both banks, with an abrupt transition to treeless tussock grassland upstream. Thus, shaded and open study sites could be located close together, minimising any changes in water temperature and chemistry associated with long reaches of riparian trees (Latta 1974; Green et al. 1989). At the sampling sites both streams were second order streams, and at the time of sampling average summer flows were $0.105 \text{ m}^3 \text{ s}^{-1}$ and $0.232 \text{ m}^3 \text{ s}^{-1}$ for Heeney Creek and Styx Creek, respectively.

For each stream, three riffles and three associated downstream pools were selected as study sites in areas shaded by riparian willows, and in open sections of stream. All sampling sites in each stream were matched as closely as possible for orientation, width, flow, and depth profiles. The first willow riffle was located at least 400 m downstream of the first willow tree, and all sampling in each stream was carried out within an 800 m reach.

Macroinvertebrates

Macroinvertebrates were sampled using a 0.0625 m^2 Surber sampler with 250 μm mesh net. To test the hypothesis that benthic macroinvertebrates increase in abundance after leaf fall, samples were taken from all riffles in summer (December), autumn (April) and winter (July). A single set of samples was taken from pools in December.

The number of samples to be collected at each site was determined from a pilot study in which 10 Surber samples had been collected from one of the study riffles in each stream. Nymphs of *Deleatidium spp.* (Ephemeroptera: Leptophlebiidae) were counted. To calculate sample size the formulae from Elliott (1983) were used, with the tolerable error set at 25%.

At each riffle, 4 sampling sites were randomly selected where current velocities were between 0.55 and 0.65 m s^{-1} , and depths ranged from 0.05 to 0.30 m. Four "pool" samples were randomly located in areas with current velocities between 0.08 and 0.18 m s^{-1} , and in depths which ranged from 0.50 to 0.80 m. Samples were preserved in 70% ethanol. In the laboratory, they were allutriated to separate organic from inorganic material, and the animals were sorted and identified using a binocular microscope at 20 \times magnification. Invertebrates were identified and sorted into functional feeding groups (Table 1), dried at 60°C to constant weight, and then ashed at 550°C for 40 min to determine the ash free dry mass (AFDM) of the different functional feeding groups.

Stone surface organic layers

Stone surface organic layers (SSOL) consist of heterotrophic and autotrophic microorganisms with an associated slime matrix, and fine particulate matter from both autochthonous and allochthonous sources (Madsen 1972). To estimate SSOL biomass, five cobbles approximately 10 cm in length were randomly selected from each study riffle, sealed in a plastic bag, and put into a dark insulated container with ice. Within 24 hours they were submerged together in a known volume (c 350 ml) of buffered 90% ethanol, scrubbed with a toothbrush and kept in darkness at 5°C for 24 h.

The sample was then mixed, and a 50 ml subsample was taken and filtered through a glass fibre filter (Whatman GFC) for chlorophyll *a* analysis. The rocks were removed and the ethanol was distilled off. The remaining material was washed into a pre-ashed crucible, dried at 60°C for 24 h, weighed, ashed, and reweighed. AFDM was calculated after correction for the 50 ml removed for chlorophyll analysis. The surface area of the rocks was determined by wrapping each rock in aluminium foil, weighing the combined foil from each riffle, and deriving area from a calibration curve. As an approximate correction for the area of the rock buried and hence not available for algal colonisation, the surface area was multiplied by 0.6.

Chlorophyll *a* concentration was calculated by the method of Lorenzen (1967), following absorption measurements at 665 and 750 nm using a Shimadzu UV-120-01 Spectrophotometer with 4 cm cells. Results are expressed as mg chlorophyll *a* m^{-2} of exposed rock.

Fine and coarse particulate organic matter

Fine and coarse particulate organic matter (FPOM and CPOM) were estimated from the Surber samples. FPOM (defined as the particulate organic material that passed through a 1 mm sieve) was collected by filtration through pre-ashed and weighed glass fibre filters (Whatman GFC), which were then dried, ashed and reweighed.

CPOM was defined as leaf and other organic material except willow roots, with a greatest dimension larger than 5 mm. This size limit was imposed because samples from shaded sites contained live willow roots, which we did not want to include as CPOM, and only particles larger than 5 mm were easily recognisable as being either root or other material. CPOM samples were sorted

Table 1 Taxa found in Styx and Heeney Creek, and the functional feeding group classification (from Ryder & Scott (1988), with modifications A. D. Huryn (pers comm)).

Functional Feeding Group	Order	Family	Taxon	
<i>Browsers</i>	Ephemeroptera	Siphonuridae	<i>Nesameletus</i>	
		Leptophlebiidae	<i>Deleatidium</i> <i>Austroclima</i>	
	Trichoptera	Hydroptilidae	<i>Oxyethira</i> ¹ <i>Paroxyethira</i> ¹	
		Helicopsychidae	<i>Helicopsyche</i>	
		Leptoceridae	<i>Oecetis</i>	
		Conoesucidae	<i>Pycnocentroides</i> <i>Pycnocentria</i> <i>Beraeoptera</i>	
		Coleoptera Diptera	Elmidae	<i>Hydora</i>
	Tipulidae		<i>Zelandotipula</i> <i>Aphrophila</i> Eriopterini Orthoclaadiinae Chironominae Diamesinae	
	Prosobranchia Decapoda	Hydrobiidae	<i>Potamopyrgus</i>	
		Parastacida Oligocheatea	<i>Paranephrops</i>	
	<i>Filterers</i>	Ephemeroptera	Oligoneuriidae	<i>Coloburiscus</i>
		Trichoptera	Hydropsychidae Philopotamidae	<i>Aoteapsyche</i> <i>Hydrobiosella</i>
<i>Shredders</i>	Diptera	Simuliidae	<i>Austrosimulium</i>	
	Plecoptera	Austroperlidae	<i>Austroperla</i> ²	
<i>Predators</i>	Trichoptera	Conoesucidae	<i>Olinga</i> ²	
	Megaloptera	Corydalidae	<i>Archichauliodes</i>	
	Plecoptera	Eustheniidae	<i>Stenoperla</i>	
	Trichoptera	Hydrobiosidae	<i>Psilochorema</i> <i>Hydrobiosis</i> <i>Hudsonema</i> ³	
		Diptera	Leptoceridae Chironomidae Tabanidae Muscidae Ceratopogonidae	Tanypodinae

¹*Oxyethira* and *Paroxyethira* are thought to be algal piercers as early instars, and browsers in later instars.

²*Olinga* and *Austroperla* are considered facultative shredders/ browsers.

³Omnivore.

manually from the Surber samples, and AFDM was determined as described above.

Physical and chemical variables

Incident illuminance was measured at all of the riffles on each sampling day. Five readings were taken immediately above the water surface on each of four transects across the stream, every 2 h from first light until dark, with a LICOR (model LI-185A) Quantum Sensor.

Water samples were taken at a depth of 10 cm in polyethylene bottles, frozen and analysed within 3 weeks for ammonia-nitrogen, nitrate and nitrite-N, and total and reactive phosphorus using a Chemlab System Four auto-analyser.

Data analysis

Data were analysed using the statistical package SAS Version 6.04 (SAS Institute Inc. 1988). For each invertebrate taxon or food type in riffles a two-way ANOVA was performed with the factors being site type (open or willow-shaded) and season (summer, autumn or winter). For pools a one way ANOVA was used with the factor being site type. All numerical data were log-transformed, and the residuals from each ANOVA were examined for normality and homogeneity of variance. Percentage data were arcsine transformed before analyses (Zar 1984). Results were considered significant for $P < 0.05$.

Power tests, which predict the chance of having committed a Type II error (the probability of not rejecting a null hypothesis when it is false), were conducted on a number of randomly selected ANOVA which failed to give a significant result for one or more factors (Zar 1984).

RESULTS

Macroinvertebrates

In both Styx and Heeney Creeks, numbers and biomass of invertebrates were higher at open sites than at willow-shaded sites, typically by a factor of 2. This effect was observed in riffles for all seasons and also for the single sample from pools (Fig. 1).

Browsers were the most abundant functional feeding group in Styx Creek, but filterers and predators were higher in biomass (Fig. 1). Open sites in Styx Creek had significantly higher numbers and biomass of all functional feeding groups, with the exception of the browser biomass (Table 2). In pools, the numbers and biomasses of shredders

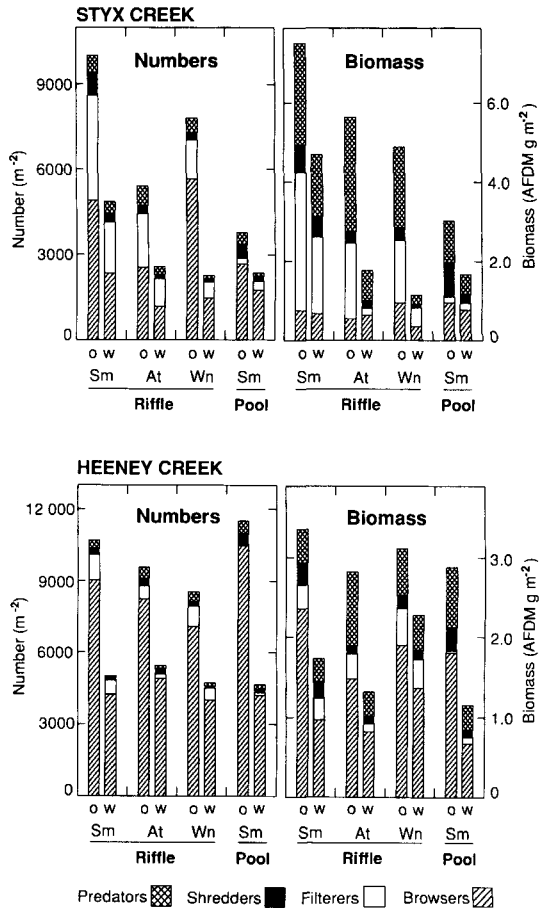
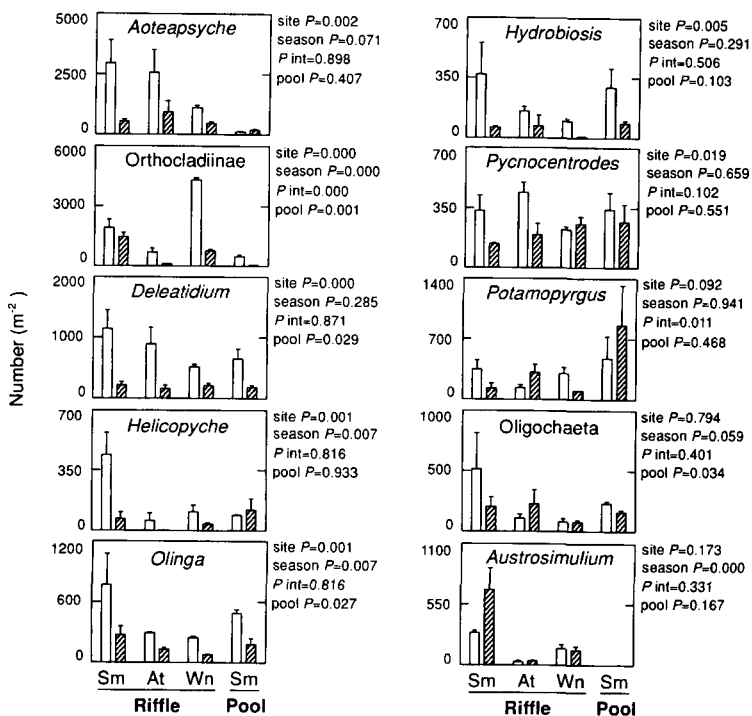


Fig. 1 Mean number and biomass of macroinvertebrates in each functional feeding group at open (o) and willow (w) sites in Heeney Creek and Styx Creek. Data are for riffles in summer (Sm), autumn (At) and winter (Wn) and for pools in summer.

and predators were significantly greater in open sites, but no difference was observed for browsers and filterers (Fig. 1, Table 2). The percentage contributions of the different functional feeding groups to the community, in terms of both biomass and numbers, were not significantly different between open and willow sites, again with the exception of browser biomass. This was the case for both riffles and the pool sample.

Heeney Creek had a rather different community, dominated by browsers in terms of both weight and abundance (Fig. 1). As in Styx Creek, open sites had significantly higher biomasses and

Fig. 2 Mean density (± 1 SE; $n = 4$) of the 10 most common macroinvertebrates in Styx Creek riffles in summer, autumn and winter, and pools in summer, at open (clear bars) and willow-shaded (hatched bars) sites. Site P , seas P , and P int, probability values from two-way ANOVA with the treatments being 'site' and 'season' are given at the side. P int, interaction probability. Pool P values are from a separate one-way ANOVA with the treatment 'site'.



numbers of predators and filterers (Table 2). They also had significantly higher numbers and biomass of browsers, but shredders were not significantly different. This trend was also observed in pools, except for filterer biomass and abundance, which were not significantly different (Fig. 1, Table 2). The relative proportions of functional feeding groups were not significantly different, either for biomass or abundance, apart from predator

abundance which was significantly higher at open sites.

Shredder abundance or biomass was not significantly correlated with CPOM on any sampling day in either stream, or for all samples combined, in Pearson r correlation tests ($P > 0.05$).

ANOVA were conducted for all of the 29 taxa found in Heeney Creek and the 30 in Styx Creek. The densities of the 10 most common genera for

Table 2 Probability values for Styx and Heeney Creek, from the ANOVA modelling functional feeding group number (or biomass) = site (open vs willow) \times season (seas). P int, interaction probability. Pool P values are from a separate one way ANOVA with the treatment 'site'.

STYX	Site P	Seas P	P int	Pool P	HEENEY	Site P	Seas P	P int	Pool P
Numbers					Numbers				
Browsers	0.000	0.166	0.400	0.197	Browsers	0.000	0.182	0.474	0.002
Filterers	0.001	0.001	0.862	0.579	Filterers	0.002	0.011	0.694	0.247
Shredders	0.001	0.006	0.721	0.027	Shredders	0.197	0.037	0.366	0.019
Predators	0.007	0.001	0.863	0.012	Predators	0.000	0.075	0.667	0.010
Biomass					Biomass				
Browsers	0.147	0.655	0.216	0.631	Browsers	0.000	0.008	0.073	0.008
Filterers	0.000	0.001	0.016	0.797	Filterers	0.057	0.244	0.358	0.146
Shredders	0.029	0.032	0.409	0.062	Shredders	0.278	0.352	0.689	0.026
Predators	0.001	0.061	0.312	0.179	Predators	0.032	0.673	0.615	0.074

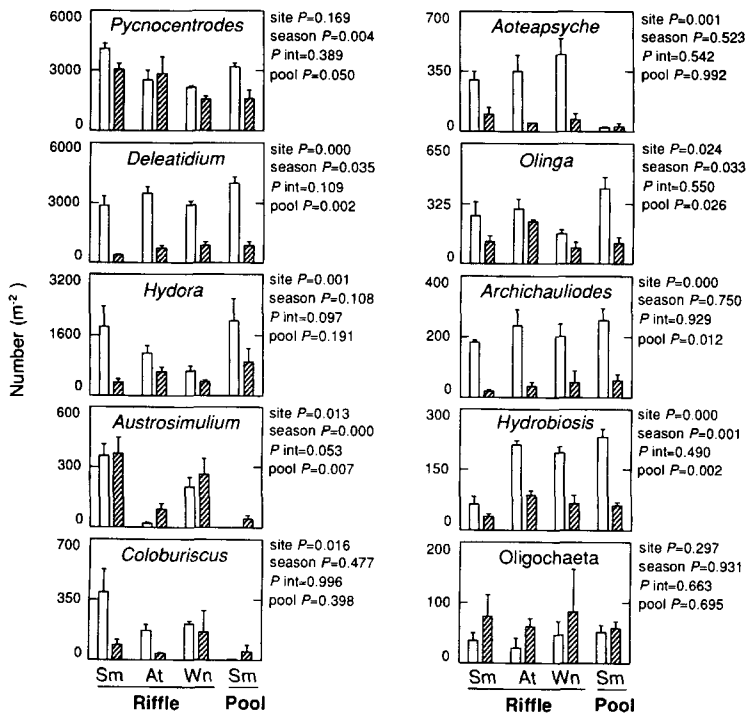


Fig. 3 Mean density (± 1 SE; $n = 4$) of the 10 most common macroinvertebrates in Heeney Creek riffles in summer, autumn and winter, and pools in summer, at open (clear bars) and willow-shaded (hatched bars) sites. Site P , seas P , and P int, probability values from two-way ANOVA with the treatments being 'site' and 'season' are given at the side. P int, interaction probability. Pool P values are from a separate one-way ANOVA with the treatment 'site'.

each season in riffles, and for the pools in summer are presented in Fig. 2 (Styx Creek) and Fig. 3 (Heeney Creek). Results from the relevant ANOVAs are presented alongside each graph.

In Heeney Creek, eight taxa were found to have significantly higher densities in open riffles than in shaded riffles (*Aoteapsyche*, *Archichauliodes*, *Beraeoptera*, *Coloburiscus*, *Deleatidium*, *Hydrobiosis*, *Orthocladiinae*, and *Olinga*). Similarly, in Styx Creek *Pycnocentroides* and all of these taxa except *Beraeoptera* were significantly more abundant in open riffles. By contrast only *Austrosimulium* and *Pycnocentria* were significantly more abundant in shaded riffles at Styx Creek, and these two genera plus *Hudsonema* in Heeney Creek. No genus was found to occur only in willow or only in open sites in either stream.

The trend in pools was similar to that in riffles. In Styx Creek, *Archichauliodes*, *Oligochaeta*, *Olinga* and *Orthocladiinae* had significantly higher numbers m^{-2} in open pools, whereas only *Paranephrops* and *Pycnocentria* were significantly more abundant at willow sites. In Heeney Creek, six genera had significantly higher densities at open sites (*Archichauliodes*, *Deleatidium*,

Hydrobiosis, *Hudsonema*, *Olinga* and *Pycnocentroides*) compared with two at willow sites (*Austrosimulium* and *Pycnocentria*) (Fig. 2, 3).

There was a notable lack of consistency in seasonal variation between streams for most genera (Fig. 2, 3). For example *Aoteapsyche* increased in abundance in riffles from Summer to Winter in Heeney Creek, but in Styx Creek it decreased in abundance over the same period. There were no notable changes in abundance of any taxa that could be clearly related to leaf fall in autumn.

Light, Periphyton, FPOM, CPOM and nutrients

The shading effect of willows was substantial in all seasons (Fig. 4). Even in winter the willow-shaded sections received less than half the illuminance of open sites (40% for Styx Creek and 47% for Heeney Creek). In summer, the corresponding figure was 20% for both streams, and in autumn it was 28% for Styx Creek and 40% for Heeney Creek. In spite of the reduction in illuminance caused by willows, there was no significant effect of site or site/season interaction on chlorophyll *a* concentration in either stream

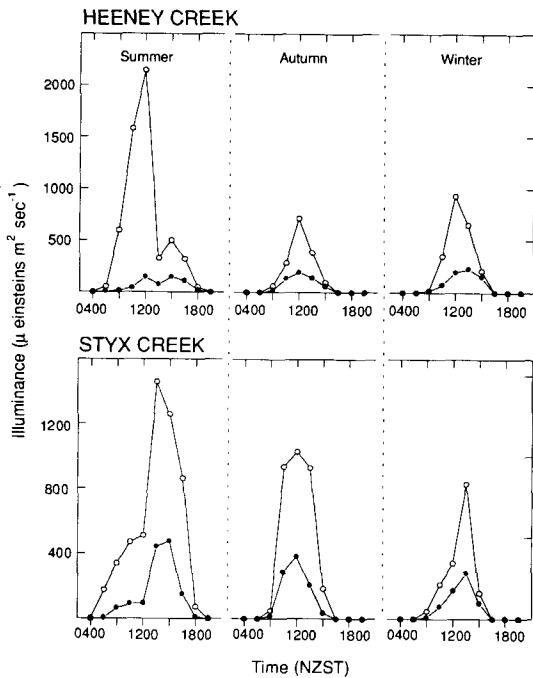


Fig. 4 Mean incident illuminance ($n = 3$ riffles, with 20 readings at each) for open (open dots) and willow-shaded (solid dots) sites on Heeneey and Styx Creek.

(Fig. 5). Seasonal effects were significant, with the most notable feature being the increase in chlorophyll *a* concentration in winter at open and shaded sites in both streams. The concentrations of plant nutrients were generally similar between open and willow sites, although there was some variation between seasons and streams (Table 3).

Amounts of SSOL and FPOM were also not significantly different between open and willow

sites in either stream, although again some seasonal effects were observed (Fig. 5).

There was a large increase at CPOM in shaded sites in autumn in both streams, though it was statistically significant only in Styx Creek (Fig. 5). This material was observed to consist largely of willow leaves or fragments of leaves, but this increase was statistically significant only in Styx Creek.

Power analysis

The power of the ANOVA analysis was calculated for *Pycnocentroides* sp. in Heeneey Creek, the biomass of shredders in Styx Creek, and the biomass of chlorophyll *a* and FPOM in Styx Creek. The chances of accepting a false null hypothesis (that there was no difference between willow and open sites, or between seasons) were 26%, 25%, 34% and 66% respectively.

DISCUSSION

The presence of riparian willow trees was clearly associated with a reduced total macroinvertebrate abundance and biomass. This effect was observed across nearly all functional feeding groups in pools and riffles of both streams in all seasons. Similar effects of riparian trees on stream invertebrate abundance have been reported elsewhere in New Zealand (Allen 1951; Hopkins 1976; Graynoth 1979; Suren 1992), and overseas (Hughes 1966; Hawkins et al. 1982; Behmer & Hawkins 1986). Two major hypotheses have been proposed to account for such results that they are a food chain effect reflecting lower primary production due to shading by trees, and/or an effect of substrate size.

Allen (1951) was probably the first to observe that riparian vegetation, through shading, could

Table 3 Concentrations of plant nutrients (mg m^{-3} ; $n = 3$) for Styx Creek and Heeneey Creek (TP, total phosphorus; RP, reactive phosphorus).

		Styx			Heeneey		
		Summer	Autumn	Winter	Summer	Autumn	Winter
Open Sites	NH ₃ -N	9.8	0	19.7	7.9	0	8.3
	NO ₃ -N	54.4	2.8	10.2	15.1	2.8	12.8
	TP	14.3	14.6	24.5	15.3	14.7	15.3
	RP	1.5	10.4	0	11.7	10.4	3.2
Willow Sites	NH ₃ -N	12.2	0	10.4	9.4	0	6.3
	NO ₃ -N	47.6	1.3	11.7	13.5	1.3	12.3
	TP	14.1	17.3	36.6	23.1	17.3	16.3
	RP	0.9	11.5	0	13.6	11.5	8.3

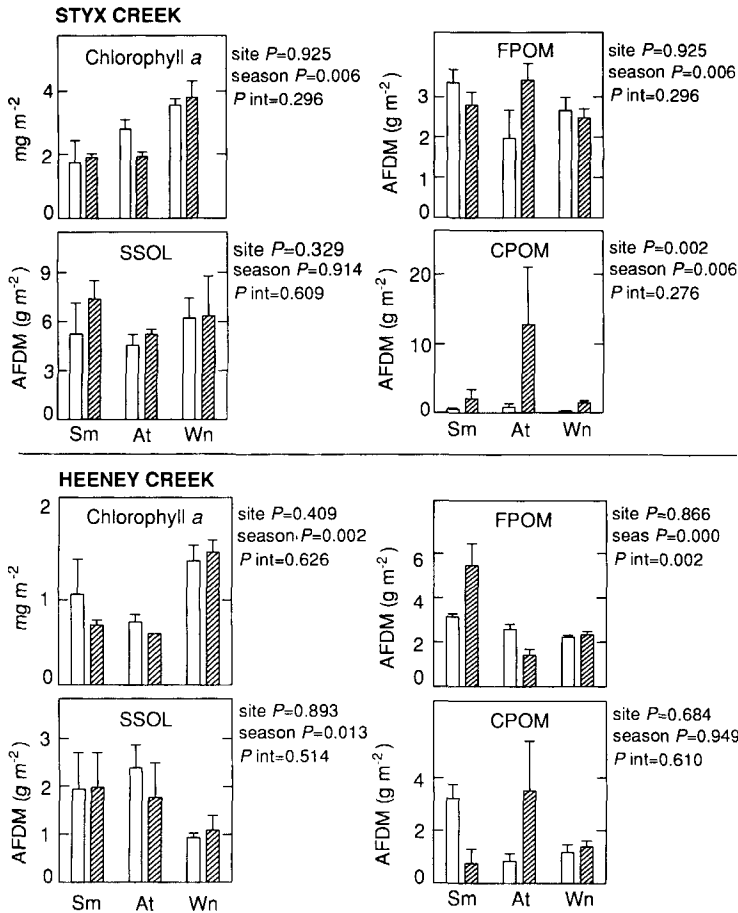


Fig. 5 Mean amount (± 1 SE; $n = 3$) of Chlorophyll *a*, FPOM, CPOM, and SSOL in open (clear bars) and willow-shaded (hatched bars) sites, in summer (Sm), autumn (At) and winter (Wn) in Heehey Creek and Styx Creek. Site *P*, seas *P*, and *P* int, probability values from two-way ANOVA with the treatments being 'site' and 'season'. *P* int, interaction probability.

significantly reduce primary production in streams. This result has been confirmed elsewhere (Hornick et al. 1981; Keithan & Lowe 1985; Hill & Harvey 1990). It has been suggested that riparian vegetation can thus indirectly reduce secondary productivity and invertebrate densities (Allen 1951; Hopkins 1976; O'Hop et al. 1984; Bøhmer & Hawkins 1986). We found that concentrations of chlorophyll *a*, SSOL and FPOM were similar at open and shaded sites, a result similar to that of Feminella et al. (1989). Those authors found, however, that when grazing animals were excluded, periphyton growth was significantly higher on tiles in open streams than on shaded tiles. Similarly, light could have played a hidden role in influencing the macro-invertebrate communities in our study by reducing primary productivity at the shaded sites, while higher grazing rates at the open sites prevented this effect from being reflected in the biomass of algae.

An increase in shredders could perhaps have been expected due to the increase in CPOM at the shaded sites in autumn. The dependence of shredders on allochthonous inputs has been well documented (Ward & Cummins 1979; Martin et al. 1980; Winterbourn 1982), and models have been developed suggesting an intimate relationship between the biomass of shredders and timing of CPOM inputs (Cummins et al. 1989). No such relationship was observed in our study, even though there was a large increase in CPOM in autumn. A similar lack of correlation between shredder abundance and leaf detritus biomass has been noted for streams in areas of evergreen native forest and forest dominated by the deciduous native *Fuchsia excorticata* in New Zealand (Winterbourn 1978; Linklater & Winterbourn 1993). The response by invertebrates to inputs of willow leaves may be delayed, however, owing to the need for the leaves

to become conditioned to increase their palatability (Collier & Winterbourn 1986; Lester et al. 1994). By winter, when conditioning could be expected to have occurred, the amounts of CPOM had declined again, and there was no apparent increase in invertebrate abundance. Any positive effects of the leaf input may therefore have been exported downstream.

The suggestion that filterers may benefit from an increase in FPOM caused by the activities of shredders (e.g. Cuffney et al. 1990) is clearly not relevant to our study, and no increase in filterer biomass or density was observed. The filterer *Austrosimulium* was, however, more abundant at willow sites in Heeneey Creek. Members of this genus have been noted to be more abundant in shaded sites by other authors (Towns 1981; Behmer & Hawkins 1986; Fuller et al. 1986). It has been suggested that this is a result of more clean attachment sites being available in shaded areas (Chutter 1968; Casey & Ladle 1976). As algal biomass was similar in shaded and open sites in Heeneey Creek this is not a reasonable explanation for the observed *Austrosimulium* distribution in our study.

Detrital food quality has long been associated with densities or growth rates of stream invertebrates (Anderson & Cummins 1979; Hawkins et al. 1982). Although we found similar levels of SSOL and FPOM at all sites, if riparian vegetation reduced the production of high quality detritus derived from algae, and replaced it with detritus of lower quality from willow leaves, then this may have contributed to the lower invertebrate densities at willow sites.

A decrease in invertebrate density is often associated with decreasing substratum size (Minshall 1984). In Heeneey and Styx Creeks, willow roots bind around rocks, occupying interstitial spaces and trapping sediment so that the streams become highly silted. This effect was observed across the entire width of the streams. It seems likely such changes to the substrate would reduce invertebrate densities through denying animals access to the interstitial spaces between stones. This may well be the most important effect of willows on stream invertebrate fauna.

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