

Vegetation on the edge: a gradient analysis of the riparian zone, Poerua River, New Zealand

C.J. Miller

Department of Conservation, Hokitika, New Zealand

Current address: CSIRO Sustainable Ecosystems, 306 Carmody Rd, St Lucia, QLD 4067, Australia.

(E-mail: craig.miller@csiro.au)

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Abstract: Forest vegetation patterns alongside the Poerua River, south Westland, were studied to determine whether a distinct riparian community could be defined either immediately adjacent to the river, or out to the limit of overbank flooding. Ten randomly located 100 m transects were established perpendicular to the river at each of two sites. Ground cover of alluvial sediment indicated that annual overbank flooding occurred up to 20 m into the forest (the flood zone). No significant difference in vascular plant species richness was found between the flood zone and non-flood zone at either site, however a significant difference in species richness was found between sites, and this was attributed to recent disturbance at the edge of one site. Detrended correspondence analysis separated plots by site and indicated a gradient of species change from the river's edge to the ends of the transects. There were inconsistent differences in the densities and/or basal areas of trees and shrubs between sites and zones. No distinct band of vegetation was recognizable as a riparian zone alongside the Poerua River. Instead, there was evidence that edge processes had influenced vegetation patterns on a gradient away from the river, fluvial processes had eroded into, and influenced the vegetated edge, and historical disturbance events had had strong effects on vascular plant community composition. The riparian zone incorporates the whole floodplain and environmental management needs to take this into consideration.

Keywords: *Dacrycarpus dacrydioides*; disturbance; edge effect; gradient; kahikatea; kamahi; riparian vegetation; *Weinmannia racemosa*.

Introduction

Riparian areas are the focus of much management interest in New Zealand because of their potential to buffer rivers and streams from adjacent land use and their perceived conservation value (Collier *et al.*, 1995; Anon., 2000). Typically, their terrestrial conservation value is attributed to their providing significant habitat and being sites of high species richness. However, few New Zealand studies have confirmed this, and their conservation value at a management level is largely an article of faith derived from the international scientific literature. This is a reasonable assumption given that riparian areas are considered to be some of "the most diverse, dynamic, and complex bio-physical habitats on the terrestrial portion of the earth" (Naiman *et al.*, 1993) and provide many species-rich habitats (Malanson, 1993). Nevertheless, managers of New Zealand's riparian areas have expressed a lack of knowledge of riparian ecology and confusion as to the limits of riparian zones and therefore their ability to manage them (Smith, 1993).

The riparian zone is defined as the land immediately

adjacent to a river, a definition that reinforces perceptions that it is a narrow linear strip (Malanson, 1993). In ecological terms, however, the riparian zone has been defined as a three-dimensional zone of direct interaction between the terrestrial and aquatic environments, with boundaries that extend out to the limits of flooding and up to the top of the vegetation (Gregory *et al.*, 1991). Consequently, it is the lateral flow of water that defines the riparian zone (Malanson, 1993). The riparian zone may be small to non-existent in steep, headwater streams that are embedded in forest or alpine vegetation, but in mid-sized rivers it tends to be represented by a distinct band of vegetation whose width is determined by topography, the annual flood regime and long-term channel dynamics (> 50 years). Kovalchik and Chitwood (1990) also defined active and inactive riparian zones within a floodplain, with the inactive zone having been formed by past fluvial activity but no longer being subject to fluvial processes. In large rivers the whole floodplain may be an active riparian zone that is flooded, periodically, e.g. parts of the Amazon River (Gregory *et al.*, 1991; Malanson, 1993; Naiman and Décamps, 1997).

Intact riparian forests of mid-sized rivers tend to be a mosaic of species-rich plant communities, a pattern attributable to a degree of flood disturbance, heterogeneous microtopography, and access to water and fertile soils (Brinson *et al.*, 1981; Nilsson, 1991; Malanson, 1993; Naiman and Décamps, 1997; Brinson and Verhoeven, 1999; Miller, 2004). Due to the proximity and frequency of floods, vegetation on surfaces close to an active river channel are likely to be characterised by younger stands of shrubs and trees, whereas floodplains further from the active channel may contain older, less species-rich plant communities (Kovalchik and Chitwood, 1990; Gregory *et al.*, 1991; Goodwin *et al.*, 1997).

Riparian zones are also natural edges, and proximity to the edge may also be responsible for some of the observed vegetation patterns. For example, stem density and/or basal area of trees and shrubs may be higher near the edge (Ranney *et al.*, 1981; Palik and Murphy, 1990; Williams-Linera, 1990; Matlack, 1994). Edge creation through lateral river movement and occasional catastrophic flooding is an ongoing process for many rivers in intact forest (Pinay *et al.*, 1990; Gregory *et al.*, 1991; Kupfer and Malanson, 1993; Malanson, 1993) and the distribution and abundance of plant species may increase, decrease, or remain constant following edge formation, depending on their characteristics or habitat requirements (Ranney *et al.*, 1981; Chen *et al.*, 1992; MacDougal and Kellman, 1992; Matlack, 1994; Young and Mitchell, 1994; Davies-Colley *et al.*, 2000; Denyer, 2000; Gehlhausen *et al.*, 2000). An edge-canopy dominated by shrubs may also form following edge creation as plants respond to the increase in light, and eventually may buffer or even seal the edge from light and wind (Matlack and Litvaitis, 1999; Norton, 2002).

Because of extensive land clearance for agriculture, few of the species rich podocarp (Podocarpaceae) forests that once occupied New Zealand's floodplains remain, and furthermore, most floodplains have been cleared to the river's edge (McSweeney, 1982; MfE, 1997; Miller, 2002a). Therefore, opportunities to study riparian ecology in intact forests are few. However, south Westland, in New Zealand's South Island (Figure 1), still retains extensive areas of podocarp-dominated alluvial floodplains where vegetation patterns can be studied (e.g. Wardle, 1977, 1980; Duncan *et al.*, 1990; Norton and Leathwick, 1990; Miller, 2002a, 2004).

In this study I examined forest vegetation composition and abundance within the first 100 m away from the river on the Poerua River floodplain with a view to determining whether: there was a distinct riparian

plant community, either immediately adjacent to the river, or out to the limits of overbank flooding; stem density and basal area of trees, shrubs and tree ferns increased or decreased with distance from the forest edge; stem density and basal area of trees and shrubs were higher or lower within the zone of overbank flooding than outside this zone; and, the riparian zone was a gradient of change in vascular plant species composition. Lastly, implications of the findings for New Zealand's riparian managers are discussed.

Methods

Study area

The study was carried out on a post-glacial floodplain on the true left of the Poerua River (Fig. 1). The Poerua floodplain was formed in a trough created by Pleistocene glaciers and lies close to sea level. The flat topography of the floodplain (variously true left and true right) is the result of alluvial deposition following glacial retreat and subsequent erosion of the surrounding mountains. The study area lies within the Saltwater Ecological Area and is part of the Harihari Ecological District (McEwen, 1987). Recent alluvial soils occupy a belt approximately three kilometres wide alongside the true left of the Poerua River; beyond this the soils have been undisturbed by river action for thousands of years (Smith and Burrows, 1977).

The floodplain forests of South Westland were formed to a large extent following catastrophic flood and earthquake damage (Duncan, 1993; Cullen *et al.*, 2003). The Poerua forest community is dominated by *Dacrycarpus dacrydioides* (kahikatea)¹, which intergrades with, and is then replaced by *Dacrydium cupressinum* (rimu) on older soils (Norton and Leathwick, 1990). The area was not cleared for farming because of its low topographical relief and imperfect drainage.

The climate is mild and wet due to the prevailing westerly winds and proximity to the coast. Mean annual precipitation at the nearest climate station (Lower Whataroa; 8 km to the south) is 3564 mm with little seasonal variation, although the Whataroa and Poerua catchments may receive >9000 mm yr⁻¹ (Duncan, 1992). Mean annual temperature is c. 11.9 °C, with a January mean of 16.3 °C and a July mean of 6.9 °C (Norton and Leathwick, 1990).

Most West Coast rivers that arise in the Southern Alps, and are not moderated by lakes, have a high baseflow and frequent large floods (Duncan, 1992). Flow data for the medium-sized Poerua River was

¹ Nomenclature follows Parsons *et al.* 1995, except for *Lagarostrobos colensoi* (aka *Manoao colensoi* (Molloy 1995); Kelch 2002).

collected from 1981 to 1993. Mean annual flow during this time was $33.7 \text{ m}^3 \text{ s}^{-1}$ compared with $139 \text{ m}^3 \text{ s}^{-1}$ for the nearby Whataroa River (Duncan, 1992). Mean maximum flow of the Poerua River was $903.7 \text{ m}^3 \text{ s}^{-1}$ and the highest maximum flow recorded was $1114.2 \text{ m}^3 \text{ s}^{-1}$ in March 1992. The mean annual "bank-full" flood in the Poerua has a return time of 2.33 years and was exceeded five times during the twelve year recording period. Dominant floods, i.e. those with most influence on the active channel (1.5–2 year return times), occurred in eight of the twelve years.

Data collection

Two forested reaches of the Poerua River floodplain, downstream of the bridge over State Highway 6, were selected for study. These sites were designated Poerua cableway (PCW) and Poerua road end (PRE) (Fig. 1). A section of PRE began actively degrading at the start of the study, whereas a grassed island largely protected PCW. A flood runner channel ran between the forest

edge and the island. The starting points for ten transects were located randomly along a 1 km reach of the river at both sites. The transects began at the forest edge and extended 100 m into the forest at right angles to the river. Ten $10 \times 5 \text{ m}$ sample plots, with their long axes oriented parallel to the river, were established at 0, 5, 10, 15, 20, 30, 40, 50, 75 and 100 m from the river along each transect.

All vascular species (except herbs) within each plot were recorded as present or absent. Hymenophyllaceae (filmy ferns) and *Carex* sedges were recorded only as *Hymenophyllum* spp. and *Carex* spp. due to difficulties with identification. The diameters of all trees $>3 \text{ cm}$ at 1.35 m (dbh) were measured (and later converted to basal area), and tree ferns $>1 \text{ m}$ tall, were counted. The outer limit of active overbank flooding, as determined by the presence of alluvial sediment deposition, extended *c.* 20 m into the forest at both sites. Therefore, plots 1–5 (0–25 m) and 6–10 (25–100 m) were referred to as the flood zone and non-flood zone, respectively.

Data analysis

The first step in the analysis focused on forest composition and its variation along transects and between sites. Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) based on species presence-absence was used to identify the dominant floristic compositional gradients and to examine the relationship of these gradients with site, plot distance from the river, and the extent of alluvial sediment. Analysis was conducted with CANOCO (ter Braak and Šmilauer, 1998), using the default options. DCA provides an indirect ordination of the species by plot data matrix and identifies the dominant floristic compositional gradients independent of other factors. The eigenvalues in DCA indicate the amount of variation accounted for by each gradient, whereas the gradient lengths indicate the amount of species turnover along a gradient. For example, a gradient length of four is equivalent to four standard deviations (SD), meaning that species located at either end of the gradient do not co-occur in the same plots, and that no species are held in common by plots at either end of the gradient (Hill and Gauch, 1980; Jongman *et al.*, 1995).

Site differences (PCW vs PRE) were compared using a split-plot Analysis of Variance (ANOVA) implemented in SPSS (SPSS, 1999). Parameters used in comparisons were species richness, total stem density (stems ha^{-1}) and basal area (m^2), and individual density and basal area of the dominant podocarp tree *Dacrycarpus dacrydioides*, the dominant angiosperm tree *Weinmannia racemosa* (kamahi), and the angiosperm shrub *Schefflera digitata* (pate).

Mean species richness and abundance values for flood zone and non-flood zone plots were calculated for each transect. One-way ANOVA was then used to

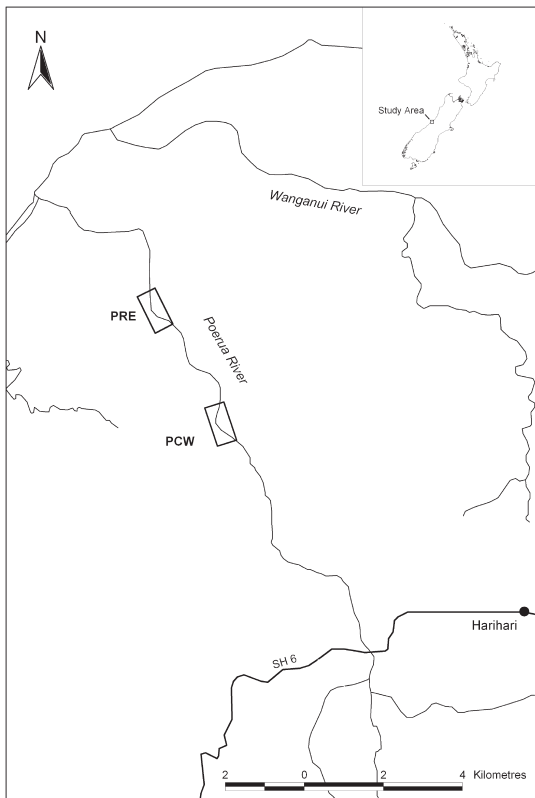


Figure 1. Location of the Poerua cableway (PCW) and Poerua road end (PRE) study sites on the Poerua River, south Westland.

test for differences in total stem density and basal area, and individual density and basal area of *Dacrycarpus dacrydioides*, *Weinmannia racemosa*, and *Schefflera digitata* between the two zones.

A reverse-Helmert contrast (or difference contrast) (SPSS, 1999) was used to identify the points of significant change ($P = 0.05$) for stem density and basal area of total species, *Dacrycarpus dacrydioides*, *Weinmannia racemosa*, and *Schefflera digitata* along the transects, from the river. This procedure is implemented through a Generalised Linear Model and compares the mean values of the plots (averaged across the 10 transects site⁻¹) at distance y against the mean of the preceding plots at distance x . The resulting P values are then used to indicate a statistically significant point of change, such as an edge effect or a distinction between riparian and non-riparian conditions.

This reverse-Helmert contrast was used because standard parametric methods cannot be used to analyse non-normal, autocorrelated, non-stationary data that are common in studies of landscape boundaries (Gosz, 1991). Various approaches have been used to circumvent such problems. For example, Norton (2002) pooled data from adjacent plots to give stability to the data and then applied a mixed model ANOVA with an autoregressive error structure (McCullagh and Nelder, 1989; Littell *et al.*, 1996), whereas Harper and MacDonald (2001) developed a 'critical values' approach that used randomisation tests to reduce the effect of spatial autocorrelation. The reverse-Helmert approach applied in this study, combined with a graph, is a conservative way to identify a point or zone of change.

Results

Species richness and composition

A total of 101 vascular plant species was recorded at the two sites, with 93 species at PCW and 87 species at PRE. Six podocarp species were recorded, five at each site. *Lagarostrobos colensoi* occurred only at the PCW site, whereas *Prumnopitys taxifolia* occurred only at the PRE

site. Thirty seven pteridophyte species were recorded, 35 at PCW and 33 at PRE. Eleven monocotyledons were recorded, nine of them at both sites. *Cordyline australis* and *Freycinetia baueriana* were found only at the PCW site, whereas *Carex* spp. and *Cortaderia richardii* were recorded only at the PRE site.

Mean species richness differed significantly between sites ($F_{1,37} = 5.078$, $P = 0.026$) and was greater at PCW where more species were recorded close to the river (Fig. 2). There was no significant difference in species richness between the flood zone and the non-flood zone at either site (PCW, $P = 0.47$; PRE, $P = 0.88$).

Ordination of plots and species

The first two axes of the DCA ordination had eigenvalues of 0.175 and 0.123, respectively, indicating they were of similar importance (Table 1). Ordination of the data separated plots on the basis of site, with PCW plots lying near the bottom of Axis 2 and PRE plots spanning the upper two thirds of Axis 2 (Fig. 3a). The plot scores were relatively evenly spread along Axis 1, although the PCW plot scores were more tightly clumped. The diagonal gradient of plots between Axes 2 and 1 was correlated weakly with the distance of plots from the river. The plots at 0 m on each transect (edge in Fig. 3a) were moderately distinct in terms of species composition and frequency of occurrence, and lie to the left of the ordination. The floristic gradient was most strongly correlated with site on Axes 1 and 2, and moderately correlated with plot distance from the river and sediment cover (Fig. 3a; Table 1).

The species ordination reflects the plot ordination (Fig. 3b). Thus, species characteristic of the forest edge, such as *Phormium tenax* and *Hebe salicifolia*, occur in the top left quadrant, whereas *Lagarostrobos colensoi* and *Phyllocladus alpinus*, which were found only 100 m from the river at PCW, lie in the bottom left quadrant. Species found only at the PRE site, such as *Leptopteris hymenophylloides*, lie on the right of the top-right quadrant, but most species common to both sites lie to the left of the right hand quadrants.

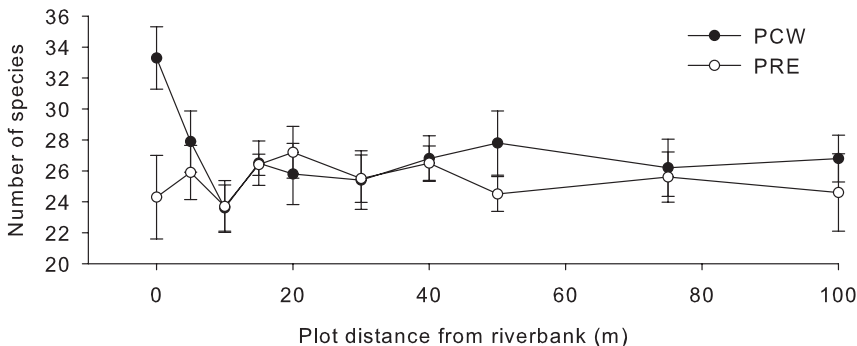


Figure 2. Mean (\pm 1SE) species richness of vascular plants in relation to distance from the riverbank at the 2 sites.

Stem density

Total stem density was significantly greater at PCW than at PRE, as were densities of *Dacrycarpus dacrydioides*, *Weinmannia racemosa* and *Schefflera digitata* (Table 2). However, significant but opposite differences in the total density of trees and shrubs were found between the flood zone and non-flood zone at both sites (PCW, $F_{1,18} = 9.29, P < 0.01$; PRE, $F_{1,18} = 4.35, P = 0.05$). Total stem density was highest in the non-flood zone at PCW, but it was highest in the flood zone at PRE (Fig. 4a). The density of *Dacrycarpus dacrydioides* was also highest in the non-flood zone at PCW, but highest in the flood zone at PRE (PCW, $F_{1,18} = 17.84, P < 0.01$; PRE, $F_{1,18} = 4.72, P < 0.05$; Fig 4b). No significant differences in stem density were observed between the two zones for *Weinmannia racemosa* at PCW, with inadequate numbers at PRE for statistical testing (Fig. 4c). The density of *Schefflera digitata* was

Table 1. Spearman rank correlation (rs) coefficients for 3 environmental variables with axes 1 and 2 of the DCA. Eigenvalues and gradient lengths (SD) for the first two axes are also shown.

	Axis 1	Axis 2
Environmental variables		
Site	0.49	0.74
Plot distance	0.18	-0.35
Sediment cover	-0.22	0.34
Eigenvalues	0.175	0.122
Gradient lengths	2.192	2.470

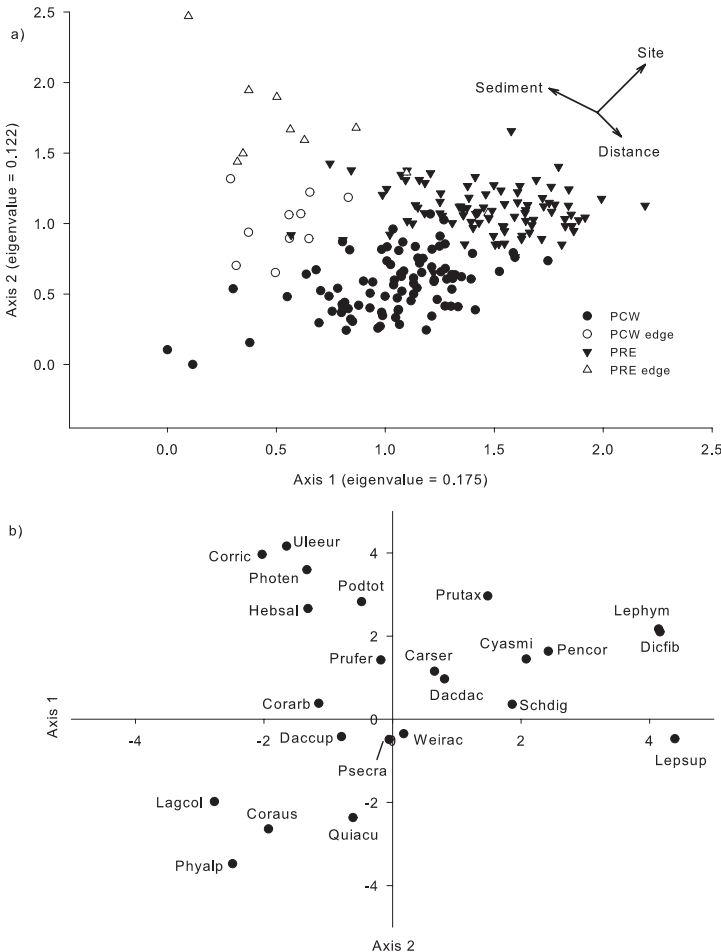


Figure 3. (a) Location of plots relative to the first 2 DCA axes. Arrows show the direction and magnitude (arrow length) of correlations with explanatory variables. Note in particular the locations of the plots at 0 m, i.e. the immediate edge plots. (b) Location of plant species relative to the first two DCA axes. Note: not all species are identified. Abbreviations: Ariser, *Aristotelia serrata*; Bleflu, *Blechnum fluviatile*; Cararb, *Carmichaelia arborea*; Corarb, *Coriaria arborea*; Corric, *Coriaria richardii*; Daccup, *Dacrydium cupressinum*; Dacdac, *Dacrycarpus dacrydioides*; Hebsal, *Hebe salicifolia*; Hohpop, *Hoheria populnea*; Lagcol, *Lagarostrobos colensoi*; Lephym, *Leptopteris hymenophylloides*; Lepsup, *L. superba*; Melram, *Melicytus ramiflorus*; Pencor, *Pennantia corymbosa*; Photen, *Phormium tenax*; Phyalp, *Phylocladus alpinus*; Podtot, *Podocarpus totara*; Quiacu, *Quintinia acutifolia*; Schdig, *Schefflera digitata*; Strhet, *Streblus heterophyllus*; Uleeur, *Ulex europaeus*; Weirac, *Weinmannia racemosa*.

significantly greater in the flood zone of PCW ($F_{1,18} = 7.68, P < 0.05$) although there was no significant difference at PRE (Fig. 4d).

The low point in total tree density at both sites (10 m, Fig. 5a) may be a riparian effect, an edge effect, or a site-age effect. Here the reverse Helmert contrast indicates that stem density in plots at 5 m was significantly greater than at 10m (PCW, $P = 0.019$; PRE, $P = 0.016$), and between plots at 75 m and 100 m at PCW ($P < 0.001$). Total stem density increased with

distance from the river, following the initial trough. *Dacrycarpus dacrydioides* followed a similar trend at PCW, although stem density at PRE did not increase following the initial decline (Fig. 5b). Changes in the density of *Weinmannia racemosa* at PCW were consistent with the trend for total tree density, and there was a significant difference between density at the 10 m plot and the 5 m plot (Fig. 5c). *Schefflera digitata* showed the opposite trend, with a peak near the edge of PCW which then declined with distance from the

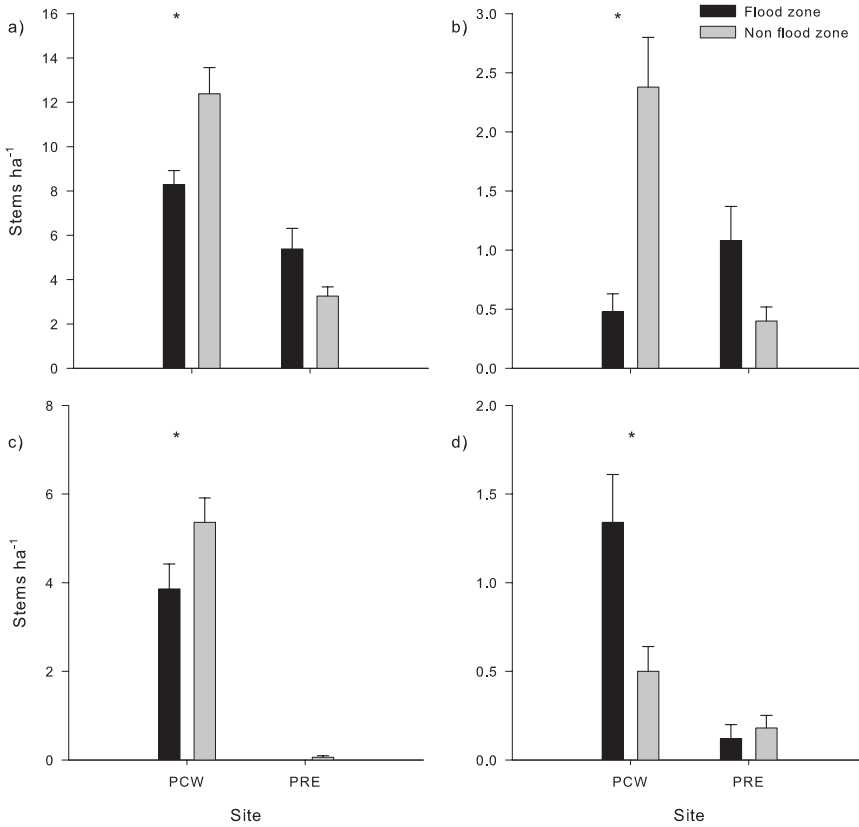


Figure 4. Mean (\pm 1SE) stem density at each site for (a) total species, (b) *Dacrycarpus dacrydioides*, (c) *Weinmannia racemosa*, and (d) *Schefflera digitata* between the flood zone and non flood zone at PCW and PRE. “*” = $P \leq 0.05$. Note different y-axis scales.

Table 2. Mean (\pm 1SE) stem density (stems ha⁻¹) and basal area (m² ha⁻¹) for all trees and shrubs and three common species at Sites PCW and PRE. Results of split-plot ANOVAs, including F and P values comparing sites are also given (d.f. = 38).

	Density				Basal area			
	PCW	PRE	F	P	PCW	PRE	F	P
All trees and shrubs	2066 \pm 126	864 \pm 92	81.99	<0.001	45 \pm 5	34 \pm 6	2.03	0.16
<i>D. dacrydioides</i>	286 \pm 41	148 \pm 28	10.43	<0.01	28 \pm 5	20 \pm 6	1.29	0.26
<i>W. racemosa</i>	922 \pm 79	6 \pm 3	182.17	<0.001	10 \pm 1	0.2 \pm 0.1	4576	<0.001
<i>S. digitata</i>	184 \pm 30	30 \pm 15	23.62	<0.001	0.3 \pm 0.1	0.05 \pm 0.02	7.68	<0.01

edge; at PRE *S. digitata* showed two small peaks, but otherwise no trend with respect to the edge (Fig. 5d).

Stem basal area

No significant difference was found between the basal area ha^{-1} of all trees at PCW and PRE (Table 2). *Dacrycarpus dacrydioides* contributed most of the basal area at both sites but, unlike stem density, there was no significant site difference. *Weinmannia racemosa* and *Schefflera digitata* had a significantly higher basal area at PCW than PRE.

The difference in total basal area of trees between the flood zone and non-flood zone was significant only at PCW, with highest basal area in the non-flood zone ($F_{1,18} = 28.18$, $P < 0.001$; Fig. 6a). Again this was due

to the dominance of *Dacrycarpus dacrydioides* ($F_{1,18} = 31.80$, $P < 0.001$; Fig. 6b). The mean basal area of *Weinmannia racemosa* and *Schefflera digitata* was significantly higher in the flood zone of PCW than in the non-flood zone ($F_{1,18} = 20.35$, $P < 0.001$; $F_{1,18} = 6.08$, $P < 0.05$, respectively; Figs. 6c, d).

The total basal area of all stems varied little with distance from the river's edge at PCW, but increased in the first 20 m and then declined, significantly at PRE (Fig. 7a) driven by the density of *Dacrycarpus dacrydioides* (Fig. 7b). The basal area of *Weinmannia racemosa* was highly variable at PCW, with a high point in the 0 m plots, although the highest density was observed in the 40 m plots (Fig 7c). The basal area of *Schefflera digitata* peaked in the 5 m plots at PCW,

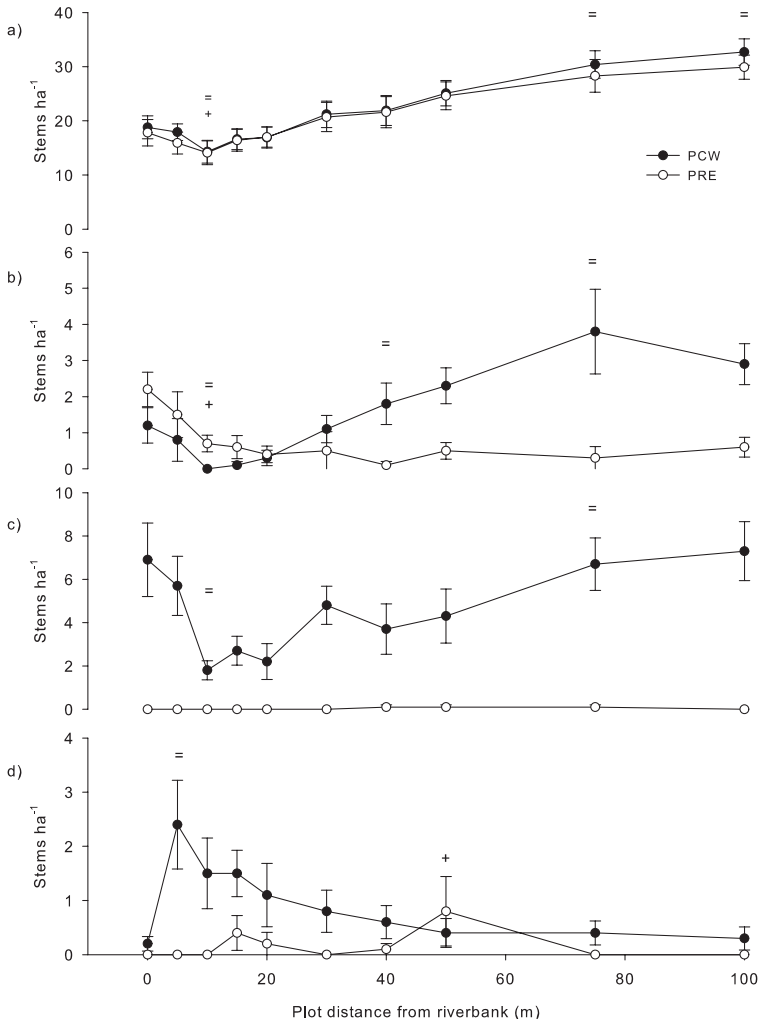


Figure 5. Mean (\pm 1SE) stem density (stems ha^{-1}) of (a) total stems, (b) *Dacrycarpus dacrydioides*, (c) *Weinmannia racemosa*, and (d) *Schefflera digitata* in relation to distance from the riverbank. “=, +” indicate that the plot mean is significantly different ($P \leq 0.05$) from the mean for the preceding plot (i.e. plot closer to the river) for PCW and PRE, respectively. Note different y-axis scales.

although this was highly variable, and subsequently leveled out at a very low level (Fig. 7d).

Discussion

Vegetation patterns

No distinct riparian plant community that could be differentiated from the conterminous vegetation was found immediately alongside the Poerua River, or out to the extent of overbank flooding. Rather, there appeared to be an edge effect, with a peak in species richness and vegetation density, followed by a gradient of change, structurally and compositionally, away from the river. The compositional and structural differences in vegetation along the transects appeared to be due to factors such as proximity to the edge, river incutting, time since establishment of canopy species, and possibly soil nutrient status. The largest differences noted were between sites, and probably reflected a history of catastrophic disturbance due to flooding or earthquakes.

Patterns associated with overbank flooding

The limit of overbank flooding at the two sites could be identified by the extent of alluvial sediment deposition, and the DCA ordination based on species presence-absence suggested a relationship between species occurrence and the extent of the flood zone. However, the relationship was one of gradual species change, rather than of distinct communities defined by the extent of flooding.

A few species were found on the riverbank that were not found elsewhere in the forest. These included *Phormium tenax* and *Cortaderia richardii*, species commonly found at the margins of rivers and swamps, and *Hebe salicifolia* and *Coriaria arborea*, species common at disturbed sites (Wardle, 1991). *Phormium tenax* and *Cortaderia richardii* typically are most abundant in the riparian zone in forested ecosystems, although they are not considered to be riparian-dependent (P. Wardle, in Collier, 1995). Introduced gorse (*Ulex europaeus*), a plant common on disturbed sites such as the floodplains of south Westland (Wardle 1980), was also present in bare sediment on the river bank. However, it was not present within the forest.

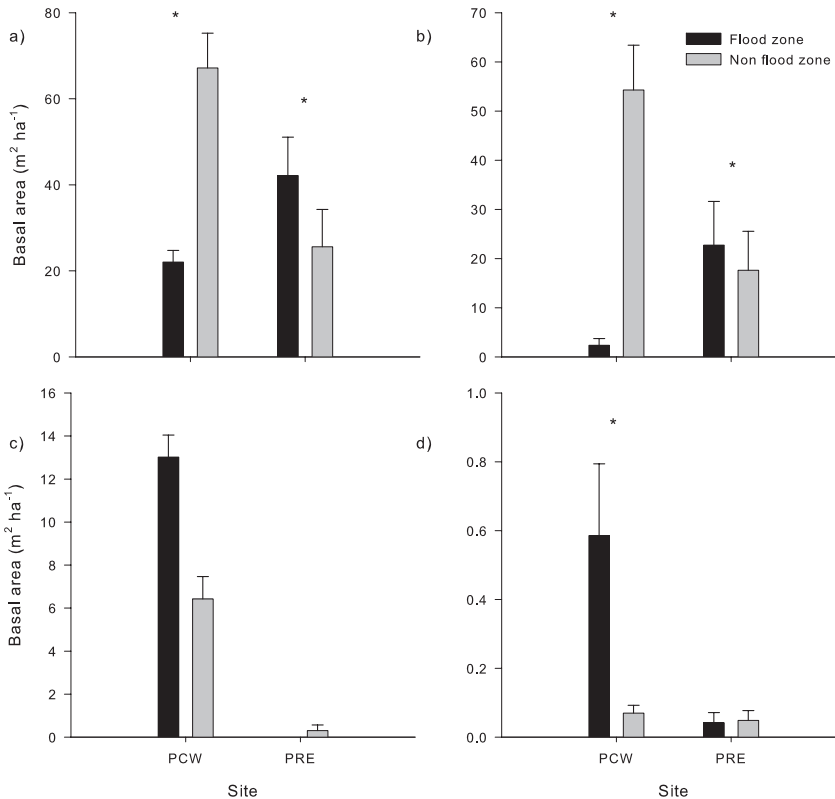


Figure 6. Mean (\pm 1SE) basal area ($m^2 ha^{-1}$) of (a) total species, (b) *Dacrycarpus dacrydioides*, (c) *Weinmanniaracemosa*, and (d) *Schefflera digitata* between the flood zone and non-flood zone at PCW and PRE. “*” = $P \leq 0.05$. Note different y-axis scales.

Species richness of vascular plants did not differ between the flood zone and non-flood zone, although the abundance of individual species changed along a gradient away from the river. However, I found no consistent general pattern or feature that stood out as an indicator of a riparian zone in its own right. For example, whereas the mean total density of trees and shrubs was higher in the non-flood zone at PCW, it was higher in the flood zone at PRE. Sapling density too was significantly greater in the non-flood zone of PCW than in the flood zone, whereas at PRE there was no significant difference in density of saplings between these two zones (Miller 2002b). There were

individual species differences too. For example, mature *Schefflera digitata* were significantly more dense in the flood zone of PCW, although their saplings were more dense in the non-flood zone of PCW (Miller 2002b). The presence of *Podocarpus totara* at PRE was the only feature that could be linked conclusively to the flood zone. *P. totara* is known to colonise the coarse free-draining sediments deposited on the river bank during overbank flooding. In contrast, they are less likely to establish on fine, poorly drained silts that are deposited further inland (Wardle, 1974; Ebbett, 1998; Miller and Wells, 2003).

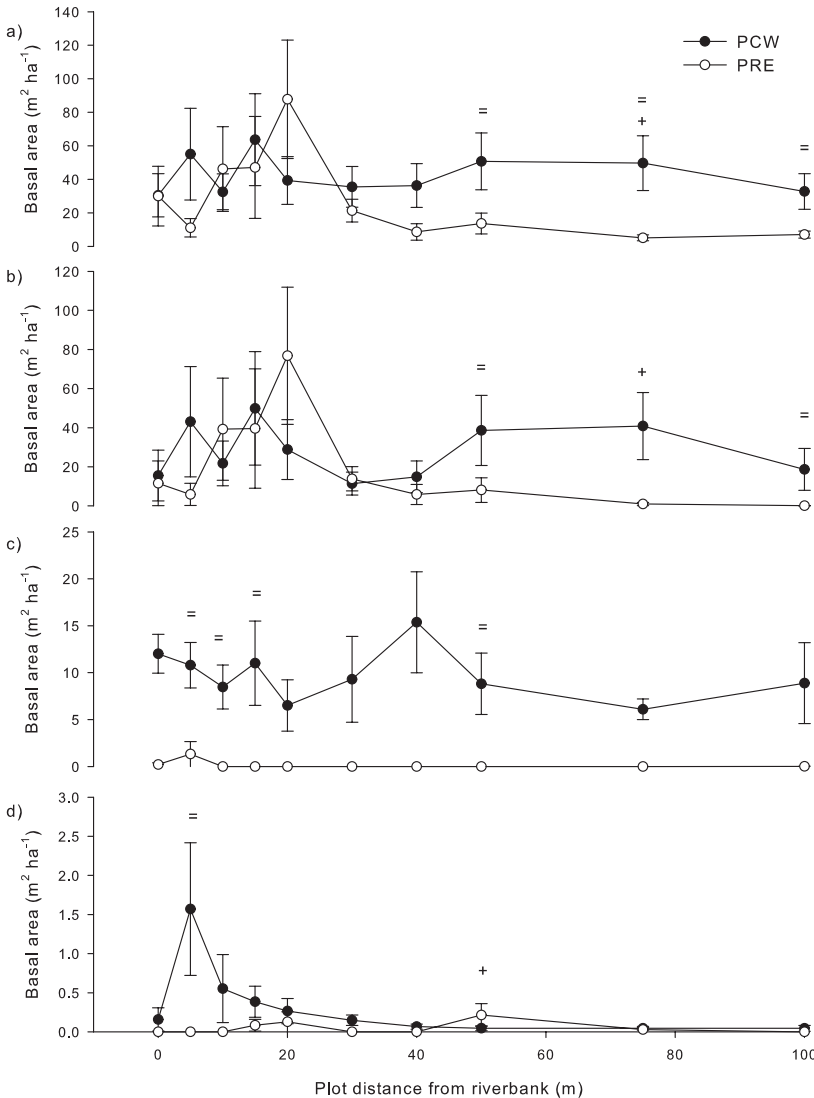


Figure 7. Mean (\pm 1SE) basal area ($m^2 ha^{-1}$) of (a) total stems, (b) *Dacrycarpus dacrydioides*, (c) *Weinmannia racemosa*, and (d) *Schefflera digitata* in relation to distance from the riverbank. “=, +” indicate that the plot mean is significantly different ($P \leq 0.05$) from the mean for the preceding plot (i.e. plot closer to the river) for PCW and PRE, respectively. Note different y-axis scales.

Although species richness of vascular plants did not differ between the flood and non-flood zones, a fertility gradient was apparent with distance from the river. For example, *Lagarostrobos colensoi* and *Phyllocladus alpinus* are common in transitions from fertile to infertile soils (Wardle, 1991), and these two species appear in the PCW plots most distant from the river. Sowden (1986) demonstrated that the nutrient status and drainability of soil decreased with time since the last flood disturbance (100s – 1000s of years), and on a gradient away from a river. Norton and Leathwick (1990) identified such a gradient on the Poerua floodplain at a larger scale than in the present study, with *Dacrycarpus dacrydioides*/*Cyathia smithii*-*Weinmannia racemosa*/*Uncinia* sp. forest and *Dacrycarpus dacrydioides*/*Coprosma* sp./*Uncinia* sp. forest close to the river, grading into *Dacrydium cupressinum*-(*Dacrycarpus dacrydioides*)/*Weinmannia racemosa*-(*Quintinia acutifolia*) forest further away. Like Sowden (1986) they attributed this gradient to edaphic properties such as nutrient status and drainage.

Whereas overbank flooding may be responsible for the presence of a distinct band of riparian zone vegetation in some water-limited environments (e.g. Kovalchik and Chitwood, 1990; Brinson *et al.*, 1981; Hupp and Osterkamp, 1996; Naiman and Décamps, 1997), this was not the case in south Westland where high rainfall combined with poor drainage has the most significant influence on species composition in forests (Duncan *et al.*, 1990; Norton and Leathwick, 1990; Miller, 2004).

Patterns associated with the river edge

New Zealand rainforests are typically shady, with canopy structure having a pronounced effect on the spatial distribution of plants (McDonald and Norton, 1992; Davies-Colley *et al.*, 2000). Consequently, elevated light levels are key drivers of floristic composition and density at the forest edge (Young and Mitchell, 1994; Davies-Colley *et al.*, 2000; Norton, 2002). A distinct forest edge of c.10 m, characterised by a peak in the density of trees and shrubs was evident in the present study, particularly at PCW. Species such as *Podocarpus totara* and *Dacrycarpus dacrydioides*, which require high light levels, and *Weinmannia racemosa* and *Schefflera digitata* that are normally found in forest canopy gaps, take advantage of the raised light levels at the forest edge (Wardle, 1991; Ebbett and Ogden, 1998). Davies-Colley *et al.* (2000) also observed a shift in species composition at a forest edge towards high light requiring pioneer species found typically in treefall gaps.

The density or frequency of occurrence of individual plant species may also increase away from a forest edge, i.e. respond negatively to the edge (Murcia, 1995). A negative response to the forest edge was noted

for a number of species on the Poerua floodplain. They included the trees *Pennantia corymbosa* and *Pseudopanax crassifolius* at the PCW site (Miller, 2002b), and the treeferns *Cyathea smithii* and *Dicksonia fibrosa* at the PRE site, despite these tree ferns being known to grow in treefall gaps and other open areas. The frequency of occurrence of ferns also tended to be lower at the edge than in plots further from the river, with species such as *Leptopteris hymenophylloides* and *Leptopteris superba* being found only in wet depressions within 15 m of the forest edge, whereas they were in more open areas further in. Davies-Colley *et al.* (2000) proposed that an increased likelihood of desiccation brought about by stronger winds restricted ferns such as *L. hymenophylloides* and *Hymenophyllum* spp. to interior rather than edge environments.

Young and Mitchell (1994), Davies-Colley *et al.* (2000) and Denyer (2000) all noted that species richness tends to be greater at the forest edge than in the interior. This was the case for the edge plots of PCW, but not for the edge plots of PRE, where mean species richness was slightly lower. This condition would appear to be due to the river at PRE cutting into the bank and creating an edge in the formerly interior (i.e. non edge) forest. A number of stems in these plots, particularly ferns, were dead, apparently due to desiccation, and were not counted. Kupfer and Malanson (1993) noted that cutbank erosion has a significant role in the creation of new forest edges in interior riparian forest, and it is likely that the small *Podocarpus totara* stand at PRE will be lost over the next few years unless the river changes course.

Changes in stem density with distance from the edge were not consistent between sites except for an initial edge effect. At PCW total stem density increased to, or beyond stem density at the edge, whereas total stem density stayed low at PRE. Increasing density away from the edge was associated with an increase in the densities of *Dacrycarpus dacrydioides* and *Weinmannia racemosa*. *Pennantia corymbosa* and *Carpodetus serratus* also contributed to this increase, although their density distribution was consistent with establishment in canopy gaps, rather than as a response to the river's dynamics or the forest edge (Miller 2002b).

Total basal area of stems also changed little from the edge to the interior at both sites, and was determined largely by the basal area of *Dacrycarpus dacrydioides*. There was no indication that basal area was necessarily lower nearer the river due to frequent disturbance (c.f. Gregory *et al.*, 1991), or higher due to increased light availability as found by Davies-Colley *et al.* (2000) in a forest edge in the Waikato region.

Patterns associated with site differences

Duncan (1991, 1993), Sowden (1986) and Cullen *et al.* (2003) demonstrated that disturbance by earthquakes

or catastrophic flooding affects the structure and composition of forests on floodplain surfaces in south Westland. This is also true of other floodplain sites throughout the world (Décamps, 1993; Naiman and Décamps, 1997; Brinson and Verhoeven, 1999). For example, the floristic composition and successional patterns of floodplain forests in the Coastal Plain Province (USA) (Hodges, 1997), western USA (Graf, 1979, 1983), and Western Australia (Pettit and Froend, 2001) are strongly influenced by past catastrophic events and the present flood regime. Graf (1979, 1983) considered that the composition and structure of western USA floodplain forest was not in a state of quasi-equilibrium with the annual flood regime, but rather they were a legacy of past catastrophic disturbances.

The dominant tree species at both my study sites on the Poerua floodplain was *Dacrycarpus dacrydioides*, a species that typically establishes after catastrophic disturbance provides large areas of exposed alluvial soils (Duncan, 1993). The site differences I observed may have been due to their different histories of catastrophic flooding, with PRE likely to have had a more recent catastrophic disturbance event and more frequent non-catastrophic flooding than PCW.

One of the most striking differences noticed between the sites was the dominance of *Weinmannia racemosa* in the canopy at PCW and its relative absence at PRE, where other species including *Carpodetus serratus* dominated. Duncan (1991, 1993) found a similar pattern in two similar aged *Dacrycarpus dacrydioides*-dominated stands and suggested that small scale disturbance events had provided *Weinmannia racemosa*, a vigorous coloniser of small gaps (Stewart and Veblen, 1982; Stewart, 1986), with the necessary raised establishment sites in only one of the stands. Species such as *Carpodetus serratus* also respond rapidly to canopy gaps, but do not require raised establishment sites (Wardle, 1977, 1979, 1991; Duncan *et al.*, 1990). This difference in canopy composition provides further, albeit circumstantial, evidence that PRE was a 'younger' site than PCW, with a history of less catastrophic flooding or disturbance.

Implications for riparian management

The term 'riparian zone' gives the impression of a linear landscape feature that is present along the length and edge of a river; a feature considered to have high conservation value (Malanson, 1993). This appears to be a typical perspective, and is manifested in New Zealand in the Resource Management Act (1991), for example, which seeks to protect the natural character of rivers and their edges as a matter of national importance. However, as seen in this study, there need not be a riparian plant community as distinct from an edge community in a floodplain forest. Other New Zealand

studies (e.g. Duncan *et al.*, 1990; Norton and Leathwick, 1990; Miller, 2004) suggest that the entire floodplain forest, as an ecosystem formed and/or maintained by fluvial processes, should be considered the riparian zone. Such a perspective is held internationally, and incorporates both older and more recent floodplain surfaces and vegetation (e.g. Goodwin *et al.*, 1997; Brinson and Verhoeven, 1999).

It follows, that the conservation value of the riparian zone lies in the entire floodplain forest, with species richness and community distinctiveness found at a landscape level rather than along the river margin *per se* (Miller, 2004). Therefore, management to protect the conservation values of a riparian zone needs to involve more than just the river's edge. An uncritical acceptance of the traditional definition of the riparian zone as a strip alongside a river is likely to lead to the loss or neglect of the values and natural character of riparian ecosystems and the species that rely on them.

Conclusion

Results of the present study suggest that the riparian zone of the Poerua River is not a simple linear strip alongside the river or even a zone extending out to the extent of overbank flooding. Rather, it supports the contention that the riparian zone for this and similar south Westland rivers is a landscape feature corresponding to the extent of the floodplain (Duncan *et al.*, 1990; Norton and Leathwick, 1990; Miller, 2004).

The creation and maintenance of a riparian community in a floodplain forest is affected by a number of factors in space and time, including the scale of flooding and river incutting, small scale disturbance events such as treefall, which create canopy gaps, and microclimatic gradients. Large-scale spatial gradients in contemporary riparian vegetation patterns along the river reflect historical factors more than recent riverine interaction, although contemporary river incutting will shape the edge community. Future studies need to account for these factors in their sampling designs. Also, it is possible that non-woody plant communities may reflect recent phenomena better than vascular plants and may provide valuable insights into recent riparian phenomena and are deserving of attention. Further research is required to evaluate this possibility and to determine the generality of the findings of the present study.

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References

- Anon. 2000. *The New Zealand biodiversity strategy: our chance to turn the tide. Whakakohukitia Te Tai Roruku Ke Te Tai Oranga*. Department of Conservation and Ministry for the Environment, Wellington, N.Z. 145 pp.
- Brinson, M.M.; Swift, B.L.; Plantico, R.C.; Barclay, J.S. 1981. Riparian ecosystems: their ecology and status. *USA Fish and Wildlife Service OBS-81/17*, Washington, U.S.A..
- Brinson, M.; Verhoeven, J. 1999. Riparian forests. In: Hunter Jr, M.L. (Editor) *Maintaining biodiversity in forest ecosystems*, pp. 265-299. Cambridge University Press, Cambridge, U.K.
- Chen, J.; Franklin, J.F.; Spies, T.A. 1992. Vegetation responses to edge environments in old-growth Douglas fir forests. *Ecological Applications* 2: 387-96.
- Collier, K.J. 1995. (unpublished) Riparian dependent plants and animals. Science and Technology Series Report. National Institute of Water and Atmospheric Research, Hamilton, N.Z.
- Collier, K.J.; Cooper, A.B.; Davies-Colley, R.J.; Rutherford, J.C.; Smith, C.M.; Williamson, R.B. 1995. *Managing riparian zones: a contribution to protecting New Zealand's rivers and streams*. Vols. 1 and 2. Department of Conservation, Wellington, New Zealand.
- Cullen, L.E.; Duncan, R.P.; Wells, A.; Stewart, G.H. 2003. Floodplain and regional scale variation in earthquake effects on forests, Westland, New Zealand. *Journal of the Royal Society of New Zealand* 33: 693-701.
- Davies-Colley, R.J.; Payne, G.W.; van Elswijk, M. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* 24: 111-122.
- Décamps, H. 1993. River margins and environmental change. *Ecological Applications* 3: 441-445.
- Denyer, K. 2000. (unpublished) Maintaining biodiversity in a production matrix: the effects of adjacent land use on indigenous forest fragments in the Waikato Region. M.Sc. thesis, University of Waikato, Hamilton, N.Z.
- Duncan, M.J. 1992. Flow regimes of New Zealand rivers. In: Mosely, M.P. (Editor) *Waters of New Zealand* pp 13-28. New Zealand Hydrological Society, Wellington, N.Z.
- Duncan, R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. *Journal of Ecology* 79: 1073-1084.
- Duncan, R.P. 1993. Flood disturbance and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand. *Journal of Ecology* 81: 403-416.
- Duncan, R.P.; Norton, D.A.; Woolmore, C.B. 1990. The lowland vegetation pattern, south Westland, New Zealand 2. Ohinemaka Forest. *New Zealand Journal of Botany* 28: 131-140.
- Ebbett, R.L. 1998. (unpublished) *The ecology of lowland totara in South Island, New Zealand. Distribution, regeneration, and future survival in a fragmented landscape*. Ph.D. thesis, University of Canterbury, Christchurch, N.Z.
- Ebbett, R.L.; Ogden, J. 1998. Comparative seedling growth of five endemic New Zealand podocarp species under different light regimes. *New Zealand Journal of Botany* 36: 189-201.
- Gehlhausen, S.M.; Schwartz, M.W.; Augsperger, C.K. 2000. Vegetation and microclimate edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147: 21-35.
- Goodwin, C.N.; Hawkins, C.P.; Kershner, J.L. 1997. Riparian restoration in the western United States: overview and perspective. *Restoration Ecology* 5: 4-14.
- Gosz, J.R. 1991. Fundamental ecological characteristics of landscape boundaries. In: Holland, M.M.; Risser, P.G.; Naiman, R.J. (Editors) *Ecotones. The role of landscape boundaries in the management and restoration of changing environments*, pp 8-30. Chapman and Hall, New York, U.S.A.
- Graf, W.L. 1979. Catastrophe theory as a model for change in fluvial systems. In: Rhodes, D.D.; Williams, G.P. (Editors) *Adjustments of the fluvial system*. pp 13-32. Kendall-Hunt, Dubuque, Iowa, U.S.A.
- Graf, W.L. 1983. The arroyo problem: paleohydrology and paleohydraulics in the short term. In: Gregory, K.J. (Editor) *Background to paleohydrology: a perspective*, pp 279-302. Wiley, New York.
- Gregory, S.V.; Swanson, F.J.; McKee, W.A.; Cummins, K.W. 1991. An ecosystem perspective of riparian zones. *BioScience* 41: 540-551.
- Harper, K.A.; Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* 82: 649-659.
- Hill, M.O.; Gauch, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.
- Hodges, J.D. 1997. Development and ecology of

- bottomland hardwood sites. *Forest Ecology and Management* 90: 117-125.
- Hupp, C.R.; Ostrerkamp, W.R. 1986. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* 14: 277-295.
- Jongman, R.H.G.; ter Braak, C.J.F.; Van Tongren, O.F.R. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge, U.K.
- Kelch, D.G. 2002. Phylogenetic assessment of the monotypic genera *Sundacarpus* and *Manoao* (Coniferales: Podocarpaceae) utilizing evidence from 18S rDNA sequences. *Australian Systematic Botany* 15: 29-35.
- Kovalchik, B.L.; Chitwood, L.A. 1990. Use of geomorphology in the classification of riparian plant associations in mountainous landscapes of central Oregon, USA. *Forest Ecology and Management* 33/34: 405-418.
- Kupfer, J.A.; Malanson, G.P. 1993. Observed and modeled directional change in riparian forest composition at a cutbank edge. *Landscape Ecology* 8: 185-199.
- Littell, R.C.; Milliken, G.A.; Stoup, W.W.; Wolfinger, R.D. (1996) *SAS system for mixed models*. SAS Institute Inc., Cary, North Carolina, U.S.A.
- MacDougal, A.; Kellman, M. 1992. The understory light regime and patterns of tree seedlings in tropical riparian forest patches. *Journal of Biogeography* 19: 667-675.
- McCullagh, P.; Nelder, J.A. 1989. *Generalised linear models*. Chapman and Hall, New York, U.S.A.
- McDonald, D.; Norton, D.A. 1992. Light environments in temperate New Zealand podocarp rainforests. *New Zealand Journal of Ecology* 16: 15-22.
- McEwen, W.M. 1987. Ecological regions and districts of New Zealand. *Publication No. 5*. New Zealand Department of Conservation, Wellington, N.Z.
- McSweeney, G.D. 1982. Matai/totara flood plain forests in South Westland. *New Zealand Journal of Ecology* 5: 121-128.
- Malanson, G.P. 1993. *Riparian landscapes*. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, U.K.
- Matlack, G.R. 1994. Vegetation dynamics of the forest edge – trends in space and successional time. *Journal of Ecology* 82: 113-123.
- Matlack, G.R.; Litvaitis, J.A. 1999. Forest edges. In: Hunter, M.L. Jr (Editor) *Maintaining biodiversity in forest ecosystems*, pp. 210-233 Cambridge University Press, Cambridge, U.K.
- MfE 1997. *The state of New Zealand's environment. 1997*. The Ministry for the Environment, Wellington, N.Z.
- Miller, C. 2002a. Conservation of riparian forest remnants, West Coast, New Zealand. *Landscape Research* 27: 125-140.
- Miller, C. 2002b. (unpublished) *Conservation ecology of riparian forest within the agricultural landscape: West Coast, New Zealand*. Ph.D, thesis, University of Canterbury, Christchurch, N.Z.
- Miller, C. 2004. Floristics and species richness of floodplain forests, south Westland, New Zealand. *New Zealand Journal of Botany* 42: 847-860.
- Miller, C.; Wells, A. 2003. Cattle grazing and the regeneration of totara (*Podocarpus totara* var *waihoensis*) on river terraces, south Westland, New Zealand. *New Zealand Journal of Ecology* 27: 37-44.
- Molloy, B.J. 1995. *Manoao* (Podocarpaceae), a new monotypic conifer genus endemic to New Zealand. *New Zealand Journal of Botany* 33: 183-201.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58-62.
- Naiman, R.J.; Décamps, H. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28: 621-658.
- Naiman, R.J.; Décamps, H.; Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3: 209-212.
- Nilsson, C. 1991. Conservation management of riparian communities. In: Hansson, L. (Editor) *Ecological principles of nature conservation*, pp. 352-372. Elsevier Science, Amsterdam, The Netherlands.
- Norton, D.A. 2002. Edge effects in a lowland temperate New Zealand rainforest. *Department of Conservation Science Internal Series* 27. 33 pp.
- Norton, D.A.; Leathwick, J.R. 1990. The lowland vegetation pattern, south Westland, New Zealand 1. Saltwater Ecological Area. *New Zealand Journal of Botany* 28: 41-51.
- Palik, B.J.; Murphy, P.G. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. *Forest Ecology and Management* 32: 187-202.
- Parsons, M.J.; Douglass, P.; Macmillan, B.H. 1995. *Current names list for wild gymnosperms, dicotyledons and monocotyledons (except grasses) in New Zealand*. Manaaki Whenua Press, Lincoln, New Zealand. 206 pp.
- Pettit, N.E.; Froend, R.H. 2001. Variability in flood disturbance and the impact on riparian tree recruitment in two contrasting river systems. *Wetland Ecology and Management* 9: 13-25.
- Pinay, G.; Decamps, H.; Chauvet, E.; Fustec, E. 1990. Functions of ecotones in fluvial systems. In: Naiman, R.J.; Decamps, H. (Editors) *The ecology and management of aquatic-terrestrial ecotones. Man and the Biosphere Series Volume 4*, pp 141-69 UNESCO, Paris & The Parthenon Publishing Group, Camforth, UK.

- Ranney, J.W.; Bruner, M.C.; Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R.L.; Sharpe, D.M. (Editors) *Forest Island Dynamics in Man-dominated Landscapes*, pp. 67-95. Springer-Verlag, New York, U.S.A.
- Smith, C.M. 1993. Perceived riverine problems in New Zealand: impediments to environmentally sound riparian zone management, and the information needs of managers. *Water Quality Centre Publication No. 24*. National Institute of Water and Atmospheric Research, Wellington, N.Z.
- Smith, K.D.; Burrows, C.J. 1977. (unpublished) *Proposed biological reserves for Saltwater Forest, South Westland*. Royal Forest and Bird Society, Wellington, N.Z.
- Sowden, J.R. 1986. (unpublished) *Plant succession and soil development, Wanganui River catchment, south Westland, New Zealand*. M.App.Sc. thesis, Lincoln College, University of Canterbury, Lincoln, N.Z.
- SPSS Inc. 1999. *SPSS Users Guide v. 10*. SPSS Inc., Chicago, USA.
- Stewart, G.H. 1986. Forest dynamics and disturbance in a beech/hardwood forest, Fiordland, New Zealand. *Vegetatio* 68: 115-126.
- Stewart, G.H.; Veblen, T.T. 1982. Regeneration patterns in southern rata (*Metrosideros umbellata*)/kamahi (*Weimannia racemosa*) forest in central Westland, New Zealand. *New Zealand Journal of Botany* 20: 55-72.
- ter Braak, C.J.F.; Šmilauer, P. 1998. *CANOCO 4.0. CANOCO reference manual and users guide to CANOCO for Windows*. Centre for Biometry, Wageningen, The Netherlands.
- Wardle, P. 1974. The kahikatea (*Dacrydium dacrydioides*) forest of South Westland. *Proceedings of the New Zealand Ecological Society* 21: 62-71.
- Wardle, P. 1977. Plant communities of Westland National Park (New Zealand) and neighbouring lowland and coastal areas. *New Zealand Journal of Botany* 15: 323-398.
- Wardle, P. 1979. Plants and landscape in Westland National Park. *National Parks Scientific Series No. 3*. Department of Lands and Survey, Wellington.
- Wardle, P. 1980. Primary succession in Westland National Park and its vicinity, New Zealand. *New Zealand Journal of Botany* 18: 221-232.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, U.K.
- Wells, A.; Stewart, G.H.; Duncan, R.P. 1998. Evidence for widespread, synchronous, disturbance-initiated forest establishment in Westland, New Zealand. *Journal of the Royal Society of New Zealand* 28: 333-345.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78: 356-373.
- Young, A.; Mitchell, N. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* 67: 63-72.

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