The response of stream ecosystems to riparian buffer width and vegetative composition in exotic plantation forests

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ABSTRACT

Riparian buffers along stream margins have been widely adopted as a management strategy to mitigate the adverse effects of plantation forestry on stream ecosystems. However, the efficacy of these riparian buffers can be compromised by adopting buffers of insufficient width, length, and vegetation. I investigated the relative influences of riparian vegetation age and composition on stream ecosystems within exotic pine plantations. Initially, a survey of physical, chemical and benthic attributes of 45 streams within pine forests of various ages and riparian composition and 5 reference indigenous forested streams, was conducted at foot-hill sites from mid-Canterbury to Hanmer Springs over the summer of 2004-2005. Additionally, terrestrial subsidies (organic matter and invertebrates) were compared between young pine, mature pine and indigenous forest streams to ascertain differences or similarities between vegetation types. For each of these streams, vegetative age and composition at catchment, riparian buffer and reach scales were determined using GIS.

Sedimentation was consistently higher and streams less stable in catchments lacking indigenous riparian vegetation, more markedly so in recently harvested catchments compared with more mature forests. Streams dominated by pine forests were generally smaller, had finer substrates with higher water temperatures and levels of turbidity, while those dominated by indigenous forest were larger with higher flows and dissolved oxygen levels, coarser substrates, and less in-stream debris. Taxonomic richness, EPT diversity, and invertebrate abundances were significantly higher in streams with considerable indigenous riparian vegetation, while benthic community composition and terrestrial subsidies were similar among vegetation types. The legacy of forestry activities declined over time but the adverse impacts upon streams with narrow riparian buffers and lacking
indigenous vegetation lasted longer. Streams with higher percentages of indigenous vegetation in their riparian zones were the least impacted and had the healthiest stream communities. Maintaining indigenous vegetation cover of >30% in the riparian zone was important for stream health. Furthermore, within young (1-2 year old) pine forest riparian vegetation comprising of native and exotic scrub was important in successfully mediating the adverse effects of forestry on stream ecosystems.
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INTRODUCTION

Plantation pine forestry activities, including harvesting and spraying, have widely recognised impacts on stream communities. Among the most well documented impacts of harvesting on streams are changes in light and temperature, reductions in allochthonous energy inputs (e.g. leaves and wood), changes to flow regimes and increased sedimentation (Graynoth 1979; Death et al. 2003; Fuchs et al. 2003; Quinn et al. 2004). Common doctrine in New Zealand, however, suggests that stream ecosystems recover from logging activities within a few years, because regeneration of the riparian vegetation re-sets these gross impacts. In contrast, several intensive studies overseas have provided evidence that long-term land-use (including forest regeneration) can leave a biological legacy that persists for many decades (Harding et al. 1998; Stone & Wallace 1998; Gomi et al. 2006).

In New Zealand, no definitive study has yet been conducted to assess the long-term affects of plantation forestry on stream ecosystems. Riparian buffer strips are frequently retained along streams in pine plantations to reduce the impacts associated with forestry activities. However, the characteristics which most strongly influence the efficacy of riparian buffers, including width, vegetative age and composition, remain unclear. This thesis investigates the gaps in our knowledge surrounding aspects of effective riparian buffers in an attempt to provide more sound recommendations to forest managers.

This thesis has been compiled as three manuscripts, each addressing different aspects of riparian buffers which are likely to influence their protective benefits. The first combines GIS derived vegetation data with a field survey of 50 streams to examine how benthic communities are influenced by vegetative age and composition at various catchment and riparian buffer scales. The second uses GIS and field survey data to explore how aspects
of stream geomorphology, water chemistry and biotic features are differentially mediated by vegetative age and composition within catchment, riparian and reach scales. Finally, the third manuscript combines a more extensive study of nine streams and an exclusion experiment to compare terrestrial subsidies from young pine, mature pine, and indigenous forests to determine the relative importance of age and composition of different riparian vegetation. The thesis concludes with a brief discussion of the value of these results to forest managers.

The first manuscript has been submitted to Marine and Freshwater Research for publication and it is formatted in that journal's layout.
The response of pine forest stream invertebrate communities to forest age and riparian composition

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Abstract. GIS-derived vegetation data and field surveys were combined to examine optimal buffer dimensions and conditions for enhancing benthic stream communities in pine plantations in Canterbury, New Zealand. Vegetative composition at 13 spatial scales, and pine forest age was determined for 50 catchments with first and second order streams. A field survey of benthic invertebrates was conducted during January-March 2005. Forty-five streams were in plantation pine forests of differing ages and riparian vegetation, whereas five reference streams were in indigenous forest.

Pearson correlations and regression analyses between riparian scales and selected biotic indices showed that riparian zones 5-10 m wide and 600 m upstream from the sampling reach had the strongest relationship with stream communities. Furthermore, the amount of indigenous vegetation within riparian buffers (at least 30%) was critical to enhancing benthic taxonomic richness. Taxonomic and EPT richness were positively influenced by increasing pine age and the amount of indigenous vegetation within the riparian zone. Community composition and dominant taxa were most similar between streams with greater proportions of indigenous riparian vegetation, compared to streams within similar aged pine forest. These results highlight the importance of protecting and enhancing the vegetation within riparian buffers 5-10 m to improve their efficacy in conserving stream diversity.

Extra keywords: stream diversity; taxonomic richness; riparian buffer; GIS
Introduction

Exotic forestry is one of New Zealand’s largest natural resource industries, accounting for more than 13% of the country’s total exports and generating $3.3 billion a year (MAF 2004). Production forests currently cover more than 1.8 million hectares, 89% of which is Pinus radiata, with 40-50,000 ha harvested each year. The effects of forest harvesting on streams have been widely documented and extensively studied both in New Zealand and internationally (Graynoth 1979; Death et al. 2003; Fuchs et al. 2003; Quinn et al. 2004; Hernandez et al. 2005). For example, harvesting can have marked impacts on the physical nature of streams, increasing light, temperature, fine sediments, channel and bank erosion, as well as a reducing terrestrial litter inputs (Murphy et al. 1981; Cummins et al. 1989; Davies-Colley and Quinn 1998; Kiffney et al. 2003; Boothroyd et al. 2004).

Campbell and Doeg (1989) suggested the most significant effects of forestry operations on stream biota occur through sediment and debris deposition, and alteration of riparian vegetation. The removal of riparian vegetation and subsequent shade in logged catchments increases levels of irradiance reaching the stream, which can lead to greater production of periphyton and higher stream temperatures (Quinn et al. 1997a; Dignan and Bren 2003; Boothroyd et al. 2004). This in turn can alter benthic invertebrate communities resulting in the replacement of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa and Crustacea with taxa more tolerant of high stream temperatures such as Diptera and Mollusca (Quinn et al. 1994).

Other factors may also explain changes in benthic communities in harvested catchments. Sweeney et al. (2004) considered that channel narrowing and subsequent loss of stream habitat associated with riparian deforestation substantially altered macroinvertebrate richness, whereas Herlihy et al. (2005) found increases in sand and fine sediments associated with forest harvesting most strongly affected taxonomic richness and the M-IBI (Macroinvertebrate Index of Biotic Integrity; Klemm et al.
Similarly, other studies have found that increases in sedimentation have lead to decreases in water quality, clarity, and suitable in-stream habitat resulting in a loss of EPT taxa (Davies and Nelson 1994; Death et al. 2003; Quinn et al. 2004; Collier and Smith 2005).

The recovery of streams following harvesting has also been well studied, although with conflicting findings (Campbell and Doeg 1989; Harding et al. 1998; Stone and Wallace 1998; Death et al. 2003; Collier and Smith 2005). Nevertheless, some differences in the magnitude and persistence of harvesting effects appear to depend largely on forest management and the harvesting techniques used (Death et al. 2003).

The maintenance of riparian buffers is a widely accepted management strategy employed by forestry companies to reduce the effects of forest harvesting on streams (Graynoth 1979; Newbold et al. 1980; Quinn et al. 2001; Flasohler et al. 2002). Riparian vegetation reduces light and in-stream temperatures, periphyton biomass and sediment accumulation, as well as stabilising stream channels and banks and maintaining terrestrial litter inputs, which help preserve stream ecosystem health (Gilliam et al. 1992; Davies and Nelson 1994; Bunn et al. 1999; Boothroyd et al. 2004; Quinn et al. 2004). Nationally, many New Zealand local authorities recommend riparian buffer widths of 5 m, however in practice the vegetation within these buffers can be highly variable in age, species, and condition. Riparian vegetation can range from grasses and exotic scrubs including Ulex europaeus (gorse), Cytisus scoparius (broom) and Rubus fruticosus (blackberry), to remnant indigenous forest, and consequently the efficacy of riparian buffers can be highly variable. One method of investigating the efficacy of riparian buffers with respect to protecting stream ecosystem health is to employ a broad landscape approach, investigating a large number of sites in a wide range of vegetative conditions (Johnson and Gage 1997;
Sponseller et al. 2001; Fausch et al. 2002; Gergel et al. 2002; Woodward and Hildrew 2002).

Catchment-based assessments that address physical and biological features of the landscape can provide useful insights into the response of stream biota to land-use stressors (Allan et al. 1997; Quinn et al. 1997b; Rios and Bailey 2006). In particular, there has been much debate on riparian buffer widths within pine forests and what sections of streams need protecting (Flasphohler et al. 2002; Lee et al. 2004; Quinn et al. 2004; Frimpong et al. 2005). Tools such as Geographic Information Systems (GIS) are becoming increasingly valuable as methods of modelling and predicting the influences of the surrounding landscape on stream ecosystems and communities (Johnson and Gage 1997; Johnson et al. 1997; Richards et al. 1997; Sponseller et al. 2001; Eikaas et al. 2005; Frimpong et al. 2005) and by coupling field surveys with GIS analysis, more detailed and precise information can be obtained about how stream communities are influenced by catchment and riparian land-use.

In this study we investigated the characteristics of effective riparian buffers, including their width, length and vegetative composition, within exotic pine forests. The objectives were (i) to determine which riparian buffer scales and vegetative composition best support healthy benthic communities, and (ii) to investigate the influence of pine forest age on stream communities.
Materials and methods

Site area

The study was conducted in the Canterbury foothills along the east coast of the Southern Alps, South Island, New Zealand (42°28' - 43°23' S, 171°4' - 172°50' E; 196-630 m above sea level). Fifty, first and second order, forested, headwater streams were surveyed on a single occasion during January-March 2005. Forty-five streams were in plantation pine forests (predominantly *Pinus radiata*) of differing ages (0-80 years) and had variable riparian vegetative composition. A further five reference steams were in mature indigenous forest, comprising either *Nothofagus solandri* - *N.fusca* forest, or mixed broadleaf forest (*Melicytus ramiflorus, Pseudopanax arboreus, P. crassifolium, Kunzea ericoides, Leptospermum scoparium, Coprosma spp*). Catchments ranged in area from 9.22 to 860.59 hectares.

Catchment and buffer vegetation

A Geographic Information System (GIS) was used to quantify catchment area and vegetative cover for each stream surveyed. Catchment boundaries were delineated with a Watershed Delineator (ArcView 3.2a) using a 25-m digital elevation model (DEM) to quantify the surface area contributing to drainage through a given point. Outputs were converted to catchment polygons, which included the entire drainage area upstream of the field sampling point.

Catchment and riparian vegetation GIS data for the pine forest catchments were obtained from Selwyn Plantation Board Ltd and Rayonier Forests, whereas data for indigenous forest catchments were sourced from the National Land-Cover Database (LCDB2).

From the combined sources of GIS data we generated twenty-five categories of vegetative cover, as well as pine forest age, by ‘clipping’ the corresponding data for each catchment to a collective GIS map. These categories were subsequently reduced
to three vegetation classes; pine forest, indigenous forest and open. Open vegetation comprised mixtures of indigenous tussock grasses (*Festuca novae-zelandiae*, *Chionochloa rigida*), and the exotic scrub plants gorse, broom and blackberry.

For comparison with benthic invertebrate data, information on vegetative cover was expressed at different spatial scales with respect to the width of the riparian zone (5, 10, 30, and 100 m), and the length of riparian buffer extending immediately upstream from the sampling point (200 m, 600 m, and the full length of the stream). Buffer lengths were based on dimensions used in studies by Sponseller *et al.* (2001) and Frimpong *et al.* (2005). Including the whole catchment and twelve buffer scales, a total of 13 spatial scales were generated (Fig. 1). In order to investigate the influence of vegetative cover on biotic indices, proportions of indigenous and pine vegetation were determined within each spatial scale giving a total of 26 land-cover variables (Table 1). Additionally, pine forest age for each catchment was divided into three age classes; young (0-7 yrs), intermediate (8-21 yrs), and mature (22+ yrs). These age classes were chosen based on local forestry knowledge of vegetation growth patterns.

**Benthic invertebrates**

Benthic invertebrate samples were taken with a triangular ‘kick-net’ (mesh 250 µm) used to sample all microhabitats within an area of 2.5 m² following ‘Protocol 1’ of Stark *et al.* (2001). Samples were preserved in the field in 80% ethanol and returned to the laboratory for processing. In the laboratory, samples were rinsed through a 500 µm mesh sieve, sorted and identified under a binocular microscope (x 6 magnification) to the lowest taxonomic level (usually genus), using standard keys (Winterbourn *et al.* 2000; Smith 2001). The abundance of each taxon was estimated using a coded abundance procedure (Stark 1998).

Several biotic indices were calculated for each site, including taxonomic richness, the Macroinvertebrate Community Index (MCI) and the Semi-quantitative
MCI (SQMCI) (Stark 1985, 1998). The MCI and its variants were developed to monitor pollution in organically enriched rivers and streams but have been applied successfully to streams in other forested and agricultural land-uses. Lower MCI and SQMCI scores refer to more polluted waterways whereas higher scores indicate cleaner water. Numbers of EPT taxa were also calculated for each site, as well as the proportions of EPT taxa, Mollusca, Coleoptera and Chironomidae.

Data analyses

Correlation, regression and ordination analyses were used to quantify the relationship between land-cover variables, including pine age and the composition of riparian vegetation (Table 1), and the eight biotic indices and benthic community composition. Correlation analyses were used to compare catchment age classes to all biotic indices, whereas sites were categorised by a single age value (the age of most trees in the catchment) for regression analyses. Ordination analysis was conducted on non-transformed benthic invertebrate data.

Pearson Correlation coefficients were initially calculated between biotic indices and the proportion of pine and indigenous forest within twelve combinations of buffer width and length. Correlation coefficients between pine cover, within each of the twelve buffers scales, and biotic indices were plotted to illustrate the scale-dependent effects of vegetative cover on benthic communities within pine forested catchments. Because multiple comparisons were made, Bonferroni corrections were applied to determine an appropriate alpha level for determining significance.

The influence of pine age on the eight biotic indices was assessed using linear regression analyses. To avoid results being confounded by the influence of indigenous riparian vegetation, only those catchments which lacked indigenous forest within riparian buffers extending 600 m upstream from the sampling reach and 10 m either side of the stream (referred to as 600 x 10 m riparian buffers) were used in regressions.
Subsequently, the influence of indigenous forest within 600 x 10 m riparian buffers on taxonomic richness was assessed using linear regression for nested subsets of catchments with increasing proportions of indigenous forest. Hence, those catchments lacking indigenous riparian vegetation were initially compared, then catchments with ≤30% indigenous forest, ≤50%, and finally all catchments. Analyses were performed using SYSTAT (SYSTAT V.10, 2000). Prior to analyses, all data were tested for normality and were transformed where necessary; proportional data were arcsine-square-root transformed, whereas MCI data were raised to the power of 6 and percent EPT taxa to the power of 4.

An ordination of the coded abundances of benthic invertebrates was undertaken using Canonical Correspondence Analysis (CCA) in order to detect underlying gradients of community composition and to assess relationships with land-cover variables (Table 1) (ter BRAAK 1986, 1994). A CCA ordination constrains sampling sites and invertebrate taxa by their relationships to environmental variables. The ordination was performed using default options in PC-ORD (McCune and Mefford 1999) for all catchments, except the five reference sites within indigenous forest.

Finally, the fifty sampled sites were grouped according to pine forest age classes (young, intermediate and mature), and proportions of indigenous forest within 600 x 10 m riparian buffers (≤30% indigenous forest = P; ≥30% indigenous forest = N). Indigenous reference streams were grouped, separately. One-way ANOVAs (with post-hoc Holm-Sidak tests) were run to compare differences using SigmaStat (Version 3.11, 2004). A cluster analysis correlating ranked, dominant taxa as a distance measure (group average linkage) was run using PC-ORD (Version 4.01, 1999), as well as a cluster analysis based on presence/absence of the ten most dominant taxa (24 taxa across all groups) and Sorensen (Bray-Curtis) distance (group average linkage).
Results

Effects of riparian buffer scales

Comparisons between proportions of forest cover (excluding indigenous reference sites) within different buffer scales and biotic indices showed a number of significant correlations. The strongest relationships were evident between biotic indices and vegetative cover within buffers 600 m long and over a range of widths. Plotted correlation coefficients of the relationships between pine cover within each buffer scale and biotic indices shows the 600 m buffer length most commonly elicits the strongest correlations (Fig. 2). Taxonomic richness, MCI, EPT taxa richness and % EPT taxa all showed significant negative correlations with pine cover at the 600 m buffer length, regardless of buffer width (Fig. 2).

Comparisons of proportions of forest cover within catchment and 200 m buffer lengths provided much weaker results. At the 200 m buffer length, MCI was most strongly correlated with pine cover within 30 m buffer widths ($r = -0.384$), whereas EPT taxa richness was most significantly correlated with pine cover within 10 m widths ($r = -0.294$), as was % Coleoptera ($r = -0.374$). Correlations of pine cover within buffers extending upstream the length of the catchment and MCI, EPT taxa richness, % EPT, and % Coleoptera were comparatively weak. MCI was correlated with pine cover within 5 and 100 m buffer widths ($r = -0.296$ and -0.305, respectively), richness and % EPT with pine cover within 100 m buffer widths ($r = -0.331$ and -0.353, respectively), and % Coleoptera with pine cover within 5 and 10 m buffer widths ($r = -0.329$ and -0.325, respectively).

In contrast to buffer lengths, there were smaller differences in correlations between biotic indices and forest cover within riparian buffer widths. Taxonomic richness, EPT taxa richness and % Coleoptera were strongly correlated with pine cover within 5 m widths at the three buffer lengths (catchment, 200 m, 600 m) ($r = -0.318$, -0.371 and -0.366, respectively), whereas MCI was most strongly correlated with pine
cover within 30 m widths ($r = -0.429$), and % EPT taxa with pine cover within 100 m widths ($r = -0.331$). Additionally, taxonomic richness was strongly correlated with pine cover within 10 m widths ($r = -0.308$), MCI with 5 and 10 m widths ($r = -0.417$ and -0.417, respectively), EPT taxa richness with 10 m widths ($r = -0.359$), % EPT taxa with 5 m widths ($r = -0.312$), and % Coleoptera with 10 m widths ($r = -0.358$).

**Pine forest age**

With the exclusion of sites having indigenous riparian vegetation with 600 x 10 m riparian buffers, significant positive relationships were found between pine forest age and taxonomic and EPT taxa richness ($r^2=0.55$ and $r^2=0.38$, respectively), indicating that older pine forests supported higher stream invertebrate diversity. However, regression coefficients between pine age and MCI, SQMCI, % EPT, % Mollusca, % Chironomidae, and % Coleoptera were not significant (Fig. 3).

**Effects of indigenous riparian vegetation**

The proportion of indigenous forest within the riparian zone had a positive influence on several biotic indices. A strong, significant relationship was found between pine forest age and taxonomic richness when comparing sites with no indigenous forest within buffers 600 x 10 m (Fig.4a; $n=12$). The relationship was still significant, although weaker, when catchments with up to 30% indigenous forest within riparian buffers were included (Fig. 4b; $n=20$). However, the relationship ceased to be significant for catchments with up to 50% indigenous forest (Fig. 4c; $n=25$) and when all catchments (including those with >50% indigenous riparian forest) were included (Fig.4d; $n=45$). Thus, increasing proportions of indigenous riparian vegetation supports higher taxonomic richness within young pine forests.
Land-cover effects on community composition

The CCA ordination based on taxonomic composition showed sites were spatially distributed across axes 1 and 2 driven by the abundance of either indigenous forest, or pine forest, within riparian buffers. Axis 1 of the CCA explained 10.1% of the total faunistic variance in the data, whereas axis 2 explained 9.2%. There was marked taxonomic turnover along both axes highlighting variation in community composition between sites (Fig. 5). The amount of pine and indigenous forest within 600 m riparian buffer corridors, over a range of widths, as well as the amount of mature (>22 years) pine forest within the catchment were most strongly correlated with the first two axes (Table 3). Correlations between stream community composition and indigenous forest within different buffer scales were distributed positively along axis 1, while correlations with pine forest were distributed negatively along the axis. Furthermore, correlations between stream communities and proportions of mature pine forest within catchments were also positively associated with axis 1 suggesting mature pine forests may support stream communities more similar to younger forested sites with indigenous riparian vegetation (Fig. 5).

Benthic communities

A total of 95 benthic taxa were collected from the 50 study streams, ranging from 15-37 per site. Benthic community composition was generally similar among groups of streams differing in pine forest age and the amount of indigenous vegetation in the riparian area, although slight differences were apparent. Proportions of Ephemeroptera generally increased with pine forest age and with greater proportions of indigenous riparian forest (Fig. 6). However, streams within young pine forest lacking indigenous riparian vegetation had some of the highest proportions of Ephemeroptera, while the lowest proportions of Plecoptera and Coleoptera (29, 4 and 4%). In contrast, proportions of Mollusca were significantly lower in streams within indigenous
reference and mature pine forested sites with more than 30% indigenous riparian vegetation (0.6 and 0.8 % respectively), compared with young and mature pine forested sites lacking indigenous riparian vegetation, and intermediate aged pine with indigenous riparian vegetation (4, 2 and 8% respectively) (KW ANOVA on Ranks, \(H=4.807, P=0.03\)).

Invertebrate abundance was consistently higher in streams with more than 30% indigenous riparian forest, than in those lacking indigenous riparian forest, regardless of pine age class (Fig. 7a). Taxonomic richness increased significantly both with pine forest age and when greater proportions of indigenous riparian forest was present (Fig. 7b) (\(F=8.462, P=0.001\)). At the taxonomic level, the mayfly Deleatidium and chironomid Orthocladiinae were the numerically dominant taxa common to all groups, while the snail Potamopyrgus was common in streams within young and intermediate aged pine forest, regardless of riparian composition (Table 2). The mayfly Coloburiscus was frequently found in streams in intermediate and mature aged pine forests, particularly for sites with greater amounts of indigenous riparian forest, whereas the Olinga caddisflies and Elmid beetles were most common in indigenous reference streams and intermediate and mature aged pine forests in which more than 30% of the riparian forest was indigenous (Table 2).

Cluster analysis, based on rank correlations of the ten most abundant taxa, indicated that stream invertebrate communities in young and intermediate aged pine forest groups with more than 30% indigenous riparian forest were most similar to one another and comparable to young pine sites lacking indigenous riparian forest (Fig. 8a). Mature pine forest stream communities with high and low proportions of indigenous riparian vegetation were also very similar to each other and not unlike those in indigenous forest streams (Fig. 8a). A second cluster analysis based on presence/absence of the ten most dominant taxa in each forest type (24 taxa in total) showed similar patterns. Communities at sites with more than 30% indigenous riparian
forest in young and intermediate pine forest were very similar, and little different from those in young pine forest lacking indigenous riparian vegetation (Fig. 8b). Mature pine forest with high proportions of indigenous riparian vegetation had similar communities to indigenous forest streams, as did intermediate and mature pine forest groups lacking indigenous riparian forest (Fig. 8b).
Discussion

Riparian buffer dimensions

These results showed that the combination of 5 - 10 m buffer width and 600 m upstream buffer length appeared to elicit the strongest relationship between forest cover and a range of biotic stream indices. Additionally, benthic invertebrate communities were influenced by the nature of forest cover within riparian buffers extending 600 m upstream. An optimal upstream buffer length of 600 m was also suggested by Frimpong et al. (2005), who in a study of sub-boreal forests in British Columbia, Canada, used GIS to assess land-cover data covering areas 300 m either side of and 2000 m upstream of their study sites. They concluded that fish communities and invertebrate indices were most strongly related to vegetative-cover within 600 m upstream from the sampling reach and at 30 m buffer widths. However, the lateral dimension of 30 m was optimal only with respect to the accuracy of the GIS resolution used to generate land-cover data (Frimpong et al. 2005). Conversely, Sponseller et al. (2001) found benthic invertebrate indices were most closely related to vegetation patterns within sub-corridors extending 200 m upstream of sampling reaches, compared with 1000 and 2000 m.

A critical problem for forest and resource managers has been to determine how wide riparian buffers need to be in plantation forests (Quinn et al. 2004). This issue has generated much discussion and has resulted in riparian buffer widths varying considerably, regionally, nationally and internationally (Lee et al. 2004; Quinn et al. 2004). A number of workers have suggested riparian buffer strips of 30 m or more, on both sides of streams, are necessary to reduce biotic and abiotic changes associated with logging and to protect benthic invertebrate communities (Newbold et al. 1980; Richardson et al. 2002; Kifiney et al. 2003). In New Zealand, Boothroyd et al. (2004) proposed that buffers 6.5 - 8 m wide could provide sufficient shading for small-moderate sized streams to prevent algal blooms following harvesting. Meleason and
Quinn (2004) found reductions in maximum daily air temperature measured mid-way within 5 and 30 m riparian buffers were virtually the same, suggesting forested buffers as narrow as 5 m can moderate air temperatures substantially, compared to a treeless environment. Riparian air temperature may affect the survival and reproductive success of stonefly and caddisfly adults thereby influencing stream community composition and structure (Collier and Smith 2000; Malmqvist 2002; Meleason and Quinn 2004). Furthermore, while forested buffer width can affect air temperatures in riparian areas, soil temperature can also be affected which may have corresponding effects on water temperature via groundwater flows (Brosofske et al. 1997).

Despite the importance of catchment-scale conditions on stream channel structure and hydrology, aquatic invertebrate life history and behaviour may be more strongly influenced by local (reach-scale) variables (Richards et al. 1997). Sponseller et al. (2001) and Rios and Bailey (2006) asserted that riparian-reach scale variables influenced benthic community structure and function more than catchment land-use variables. However, the riparian buffers examined by these workers were all 30 m wide and the results of the present study showed that community composition was affected similarly by forest cover within shorter (200 m), wider buffers (30-100 m), and longer buffers (600 m) varying in width. Thus, vegetation within short, wide buffers and longer, narrower buffers may equally affect stream communities suggesting a dependence on total buffer area. Greater adverse edge effects associated with smaller buffer areas (e.g. 200 m long and 5-10 m wide) can affect vegetation composition, condition and microclimates (including temperature, humidity, light, and wind exposure) which may therefore reduce their buffering capacity (Deans et al. 2005).

On the whole, the results reported here indicate long buffers (600 m) with 5-10 m widths for small, first and second order headwater streams within plantation forests can adequately buffer stream communities from the effects of forestry activities, particularly harvesting, within the surrounding catchment.
Pine forest age

Taxonomic richness and numbers of pollution sensitive taxa (e.g. EPT) increased significantly with pine forest age. This is consistent with another New Zealand study in which older, more mature pine plantations supported greater benthic diversity, and that after harvesting, stream communities recovered rapidly (Winterbourn 1997). Similarly, Fuchs et al. (2003) suggested that following canopy closure, stream communities within sub-boreal forests of British Columbia, Canada, recovered to pre-harvest condition within two decades, whereas studies in New Zealand have found considerable improvements to in-stream health and community composition after ten to fifteen years (Friberg et al. 1997; Harding et al. 2000; Death et al. 2003). However, in eastern USA, Harding et al. (1998) found that stream communities in forested catchments previously subjected to long-term agriculture did not fully recover even after 50 years of forest growth. As the rotation of P. radiata in New Zealand is approximately twenty to thirty years (from planting to harvest), such findings could imply there may be confounding long-term impacts of plantation forestry on streams not yet detectable to researchers.

However, in the present study results indicate that benthic community composition was similar in mature pine forest and indigenous forest. Common taxa such as the mayfly Coloburiscus and cased caddis Olinga were abundant among intermediate and mature pine forested sites, with and without indigenous riparian vegetation, as well as in indigenous reference sites. These species are common to forested streams within New Zealand, while the gastropod snail Potamopyrgus, which commonly occurred in young and intermediate age pine forested streams, are found more readily within open streams (Collier and Winterbourn 2000). These results are consistent with earlier findings that suggest stream invertebrate faunas in mature New Zealand pine forests can be very similar to those in nearby indigenous forest catchments (Friberg et al. 1997; Quinn et al. 2004; Collier and Smith 2005), although
along the "ecological gradient" suggested by Harding and Winterbourn (1995) stream communities within mature pine forests may not recover to those in indigenous forests.

**Effect of native riparian forest**

The positive influence of riparian vegetation on stream biotic indices was contingent on the amount of indigenous forest within the riparian buffer. Negative changes in biotic indices associated with pine forest age were noticeably reduced at sites with increasing proportions of indigenous vegetation within their riparian buffers. For sites with up to 30% indigenous vegetation within their riparian buffers, pine age explained less of the variation in taxonomic richness (41%) compared to sites with no indigenous riparian vegetation (55%). This degree of explanation is considerably stronger than that reported by Frimpong *et al.* (2005), who found that forest cover within riparian buffers 30 m wide and 600 m long accounted for approximately 10% of the variation in IBI at the eco-regional scale. This suggests that other physico-chemical and/or biological factors may have had greater effects on stream communities than riparian forest cover in the Canadian study. When sites with up 50% of indigenous vegetation within riparian buffers were considered in this study, the relationship between taxonomic richness and pine forest age was weak and not significant, as it was when all sites were included. These results and the broader scale analysis indicate that benthic taxonomic richness is greater within young and intermediate aged pine plantations in which indigenous forest makes up at least a third of the riparian vegetation. Additionally, community composition may be similarly influenced as indicated by the dominance of Elmid beetles in indigenous reference streams as well as young, intermediate, and mature pine forested streams with more than 30% indigenous riparian vegetation. Because much of the indigenous vegetation in the riparian buffers of the present study streams was remnant beech forest, the protective benefits of maintaining original, intact forest within riparian buffers is apparent.
Rios and Bailey (2006) examined the influence of riparian vegetation on macroinvertebrate community structure, in first and second order streams in Southwestern Ontario, and found taxonomic richness and diversity increased with increasing tree cover within the 30 m riparian buffer. Furthermore, Boothroyd et al. (2004) found that streams ranging in width from 1.8 – 9 m, within plantation pine forests had greatly reduced changes to in-stream geomorphology, temperature, lighting, and periphyton biomass normally associated with logging effects with riparian buffers comprised of indigenous vegetation. The presence of buffers also reduced changes to stream invertebrate community structure. Streams with continuous riparian buffers have greater invertebrate diversity, taxon richness, relative abundances and numbers of EPT taxa, compared to clear-cut reaches (Quinn et al. 2004). Similarly, in this study found benthic invertebrate abundance increased with pine age when up to 30% indigenous riparian forest was present, suggesting that maintaining riparian buffers comprised of at least a third indigenous vegetation, will provide valuable tools for reducing disturbance effects associated with plantation forestry on stream communities.

Few guidelines exist in New Zealand for the protection of riparian buffer zones, and the presence of indigenous riparian vegetation in pine forests is often largely due to other factors such as difficulty of access for logging or planting (Boothroyd et al. 2004). In this study, riparian buffers without native vegetative cover were dominated largely by grasses and exotic scrub, including gorse, broom, and blackberry, most of which are present only during the early part of the plantation cycle. Grasses and exotic scrub within riparian buffers do not adequately protect benthic stream communities from harvesting and associated forestry activities, and the occurrence of this type of vegetation significantly reduces the effectiveness of riparian buffers. This view is supported by Boothroyd et al. (2004) who found that bank erosion at grassed sites was significantly higher than at sites with indigenous riparian vegetation. Increased bank erosion results in higher contributions of sediment and so adversely affect in-stream
The establishment of regenerating, indigenous vegetation within riparian buffers in production pine forests may be inhibited by the presence of pine trees, which grow more quickly and reach maturity much faster than native conifers and hardwoods (Boothroyd et al. 2004). Moreover, the uniform height of mature plantation pines can create denser canopies than found in indigenous forests and so provide less variable shading (Boothroyd et al. 2004). Thus, the lack of variation in height, found naturally within indigenous forests, is likely to contribute to less spatial and temporal variation in light penetration, diminishing patches of sunlight, or sunflecks, which are important for the establishment and growth of under-storey plants (Chazdon and Pearcy 1991).

Coupled with the disturbance of forest harvesting, which increases exposure of riparian vegetation and often leads to desiccation of indigenous undergrowth and invasion by exotic plant species, the successful establishment of regenerating indigenous forest within riparian buffers may require a new management approach. For example, incorporating a protective pine tree “fence” 5-10 m from the edge of streams (depending on their size), which remains un-logged and stands as the definitive edge of the riparian buffer, may enhance succession and regeneration of native vegetation within riparian buffers throughout the plantation cycle. Furthermore, a clear boundary between riparian buffers and productive forestry terrain would benefit streams and their communities, as well as forestry companies by eliminating concerns that regenerating riparian buffer zones may be encroaching into productive plantation land.

Maintaining and enhancing adequate proportions of indigenous vegetation within riparian buffers may be pivotal to their worth, and we suggest the efficacy of riparian buffers may lie not so much in their widths, but in the quality and composition of the vegetation within them.
Acknowledgements

We thank Hugh Stevenson (Selwyn Plantation Board Ltd) and Simon Rapley (Reyonier Forests) for access to study streams and for providing land-cover information. Thanks to Hans Eikaas for assistance with GIS and Raphael Didham for statistical advice. Special thanks also to Mike Winterbourn and Tanya Blakely for providing valuable comments on drafts of this manuscript.
References


*Freshwater Biology 47, 777–798.*
FIGURE CAPTIONS

Fig. 1. Thirteen spatial scales and vegetative-cover variables generated using GIS for correlations with biotic indices.

Fig. 2. Pearson correlation coefficients between pine-cover, within riparian buffers differing in width (5, 10, 30 and 100 m) and length (catchment, 200 and 600 m), and eight biotic indices; taxonomic richness, SQMCI, MCI, EPT taxa, % EPT taxa, % Coleoptera, % Chironomidae, and % Mollusca. Shaded area indicates significant correlations ($P<0.05$), where $r$ values were greater than $\pm0.294 (n=45)$.

Fig. 3. Relationship between pine age and eight biotic indices; taxonomic richness, MCI, SQMCI, number of EPT taxa, % EPT taxa, % Molluscs, % Chironomids, and % Coleoptera. Sites with any indigenous vegetation (within 600 x 10 m riparian buffers) are excluded. ($n=12; * = P <0.05$).

Fig. 4. Relationship between pine age, presence of indigenous vegetation (within 600 x 10 m riparian buffers), and taxonomic richness. a) Sites with pine only ($n=12$), b) sites with $\leq30\%$ indigenous ($n=20$), c) sites with $\leq50\%$ indigenous ($n=25$), d) all sites included ($n=45; * = P <0.05$).

Fig. 5. Canonical Correspondence Analysis of study streams with the directions of correlations with major land-cover variables highlighted by arrows (plotted using biplot values) and labeled using appropriate codes (see Table 1).

Fig. 6. Benthic community composition for streams within young (0-7 years), intermediate (8-21 years) and mature (>22 years) pine forest. ‘N’ indicates sites with $\geq30\%$ indigenous vegetation within 600 x 10 m riparian buffers; ‘P’ indicates sites with
≤30% indigenous vegetation. The ‘Indigenous’ group refers to reference streams within entirely indigenous forest. Proportions are calculated from mean densities based on coded abundances.

**Fig. 7.** Mean (±1 se) a) benthic invertebrate abundance and, b) taxonomic richness for streams within young (0-7 years), intermediate (8-21 years) and mature (>22 years) pine forest. ‘N’, ‘P’ and ‘Indigenous’ as in Figure 6. Superscript letters indicate significant differences resulting from Post-hoc Holm-Sidak tests (n=7, P<0.05).

**Fig. 8.** Similarity of invertebrate stream communities within young (0-7 years), intermediate (8-21 years) and mature (>22 years) pine forest. Cluster a) based on rank correlation of the ten most dominant taxa in the full data set and group average linkage, b) based on presence/absence of the ten most dominant taxa in each stream (24 taxa in total), Sorensen (Bray-Curtis) distance and group average linkage. ‘N’, ‘P’ and ‘Indigenous’ as in Figure 6.
Spatial scale generation

Buffer length

Whole catchment
- Catchment
- 600 m
- 200 m

Buffer width

- 5 m
- 10 m
- 30 m
- 100 m

Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.

Figure 6.
Figure 7.

Figure 8.
Table 1. Codes and their descriptions for GIS-derived data describing vegetative cover at 13 different spatial scales for 45 study catchments.

<table>
<thead>
<tr>
<th>Codes</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>% NativeWC</td>
<td>Proportion of the whole catchment in indigenous forest</td>
</tr>
<tr>
<td>% PineWC</td>
<td>Proportion of the whole catchment in pine forest</td>
</tr>
<tr>
<td>% Ncatch5</td>
<td>Proportion of 5m buffer, extending full catchment length, in indigenous</td>
</tr>
<tr>
<td>% Peatch5</td>
<td>Proportion of 5m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
<td>% Ncatch10</td>
<td>Proportion of 10m buffer, extending full catchment length, in indigenous</td>
</tr>
<tr>
<td>% Peatch10</td>
<td>Proportion of 10m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
<td>% Ncatch30</td>
<td>Proportion of 30m buffer, extending full catchment length, in indigenous</td>
</tr>
<tr>
<td>% Peatch30</td>
<td>Proportion of 30m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
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</tr>
<tr>
<td>% Peatch100</td>
<td>Proportion of 100m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
<td>% N200x5</td>
<td>Proportion of 5m buffer, extending 200m upstream, in indigenous</td>
</tr>
<tr>
<td>% P200x5</td>
<td>Proportion of 5m buffer, extending 200m upstream, in pine</td>
</tr>
<tr>
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<td>Proportion of 10m buffer, extending 200m upstream, in indigenous</td>
</tr>
<tr>
<td>% P200x10</td>
<td>Proportion of 10m buffer, extending 200m upstream, in pine</td>
</tr>
<tr>
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</tr>
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<td>Proportion of 30m buffer, extending 200m upstream, in pine</td>
</tr>
<tr>
<td>% N200x100</td>
<td>Proportion of 100m buffer, extending 200m upstream, in indigenous</td>
</tr>
<tr>
<td>% P200x100</td>
<td>Proportion of 100m buffer, extending 200m upstream, in pine</td>
</tr>
<tr>
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<td>Proportion of 5m buffer, extending 600m upstream, in indigenous</td>
</tr>
<tr>
<td>% P600x5</td>
<td>Proportion of 5m buffer, extending 600m upstream, in pine</td>
</tr>
<tr>
<td>% N600x10</td>
<td>Proportion of 10m buffer, extending 600m upstream, in indigenous</td>
</tr>
<tr>
<td>% P600x10</td>
<td>Proportion of 10m buffer, extending 600m upstream, in indigenous</td>
</tr>
<tr>
<td>% N600x30</td>
<td>Proportion of 30m buffer, extending 600m upstream, in indigenous</td>
</tr>
<tr>
<td>% P600x30</td>
<td>Proportion of 30m buffer, extending 600m upstream, in indigenous</td>
</tr>
<tr>
<td>% N600x100</td>
<td>Proportion of 100m buffer, extending 600m upstream, in indigenous</td>
</tr>
<tr>
<td>% P600x100</td>
<td>Proportion of 100m buffer, extending 600m upstream, in indigenous</td>
</tr>
</tbody>
</table>

N = Indigenous forest; P = Plantation pine forest; WC = Whole catchment
Table 2. Dominant taxa (in rank order highest to lowest) in streams within young (0-7 years), intermediate (8-21 years) and mature (>22 years) pine forests. ‘N’ indicates sites with ≥30% indigenous vegetation within riparian buffers extending 600 m upstream from the sampling reach, and 10 m wide; ‘P’ indicates sites with ≤30% indigenous riparian vegetation. ‘Indigenous’ refers to reference streams within entirely indigenous forest. Densities were derived from coded abundances (Stark 1998) and summed for each group.

<table>
<thead>
<tr>
<th>Sites</th>
<th>P0-7</th>
<th>N0-7</th>
<th>P8-21</th>
<th>N8-21</th>
<th>P22+</th>
<th>N22+</th>
<th>Indigenous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deleatidium</td>
<td>Orthocladiinae</td>
<td>Hydrobiosella</td>
<td>Elmidae</td>
<td>Orthocladiinae</td>
<td>Deleatidium</td>
<td>Deleatidium</td>
<td>Deleatidium</td>
</tr>
<tr>
<td>Orthocladiinae</td>
<td>Deleatidium</td>
<td>Orthocladiinae</td>
<td>Deleatidium</td>
<td>Orthocladiinae</td>
<td>Coloburiscus</td>
<td>Chironominae</td>
<td></td>
</tr>
<tr>
<td>Archichadoides</td>
<td>Elmidae</td>
<td>Hydraenidae</td>
<td>Coloburiscus</td>
<td>Olinga</td>
<td>Orthocladiinae</td>
<td>Orthocladiinae</td>
<td>Olinga</td>
</tr>
<tr>
<td>Aoteapsyche</td>
<td>Coloburiscus</td>
<td>Helicopsyche</td>
<td>Orthocladiinae</td>
<td>Coloburiscus</td>
<td>Neozephlebia</td>
<td>Neozephlebia</td>
<td>Neozephlebia</td>
</tr>
<tr>
<td>Chironominae</td>
<td>Tanypodinae</td>
<td>Potamopyrgus</td>
<td>Potamopyrgus</td>
<td>Amphipoda</td>
<td>Tanypodinae</td>
<td>Olinga</td>
<td>Tanypodinae</td>
</tr>
<tr>
<td>Pycnocentrodes</td>
<td>Potamopyrgus</td>
<td>Deleatidium</td>
<td>Tanypodinae</td>
<td>Austroperla</td>
<td>Olinga</td>
<td>Olinga</td>
<td>Hydrolebidae</td>
</tr>
<tr>
<td>Potamopyrgus</td>
<td>Aoteapsyche</td>
<td>Stenoperla</td>
<td>Olinga</td>
<td>Hydromicidae</td>
<td>Amphipoda</td>
<td>Helicopsyche</td>
<td></td>
</tr>
<tr>
<td>Austroslimulium</td>
<td>Austroperla</td>
<td>Tanypodinae</td>
<td>Austroslimulium</td>
<td>Tanypodinae</td>
<td>Chironominae</td>
<td>Austroslimulium</td>
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</tr>
<tr>
<td>Elmidae</td>
<td>Tricladida</td>
<td>Pilodactylidae</td>
<td>Aoteapsyche</td>
<td>Helicopsyche</td>
<td>Elmidae</td>
<td>Austroslimulium</td>
<td></td>
</tr>
<tr>
<td>Plephorema</td>
<td>Helicopsyche</td>
<td>Coloburiscus</td>
<td>Hydraenidae</td>
<td>Stenoperla</td>
<td>Polyelectropus</td>
<td>Elidae</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. CCA derived Pearson correlation coefficients between benthic community composition and land-cover variables. Significant relationships are given (p<0.05).

<table>
<thead>
<tr>
<th>Land-cover variable</th>
<th>r value</th>
</tr>
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<tbody>
<tr>
<td>Pine &gt;22 yrs</td>
<td>0.517</td>
</tr>
<tr>
<td>600x5N</td>
<td>0.422</td>
</tr>
<tr>
<td>600x10N</td>
<td>0.442</td>
</tr>
<tr>
<td>600x30N</td>
<td>0.494</td>
</tr>
<tr>
<td>600x100N</td>
<td>0.523</td>
</tr>
<tr>
<td>200x30P</td>
<td>0.499</td>
</tr>
<tr>
<td>600x10P</td>
<td>-0.419</td>
</tr>
<tr>
<td>600x30P</td>
<td>-0.438</td>
</tr>
<tr>
<td>600x100P</td>
<td>-0.476</td>
</tr>
<tr>
<td>200x100P</td>
<td>-0.445</td>
</tr>
</tbody>
</table>
The influence of vegetation age and composition at multiple scales on stream geomorphology and water chemistry in pine plantations.

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ABSTRACT

Catchment land use, specifically plantation forestry and the composition of riparian buffers can differentially influence stream geomorphology and water chemistry. We correlated GIS and field survey data to assess catchment, riparian and reach scale effects of vegetative age and composition on fifty small headwater streams in the Canterbury foothills, New Zealand. Streams ranged from young pine forest (1-2 years old) to indigenous forest. Where pine trees dominated riparian areas, streams were small, had poor bank and channel stability and predominantly sandy, silted substrates. Younger forests had riparian vegetation comprising mainly of low shrubs, such as gorse, broom, bracken and blackberry. However, following canopy closure as forests matured shade-intolerant low shrubs were replaced by patches of bare ground and grasses. Streams with greater proportions of indigenous riparian vegetation were generally larger, with cooler water temperatures and more stable channels, as well as coarser, boulder dominated substrates. In this study, riparian buffer zones were clearly defined along larger streams but poorly so for smaller streams. We suggest, despite the small size and often intermittent nature of headwater streams, their place within river networks is fundamental to clean waterways. Thus, it is important for foresters to manage even the smallest streams in order to achieve more comprehensive protection of stream ecosystems.
INTRODUCTION

Plantation forestry is one of New Zealand’s largest natural resource industries with production forests currently covering more than 1.8 million hectares. Both within New Zealand and internationally a number of workers have investigated the effects of production pine forestry on stream ecosystems (Morgan & Graynoth 1978; Newbold et al. 1980; Gilliam et al. 1992; Growns & Davis 1994; Harding et al. 2000; Boothroyd et al. 2004). Forestry activities including planting, spraying and harvesting can lead to a multitude of direct and indirect effects on stream habitats and ecosystems operating at different spatial and temporal scales.

Stream ecosystems are strongly influenced by physical, chemical and geomorphic features of stream habitats (Richards et al. 1996; Allan et al. 1997; Death et al. 2003). These features are in turn affected by riparian and catchment conditions including hydrology, topography and vegetation (Townsend et al. 1997; Harding et al. 1998). At broad, catchment scales forestry activities can directly alter hydrologic patterns, increase catchment erosion and sedimentation, which influence streams by reducing channel stability and substrate heterogeneity, and can impact on water quality indirectly via elevated turbidity and decreased dissolved oxygen levels (Graynoth 1979; Fahey & Watson 1991; Harding & Winterbourn 1995; Richards et al. 1996; Quinn & Stroud 2002).

At the reach scale, forest harvesting can directly affect physical habitats increasing in-stream debris, channel instability, and fine sediments, often indirectly reducing substrate heterogeneity (Collier & Bowman 2003; Quinn et al. 2004). Furthermore, removal of riparian vegetation directly reduces leaf litter inputs and increases light levels reaching the stream surface, often elevating water temperatures and indirectly promoting algal growth (Rutherford et al. 1997; Dignan & Bren 2003; Boothroyd et al. 2004; Kiffney et al. 2004). The subsequent alteration of food sources
can have corresponding effects on stream food web structure and community composition. Declines in water quality and warmer temperatures frequently result in the loss of pollution sensitive Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa (Cummins et al. 1989; Davies & Nelson 1994; Wallace et al. 1997; Fuchs et al. 2003; Melody & Richardson 2004).

The extent of these effects on stream systems are largely dependant on management practices. Maintaining riparian buffers alongside streams within production forests has been widely implemented to protect stream ecosystems from the adverse effects of forestry activities. However, the effectiveness of riparian buffers can be largely moderated by local variations in width, length and vegetative composition (Gilliam et al. 1992; Quinn et al. 2004), resulting from differences between management within and among forestry companies, both nationally and internationally (Davies & Nelson 1994; Lee et al. 2004). Different workers have emphasised the importance of different aspects of riparian buffers, such as width or vegetative composition. Boothroyd et al. (2004) proposed riparian vegetation condition was an important feature in the functioning and productivity of stream ecosystems, while Davies & Nelson (1994) suggested the intensity and type of impacts associated with forestry were directly related to riparian buffer width.

Detecting the impacts of forestry on stream habitats and ecosystems can be challenging due to the diverse biological, chemical, climatic, hydrological and geophysical components that must be assessed (Gergel et al. 2002; Power & Dietrich 2002). Both large scale physical processes and local biotic processes affect stream communities, thus the best prediction of the structure and function of streams should be based on variables acting at a range of different scales (Malmqvist 2002). Geographic information systems (GIS) allow quantitative assessment of lateral, longitudinal and vertical components of the landscape that interact at several spatial
and temporal scales to influence streams (Johnson & Gage 1997). Coupling GIS with extensive field surveys can allow complex relationships between streams and catchment variables to be elucidated and predicted.

The objectives of this study were to examine how physical, chemical and geomorphic aspects of stream habitats may be differentially mediated by riparian buffers of different widths, lengths and vegetative composition. Specifically, we investigated catchment, riparian and reach scale effects of vegetative age and composition on stream geomorphology, water chemistry, and biotic attributes. The influence of pine forest age on stream habitats (specifically time since last harvested) was also investigated to determine how forestry effects may vary temporally.
METHODS

Site design

The study was conducted in the foothills of Canterbury on the east coast of the South Island of New Zealand (42°28’ S-43°23’ S, 171°43’ E-172°50’ E). Fifty, first and second order forested headwater streams were surveyed on a single occasion during January-March 2005. Forty-five streams were selected in plantation pine forests (predominantly *Pinus radiata*) with differing ages and composition of riparian vegetation. Five reference streams were selected in mature, undisturbed, indigenous forest (predominantly *Nothofagus* spp.). Catchments ranged from 196 to 630 m above sea level, and from 9.22 to 860.59 hectares.

Catchment and buffer vegetation

A Geographic Information System (GIS) was used to quantify catchment area and vegetative cover for each surveyed stream. Catchment boundaries were delineated with a Watershed Delineator (ArcView 3.2a) using a 25-m digital elevation model (DEM) to quantify the surface area contributing to drainage through a given point. Outputs were converted to catchment polygons, which included the entire drainage area upstream of the field sampling point. GIS data for the pine forested catchments were obtained from Selwyn Plantation Board Ltd and Rayonier Forests, while data for areas of indigenous mixed beech and podocarp forest were sourced from the National Land-cover Database (LCDB2, 2004).

From the combined sources of GIS data we generated twenty five categories of vegetative cover, as well as pine forest age, by ‘clipping’ the corresponding data for each catchment polygon to a collective GIS map. These categories were reduced to three, including pine, indigenous and open. Open vegetation comprised mixtures of indigenous tussock grasses (*Festuca novae-zelandiae*, *Chionochloa rigida*), and the
exotic scrubs *Ulex europaeus* and *Cytisus scoparius*. Vegetative data was used to characterise vegetation at multiple scales including; the whole catchment scale and at four riparian buffer widths (5, 10, 30, and 100 m), and three riparian buffer lengths extending upstream from the sampling reach (200 m, 600 m, and the full length of the stream). The buffer lengths were selected based on buffer dimensions used in studies by Sponseller et al. (2001) and Frimpong et al. (2005). Thus, a total of 13 GIS derived spatial scales were generated (Fig. 1). In the final analysis, proportions of indigenous and pine vegetation were determined for each giving a total of 26 land-cover variables (Table 1).

The age of the pine forest at each site was also determined. Ages ranged both within and between catchments from 0 - 80yrs which were divided into age classes corresponding to young (0-7 yrs), intermediate (8-21 yrs), and mature (≥ 22 yrs) stages of pine tree growth for each catchment. These age classes were based on local forestry knowledge of vegetation growth. Each catchment was also given a single value of pine age using the dominant age for most of the trees in the catchment.

*Reach-scale riparian buffer characteristics*

In the field, riparian buffer width (defined as the area between the stream edge and the nearest planted pine tree) was measured and vegetation categorized along a 25 m reach. The riparian width was measured on either side of the stream and proportions of four categories of vegetative cover recorded; grass/bare ground, low shrubs (<2 m high), tall shrubs (≥2 m high), and tree cover.

*Physico-chemical factors*

Spot water temperature, pH and specific conductivity (YSI 63 pH/conductivity meter), and dissolved oxygen (DO) (YSI 550 DO meter) were measured. A 100 ml
grab water sample was also collected and turbidity (HACH 2100P Turbidimeter) measured in the laboratory. Mean light levels were measured directly at the stream surface over 15s using a LICOR LI-250 light meter, while canopy cover over the stream was measured from digital photographs taken with a fish-eye lens; photos were analysed using HemiView 2.1 (Canopy Analysis Software; Delta-T Devices) giving values of gap fraction and visible sky (canopy gaps).

Within the stream several physical characteristics were recorded at each site, including three measures of width, depth, and surface velocity, from which mean discharge was calculated. Substrate composition was estimated from visual observations of the relative percentage of six size classes (bedrock, boulder, cobble, pebble, gravel, and sand/silt) within a 10 m reach. From this a Substrate Index, ranging between 3 and 8 (where 3 indicates 100% sand/silt and 8 indicates 100% bedrock) was calculated (Jowett & Richardson 1990). Additionally, stream channel stability was assessed using methods described by Pfankuch (1975). This method assesses fifteen characteristics of the upper banks, lower banks, and stream bed which are visually evaluated, and include the degree of vegetation cover, bank undercutting, the occurrence of in-stream deposition zones, and the amount of substrate compactness. Scores assigned to each characteristic are summed to give a total score interpreted as; <38 = excellent channel stability and >114 = poor. Additionally, in each 10 m reach the number of debris jams and percent of the stream bed covered by woody debris (leaf and wood jams > 1 m²) were counted and measured.

**Biological attributes**

Coarse particulate organic matter (CPOM >500 μm), fine particulate organic matter (FPOM <500 μm), and deposited sediment were measured at each site. Three CPOM samples were randomly taken using a small Surber sampler, (225 cm²; 250 μm mesh).
Samples were returned to the laboratory, washed through a 500\,\mu m sieve, oven dried over 24 hours at 40{\degree}C and weighed. FPOM and deposited sediment were sampled at five random locations at each site by stirring bed sediment within a cylinder (0.30 m diameter) with a rod to a depth of c. 5 cm so that fines were suspended in the known volume of water in the cylinder (determined from two depth measurements). When the suspended fines were well mixed, a 10 ml sample was collected following the method described in Quinn & Cooper (1997). In the laboratory, samples were oven dried over 24 hours at 40{\degree}C, then ashed at 450{\degree}C for four hours, to determine ash-free-dry-weight (AFDW). Dried and ashed samples were weighed (\pm 0.001 g) and expressed as (g/l) using the following equation:

\[
\text{Sediment/FPOM (g/l)} = \frac{\text{cylinder water vol. cm}^3 \times \text{weight(g)}}{\text{Sample water volume cm}^3} \times \frac{\text{cylinder water vol. cm}^3}{1000}
\]

Algal biomass was estimated at each site from five randomly selected cobbles. Chlorophyll \( \alpha \) was extracted from each cobble in 90% ethanol for 24 hours at 4{\degree}C in the dark, and absorbances at 665 and 750 nm were measured by spectrophotometer (APHA 1989). Chlorophyll \( \alpha \) concentrations were calculated as described by Hach (1990) and expressed as \( \mu g/cm^2 \).

**Data analysis**

Pearson correlation analyses were used to relate reach-scale riparian buffer characteristics, physico-chemical factors, and biological attributes with GIS generated vegetative composition within buffer and catchment spatial scales as well as pine forest age. To illustrate the scale-dependent effects of vegetative cover we plotted correlation coefficients between vegetative cover within each of the twelve buffer scales against reach-scale riparian buffer width, proportions of trees within riparian buffers, substrate index scores, boulder substrate, gravel substrate, and water.
temperature. Additionally, reach-scale riparian buffer, physico-chemical and biological characteristics were correlated with each other to investigate local scale relationships. Analyses were performed using SYSTAT version 10 (Wilkinson 1989). Data were tested for normality and were transformed where necessary. Proportional data were arcsine-square-root transformed.
RESULTS

Reach-scale riparian buffer characteristics

The width of riparian buffers measured in the field ranged from 0.6 to 30 m (mean 9.6 m, S.E.±1.4) and were significantly correlated with several GIS generated riparian buffer dimensions, indicating the accuracy of the vegetative cover data produced using GIS. In general, indigenous vegetation was positively correlated and pine negatively with riparian buffer widths indicating a prevalence of indigenous vegetation within riparian areas. Both indigenous and pine vegetation were strongly correlated with each GIS generated buffer width, particularly 5 m, as well as buffer lengths extending 200 m upstream from the sampling reach in addition to whole catchment lengths (Fig. 2).

Grass/bare ground within riparian buffers was negatively correlated with indigenous vegetation along the length of the catchment and at 5, 10, and 30 m widths, as well as vegetation within buffers 100 m wide and continuing 200 m upstream of the sampling site (Table 2). In contrast, low shrubs (<2 m) within riparian buffers were positively correlated with pine cover within buffers 5 m wide and extending 200 m upstream (Table 2), while, tall shrubs within riparian buffers were not correlated with any GIS generated vegetative cover (Table 2). The proportion of trees within riparian buffers declined with pine cover and increased with indigenous cover within all but one GIS generated buffer dimension (Table 2, Fig. 2b). The strongest correlation between proportions of riparian trees and GIS vegetative cover also occurred with buffers 5 m wide and extending 200 m upstream.

Riparian composition showed few significant relationships with pine forest age. The amount of grass/bare ground was greatest within intermediate aged pine forest (8-21 years), while low shrub cover was minimal (Table 3). Alternatively, tall shrubs and tree cover within riparian buffers showed no relationship with pine forest
age (Table 3). Furthermore, the composition of riparian vegetation changed with buffer width. The occurrence of grass/bare ground significantly decreased as riparian buffers widened while proportions of tall shrubs (>2 m) and indigenous trees increased (Table 4).

Surprisingly, although the amount of canopy cover over the study streams varied, no correlations with either pine or indigenous vegetation at any scale were evident (Table 2), however canopy gaps declined within mature pine forest (≥22 years) and with increasing pine age (Table 3). This relationship with pine age was strengthened with the removal of sites with greater than 25% indigenous cover within buffers 10 m wide and extending 600 m upstream \( r = -0.438, P = 0.05, n=20 \).

Moreover, canopy gaps above the stream channel significantly increased with watershed area indicating that larger watersheds had wider streams, creating larger openings in the overhead canopy (Table 4).

Stream geomorphology

Stream channel stability scores and the upper and lower bank, and stream bed component scores were significantly correlated with a number of vegetative buffer variables. Stream channel stability decreased with increasing pine cover within buffers 30 and 100 m wide and extending 200 and 600 m upstream (Table 2). Surprisingly, upper and lower bank stability showed no relationship with vegetation, regardless of buffer dimensions. However, stream bed stability improved significantly with greater proportions of indigenous vegetation within most buffer widths extending 600 m upstream, and decreased with pine cover within similar buffers (Table 2).

Contrary to our expectations, no relationships were found between pine age and stream channel stability (Table 3), possibly due to the influence of indigenous riparian vegetation. Not surprisingly upper and lower bank, and stream bed stability was less
with greater cover of grass/bare-ground within riparian buffers as well as in-stream debris and sand/silt substrate. However, stream stability improved with wider, reach-scale riparian buffers dominated by tall shrubs and trees (Table 4).

The amount of in-stream debris in our streams was not related to vegetation within GIS generated riparian buffer scales, however it did decline within intermediate and mature aged pine forest (Table 2 & 3). Furthermore, the proportion of debris and number of jams increased with sand/silt, turbidity, deposited sediment, and FPOM, but decreased in larger streams with increasing channel width, surface velocity, discharge, watershed area, and greater proportions of tall shrubs within riparian areas (Table 4).

Channel width was positively correlated with the amount of indigenous vegetation within buffers extending the length of the catchment and 30 m wide, while negatively correlated with pine cover within a number of catchment and buffer dimensions (Table 2). Channel width was also strongly correlated with watershed area and a range of physical characteristics influenced by stream size including; stream discharge, depth, substrate index scores, deposited sediment, and lower bank stability (Table 4). Additionally, as stream depth and discharge increased, low shrubs in the riparian area declined significantly (Table 4).

Stream substrate among our 45 sites was dominated by cobbles, boulders, and sand/silt (25%, 23%, and 19%, respectively). Streams with more indigenous riparian vegetation had higher substrate index scores, indicating larger substrates, while streams where riparian areas were dominated by pine forest had more fine, sand/silt dominated substrates (Table 2, Fig. 3); however no relationship was evident with pine forest age (Table 3). Naturally, substrate index scores declined as stream stability worsened (channel, upper bank, lower bank, and stream bottom stability), and debris cover and sand/silt increased (Table 4).
Substrate size was strongly correlated with vegetative cover. Boulder substrate increased with indigenous vegetation within the whole catchment and most GIS generated buffer dimensions, however declined with pine cover (Table 2 & Fig. 3). Additionally, boulder substrate was positively correlated with proportions of trees within riparian areas (Table 4). No relationship was found between boulders and pine forest age. However, the proportion of cobbles was positively correlated with intermediate aged forest (Table 3), though decreased with greater proportions of tall shrubs in riparian areas (Table 4). Pebble substrate became more common as pine cover increased within the entire catchment and within buffers 30 and 100 m wide and extending 200 m upstream (Table 2), while gravel was correlated with vegetative cover within a greater number of buffer dimensions (Fig. 3), and intermediate aged pine forest (Table 3). Sand/silt substrate showed no relationship with GIS generated vegetative cover or pine forest age however was negatively correlated with proportions of tall shrubs in riparian areas and watershed area, while positively related to in-stream debris, deposited sediment, and FPOM (Table 4).

Deposited sediment showed no relationship with GIS generated vegetative cover (Table 2), however was negatively correlated with intermediate aged pine forest (Table 3). We further investigated the relationship between deposited sediment and indigenous vegetation within riparian buffers by comparing sites with either greater than or less than 50% indigenous vegetation within 10 m wide buffers extending 600 m upstream, as well as indigenous reference streams (Fig. 4). Streams with <50% indigenous vegetation within riparian buffers had significantly greater quantities of deposited sediment compared to streams with >50% indigenous riparian vegetation, and indigenous reference streams (Kruskal-Wallis ANOVA; $H=4.870, P=0.027$; $H=7.68, P=0.006$, respectively). Additionally, deposited sediment increased with FPOM and grass/bare ground within riparian buffers, while negative relationships
were evident with tall shrubs within riparian buffers, cobbled substrate, substrate index scores, channel width, and watershed area (Table 2 & 4).

Stream water chemistry
In general, water chemistry (excluding temperature) was not strongly influenced by GIS generated riparian and catchment vegetative cover. pH showed no relationships with vegetative cover or pine forest age (Table 2 & 3), however was positively correlated with conductivity (Table 4). Conductivity showed no relationship with vegetative cover, however it declined as forests matured (Table 3). Turbidity showed no relationship with vegetative cover or pine forest age (Table 2 & 3), while DO was also unrelated to vegetative cover (Table 2), but positively correlated with increasing pine age and mature pine forest within the catchment (Table 3).

Stream water temperature was significantly correlated with vegetative cover within a number of different buffer dimensions, positively with pine and negatively with indigenous (Table 2 & Fig.5). As expected, water temperature decreased significantly with increasing pine age as canopies closed, the occurrence of canopy gaps above the stream channel and light reaching the stream surface decreased, and streams became more shaded (Table 3 & 4).

Light levels at the stream surface were significantly, positively correlated with pine cover within buffers 200 m long by 5 and 30 m wide, and negatively correlated with indigenous vegetation within buffers 600 m by 100 m wide (Table 2). No relationship was initially evident between light levels and pine forest age (Table 3; \( r = -0.264, P = 0.08, n = 45 \)), however, when sites with indigenous vegetation within their buffer 600 m by 10 m were removed, there was a significant, negative relationship \( (r = -0.619, P = 0.04, n = 11) \). Furthermore, streams with greater proportions of trees
within riparian buffers had more FPOM and CPOM, and lower light levels at the stream surface (Table 4).

*Biological attributes*

Quantities of FPOM showed no relationship with vegetative cover within catchment or buffer dimensions, or pine forest age (Table 2 & 3), however were lowest in larger, deeper, more swiftly flowing streams with few canopy gaps (Table 4).

Similarly, quantities of CPOM showed no correlated relationships with vegetative cover within GIS generated catchment or buffer scales, or pine forest age (Table 2 & 3), but at the reach-scale was negatively associated with grass/bare ground cover within riparian areas (Table 4).

Algal biomass as determined by chlorophyll *a* did not change with vegetative cover or pine forest age (Table 2 & 3), however it was positively correlated with watershed area, and negatively with debris cover (Table 4). No relationship was found with stream light levels (*r* = 0.204, *P* = 0.18, *n*=45).
DISCUSSION

The influence of catchment land use and vegetative cover on stream ecosystems and habitats has been widely studied in New Zealand and overseas (Richards et al. 1996; Huryn et al. 2002). Specifically, stream geomorphology and water chemistry in a range of land uses, including native forest, tussock grassland, pine plantations and agricultural pasture, has been investigated in the South Island by Harding & Winterbourn (1995), and Townsend et al. (1997), and by several workers in the North Island (Quinn et al. 1997; Searsbrook & Halliday 1999; Quinn & Stroud 2002). Townsend et al. (1997) found that land uses differed in elevation, habitat structure, coarse substrates, phosphorus concentrations and alkalinity, as well as canopy cover and relative abundances of CPOM. Similarly, Collier & Smith (2005) suggested the major effects of pine forest harvesting were evident in different hydrologies and bed-substrate stabilities. Conversely, Friberg et al. (1997) suggested that geographical factors such as climate and location, may be more important than forest type in South Island streams. Although the variable impacts of these land uses on stream ecosystems have been well studied, the importance of catchment and riparian vegetative composition and age, is still poorly understood. In this study we addressed this gap in our knowledge by investigating the catchment, riparian and reach scale effects of vegetative age and composition on stream geomorphology, chemistry and biotic attributes.

Within our study, we found pine and indigenous forests strongly influenced stream geomorphology and water chemistry. Not surprisingly, in streams where indigenous forest dominated the catchment, riparian vegetation at the reach-scale was comprised commonly of trees (non-pine) and tall shrubs with little grass/bare ground. This suggests indigenous vegetation may inhibit the growth of light-limited grasses and instead promote shade-tolerant undergrowth, reducing patches of bare ground and
possibly help to stabilise banks. Streams with predominantly pine forested catchments were generally smaller, with higher water temperatures and finer substrates consisting of pebbles and gravel, and riparian vegetation which changed throughout the plantation cycle.

Within young pine forests, low shrubs including early successional, native and exotic scrub species such as *Pteridium esculentum* (bracken), *Ulex europaeus* (gerse), *Cytisus scoparius* (broom) and *Rubus fruticosus* (blackberry) frequently dominated riparian areas. Moreover, streams with low shrubs common within riparian areas were generally shallow, small, with fine sand/silted substrates. Gibb (1994) suggested catchments with fine, sandy substrates may be more readily colonised by early successional plant species and if undamaged by natural or anthropogenic disturbances, can lead to the establishment of secondary successional plants such as *Kunzea ericoides* (kanuka) and *Leptospermum scoparium* (manuka). The potential for natural succession within riparian areas, which can favour indigenous vegetation with minimal disturbance (Moles & Drake 1999), highlights the importance of protecting riparian vegetation particularly during harvesting and spraying operations, in order to enhance and preserve their integrity throughout forestry cycles.

As pine forests matured, riparian areas were often covered by grass and bare ground with few low shrubs. This may have been due to less light associated with canopy closure suppressing shade-intolerant, early successional plants (Boothroyd et al. 2004). Furthermore, where grass/bare ground dominated the riparian vegetation, there was less in-stream CPOM. Terrestrial litter inputs from riparian vegetation are of fundamental importance to stream ecosystems. Small headwater streams in particular are dependent on the input of allochthonous material as an energy source (Cummins et al. 1989; Wallace et al. 1999; Karlsson et al. 2005). Additionally, leaf litter and small, woody debris retained within stream can provide important
microhabitats for invertebrates and fish (Collier & Smith 2003; but see Gjerlov & Richardson 2004). Furthermore, channel instability and higher sediment yields associated with more grass/bare ground within riparian buffers may be detrimental to stream ecosystems within pine forested catchments.

Following canopy closure in mature forests, stream shading increased, effecting water quality by reducing water temperatures and increasing DO levels. Additionally, physical changes resulted in less deposited sediment and in-stream debris, and stream substrates dominated by cobbles and gravel. Although physical and chemical stream attributes improved as pine forests aged towards conditions found in more pristine, indigenous forest streams, forestry impacts remained evident. These findings support the view suggested by Harding & Winterbourn (1995), that the structure of the stream communities may change along an "ecological gradient", within which pine forested streams occupy an intermediate condition.

There has been some debate about whether catchment, riparian, or reach scale characteristics best shape the structure of stream communities (Richards et al. 1996; Sponseller et al. 2001; Weigel et al. 2003; Rios & Bailey 2006). Following a study of first order streams in southeastern Michigan, Lammert & Allan (1999) suggested riparian land use may better predict overall biotic conditions than catchment land use. However, they go on to assert that reach-scale habitat variables seemed more important than catchment land use in explaining variability in fish and macroinvertebrate assemblages. Similarly, Richards et al. (1997) found that life history and behavioural attributes of aquatic insects, were best related to reach-scale physical features than catchment-scale variables. Although, they suggested catchment-scale variables may have direct or indirect influences on reach-scale properties, particularly channel morphology and hydrologic patterns. Conversely, Roth et al. (1996) suggested the biological integrity of stream ecosystems depend on
land use influences at catchment rather than reach scales. From our study, some aspects of stream habitats including reach-scale riparian vegetation, substrate composition, sedimentation, debris jams and water chemistry (water temperatures and DO levels) were similarly influenced by both catchment and riparian scales variables. However, other attributes of stream geomorphology and water chemistry were more strongly influenced by vegetation type within riparian buffer scales.

Streams with a predominance of indigenous vegetation within riparian buffers, particularly those of greater lengths (extending 600 m and the full length of the catchment upstream), generally had wider, deeper, more stable channels, with higher discharges and more heterogeneous substrates. Furthermore, quantities of FPOM, turbidity and deposited sediment were lower. These conditions are consistent with the findings of other New Zealand studies of streams in indigenous beech and podocarp forests (Harding & Winterbourn 1995; Quinn et al. 1997; Scarsbrook & Halliday 1999). Conversely, streams with greater proportions of pine forest within riparian buffers (particularly at more broad scales) were smaller, with lower flows, less stable channels, larger quantities of in-stream debris and higher turbidity. Moreover, streams with greater than 50% pine forest within extensive riparian buffers had significantly greater sediment deposits compared to those with greater than 50% indigenous riparian vegetation, which were comparable to reference streams within entirely indigenous catchments. Similarly, (Quinn et al. 1997) found pine forest streams in Waikato had 3-fold higher suspended solids and fine sediment stored in streambeds than native forest streams.

The planting of pine trees close to the streams edge is often associated with less stable stream banks and channel erosion. Murgatroyd & Ternan (1983) found coniferous afforestation lead to more active bank erosion along forested reaches compared with non-forested reaches with marked effects on channel form. These
changes were attributed to reduced bank stability resulting from lost sediment-stabilising ground cover (Trimble 1997; Scarsbrook & Halliday 1999). Stream systems do recover from afforestation, eventually returning to more stable, wider channels, typical of streams within pristine, indigenous forest (Quinn et al. 1997). Although channel adjustments can cause increased sedimentation in the interim, as suggested by Scarsbrook & Halliday (1999), streams may eventually reach an equilibrium with stable cross-sections (Allmendinger et al. 2005) and heterogeneous substrates, which provide greater stream habitats to which stream communities are likely to respond positively (Sweeney et al. 2004).

The smallest streams in this study often had pine trees were planted close to stream edge. Maintaining an adequate riparian buffer in these small streams is likely to have positive consequences on the functionality of the greater stream network, as these smaller headwater streams are sources of water, sediment and energy for larger downstream waterways. Research has shown that despite the intermittent nature of small head water streams, they are fundamental to healthy river ecosystems (Moore & Richardson 2003; Price et al. 2003).

The trends evident in this study suggest buffers of greater widths (e.g. >10 m) can support more mature, secondary successional vegetation, such as K. ericoides and L. scoparium, possibly with deeper roots systems which are likely to enhance stream bank stability and the protective capacity of riparian buffers. Root systems of riparian vegetation stabilise banks, providing protection from undercutting and enhance channel stability (Boothroyd et al. 2004; Allmendinger et al. 2005). Clearly the careful management and planning of riparian areas within pine forest catchments including maintaining riparian buffers of adequate width, is likely to reduce the incidence of bank erosion and sedimentation (Davies-Colley 1997; Trimble 1997). Furthermore, protecting vegetation within riparian buffers is likely to encourage
natural regeneration and succession of plant communities toward compositions more similar to indigenous forest, almost certainly enhancing the protection of stream ecosystems.
REFERENCES


Roth NE, Allan JD, Erickson DL 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11(3): 141-156.


FIGURE CAPTIONS

Figure 1. Thirteen spatial scales and vegetative-cover variables generated using GIS for correlation in various combinations with reach-scale riparian buffer characteristics, physico-chemical factors, and biological attributes.

Figure 2. Pearson correlation coefficients of (a) mean reach-scale riparian buffer widths and, (b) proportions of tree cover within riparian buffers compared to GIS generated vegetation cover within different buffer scales. N/Pcatch = Proportion of the whole catchment in indigenous/pine forest, N/P200 = Proportion of the buffer, extending 200 m upstream, in indigenous/pine, N/P600 = Proportion of the buffer, extending 600 m upstream, in indigenous/pine. r values greater than ± 0.286 (i.e. those within shaded areas) represent significant correlations (P<0.05, n = 45).

Figure 3. Pearson correlation coefficients between substrate composition and GIS generated vegetative cover within different buffer scales, codes are as in Fig.2. Correlations with (a) substrate index scores, (b) proportion of boulders within streams' substrate and, (c) proportion of gravel within streams' substrate are shown; where r values greater than ± 0.286 (i.e. those within shaded areas) represent significant correlations (P<0.05, n = 45).

Figure 4. Mean (±1 S.E.) levels of deposited sediment (g/l) at sites with ≤50%, >50% indigenous vegetation within 600x10 m buffer, and indigenous reference streams. Subscript letters indicate significant differences between means resulting from Kruskal-Wallis ANOVA and Post-Hoc Dunn's test (H = 4.870, P = 0.027).

Figure 5. Pearson correlation coefficients between stream water temperature, and GIS generated vegetative cover within different buffer scales, codes are as in Fig.2. r values greater than ± 0.286 (i.e. those within shaded areas) represent significant correlations (P<0.05, n = 45).
FIGURES

Spatial scale generation

Buffer length

Whole catchment

catchment

600 m

200 m

Buffer width

5 m

10 m

30 m

100 m

Figure 1.

Figure 2.
Figure 3.
Figure 4.

Figure 5.
Table 1. Codes and their descriptions for GIS-derived data describing vegetative cover at 13 different spatial scales for 45 study catchments.

<table>
<thead>
<tr>
<th>Codes</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>% NativeWC</td>
<td>Proportion of the whole catchment in indigenous forest</td>
</tr>
<tr>
<td>% PineWC</td>
<td>Proportion of the whole catchment in pine forest</td>
</tr>
<tr>
<td>% Ncatch5</td>
<td>Proportion of 5m buffer, extending full catchment length, in indigenous</td>
</tr>
<tr>
<td>% Pcatch5</td>
<td>Proportion of 5m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
<td>% Ncatch10</td>
<td>Proportion of 10m buffer, extending full catchment length, in indigenous</td>
</tr>
<tr>
<td>% Pcatch10</td>
<td>Proportion of 10m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
<td>% Ncatch30</td>
<td>Proportion of 30m buffer, extending full catchment length, in indigenous</td>
</tr>
<tr>
<td>% Pcatch30</td>
<td>Proportion of 30m buffer, extending full catchment length, in pine</td>
</tr>
<tr>
<td>% Ncatch100</td>
<td>Proportion of 100m buffer, extending full catchment length, in indigenous</td>
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<tr>
<td>% Pcatch100</td>
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</tr>
<tr>
<td>% N200x5</td>
<td>Proportion of 5m buffer, extending 200m upstream, in indigenous</td>
</tr>
<tr>
<td>% P200x5</td>
<td>Proportion of 5m buffer, extending 200m upstream, in pine</td>
</tr>
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<td>% N200x10</td>
<td>Proportion of 10m buffer, extending 200m upstream, in indigenous</td>
</tr>
<tr>
<td>% P200x10</td>
<td>Proportion of 10m buffer, extending 200m upstream, in pine</td>
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<td>Proportion of 30m buffer, extending 200m upstream, in indigenous</td>
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<td>% P200x30</td>
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</tr>
<tr>
<td>% P600x100</td>
<td>Proportion of 100m buffer, extending 600m upstream, in pine</td>
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</table>

N = Indigenous forest; P = Plantation pine forest; WC = Whole catchment
Table 2. Significant ($P<0.05$) Pearson correlations between GIS generated vegetative cover within different buffer dimensions and; riparian characteristics, stream geomorphology, physico-chemical and biological attributes, where * indicates $P<0.001$.

<table>
<thead>
<tr>
<th>Attributes</th>
<th>Native WC</th>
<th>Neath</th>
<th>N200</th>
<th>N600</th>
<th>N100</th>
<th>Pine WC</th>
<th>Petch</th>
<th>P200</th>
<th>P600</th>
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<td>0.45</td>
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<td>0.52*</td>
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N = Indigenous forest; P = Plantation pine forest; WC = Whole catchment
Table 3. Significant (P<0.05) Pearson correlations between increasing pine age, young, intermediate, and mature forest and, riparian characteristics, stream geomorphology, physico-chemical and biological attributes, where * indicates p<0.001.

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<th>Pine age</th>
<th>Young 0-7 yrs</th>
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<tr>
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The influence of terrestrial subsidies on stream communities within young pine, mature pine, and indigenous forest: how do they compare?

R. S. Eivers, J.S. Harding

School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
ABSTRACT

This study investigated the influence of variable terrestrial subsidies from riparian vegetation in young pine, mature pine, and indigenous forests on benthic stream communities. We compared inputs of leaf litter and terrestrial invertebrates in nine streams within the three forest types, and measured the response of physico-chemical and biotic indices. Additionally, terrestrial inputs were experimentally excluded from three young pine forest streams with early successional, riparian scrub species, to investigate the influence of these subsidies on stream communities. Indigenous forest streams were more stable, with higher flows and dissolved oxygen levels, and water temperatures on average 2 °C cooler than pine forest streams. Inputs of coarse particulate organic matter (CPOM) and terrestrial invertebrate abundances were comparable between forest types, however young pine forest contributed significantly more CPOM than mature pine and indigenous forests. Benthic invertebrate densities in indigenous forest streams were more than twice those of pine forests, while mean taxonomic richness was highest in indigenous forest (34 taxa) and lowest in young pine forest streams (19 taxa). Observed similarities in community composition among forest types may be due to the generalist feeding nature of New Zealand benthic invertebrates. Our findings suggest that even exotic scrub species, such as gorse, broom and blackberry, in young pine forests may provide essential subsidies to stream communities and enhance their recovery from harvesting activities.
INTRODUCTION

Subsidies of organic matter and terrestrial invertebrates are an important link between stream food webs and the riparian ecotone. Nutrient, terrestrial invertebrate and detrital subsidies have been shown to increase primary and secondary productivity in recipient ecosystems, both directly and indirectly (Polis et al. 1997). The relative productivity of riparian habitats affects the magnitude and importance of terrestrial subsidies, which are explicitly linked to the age and composition of riparian vegetation. Baxter et al. (2005) suggested there is a need to determine whether reciprocal prey fluxes stabilise stream-riparian ecosystems, explore how landscape context affects the magnitude and importance of subsidies, and determine how impacts of human disturbance may influence streams and riparian networks via trophic linkages.

Wallace et al. (1997; 1999) extensively studied the importance of terrestrial-aquatic linkages through excluding terrestrial leaf litter inputs from a forest stream in the Coweeta Hydrologic Laboratory, in western North Carolina, U.S.A. Excluding leaf-litter was found to have a strong bottom-up effect on detritivores and predators within the detrital based ecosystem, demonstrating the importance of terrestrial-aquatic linkages in maintaining productivity of detrital based, headwater ecosystems draining forested catchments.

A number of workers within New Zealand and internationally have studied the influence of riparian vegetative composition and land use on terrestrial subsidies and their subsequent influences on stream food webs (McDowall et al. 1996; Nakano et al. 1999; Siler et al. 2001; Kawaguchi et al. 2003). However, studies exploring the relationship between riparian vegetation age and composition, terrestrial invertebrates and stream communities have been inconclusive. Wipfli (1997) investigated terrestrial subsidies from streams within conifer dominated old-growth forests and alder dominated young-growth forests in southeastern Alaska, and found terrestrial
invertebrate biomass was similar and contributed to at least half of the prey ingested by salmonids. Furthermore, Wipfli & Gregovich (2002) suggested subsidies to fishless headwaters, including terrestrial invertebrates and detritus, are exported to downstream food webs, increasing aquatic productivity within larger streams. In small hill country streams in Waikato, New Zealand, Scarsbrook et al. (2001) found litter inputs to pasture streams were significantly lower than those within native and exotic pine forests, whereas Edwards & Huryn (1996) found that the amount of terrestrial invertebrate biomass entering forested and native tussock streams were very similar and significantly greater than in grazed, pasture grassland streams.

Previous research has examined how terrestrial subsidies vary seasonally, with differing vegetation and land-uses. However, few studies have examined how these inputs change throughout plantation forestry cycles and how they compare to those within indigenous forest. Harvesting and replanting within plantation forests often changes riparian plant community composition and structure, inadvertently altering terrestrial subsidies to stream communities.

Vegetated riparian buffers are often maintained along streams within production pine forests to mitigate adverse effects on stream ecosystems associated with production forestry, for example, by reducing increases in irradiance, temperature, and sedimentation (Davies & Nelson 1994; Boothroyd et al. 2004; Quinn et al. 2004). Forest harvesting can shift the source of energy within streams from allochthonous to autochthonous based systems. Riparian buffers help to maintain natural energy sources within stream ecosystems, preventing algal blooms often associated with more light and higher stream temperature following harvesting, whilst sustaining leaf litter inputs (Cadwallader et al. 1980; Boothroyd et al. 2004). Effects on community dynamics are likely to vary with the relative amount of allochthonous inputs as well as local food web structure (Polis et al. 1997). For example, whether or
not the stream ecosystem is based primarily on detrital resources, as was apparent in
the study of Wallace et al. (1997; 1999).

Several New Zealand studies have suggested indigenous vegetation within
riparian buffers ranging from 5-30 m may be most effective at buffering streams from
forestry effects (Graynoth 1979; Boothroyd et al. 2004; Meleason & Quinn 2004).
Despite these findings, improving our understanding of the effectiveness of riparian
buffers differing in width, length and vegetative composition is required to provide
forest managers with more accurate advice. Few studies have investigated the
potential of riparian buffers comprised of early successional, native and exotic scrub,
to adequately protect streams from the impacts associated with plantation forestry.

In this study we compared terrestrial subsidies from young pine (1-2 years old
with riparian areas dominated by native and exotic scrub species), mature pine (>22
years old), and indigenous forests to small headwater streams within the Canterbury
foothills in the South Island, New Zealand. Our objectives were to determine how
inputs of leaf litter and terrestrial invertebrates compared between forest types, and
what influence, if any, differences may have on benthic stream communities. We
adopted two approaches to compare inputs from each forest type. Firstly, the quantity
of terrestrial leaf litter and invertebrates was compared by sampling representative
streams in each forest type. Secondly, an exclusion experiment was conducted to test
the importance of terrestrial subsidies from young riparian vegetation on stream
communities.
METHODS

Site Description

The study was conducted in the Canterbury foothills along the east coast of the Southern Alps, South Island, New Zealand (42°28' - 43°23' S, 171°4' - 172°50' E). Firstly, nine streams were studied including, three streams within young pine forest (1-2 years old), predominantly Pinus radiata, three within mature pine forest (>22 years old) and three within mature indigenous forest, comprised of Nothofagus solandri - N.fusca (mountain and red beech), and mixed broadleaf forest (Melicytus ramiflorus, Pseudopanax arboreus, P. crassifolium, Kunzea ericoides, Leptospermum scorparium, Coprosma spp). The young pine forest streams had riparian vegetation consisting of grasses, native and exotic scrub including, Pteridium esculentum (bracken), Ulex europaeus (gorse), Cytisus scoparius (broom) and Rubus fruticosus (blackberry). Streams were small, first and second order headwater tributaries of the Ashley and Percival rivers, similar in size and physical condition. Catchments ranged from 19-162 ha and were between 280-477 m above sea level. For the initial component of the study, each stream was sampled twice, in September and November, 2005.

Exclusion Tunnels

Three 50 m exclusion tunnels were constructed over a 50 m reach in each of the three young pine forest streams to prevent terrestrial inputs of organic matter and invertebrates from entering the streams. The tunnels were constructed using 2.1 m fiberglass rods, shade cloth 3.6 m wide and 50 m long which reduced light intensity by 50% (Fig. 1). Exclusion tunnels were left for two months before sampling. In each stream, an upstream control and exclusion tunnel reach (approximately 40 m downstream beneath the tunnel) were sampled twice in September and November, 2005. Physico-chemical, biological, benthic invertebrate and drift samples were taken
within 10 m reaches at the downstream end of the exclusion tunnel and in the 
upstream control reach.

*Physico-chemical factors*

Spot water temperature, pH and conductivity were measured at each of the nine 
streams using a calibrated YSI 63 pH/conductivity meter, and dissolved oxygen (DO) 
a YSI 550 meter. Mean light intensity and air temperature at the stream surface were 
measured every hour for two months using HOBOware light intensity/temperature 
loggers (Onset U-series data loggers 2005).

Within the nine streams several physical characteristics were recorded at each 
site, including three measures of width, depth and surface velocity, from which mean 
discharge was calculated. Substrate composition was estimated from visual 
observations of the relative percentage of six size classes (bedrock, boulder, cobble, 
pebble, gravel, and sand/silt, according to the Wentworth scale) within a 10 m reach. 
From this a Substrate Index, ranging between 3 and 8 (where 3 indicates 100% 
sand/silt and 8 indicates 100% bedrock) was calculated using Jowett & Richardson 
(1990). Additionally, stream channel stability was assessed using the method 
described by Pfankuch (1975). This method assesses fifteen characteristics of the 
upper banks, lower banks, and stream bed which are visually evaluated, and include 
the degree of vegetation cover, bank undercutting, the occurrence of in-stream 
deposition zones, and the amount of substrate compactness. Scores assigned to each 
characteristic are summed to give a total score interpreted as; <38 = excellent channel 
stability and >114 = poor.

Deposited sediment was measured in conjunction with algal biomass from five 
randomly selected cobbles from each site. Cobbles were scrubbed vigorously using a 
wire brush in 10-20 ml of water which was then filtered through weighed glass 
microfibre filters (GF/C 47 mm; ~1μm pore size). Samples were oven dried at 40 °C
for 24 hours, weighed and ashed at 450 °C for four hours, to determine ash-free-cry-
weight (AFDW).

**Biological characteristics**

Samples of periphyton, fine particulate organic matter (FPOM <500 μm) and coarse
particulate organic matter (CPOM >500μm) were collected from each site.
Periphyton was measured by randomly selecting ten cobbles from which five were
used to measure chlorophyll a and five to measure biofilm and inorganic sediment
mass. In the field, individual cobbles were placed in zip-lock bags, kept cool and
refrigerated upon return to the laboratory. In the laboratory, chlorophyll a was
extracted from each cobbles in 90% ethanol for 24 hours at 4 °C in the dark, and
absorbance's at 665 and 750 nm were measured by spectrophotometer (APHA 1989).
Chlorophyll a concentrations were calculated as described by Hach (1990) and
expressed as μg/cm². Biofilm was determined using the same methods that were used
to measure deposited sediment.
FPOM was collected from each site using a plankton net (diameter 20 cm;
~50μm mesh) placed in the stream where most of the flow traveled through the net.
Time, velocity, and three depth measurements were made to determine the volume of
water sampled. In the laboratory, the sample was sieved through a 500 μm mesh
sieve to remove large particles, and then filtered through weighed GF/C microfibre
filters. Samples were oven dried at 40 °C for 24 hours, weighed, and converted to
milligrams per volume of water (mg/m³).

Four samples of deposited CPOM were taken randomly with a Surber sampler
(625 cm²; mesh 250 μm). Samples were returned to the laboratory, rinsed through a
500 μm sieve, invertebrates were removed, then samples were oven dried at 40 °C,
and weighed.
CPOM and invertebrate drift were sampled simultaneously. A sample was taken from each site using drift nets (0.075 m², 250 μm), left overnight for a minimum of ten hours. CPOM was separated from invertebrates, oven dried for 48 hours at 40 °C and weighed.

Terrestrial CPOM was measured along with terrestrial invertebrates in the riparian area using pitfall traps (plastic pottles 10 cm diameter; 10 cm deep). Six traps were placed alongside each stream, three on either side roughly 2 m apart and half a meter from the waters edge. Traps were dug into the ground, so that the edge of the pottle sat flush with the surface; the lip of the pottle was smoothed over with dirt. Approximately 25 ml of ethylene diluted glycol was placed in each pitfall trap. Traps were retrieved after one week and were returned to the laboratory where their contents were rinsed through a 500 μm sieve, and preserved in 90% ethanol. CPOM was separated from invertebrates, dried for 48 hours at 40 °C and weighed. Terrestrial invertebrates were counted and identified to order using New Zealand Insect keys (Grant 1999; Gullan & Cranston 2000). Adult aquatic insects were grouped with terrestrial invertebrates.

Benthic invertebrates

Four benthic invertebrate samples were taken randomly from each stream using a Surber sampler (625 cm², 250 μm mesh). Samples were preserved in the field in 80% ethanol and returned to the laboratory for processing. In the laboratory, samples were rinsed through a 500 μm mesh sieve, sorted, counted and identified under a binocular microscope (x 6 magnification) to the lowest taxonomic level (usually genus), using standard keys (Winterbourn et al. 2000; Smith 2001).

Seven biotic indices were calculated including taxonomic richness, the Macroinvertebrate Community Index (MCI) and Quantitative MCI (QMCI). The MCI and its variants were developed to monitor pollution in organically enriched rivers and
streams but have been applied successfully to streams in some other land-uses. Lower MCI and QMCI scores refer to more polluted waterways, whereas higher scores indicate cleaner water (see Stark 1985). Numbers of pollution sensitive Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa were calculated for each site, as well as the proportions of EPT taxa.

Drift

Drifting invertebrates (both aquatic and terrestrial) and suspended CPOM were sampled using drift nets (square frame 0.075 m², net 85 cm long; 250 μm mesh). Nets were secured to the stream bed using aluminum poles, the opening of the net lying flush with the stream bed. Nets were positioned to sample the entire stream discharge which was calculated from two depth measurements and mean velocity. Drift nets were left over night (for a minimum of 10 hours) following which, samples were preserved in 80% ethanol in the field. In the laboratory, samples were rinsed through a 500 μm mesh sieve and sorted. CPOM was oven dried at 40 °C and weighed. Drifting stream and terrestrial invertebrates were counted and identifications were made as described for benthic and pitfall trap samples.

Data analysis

One-way ANOVAs (with post-hoc Holm-Sidak tests) were used to compare differences in physico-chemical, biological, benthic invertebrate, and drift samples between forest types using SigmaStat (Version 3.11, 2004). Data were tested for normality and if non-normal, were compared using a non-parametric test (Kruskal-Wallis ANOVA on Ranks, with post-hoc Tukey tests). Differences were displayed in tabular form or graphically using SigmaPlot (Version 9.0, 2005). Similarly, One-way ANOVAs were run to compare differences between samples from exclusion tunnel and upstream control reaches within the young pine forest streams.
RESULTS

Physico-chemistry

Streams within each forest type (young pine, mature pine, and indigenous forest) were of similar widths, however indigenous forest streams were significantly deeper with greater velocities and discharge (Table 1). Streams within indigenous forest were also significantly more stable with coarse, boulder dominated substrates. Furthermore, indigenous streams had significantly higher pH, specific conductance, and DO levels and cooler temperatures (Table 1).

Terrestrial Subsidies

Suspended FPOM was greatest in streams within mature pine and least within indigenous forest (Fig. 2a). Quantities of benthic and pitfall trapped CPOM were significantly higher at young pine streams than mature pine and indigenous forest streams (Fig. 2b, c), whereas the amount of suspended CPOM was lowest in young pine forest streams (Fig. 2d).

Densities of pitfall trapped terrestrial invertebrates were highest in mature pine forest streams (Fig. 2e), largely due to high numbers of Collembola which accounted for more than 75% of all terrestrial invertebrates (Table 2). Representatives of 21 orders were collected in pitfall traps, with Collembola making up the largest proportion of total densities from 17-75% per forest type (Table 2). Approximately, 7% of invertebrates collected in pitfall traps were aerial stages of aquatic insects, including EPT taxa and Diptera. Densities of drifting terrestrial invertebrates (i.e. those that had fallen into the streams) were variable among and within forest types, but tended to be higher in indigenous forested streams (Fig. 2f).

Stream communities

Levels of chlorophyll a and biofilm biomass were highest on cobbles from streams in young pine, intermediate in mature pine and lowest in indigenous forest (Fig. 2g, h),
however due to high variability, seemingly large differences between young pine and indigenous forested streams were not significant.

Community composition of benthic macroinvertebrates was similar among streams within different forest types although some differences were evident (Fig. 3). Young pine forest streams had significantly greater proportions of Ephemeroptera than mature pine and indigenous forest streams ($n=3, F=9.49, P=0.014$), largely because of high densities of *Deleatidium* which accounted for 35% of the total benthic invertebrates in young pine forest streams (Table 3). Conversely, young pine streams had fewer Plecoptera whereas mature pine forest streams had the highest densities of stoneflies ($n=3, F=4.98, P=0.053$). Trichoptera abundances were similar in young pine and indigenous forest streams and slightly higher than those within mature pine (Fig. 3). Diptera comprised similar proportions within streams of all three forest types, but proportions of Mollusca were significantly lower in indigenous forest streams ($n=3, H=7.2, P=0.004$, Tukey test). Numbers Coleoptera of were highest in indigenous forest streams and lower in young pine forest streams ($n=3, F=8.48, P=0.018$).

The ten numerically dominant taxa in streams of each forest type included three taxa in common; *Deleatidium*, which was dominant in all three forest types, Orthocladiinae and Hydraenidae (Table 3). In young pine forest streams larvae of the caddisflies *Polypelectrobus* and *Psilochorema* were abundant and most likely were feeding on the high densities of *Deleatidium* nymphs and Orthocladiinae, which are known to be among their major prey species (Winterbourn 2000). Deposit-feeding Oligochaeta and grazing *Helicopsyche* larvae were also common in young pine forest streams (Table 3). The stonefly *Austroperla* and Tanypodinae were common only in mature pine forest streams, whereas Elmid beetles, detritivorous *Olinga* and predatory *Philorheitthus* caddisflies, and Empididae, were only important in indigenous forest streams (Table 3).
Benthic invertebrate densities were significantly higher in indigenous forest streams than pine forest streams, but were similar in young and mature pine forest streams \((n=3, F=5.182, P=0.049; \text{Fig. 4a})\). Similarly, benthic taxonomic richness increased as pine forests matured and was significantly greater within indigenous forested than young pine forest streams \((n=3, F=8.463, P=0.018; \text{Fig. 4b})\). MCI and QMCI scores indicated clean-water streams within indigenous forest and possible mild pollution in young pine and some mature pine forested streams (see Stark 1985 for definitions), however neither MCI nor QMCI differed significantly among forest types \((\text{Fig. 4c, d})\). EPT taxa richness increased with pine forest age and was greatest in indigenous forest streams, however varied considerably among young and mature pine forest streams so that differences between the three stream types were not significant. Similarly, the percentage of EPT individuals in the total stream fauna did not differ among stream types \((\text{Fig. 4e, f})\).

Densities of drifting invertebrates were highly variable among streams, although they tended to be lowest in mature pine forest streams \((\text{Fig. 4g})\). Meanwhile, taxonomic richness of drift invertebrates was significantly higher in indigenous forest streams than pine forest streams \((n=3, F=11.371, P=0.009; \text{Fig. 4h})\).

*Exclusion experiment*

The physico-chemistry of exclusion and upstream control reaches within the young pine forested streams was very similar, although light intensity was significantly reduced to roughly half that of upstream control reaches as expected from the 50% shade cloth (Table 4).

Quantities of suspended FPOM and benthic CPOM were reduced on average by 50% and 38%, respectively within exclusion reaches, however, differences between reaches were not significant due to high variation and low statistical power \((\text{Fig. 5a, b})\). Conversely, the amounts of pitfall trapped CPOM and drifting CPOM
were significantly reduced (by 74% and 79%, respectively) within exclusion reaches illustrating the effectiveness of the exclusion tunnels ($n=3$, $F=13.01$, $P=0.02$; $n=3$, $F=21.36$, $P=0.01$, respectively; Fig. 5c, d). Densities of pitfall trapped terrestrial invertebrates were also reduced within exclusion reaches by 23%, but not significantly, while numbers of drifting terrestrial invertebrates tended to be greater beneath exclusion tunnels (Fig. 5e, f). Emerging aquatic invertebrates, which were often caught beneath the tunnels, most likely contributed to greater numbers of adult aquatic insects present in drift samples from the tunnel exclusion reaches.

Both levels of chlorophyll a and biofilm biomass did not differ between exclusion and upstream control reaches (Fig. 5g, h).

Benthic community composition was also similar between exclusion and upstream control reaches (Fig. 6). However, the abundance of Trichoptera was greater within upstream reaches, whereas numbers of Mollusca were higher within exclusion reaches. Though due to high variability, neither of the observed differences was significant. The ten dominant taxa within exclusion and upstream reaches were also similar, although the snail *Potamopyrgus* and caddisflies *Oxyethira* were relatively more abundant within exclusion reaches, while *Polyplectropus* and caddisflies *Helicopsyche* accounted for greater proportions of the overall community within upstream reaches (Table 5).

Densities of benthic invertebrates were generally greater within exclusion reaches, but biotic indices including taxonomic richness, MCI, QMCI, EPT richness and proportions of EPT individuals, did not differ between exclusion and upstream control reaches (Fig. 7). Furthermore, although drifting invertebrate abundance and taxonomic richness were slightly higher within exclusion reaches, they were highly variable (Fig. 7g, h).
DISCUSSION

In recent years research has confirmed the significance of terrestrial inputs of organic matter as an important trophic link between riparian habitats and stream food webs, providing energy subsidies in the form of leaf litter and terrestrial invertebrates. The amount and quality of these inputs have been found to differ markedly with the age and composition of riparian vegetation (Edwards & Huryn 1996; Wipfli 1997; Kawaguchi & Nakano 2001; Allan et al. 2003). In a study of three native riparian tree species in streams on Banks Peninsula, New Zealand, Linklater (1995) found peaks in shredder biomass feeding on red beech and mahoe leaves, however none were recorded on fuchsia leaves indicating that leaf litter sourced from different plant species can vary in importance to stream taxa. While an essential food source for stream detritivores, leaves can also provide microhabitats which are readily colonized by invertebrates and can lead to increased abundance and species richness (Quinn et al. 2000). Parkyn & Winterbourn (1997) found greater densities of invertebrates colonized leaves of introduced elm and native mahoe, although shredders were most abundant on introduced willow and native red beech leaves. Similarly, the shredder Olinga jeanae showed a preference for both elm and red beech leaves as food sources, thus no strong associations were apparent between shredders and native trees, rather leaves from introduced and native trees may be equally preferred by shredders (Parkyn & Winterbourn 1997).

In this study we investigated the relative contribution of organic matter and terrestrial invertebrates to streams with differing riparian age and vegetative composition and found quantities of CPOM were significantly greater in young pine forest streams than in mature pine and indigenous forests. Inputs of CPOM within young pine forests were approximately 6 times greater than those from mature pine and 14 times greater than those from indigenous forest. We also observed significant amounts of slash retained in young pine streams following forest harvesting. Slash, in
particular wood, leaves and pine needles are known to contribute to benthic and
drifting CPOM for a number of years following harvesting (Collier & Bowman 2003;
Collier & Smith 2003). We also observed that much CPOM originated not from
young pine seedlings, but from native and exotic scrubs including bracken, gorse,
broom and blackberry within riparian areas, which provided leaves, dead flower heads
and seedpods.

Similarly, Wipfli & Musslewhite (2004) found that red alder, which
commonly regenerates following soil disturbance such as forest harvesting,
contributed significantly more detritus to headwater streams within young growth,
conifer forests in southeastern Alaska, than those lacking riparian alder. Piccolo &
Wipfli (2002) go on to suggest maintaining alder vegetation in previously harvested
stands, while significantly increasing numbers and biomass exports of
macroinvertebrates (terrestrial and aquatic) compared to young-growth conifer
streams, may also offset other potentially negative effects of harvesting (such as
sedimentation and loss of coarse woody debris) on downstream food webs.

In New Zealand, terrestrial invertebrates are an important food source for
native fishes, particularly adult banded kokopu and shortjawed kokopu, as well as
introduced trout, highlighting the importance of maintaining terrestrial inputs in order
to support stream food webs (Edwards & Huryn 1995; McDowall et al. 1996; West et
al. 2005). Edwards & Huryn (1996) found that taxonomic richness of terrestrial
invertebrates did not differ between land-use types. Although, they found in pasture
and tussock grassland streams, Hemiptera and Diptera together comprised 55% and
59% of biomass, while in forest streams Lepidoptera comprised 46% of total biomass
of terrestrial invertebrates. In our study, Hemiptera, Diptera and Collembola were
common among all three forest types, as well as Acari and Arachnida in mature and
indigenous forest, and Diplopoda and Thysanoptera in young pine forests.
Similar to findings of Allan et al. (2003) who found no significant difference in terrestrial invertebrate biomass ingested by juvenile coho salmon (*Oncorhynchus kisutch*) between streams in deciduous alder and coniferous forests, or young and old growth forests, terrestrial invertebrate inputs from young pine in our study streams were comparable to those in mature pine and indigenous forest streams. Although mature pine had significantly greater densities of terrestrial invertebrates than indigenous forested streams, this was due to large numbers of Collembola which accounted for more than 75% of terrestrial invertebrates. Similarly, Edwards & Huryn (1996) reported no significant difference between terrestrial invertebrate abundance contributed from pasture, tussock and native forest streams. However, in other studies which compared invertebrate biomass (which we did not measure), differences between vegetation types have been found (Mason & Macdonald 1982; Edwards & Huryn 1996; Kawaguchi & Nakano 2001). Furthermore, in a study investigating the diet of *Galaxias olidus* in the Seven Creeks river system in Australia, Cadwallader et al. (1980) found terrestrial invertebrates were much less common in the diet of fish from streams with little overhanging riparian vegetation, suggesting the extent to which riparian vegetation overhangs streams may influence the amount of terrestrial invertebrate inputs.

Wipfli (1997) also compared terrestrial invertebrate inputs to streams with riparian habitats of either old-growth conifer or young-growth red alder in southeastern Alaska and found no significant difference between them. Like bracken, gorse and broom, red alder is a relatively short-lived, shade-intolerant pioneer species with rapid juvenile growth and prolific seed production, and is typically confined to riparian areas. Red alder is an early successional species favoured by disturbance, and like the native and scrub species in our study, often increase in abundance after logging (Newton & Cole 1994). Wipfli (1997) and Wipfli & Musslewhite (2004) suggested that headwater streams with more riparian alder and denser, diverse shrub
understoreys may provide more terrestrial invertebrates and thus support more
downstream fish biomass. Downstream food webs in New Zealand stream networks
may similarly rely on subsidies of terrestrial invertebrates exported from headwater
streams.

Moreover, terrestrial invertebrates may be more important to stream predators
in pine forests as benthic taxonomic richness and abundance is frequently lower than
in indigenous forest streams as shown by our study and the findings of others
(Harding & Winterbourn 1995; Townsend et al. 1997; Fuchs et al. 2003; Quinn et al.
2004). While benthic community composition was similar between forest types,
densities and richness of EPT taxa were lowest in young pine forest streams. England
& Rosemond (2004) assessed the impacts of deforestation on the energy base of
headwater food webs in the Upper Chattahoochee, U.S.A., by measuring the
deendence of crayfish and insectivorous fish on terrestrial versus aquatic food. They
found consumption of CPOM decreased with reductions in canopy cover and
suggested relatively low levels of riparian deforestation along headwater streams can
lead to marked reductions in stream food web dependence on terrestrial subsidies.
Hence, we might expect stream predators to shift their dependence to aquatic prey,
which if also reduced by forestry activities, could have negative impacts on
populations of predatory species.

The understorey in pine plantations can contribute more shade to streams than
the pines themselves and damage to this understorey (e.g. from harvesting) can
markedly increase light, effecting stream ecosystems (Davies-Colley & Quinn 1998).
Riparian vegetation comprised of early successional species can promote more
productive understorey vegetation, encouraging the growth of species which are
otherwise difficult to maintain in conifer forests. These may have the added benefit
of supporting greater aquatic invertebrate densities and diversity with reciprocal
effects on terrestrial invertebrate production and stream bank stability (Hernandez et
al. 2005; Hanley et al. 2006). Forest management often involves regular spraying of invasive plant species, particularly “nuisance” native and exotic scrub species. The spraying usually occurs prior to planting pine seedlings and during the first few years following planting to prevent competition with the establishing pine seedlings. Barton & Davies (1993) suggested spraying requires intact riparian buffers with widths of at least 30 m, to reduce atrazine concentrations within streams to levels unlikely to harm in-stream biota. Furthermore, they recommend widths of at least 50 m to minimise mortality of stream invertebrates from pyrethroid spraying. Moreover, Barton & Davies (1993) suggest buffer width, rather than vegetative composition and quality, may be more important to ensure adequate protection of stream communities from spraying. The potential benefits to stream ecosystems from native and exotic scrub within riparian areas suggest care should be taken when spraying to prevent reducing the integrity of riparian buffers.

As well as terrestrial subsidies of leaf litter and invertebrates, other factors including algal biomass, channel instability and stream temperatures also seemed to have influenced benthic stream communities in this study. Levels of chlorophyll $a$ and biofilm biomass tended to be higher within pine forested streams in which grazers such as Potamopyrgus and Helicopsyche were dominant, whereas, richness and abundance of sensitive EPT taxa were significantly greater within indigenous forested streams. The response of these taxa to more stable stream channels and cooler temperatures is consistent with the findings of other workers in New Zealand (Harding & Winterbourn 1995; Quinn et al. 1997; Scarsbrook & Halliday 1999).

To investigate how benthic communities may be influenced by terrestrial subsidies from differing riparian vegetation, we excluded inputs of leaf litter, FPOM and terrestrial invertebrates to streams within young pine forests. Results showed that the exclusion tunnels significantly reduced CPOM inputs by approximately 75%, and reduced FPOM and terrestrial invertebrates, but not significantly. Despite a degree of
resource limitation, benthic invertebrate communities showed little response in terms of community composition or abundance during the 6 months of this exclusion, although, densities of benthic and drift invertebrates were slightly higher within exclusion reaches compared with upstream controls. This limited response may be attributed to slightly higher levels of chlorophyll a in reaches beneath exclusion tunnels, although once more this difference was not significant. Certain taxa appeared to be more abundant in upstream control reaches, such as the net spinning caddisfly *Polyplectropus*, while others including the algal-piercing caddis *Oxyethira* and gastropod snail *Potamopyrgus* were more prominent in exclusion reaches. Increasing the number of experimental treatments and extending the exclusion experiment over a year to encompass the full life cycle of most aquatic invertebrates, may have yielded a greater response from the benthic community. Furthermore, many aquatic invertebrates within New Zealand streams are relative generalists in habitat and feeding so sizeable changes in energy resources may be needed to elicit a definitive response.

Gomi et al. (2006) suggested that early successional vegetation within riparian areas of young-growth forests may benefit wood and detrital production, and enhance the biological recovery of disturbed headwater streams following forest harvesting. In contrast, streams with no riparian vegetation, including those in pasture grasslands and adjacent to urban development, have been found to have fewer terrestrial invertebrate inputs compared to indigenous and exotic forest streams, as well as those within native tussock grasslands (Edwards & Huryn 1996; Kawaguchi & Nakano 2001; Romanuk & Levings 2003). These findings and ours highlight the importance of maintaining adequate buffers along streams within pine forests to enhance riparian vegetation and composition. Our results show, while inputs of leaf litter can vary significantly between young and mature production pine forests, the contribution of leaf litter from early successional, native and exotic scrub species such as, bracken,
gorse, broom and blackberry, which are often prolific within the riparian areas of the young pine forests, may maintain important energy subsidies of leaf litter and terrestrial invertebrates following forest harvesting.
REFERENCES


FIGURE CAPTIONS

Figure 1. The exclusion tunnels replicated in three young (1-2 years old) pine forest streams.

Figure 2. Mean (±1SE) values of (a) FPOM, (b) Surber CPOM, (c) pitfall CPOM, (d) drifting CPOM, (e) invertebrate pitfall density, (f) drifting invertebrate density, (g) chlorophyll a, and (h) biofilm for streams within young pine, mature pine and indigenous forest. Superscript letters indicate significant differences resulting from post-hoc Holm-Sidak tests (n=3, P<0.05).

Figure 3. Benthic community composition of streams within young pine, mature pine and indigenous forests. Communities are grouped into the six most common insect orders and others.

Figure 4. Mean (±1SE) values of (a) benthic invertebrate density, (b) benthic taxonomic richness, (c) MCI, (d) QMCI, (e) EPT taxa richness, (f) % EPT, (g) drifting invertebrate density, and (h) drifting invertebrate taxonomic richness for streams within young pine, mature pine and indigenous forest. Superscript letters indicate significant differences resulting from post-hoc Holm-Sidak tests (n=3, P<0.05).

Figure 5. Mean (±1SE) values of (a) FPOM, (b) Surber CPOM, (c) pitfall CPOM, (d) drifting CPOM, (e) terrestrial invertebrate pitfall density, (f) drifting invertebrate density, (g) chlorophyll a, and (h) biofilm for exclusion tunnel and upstream control reaches within young pine forest. Superscript letters indicate significant differences resulting from post-hoc Holm-Sidak tests (n=3, P<0.05).

Figure 6. Benthic community composition for exclusion tunnel and upstream control reaches within young pine forest. Communities are grouped into the six most common insect orders and others.
Figure 7. Mean ($\pm$1SE) values of (a) benthic invertebrate density, (b) benthic taxonomic richness, (c) MCI, (d) QMCI, (e) EPT taxonomic richness, (f) % EPT taxa, (g) drifting invertebrate density, and (h) drifting invertebrate taxonomic richness for exclusion tunnel and upstream control reaches within young pine forest. Superscript letters indicate significant differences resulting from post-hoc Holm-Sidak tests ($n=3$, $P<0.05$).
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.
Table 1. Physico-chemical attributes of streams within young pine, mature pine and indigenous forest. Channel instability is the Pfankuch score (1975), DS=deposited sediment, SS=suspended sediment. (*) indicates a significant difference among the three stream types (P<0.05).

<table>
<thead>
<tr>
<th>Physical</th>
<th>Young mean</th>
<th>SE</th>
<th>Mature mean</th>
<th>SE</th>
<th>Indigenous mean</th>
<th>SE</th>
<th>One-way ANOVA F stat</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Width (m)</td>
<td>0.59</td>
<td>0.10</td>
<td>0.67</td>
<td>0.06</td>
<td>1.01</td>
<td>0.17</td>
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<td>Depth (m)</td>
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<td>0.007</td>
<td>0.05</td>
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<td>0.09</td>
<td>0.012</td>
<td>8.115</td>
<td>0.02*</td>
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<td>Velocity (m/s)</td>
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<td>0.36</td>
<td>0.08</td>
<td>0.48</td>
<td>0.01</td>
<td>6.621</td>
<td>0.03*</td>
</tr>
<tr>
<td>Discharge (m³/s)</td>
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<td>0.20</td>
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<td>0.68</td>
<td>10.252</td>
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<td>4.05</td>
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<td>0.10</td>
<td>5.876</td>
<td>0.04*</td>
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<td>93</td>
<td>5.46</td>
<td>56</td>
<td>3.61</td>
<td>7.819</td>
<td>0.02*</td>
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<td>DS (mg/cm²)</td>
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<td>0.85</td>
<td>5.79</td>
<td>0.72</td>
<td>2.26</td>
<td>0.48</td>
<td>3.762</td>
<td>0.09</td>
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<td>SS (mg/m³)</td>
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<td>87.3</td>
<td>162.4</td>
<td>61.2</td>
<td>27.4</td>
<td>10.7</td>
<td>1.79</td>
<td>0.25</td>
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</table>

Chemical

<table>
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<th>Mature mean</th>
<th>SE</th>
<th>Indigenous mean</th>
<th>SE</th>
<th>One-way ANOVA F stat</th>
<th>P value</th>
</tr>
</thead>
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<td>pH</td>
<td>7.3</td>
<td>0.1</td>
<td>7.8</td>
<td>0.2</td>
<td>7.9</td>
<td>0.1</td>
<td>6.901</td>
<td>0.03*</td>
</tr>
<tr>
<td>Conductivity (µS/cm⁻¹)</td>
<td>130.6</td>
<td>11.7</td>
<td>74.8</td>
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<td>155.9</td>
<td>14.6</td>
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<td>0.03*</td>
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<tr>
<td>DO (mg/l)</td>
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<td>0.2</td>
<td>10.3</td>
<td>0.1</td>
<td>11.4</td>
<td>0.2</td>
<td>8.113</td>
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<td>Temperature (°C)</td>
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<td>8.4</td>
<td>0.2</td>
<td>6.3</td>
<td>0.2</td>
<td>17.973</td>
<td>0.00*</td>
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Table 2. Proportions of terrestrial invertebrate higher taxa collected from pitfall traps (in ranked order, highest to lowest) within young pine, mature pine and indigenous forest riparian areas.

<table>
<thead>
<tr>
<th>% Young</th>
<th>% Mature</th>
<th>% Indigenous</th>
</tr>
</thead>
<tbody>
<tr>
<td>17.9 Hemiptera</td>
<td>75.8 Collembola</td>
<td>28.0 Collembola</td>
</tr>
<tr>
<td>17.4 Collembola</td>
<td>6.9 Acari</td>
<td>13.6 Acari</td>
</tr>
<tr>
<td>16.2 Diplopoda</td>
<td>3.2 Diptera</td>
<td>13.3 Protura</td>
</tr>
<tr>
<td>13.7 Thysanoptera</td>
<td>2.5 Hemiptera</td>
<td>10.6 Diptera</td>
</tr>
<tr>
<td>12.0 Diptera</td>
<td>2.3 Arachnida: Araneae</td>
<td>6.4 Arachnida: Araneae</td>
</tr>
<tr>
<td>5.6 Acari</td>
<td>2.2 Diplopoda</td>
<td>5.5 Hemiptera</td>
</tr>
<tr>
<td>5.6 Arachnida: Araneae</td>
<td>1.2 Hymenoptera</td>
<td>4.7 Hymenoptera</td>
</tr>
<tr>
<td>4.1 Protura</td>
<td>1.2 Oligochaeta</td>
<td>4.6 Amphipoda</td>
</tr>
<tr>
<td>1.7 Hymenoptera</td>
<td>0.7 Amphipoda</td>
<td>3.1 Oligochaeta</td>
</tr>
<tr>
<td>1.4 Amphipoda</td>
<td>0.7 Coleoptera</td>
<td>2.1 Nematomorpha</td>
</tr>
<tr>
<td>1.1 Oligochaeta</td>
<td>0.7 Lepidoptera</td>
<td>1.7 Ensetera</td>
</tr>
<tr>
<td>1.0 Coleoptera</td>
<td>0.6 Protura</td>
<td>1.7 Thysanoptera</td>
</tr>
<tr>
<td>1.1 Lepidoptera</td>
<td>0.5 Nematomorpha</td>
<td>1.4 Coleoptera</td>
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<tr>
<td>0.9 Nematomorpha</td>
<td>0.3 Mollusca</td>
<td>1.4 Lepidoptera</td>
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<td>0.1 Trichoptera</td>
<td>0.3 Pseudoscorpioidae</td>
<td>0.9 Mollusca</td>
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<td>0.2 Ensetera</td>
<td>0.2 Thysanoptera</td>
<td>0.2 Blattodea</td>
</tr>
<tr>
<td>0.2 Plecoptera</td>
<td>0.2 Blattodea</td>
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</table>

Table 3. Proportions of the ten dominant benthic taxa (in ranked order, highest to lowest) within young pine, mature pine and indigenous forest streams.

<table>
<thead>
<tr>
<th>% Young</th>
<th>% Mature</th>
<th>% Indigenous</th>
</tr>
</thead>
<tbody>
<tr>
<td>35 Deleatidium</td>
<td>18 Deleatidium</td>
<td>19 Deleatidium</td>
</tr>
<tr>
<td>17 Orthocladiinae</td>
<td>9 Orthocladiinae</td>
<td>13 Elmidae</td>
</tr>
<tr>
<td>8 Polyplectropus</td>
<td>9 Potamopyrgus</td>
<td>13 Orthocladiinae</td>
</tr>
<tr>
<td>5 Oligochaeta</td>
<td>7 Austroperla</td>
<td>10 Olinga</td>
</tr>
<tr>
<td>4 Tricladida</td>
<td>7 Tricladida</td>
<td>9 Chironominae</td>
</tr>
<tr>
<td>4 Hydraenidae</td>
<td>5 Zelandobius</td>
<td>3 Zelandobius</td>
</tr>
<tr>
<td>3 Helicopsyche</td>
<td>5 Stenoperla</td>
<td>3 Stenoperla</td>
</tr>
<tr>
<td>2 Austrostigmum</td>
<td>4 Hydraenidae</td>
<td>2 Philorheithrus</td>
</tr>
<tr>
<td>2 Potamopyrgus</td>
<td>4 Chironominae</td>
<td>2 Empididae</td>
</tr>
<tr>
<td>2 Psilocheirema</td>
<td>4 Tanypodinae</td>
<td>2 Hydraenidae</td>
</tr>
</tbody>
</table>
Table 4. Physico-chemical attributes biofilm for exclusion tunnel and upstream control reaches within young pine forest streams. Channel instability is the Pfankuch score (1975), DS—deposited sediment, SS—suspended sediment. (*) indicates a significant difference (P<0.05).

| Physical | Exclusion | | | Upstream | | | One-way ANOVA | | |
|----------|-----------|---|---|-----------|---|---|----------------|---|
| Width (m) | 0.59 | 0.095 | 0.59 | 0.098 | 0.001 | 0.98 |
| Depth (m) | 0.04 | 0.002 | 0.04 | 0.007 | 0.000 | 1.00 |
| Velocity (m/s) | 0.21 | 0.048 | 0.21 | 0.044 | 0.001 | 0.97 |
| Discharge (m³/s) | 0.17 | 0.03 | 0.14 | 0.02 | 0.686 | 0.45 |
| Substrate Index | 4.21 | 0.22 | 4.21 | 0.22 | 0.000 | 1.00 |
| Channel instability | 92 | 11.4 | 92 | 11.4 | 0.000 | 1.00 |
| DS (mg/cm²) | 3.73 | 0.44 | 3.75 | 0.85 | 0.001 | 0.98 |
| SS (mg/m³) | 164.8 | 80.6 | 177.8 | 87.3 | 0.012 | 0.92 |

Chemical

| pH | 7.4 | 0.2 | 7.3 | 0.1 | 0.486 | 0.52 |
| Conductivity (µS/cm⁻¹) | 129.6 | 10.3 | 130.6 | 11.7 | 0.004 | 0.95 |
| DO (mg/l) | 11.2 | 0.4 | 10.5 | 0.2 | 3.250 | 0.15 |
| Temperature (°C) | 8.7 | 0.4 | 8.5 | 0.4 | 0.233 | 0.66 |
| Light intensity (Lux) | 4280 | 135.6 | 10270 | 333.4 | 83.25 | 0.00* |
| Air temperature (°C) | 10.0 | 0.07 | 10.3 | 0.08 | 1.408 | 0.24 |

Table 5. Proportions of the most dominant benthic taxa (in ranked order, highest to lowest) for exclusion tunnel and upstream control reaches of young pine forest streams.

<table>
<thead>
<tr>
<th>%</th>
<th>Exclusion</th>
<th></th>
<th></th>
<th>%</th>
<th>Upstream</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>37</td>
<td>Deleatidium</td>
<td>35</td>
<td>Deleatidium</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>Potamopyrgus</td>
<td>17</td>
<td>Orthocladiinae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>Orthocladiinae</td>
<td>8</td>
<td>Polyplectropus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Oligochaeta</td>
<td>5</td>
<td>Oligochaeta</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Tricladida</td>
<td>4</td>
<td>Tricladida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Psilochorema</td>
<td>4</td>
<td>Hydraenidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Austrosimulium</td>
<td>3</td>
<td>Helicopsycha</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Hydraenidae</td>
<td>2</td>
<td>Austrosimulium</td>
<td></td>
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</tr>
<tr>
<td>2</td>
<td>Oxyethira</td>
<td>2</td>
<td>Potamopyrgus</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Tanypodinae</td>
<td>2</td>
<td>Psilochorema</td>
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</tbody>
</table>
CONCLUDING REMARKS

In 1991, the New Zealand Government developed and implemented the Resource Management Act which requires forestry companies ensure mitigation of any adverse effects of forestry activities on stream communities. One result of this is that forest managers are increasingly seeking advice and guidance from scientists to assist them in designing and applying best management practices. Increased competition from overseas has also encouraged many New Zealand forestry companies to improve their environmental management. Proof of good environmental practices is becoming an important component of forestry marketing, and schemes such as the Forest Stewardship Council (FSC) certification are gaining popularity. FSC audits include promoting sustainable forest management, sound riparian practices and monitoring the health of streams within plantation forests. Maintaining riparian buffers within pine plantations is widely accepted as an essential management tool for mitigating the impacts of forestry operations on stream ecosystems (Gilliam et al. 1992; Davies & Nelson 1994; Quinn et al. 2004). Considerable research is still being done to determine what aspects of riparian buffers are important to ensure their efficacy. The aims of this thesis were to improve our understanding of some of these issues.

Initially I combined a field survey of benthic invertebrates and GIS generated vegetative data over a range of spatial scales, to determine optimal buffer dimensions. My results revealed benthic communities strongly respond to vegetation within riparian buffers of 5-10 m widths and which extend 600 m upstream. In practice, this suggests that continuous lengths of riparian forest at the reach scale are very important in effecting benthic communities of small, headwater streams. Similar suggestions have been made by Quinn et al. (2004) who found streams with continuous buffers did not differ in biometrics from those in intact native or mature plantation forest. Additionally my
results showed the importance of maintaining or enhancing indigenous riparian vegetation, particularly for reducing the effects of pine age (specifically time since last harvested) and improving benthic taxonomic richness and diversity.

The second component of this thesis examined how vegetative composition over a range of spatial scales influenced stream ecosystems, concentrating on geomorphology and water chemistry. My results support the concept that where indigenous vegetation is absent, riparian buffers of greater widths may be more important to provide adequate protection from forestry operations. Moreover, maintaining wider riparian areas may encourage natural regeneration leading to more diverse plant communities, which are likely to improve the protective capacity of buffers. Many of the smallest streams in this study lacked adequate riparian buffers and instead pine trees were often planted close to the channel edge. Other researchers have reported similar findings and suggest despite their size, small streams are a fundamental part of river networks and it is important they are not overlooked by forest management (Moore & Richardson 2003; Price et al. 2003).

The final part of this thesis compared terrestrial-aquatic linkages within forests of different age and riparian composition. Indigenous forest stream communities have frequently been reported to have greater diversity than those within pine forests, similar findings are apparent in this study (Harding & Winterbourn 1995; Quinn et al. 1997; Searsbrook & Halliday 1999). Surprisingly, I found contributions of terrestrial inputs of detritus and invertebrates from indigenous forest were comparable to those in young and mature forests. Inputs provided by riparian vegetation of early successional native and exotic scrub species within young pine forests appeared to adequately maintain energy subsidies. In effect, the rapid growth of these scrub plants in riparian areas may speed recovery of stream ecosystems following forest harvesting. Thus, where streams lack indigenous riparian vegetation it seems imperative forest managers take steps to ensure
the boundaries of riparian buffers are carefully maintained during spraying, planting and harvesting. Several key findings might be of particular relevance to forest managers;

1. Riparian buffer widths of 5-10 m and continuous lengths of at least 600 m are very important for small streams ~0.3-1.5 m wide.

2. Wider buffers (>10 m) are needed along streams where indigenous vegetation is absent to encourage the establishment of successional plants as well as regeneration.

3. It is important to maintain the integrity of riparian vegetation during forestry activities, especially harvesting and spraying, regardless of composition (whether indigenous or exotic scrub plants).
ACKNOWLEDGMENTS

Over the past 18 months while I have battled my way through a sea of unknowns from field work, countless invertebrate identifications, crucial yet mind boggling and exasperating data analysis, and finally the most stressful and difficult stage for me, writing up, I have had huge support from so many people. Naturally, my main supervisor Jon Harding has been there every step of the way, never failing to help me and provide guidance, always quick with a good pep talk when needed. To him I am most sincerely thankful as I am sure I was one of his more challenging students, full of enquires and always after the best! "Why only three 50 m tunnels Jon? Can't I have more??". I am also grateful to the rest of the FERG group for their support and advice, particularly Tanya who is always so generous with her time and knowledge, and Mike Winterbourn for helping with my identifications and most importantly providing valuable feedback on my manuscripts. Thanks also to Rebecca and Ingra who were so great helping me with my field work.

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REFERENCES (From introduction and concluding remarks.)


