Hydrologic and hydraulic control of macrophyte establishment and performance in streams

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Abstract

   Macrophytes play a key role in many unshaded lotic ecosystems, but little is known of the factors controlling their presence, abundance, and composition. Macrophyte abundance, diversity, and composition were studied in 15 New Zealand streams to test the hypotheses that the presence and development of macrophytes in lotic systems is primarily controlled by the hydrologic regime (frequency of high-velocity flood events) and that the interflood spatial distribution and performance of taxa in more stable systems is strongly influenced by local hydraulic conditions (depth/velocity/sediments). Both hypotheses were supported by our results. We found that the abundance and diversity of macrophytes decreased as flood disturbance frequency increased ($r^2 = 0.52$, $P = 0.002$ for abundance; $r^2 = 0.53$, $P = 0.022$ for diversity) and that vegetation was absent in streams with more than ~13 high-flow disturbances per year. An experiment in an ecohydraulics flume identified that the main mechanism causing these effects was not stem breakage at high water velocity but probably uprooting associated with bed sediment erosion. We found that plants with high propagule production constituted a greater proportion of the vegetation in more flood disturbed streams than in stable streams, suggesting that this species trait is important for the maintenance of macrophyte communities in flood prone streams. Distinct velocity, depth, and substrate particle size habitat preferences were displayed by four common species in the study streams. None of the macrophytes showed overlapping preferences for all three habitat variables, suggesting coexisting of the species in streams by physical niche separation. These results significantly expand our understanding of the role of flow regimes in determining lotic ecosystem structure and functioning.

Macrophytes play a key role in unshaded streams by increasing physical heterogeneity, trapping fine sediments, and providing extensive habitat for periphyton, invertebrates, and fish (Biggs 1996*a*). However, macrophytes can also proliferate and severely impede water flow, degrade water quality through their effects on pH and dissolved oxygen, and degrade aesthetic/recreational values in streams (Haslam 1978; Nichols and Shaw 1986; Biggs 1996*a*). Optimal management of streams will require information to predict macrophyte abundance and diversity. At present, we cannot even answer basic questions such as why macrophytes colonize and grow successfully in some streams but not others, and once they do colonize what controls patchiness, overall biomass, and community structure. Obtaining such knowledge is very important because stream macrophytes can drive physical conditions, periphyton, benthic invertebrates, and (possibly) fish communities to quite different states compared with unvegetated channels (e.g., Burkholder 1996; Death 2000).

   Biggs (1996*a*) posited a hierarchical conceptual model of factors that may strongly influence macrophyte development in streams based on components of the flow regime. In this model, flow variability (frequency of flood events) and degree of substrate stability were put forth as the primary factors controlling colonization of unshaded streambeds by macrophytes. Infrequent high-velocity events and long periods with stable bed sediments were predicted to be necessary for significant macrophyte colonization. Once established, Biggs (1996*a*) suggested that reach-scale velocities should be an important controller of local biomass through effects on drag and dislodgement. Indeed, different macrophyte species are likely to have optimized their morphological and physiological functioning to be more competitive within specific ranges of water velocities such as occurs for periphyton, invertebrates, and fish (Stevenson 1996; Jowett 2000). This should result in specific hydraulic habitat preferences for different taxa and, thus, at reach scales, a mosaic of patches on the stream bed as a result of heterogeneous flow conditions.

   There is some empirical support for these predictions. Haslam (1978) reported that a flood 2.5 times the normal flow removed some of the dominant macrophytes (*Myriophyllum spicatum*) in a stream reach, but a flood of four times the normal flow removed half the dominant species and most of the small plants (including severely reducing stem lengths of the remaining plants). Bilby (1977) and Henry et al. (1994) also report a reduction in vegetation cover following flooding. In relation to interflood water velocity, Henriques (1987) and Chambers et al. (1991) have demonstrated negative relationships between velocity and biomass. For example, Henriques (1987) found that where mean velocities were <0.2 m s^{-1}, up to 75% of a reach was occupied by vegetation, whereas <10% of a reach was occupied where velocities were >0.9 m s^{-1}.

Table 1. Physical and chemical conditions in the 15 surveyed stream reaches.

Stream	FRE 7 (yr^{-1})	FLOW $(m^3\ s^{-1})$	WOLM (mm)	ALK $(g\ CaCO_3\ m^{-3})$	TOTP $(mg\ m^{-3})$	TOTN $(mg\ m^{-3})$	DIST (m)
Gibson	0	0.55	45.0	32.7	12.4	155.3	205
Hakataramera	2.4	3.41	22.6	30.4	5.8	135.4	68,317
Kakanui	5.2	1.90	45.0	25.6	7.9	148.4	68,056
Nenthorn	6	0.32	32.0	17.8	16.3	418.4	5,970
Selwyn	4.6	1.30	22.6	37.6	23.4	4,414.5	90,581
Shag	4	0.83	22.6	52.5	12.3	287.5	61,653
Silver	0	0.33	22.6	29.5	9.3	3,796.7	200
Spring	0	3.67	32.0	22.6	9.8	286.4	2,857
Stanton	8	0.13	32.0	123.5	7.2	128.2	15,165
Taranaki	0	0.14	32.0	34.5	12.9	1,224.1	2,299
Tokomairiro	7.7	0.42	0.0	22.5	22.2	355.2	26,299
Waihopai	7.6	1.23	22.6	26.9	37.9	2,275.4	36,157
Waikawa	5.6	2.57	32.0	22.8	21.9	636.3	23,328
Waimea	8.8	1.70	32.0	37.9	25.5	486.8	53,554
Waipahi	4.6	3.15	45	32.3	32.0	351.5	46,468

Our goal was to test and provide empirical quantification of the hydraulic habitat conceptual model defined by Biggs (1996*a*). Specifically, our objectives were to (a) identify the relationships between flood disturbance frequency and summer peak macrophyte biomass and species diversity to establish the degree of hydrological stability required to enable colonization and growth of macrophytes in streams; (b) investigate the importance of stem fragility as a disturbance resistance trait in macrophytes and relate the proportion of plants on reaches possessing this and two other disturbance-resistant/resilience traits to flood frequency; and (c) determine the relationships between interflood maximum biomass and the hydraulic characteristics of hydrologically stable streams, including attempting to define hydraulic habitat preferences for common species in our field surveys.

We completed detailed surveys of macrophyte cover/volume in 15 streams covering a gradient in flood disturbance frequency and conducted an experiment on stem fragility in seven macrophyte taxa common to New Zealand streams.

Methods

Field measurements—We surveyed reach-scale (50 m) vegetation and physical conditions in 15 streams on the South Island of New Zealand (Table 1). Flow was monitored at all sites for 3 to 6 yr prior to the survey. No weed cutting took place at the sites, and no major shading was present to influence macrophyte growth. In each reach, plant species cover was recorded for at least 150 quadrats (25 × 25 cm). The quadrats were placed side by side from one bank to the other in transects evenly distributed along the reach. The number of transects varied from 3 to 15 depending on the width of the stream.

For each quadrat, plant species coverage and biomass volume under the mean plant height was assessed by a modified Braun-Blanquet (1932) scale: <5%, 5%–25%, 25%–50%, 50%–75%, >75%. The percentage vegetation cover (COVER) and volume (VOLUM) at each reach were calculated from the proportion between the total recorded vegetation cover and volume and the total possible vegetation cover and volume in all quadrats. The total cover was calculated by assuming 100% cover, and total volume by assuming total volume of the water body in each quadrat. Only quadrats present in the middle 80% of the channels were included because the area near the bank was often influenced by local riparian vegetation and was less susceptible to flood effects because near-bank water depth was low.

Median flows in the reaches were obtained from daily flow records 3–6 yr prior to the survey (FLOW). We determined the median size of the bed sediment not covered with vegetation (intermacrophyte area) for each reach using the Wolman (1954) method (WOLM). The cover of the dominant substrate types (>30% area cover) was also recorded in each quadrat. Substrate was characterized into the following classes: boulders (>250 mm), stones (60–250 mm), gravel (10–60 mm), small gravel (3–10 mm), sand (0.25–3 mm), and silt (<0.25 mm). The distance from the survey reach to the headwaters (DIST) was determined using GIS (Geographic Information System). This variable was included to assess the relative probability of a species being present upstream of the reach and thereby a relative measure of the potential extent of the upstream species pool.

Water samples were collected on the sampling day for analysis of total P (TOTP), total N (TOTN) (Gibbs and Pickmere 1987; Downes 1988), and alkalinity (ALK; potentiometric end-point titration with 0.2N HCL on 200-ml samples of stream water) in the laboratory. Physical and chemical conditions in the 15 stream reaches are shown in Table 1.

Disturbance measurement—Disturbance in the stream reaches was measured as the frequency of high-flow events. This was calculated as the mean number of events where flow exceeded seven times the median flow per year (FRE 7; after Clausen and Biggs 1997). We only included events with at least a 2-week interval to avoid consecutive flood peaks within one overall period of high flow. FRE 7 was chosen after testing the explanatory power of events 3, 5, 7, and 9 times median flow. Mean reach FRE 7 was determined from hydrographs based on continuous flow records for 3 to 6 yr prior to the surveys (Table 1).

Table 2. Variables describing the vegetation at the 15 surveyed stream reaches. The cover and volume are as percentage of the stream reach. Species richness and Shannon diversity are based on all species present in the stream on the survey day. The proportion of vegetation cover in each reach possessing the different species traits is also given.

Stream	COVER (%)	VOLUM (%)	RICH TOT (No.)	RICH AQU (No.)	SHAN	STEM low	PROP high	RT:SH high
Gibson	69.5	21.4	11	4	1.54	0.86	0.45	0.00
Hakataramera	21.0	2.6	15	7	1.88	0.80	0.22	0.07
Kakanui	56.4	13.3	14	11	1.19	0.94	0.63	0.06
Nenthorn	20.5	5.6	16	7	2.05	0.69	0.01	0.11
Selwyn	13.1	9.7	9	6	1.51	0.83	0.92	0.00
Shag	76.4	39.9	10	9	1.41	0.84	0.06	0.08
Silver	48.9	26.3	14	8	2.25	0.44	0.02	0.06
Spring	65.1	31.2	13	10	2.08	0.71	0.57	0.00
Stanton	0	0	4	2	1.17	0.15	0.00	0.00
Taranaki	55.3	35.7	15	8	2.26	0.40	0.00	0.00
Tokomairiro	29.7	8	10	4	1.44	0.95	0.92	0.00
Waihopai	31.0	21.6	12	9	1.90	0.81	0.59	0.01
Waikawa	33.8	9.55	3	2	0.12	1.00	0.00	0.00
Waimea	12.4	2.0	5	5	0.79	0.97	0.80	0.02
Waipahi	58.4	17.9	12	8	1.70	0.91	0.39	0.09

Vegetation analysis—For the data analysis, it was necessary to convert abundance classes into one value for each quadrat; we assigned a value halfway between limits for the range in the Braun-Blanquet scale within which the value occurred. For example, if vegetation cover was assessed as 25%–50% in a quadrat we assigned the value 37.5%. Species richness was defined with two components: total species number (RICH TOT) and number of submerged species (RICH AQU) in the full stream width (Table 2). Diversity was calculated using the Shannon-Wiener diversity index (SHAN) (Kent and Coker 1992).

Species living in disturbed environments are expected to have a higher resistance to disturbance and/or a better resilience after disturbance (Grime 1979). We tested this hypothesis by determining whether there was a significant relationship between disturbance frequency and the percentage cover of species possessing disturbance resistance/resilience traits. Traits included (after Riis and Biggs 2001): fragility of stems (STEM), root:shoot ratio (RT:SH), and production of vegetative propagules (seed and vegetative propagules: PROP). Fragility of stems was determined experimentally, and root:shoot ratios were measured for seven species commonly found in the field survey (*see below*). Information about the ability of the common species to produce propagules was obtained from the literature for 13 of the 18 aquatic species (Table 3).

Plant species for which information was obtained on stem fragility and vegetative propagule production comprised, on average, 92% of the total vegetation cover in our study reaches. In the calculations we made three assumptions. First, we assumed that the traits for *Elodea canadensis, Myriophyllum triphyllum,* and *Rorippa nasturtium-aquatica* would be similar to those reported for the morphologically similar species of *Lagorosiphon major, Myriophyllum propinquum,* and *Veronica anagallis-aquatica,* respectively. This expanded our information on disturbance resistance/resilience traits to 10 species. Second, we excluded terrestrial

or floating plants (*Lemna minor* and *Azolla pinnata*) because we assumed their frequency at a site was influenced more by local factors (including disturbance of the site during vegetation surveys). Third, we assumed that the regional species pool was the same for the whole South Island and the probability of species presence at a site was equal for all sites.

The next step was to obtain a single value for each stream describing the proportion of the vegetation possessing each trait. First, we normalized the frequencies of each species present at a site to the total frequencies of species for which we had species trait information. Second, we classified the degree of development of each trait for each species into three categories from low to high. Third, we added the frequencies of species possessing each trait category. For example, high susceptibility to stem breakage was possessed by *Potamogeton cheesemanii, Rorippa nasturtium-aquatica,* and *Veronica anagallis-aquatica.* We therefore added the normalized frequencies of these species together for each site to give an overall value for this trait for each stream (Table 2). This value from all sites was then related to disturbance frequency over all the sites.

Species traits experiment/measurements—We measured the root:shoot ratio for seven common species and their abilities to resist stem breakage during high water velocities. Plants usually form beds in streams, and therefore experiments on stem fragility were performed on whole macrophyte beds (i.e., mats comprising ~300 stems m^{-2}). The test species (i.e., *Callitriche stagnalis, Lagarosiphon major, Myriophyllum propinquum, Potamogeton cheesemanii, Potamogeton crispus, Ranunculus trichophyllus,* and *Veronica anagallis-aquatica*) were grown for 3 months in three replicate trays (400 mm × 250 mm) in 0.7-m deep water at a water velocity of 0.2 m s^{-1}. The mean biomass (g dry weight) for each species in the three trays after 3 months was *C. stagnalis,* 39.5 ± 4.9; *L. major,* 36.0 ± 8.6; *M. propinquum,* 33.8 ± 11.2; *P. cheesemanii,* 11.8 ± 3.8; *P.*

Table 3. Species found in the 15 surveyed stream reaches. Species regarded as being primarily aquatic and species used in the species trait experiment are denoted with a √. Information on propagules production rate was obtained from the literature and grouped from 1–3 as low to high. Sources are Barrat-Segretain et al. 1998 and 1999; Bornette et al. 1994; Nichols and Shaw 1986.

Species	Aquatic species	Species trait experiments	Propagule production
Agrostis sp.			
Alisma plantago-aquatica L.	√		
Alopecurus geniculatus L.			
Azolla rubra R. Br.	√		
Callitriche stagnalis Scop.	√	√	2
Carex sp.			
Elodea canadensis Michaux	√		3
Eleocharis acuta R. Br.			
Glyceria declinata Breb.	√		
Glyceria fluitans (L.) R. Br.	√		
Juncus articulatus L.			
Juncus effusus L.			
Lagorosiphon major (Ridl.) Wag.	√	√	3
Lemna minor L.	√		
Lilaeopsis ruthiana Affolter	√		1
Mentha sp.			
Mimulus guttatus DC.			
Myosotis laxa Lehm. subsp. *caespitosa* (C. F. Schultz) Nordh.			
Myriophyllum propinquum Cunn.	√	√	2
Myriophyllum triphyllum Orch.	√		2
Nitella hookerii A. Br.	√		2
Phalaris arundinaceae L.			
Poa palustris L.			
Polygonum sp.			
Potamogeton crispus L.	√	√	3
Potamogeton cheesemanii A. Benett	√	√	2
Potamogeton ochreatus Raoul	√		2
Pratia perpusilla Hook f.			
Ranunculus trichophyllus Chaix	√	√	2
Ranunculus repens L.			
Rorippa nasturtium-aquaticum (L.) Hayek	√		2
Rumex obtusifolius L.			
Veronica anagallis-aquatica L.	√	√	2

crispus, 15.3 ± 1.7; *R. trichophyllus,* 76.9 ± 18.2; *V. anagallis-aquatica,* 25.7 ± 9.3. Each tray was then placed in an outdoor ecohydraulics flume (dimensions: 10-m long, 0.75-m wide, and 0.5-m deep; Nikora et al. 1998) and exposed for 15 min to current velocities of 1.5 m s⁻¹, this being around the upper limit for velocity observed during high flows in New Zealand lowland stream habitats (Riis and Biggs unpubl. data). Fragments broken from the mats were collected in a downstream net and later dried at 105°C and weighed in the laboratory. The velocity treatment was only run for 15 min because an initial analysis over a 2-h period showed that more than 70% of the total biomass loss occurred in the first 15 min of treatment for all species.

The root:shoot ratio was measured on each replicate used in the flume experiment. Species were grouped according to root:shoot ratios as low (<0.7, $n = 5$ species), medium (0.7–1.4, $n = 3$), and high (>1.4, $n = 2$) ratio.

Data analysis—Relationships between environmental and vegetation variables were tested by linear and nonlinear regression based on the best goodness of fit. The analysis was performed with the following dependent variables: vegetation cover, vegetation volume, total species richness, aquatic species richness, and Shannon diversity. We analyzed the effect of selected independent variables on the presence of species traits using the following dependent variables: proportion of vegetation possessing low stem breakage potential (STEM low), high root:shoot ratio (RT:SH high), and high vegetative propagule production (PROP high).

To test whether vegetation abundance is controlled by local-scale water velocity in hydrologically stable streams, we analyzed the relationship between velocity in vegetation-free space and percentage of transect area occupied by vegetation in each transect from the five most stable streams. Habitat preference was analyzed for *Elodea canadensis, Myriophyllum triphyllum, Potamogeton cheesemanii,* and *Ranunculus trichophyllus.* Hydraulic habitat preferences were determined as described by Jowett (2000). The number of quadrats with each species was calculated for each habitat class based on intervals of water velocity, depth, and substrate size. For
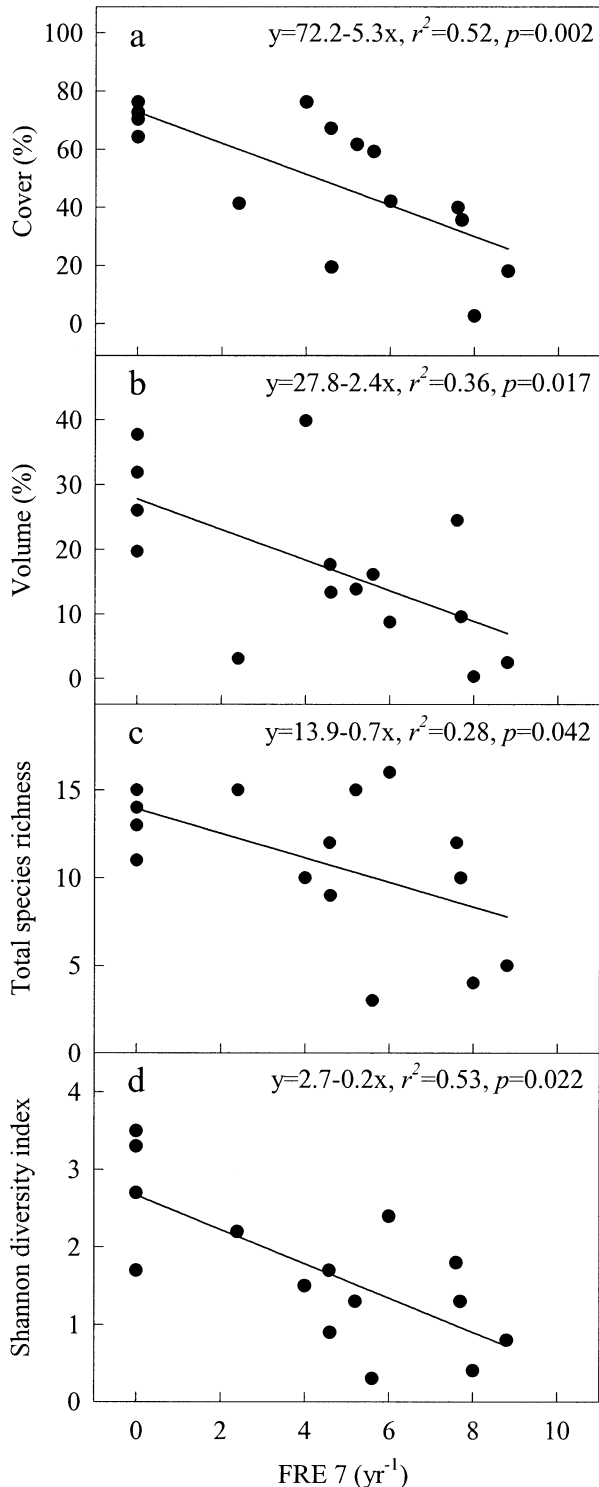
Fig. 1.   (a) Vegetation cover, (b) volume, (c) total species richness, and (d) Shannon diversity in the stream study reaches in relation to flood disturbance frequency. FRE 7 is the mean number of events per year where flow is >7 × median flow in the streams.

example, *Elodea canadensis* was present in 76% of quadrats that fell within the velocity interval 0.3–0.4 m s^{-1}. The probability of species being present in a stream in this velocity interval therefore became 0.76, and this was interpreted as its hydraulic habitat preference or weighting value (Jowett 2000). In the same way, preference values for each species were assigned for other velocity intervals as well as for classes of depth and substrate size. The preference values were scaled to a maximum by dividing all values by the maximum recorded value. In preparing preference curves, any preference value >0.8 was given a value of 1 (Jowett and Richardson 1995).

The preference curves for *Elodea canadensis* and *Ranunculus trichophyllus* are based on data from four stable rivers with no floods over the previous 3–6 yr and high vegetation cover: Gibson, Silver, Spring, and Taranaki (Tables 1 and 2). In order to obtain enough data for *Ranunculus trichophyllus,* the Shag River (FRE 7 = 4) was also included. To obtain enough data to calculate preference curves for *Myriophyllum triphyllum* and *Potamogeton cheesemanii,* we included four additional streams where these species were common (Hakataramera, Nenthorn, Waihopai, and Wapahi). However, these streams had a mean flood frequency ranging from 2.4 to 7.6 per year and only moderate vegetation cover (Tables 1 and 2), so macrophyte colonization of suitable habitats may not have been complete in these streams.

Results

Vegetation abundance, diversity, and disturbance frequency—Vegetation abundance within stream reaches was negatively correlated with flood frequency (Fig. 1a,b). When common species were examined individually, no significant correlations between species cover and FRE 7 (linear and nonlinear regressions; $P > 0.05$) were found. However, intermediate to frequently flooded streams were consistently dominated by *Elodea canadensis, Potamogeton ochreatus,* and *Ranunculus trichophyllus,* with other species only sparsely represented.

Thirty-three macrophyte taxa (including the characean macroalga *Nitella hookerii*), 18 of which were regarded as primarily aquatic, were found in the 15 stream reaches surveyed (Table 3). Total species richness and Shannon diversity were negatively correlated with flood frequency (Fig. 1c,d). At low flood frequency, more species were abundant, contributing to a higher Shannon diversity, whereas at high flood frequency only a few species were abundant, contributing to a low Shannon diversity. Aquatic species richness did not correlate with flood frequency.

There were no significant correlations between vegetation variables (COV, VOL, RICHTOT, RICHAQ, SHAN, STEM-low, PROP-high, RT : SH high) and environmental variables describing stream size (FLOW), water chemistry (TOT P, TOT N, ALK), or distance from stream source (DIST; Spearman rank correlation $P > 0.05$).

Disturbance experiments—For all species, loss of biomass from macrophyte beds during high-velocity perturbations (1.5 m s^{-1}) was very low (<1% of total biomass removed; Fig. 2). This indicates that the overall importance of stem
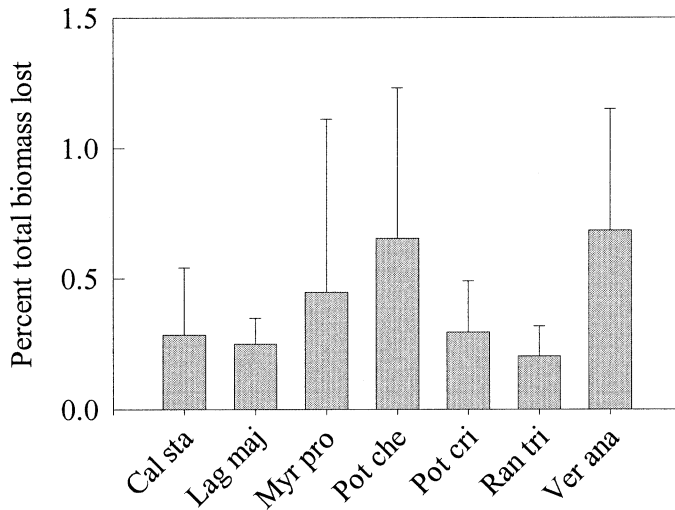
Fig. 2. The percentage of total biomass lost from experimental trays for seven different macrophyte species exposed to a velocity of 1.5 m s^{-1} (data are means of three replicates and SD). Cal sta, *Callitriche stagnalis*; Lag maj, *Lagorosiphon major*; Myr pro, *Myriophyllum propinquum*; Pot che, *Potamogeton cheesemanii*; Pot cri, *Potamogeton crispus*; Ran tri, *Ranunculus trichophyllus*; Ver ana, *Veronica anagallis-aquatica.*
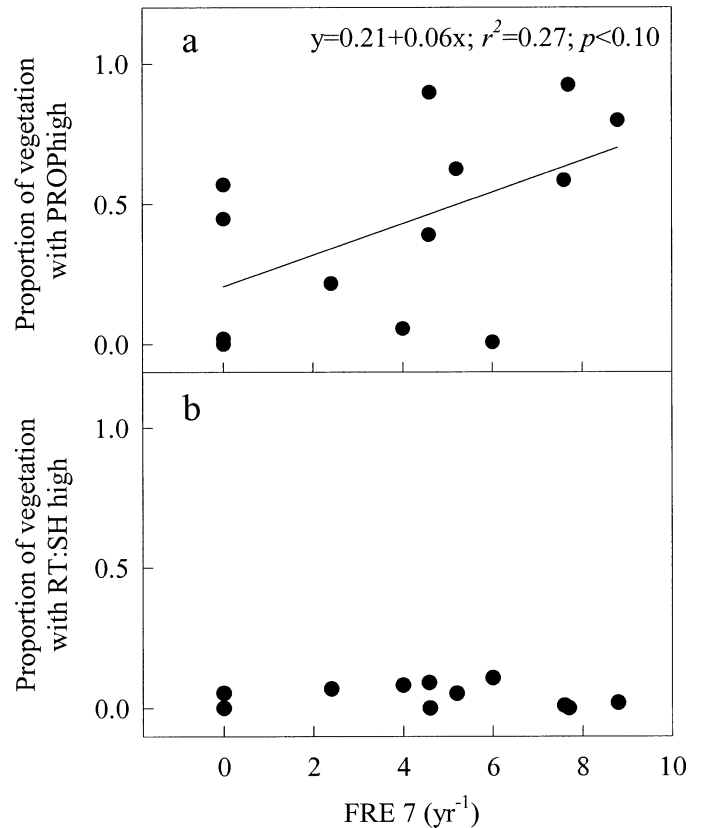

Fig. 3. Proportion of vegetation constituting (a) high propagule production and (b) high root:shoot ratio related to disturbance frequency in the streams. FRE 7 is the mean number of events per year where flow is >7 × median flow in the streams. One site (Stanton) with very low cover and one site with an almost dominance of only one species (Waikawa) have been omitted from the analyses.

breakage in controlling vegetation abundance by floods is small. There was no significant difference ($P > 0.05$, *t*-test) in total biomass lost among the seven species.

The root:shoot ratio was lowest in *Callitriche stagnalis, Lagorosiphon major, Myriophyllum propinquum,* and *Ranunculus trichophyllus* (0.42–0.63), intermediate in *Veronica anagallis-aquatica* (0.86), and highest in *Potamogeton cheesemanii* and *Potamogeton crispus* (2.54 and 1.58, respectively). This suggested a better bed sediment anchorage strength and therefore a higher resistance to disturbance in the latter two species.

From root:shoot ratios and literature information about propagule production (Table 3), we calculated the proportion of plants in each reach possessing the different disturbance resistance/resilience traits and compared these with flood frequency at the sites. The proportion of plants with high vegetative propagule production in a reach was significantly correlated with flood frequency (linear regression, $P < 0.10$; Fig. 3a). Vegetation present at sites with low flood frequency usually had low to intermediate proportions of species with high propagule production, and the three streams with the highest flood frequency were dominated by species with a high propagule production. There was no relationship between disturbance frequency and root:shoot ratios (linear regression, $P > 0.05$; Fig. 3b).

Interflood vegetation abundance and hydraulic habitat preferences—Interflood vegetation abundance showed a negative, quadratic relationship with mean water velocity in the vegetation-free space in hydrological stable streams (Fig. 4). Water velocity in the transects ranged from 0.04 to 0.58 m s^{-1}, and the vegetation abundance peaked at 0.3–0.5 m s^{-1}.

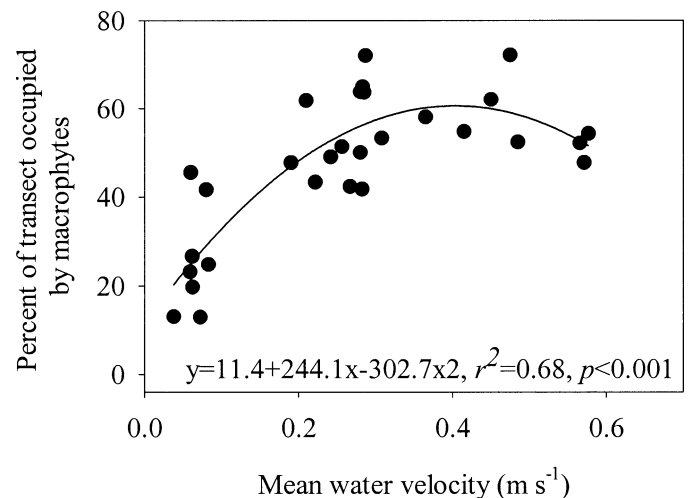All species showed well-defined water velocity preferenc-

Fig. 4. Percentage cover occupied by vegetation in 29 transects in five hydrological stable streams in relation to mean water velocity in the vegetation-free space of the transects.
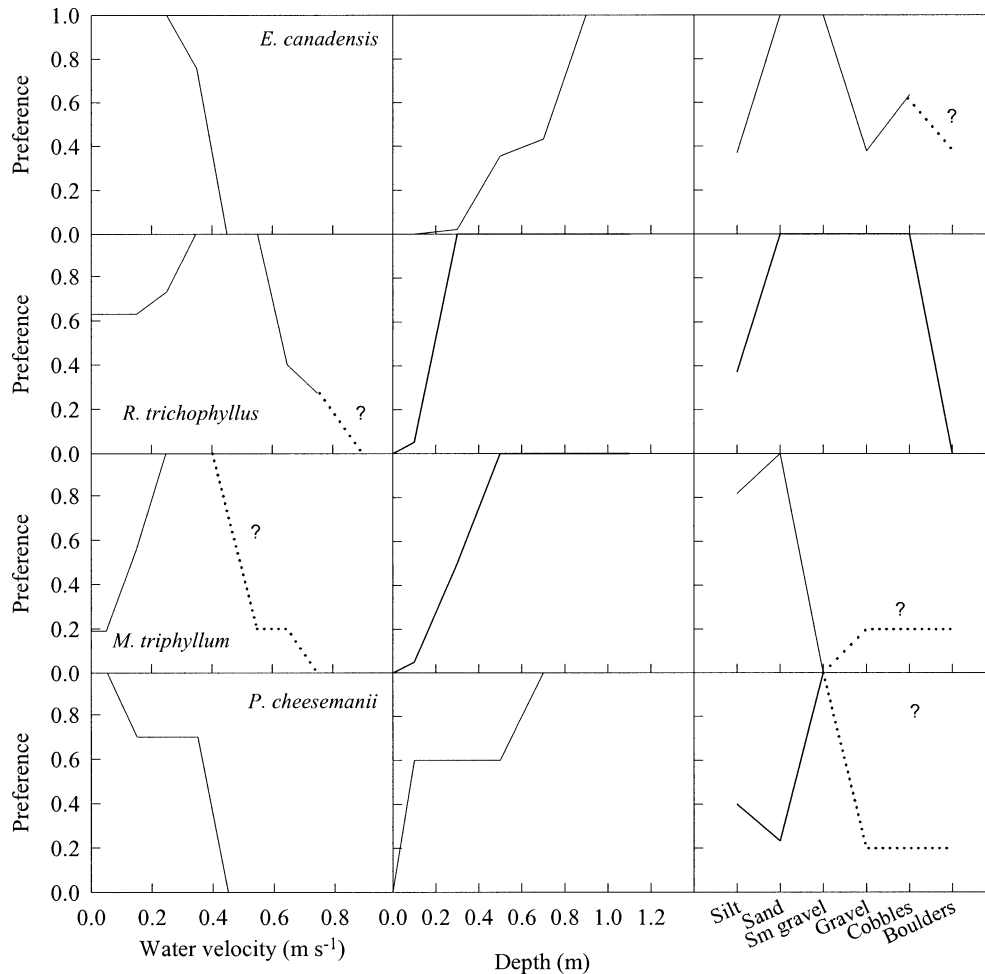
Fig. 5. Habitat preference curves for four common stream macrophytes with respect to water velocity, depth, and substrate size. Dotted lines mark extrapolations based on extensive field observations, but where no data were available in the present study.

es (Fig. 5). Optimum water velocity for *Elodea canadensis, Myriophyllum triphyllum,* and *Potamogeton cheesemanii* was between <0.1 and 0.4 m s⁻¹ but was 0.4–0.6 m s⁻¹ for *Ranunculus trichophyllus.* The lowest optimum depth preference varied among the four species, being 0.3 m for *R. trichophyllus,* 0.5 m for *M. triphyllum,* and 0.7 m for *P. cheesemanii,* whereas *E. canadensis* preferred deeper water (0.9 m optimum; Fig. 5). Substrate preference also differed among species. *E. canadensis* preferred sand and small gravel as substrate, sharing the sandy preference with *M. triphyllum* and small gravel preference with *P. cheesemanii. R. trichophyllus* had no specific substrate preference, since it ranged equally from sand to cobbles. Some habitat classes were not observed in our study reaches, and thus no habitat preferences could be derived for velocities >0.4 m s⁻¹ for *M. triphyllum* and >0.75 m s⁻¹ for *R. trichophyllus,* and in coarse substrate for *M. triphyllum* and *P. cheesemanii.* The dotted lines in Fig. 5 are best estimates based on personal observations under these conditions. Similarly, no habitat preferences could be determined for water >0.8-m deep for *R. trichophyllus, M. triphyllum,* and *P. cheesemanii* and >1.2 m for *E. canadensis.* However, if the light conditions

are sufficient for plant growth, all species are likely to be present to >1.2 m.

Discussion

Disturbance frequency in streams—Biggs (1996*a*) hypothesized that successful colonization of macrophytes in streams is primarily controlled by flood frequency because macrophyte immigration and growth rates are relatively slow (months to years) compared with other stream biota such as periphyton and invertebrates (days to months). Thus, prolonged periods of hydrological stability are required for macrophyte propagules to arrive and develop into substantial cover. Our study supported this hypothesis and provides an empirical basis for predicting the potential occurrence of macrophytes in streams. Based on an extrapolation of data in Fig. 1, we suggest that significant macrophyte development is restricted to streams with less than an average of ~13 flood events (of >7 × median flow) per year (*x*-axis intercept; Fig. 1). This result is supported by previous, more extensive, surveys in New Zealand that have indicated that even though interflood water velocity and growth resources

might be suitable, few or no macrophytes will be present soon after intense floods or if flood frequency is high (Biggs and Price 1987). For example, only 15% of 378 New Zealand streams surveyed during summer low flows contained macrophytes even though all growth conditions appeared suitable.

The present study also suggests strong effects of disturbance frequency on total macrophyte biomass. For example, there was approximately a threefold decrease in vegetation abundance in streams with eight disturbances per year compared to streams with no disturbances (Fig. 1). A similar relationship between disturbance and biomass has been found for periphyton, with a threefold change in abundance over the range from 0 to 8 disturbances per year (Biggs 1995). Despite low biomass, periphyton was still present in streams with >40 disturbances per year, yet our present work suggests that macrophytes are rare in streams with only ~13 disturbances per year. This difference most likely reflects the rapid colonization of periphyton after disturbance (1–2 weeks; Peterson 1996) compared with slower colonizing macrophytes and the effects of this differential on time available for lateral growth and biomass accrual. In related experiments we have found that 10–20 weeks are required for macrophytes to establish to >1% cover (Riis and Biggs unpubl. data). Thus, a long interflood period may be required for maximum possible vegetation biomass, and even a small number of floods within a year will decrease macrophyte abundance (Fig. 1). Conversely, maximum biomass of periphyton can accrue in under 3 months following flood disturbances in streams (e.g., Biggs 1996*b*). Thus, it would be expected that for a given stream, the longer the time since the last flood disturbance the higher the abundance of macrophytes.

There was no relationship between disturbance frequency and number of aquatic obligate species for eight common species occurring over a large range in flood disturbance frequency (Fig. 1). However, we found that only *Elodea canadensis, Potamogeton ochreatus,* and *Ranunculus trichophyllus* were able to dominate communities in more disturbed streams (resulting in a low variation in Shannon diversity at high flood frequency, Fig. 1), suggesting that they are the most disturbance-resistant/resilient species. This conforms to previous predictions that *Elodea canadensis* is one of the most disturbance-resilient species in streams (Riis and Biggs 2001).

To explore what mechanisms may be responsible for variation in macrophyte abundance and diversity across gradients of flood disturbance frequency, we asked if certain species traits allow macrophytes to cope with floods. We found that species constituting the highest proportion of the vegetation in disturbed stream reaches have high vegetative propagule production. This has also been found in a former channel of the River Rhone, where all species that were first to reestablish after a flood were capable of producing turions or other dispersal organs (Henry et al. 1994). A high rate of propagule production appears to be beneficial for species living in disturbed habitats because it increases the probability of postdisturbance dispersal and reestablishment (Barrat-Segretain 1996). However, a range of other species traits is also likely to be important for recolonization success, such

as the dispersal and survival ability of propagules, establishment success, rooting success, and growth rate when first established (Grime 1979).

We found a very low loss of biomass due to stem breakage during high water velocities (1.5 m s^{-1}), suggesting that stem breakage is not significant for stream macrophytes during most floods. Thus, relative resistance to stem breakage is probably not a useful trait to typify disturbance resistance (cf. stream periphyton; Biggs and Thomsen 1995). It is possible that uprooting of the plants by sediment erosion is a more important loss mechanism for macrophytes during floods than stem breakage.

Similarly, root : shoot ratio did not show any relationship to disturbance frequency and therefore cannot be considered as a disturbance-resistant species trait (e.g., by enhancing anchorage strength to resist high velocities). It is possible that anchorage depth may be of more importance, and this should be tested in future studies. Overall our study partly supported the hypothesis that species possessing traits that increase disturbance resistance or resilience will constitute a higher proportion of the vegetation in disturbed streams.

Interflood spatial water velocity effects—In hydrologically stable streams with long interflood periods, macrophytes will eventually reach a maximum abundance for the suitable habitat space available. Biggs (1996*a*) suggested that this space/maximum abundance is controlled by water velocity in unshaded streams, and our study confirmed this. As macrophytes establish and grow they occupy increasingly more of the stream volume, influencing velocity and turbulence fields, and, in turn, these are expected to influence processes such as mass transfer and drag (as has been quantified for periphyton and bryophytes; Stevenson 1996; Nikora et al. 1998, 2002). Indeed, the quadratic relationship we found between vegetation abundance and vegetation-free water velocity probably reflects these two conflicting processes of mass transfer and drag. First, within the range of 0–0.2 m s^{-1}, increased velocity can increase photosynthetic rates by controlling the thickness of the diffusive boundary layer and increasing resource supply within the macrophyte beds (Westlake 1967; Madsen and Søndergård 1983). In our study, this was evidenced by an increase in vegetation abundance at velocities between 0 and 0.3 m s^{-1} (Fig. 4). Second, at high velocities, drag forces increase greatly, which can result in biomass losses. In our study, this was evidenced by a reduction in abundance at velocities >0.4 m s^{-1}. Indeed, in a given stream cross-section, the velocity in vegetation-free flow paths will be much higher than the cross-section mean as macrophyte occupation of the channel increases and flows through the beds decrease (Sand-Jensen and Mebus 1996; Dodds and Biggs 2002). There will even be a threshold in the vegetation-free water velocity above which macrophyte development into the free-stream will be almost eliminated by forces of the flow. In our study, we found this velocity threshold to be around 0.80 m s^{-1} (*x*-axis interception, Fig. 4). The above velocity effects of growth stimulation and drag/biomass loss also occur in stream periphyton communities (Stevenson 1996).

It is tempting to explain the decreasing macrophyte abundance with higher velocities as a result of increasing plant

fragmentation. However, as noted earlier we found that almost no plant material was lost by breakage at velocities as high as 1.5 m s^{-1}. It is possible that increased drag and turbulence at high velocities may result in increased lateral sediment erosion in the vegetation-free zones around the macrophyte beds. This could then lead to biomass loss through progressive undermining and uprooting of plants along the edges of the beds resulting in lower overall transect-scale macrophyte abundances at higher velocities. We predict this to be the most likely mechanism controlling biomass at high velocities and causing the decline in abundance recorded at velocities >0.4 m s^{-1} (Fig. 4).

Nilsson (1987) also found that macrophyte cover in a Swedish river increased up to velocities of around 0.3 m s^{-1} but decreased at higher velocities. Conversely, Chambers et al. (1991) found that vegetation biomass in two Canadian rivers decreased linearly with increasing water velocity in the range 0.01–1 m s^{-1}, and Henriques (1987) found an overall decrease in macrophyte abundance in the range 0.1–0.9 m s^{-1} at 22 sites in New Zealand streams. We cannot explain the discrepancy between the latter results and our study except for the possibility that diffusive boundary layer limitation (e.g., of carbon supply) was not limiting macrophyte growth at the low velocity sites in Henriques (1987) (and perhaps also in Chambers et al. 1991).

At the species level, different macrophytes are known to live in areas of different water velocity (e.g., Butcher 1933; Haslam 1978), suggesting that total stream macrophyte abundance is tightly coupled not only to spatial variations in hydraulic parameters but also to the performances of individual macrophyte species. The water velocity preferences we observed for *Elodea canadensis, Ranunculus trichophyllus, Myriophyllum triphyllum,* and *Potamogeton cheesemanii* agree with those reported previously. As in our study, French and Chambers (1996) found that *E. canadensis, Myriophyllum exalbescens* (morphologically comparable to *Myriophyllum triphyllum*), and *Potamogeton gramineus* (morphologically comparable to *Potamogeton cheesemanii*) were most abundant in the velocity range 0–0.4 m s^{-1}, and *Ranunculus aquatilis* (morphologically comparable to *Ranunculus trichophyllus*) was most abundant from 0.4 to 0.6 m s^{-1}. Similarly, Butcher (1933) and Haslam (1978) found that *Ranunculus* spp. prefer fast-flowing water, and Bilby (1977) and Haslam (1978) observed that *E. canadensis* prefer slow-flowing waters. Since drag increases the risk of plants becoming uprooted, species most susceptible to high velocities should have high drag coefficients and will therefore show a preference for low water velocities.

Regarding the habitat preference for substrate types in the present study, we found that sand and small gravel are preferred by *E. canadensis, M. triphyllum,* and *P. cheesemanii,* whereas *R. trichophyllus* prefer gravel and cobble substrata. These findings conform to Haslam (1978), who found that *E. canadensis* prefer silt and *Ranunculus* spp. prefer gravel.

For each of the measured variables (water velocity, depth, and substrate) some species had overlapping maximum preferences. For example, *E. canadensis* and *P. cheesemanii* preferred similar water velocities; *R. trichophyllus, M. triphyllum,* and *P. cheesemanii* preferred similar depths; and *E. canadensis* and *M. triphyllum* preferred similar substrate

types. However, no pairs of the four species had the same maximum preference ranges for all three variables, suggesting that the species are likely to coexist in stable rivers due to niche separation.

In conclusion, we have confirmed two important hypotheses about hydrologic and hydraulic factors controlling macrophyte colonization and development in temperate stream environments, as posed by Biggs (1996*a*). First, we found that hydrologic regime (and associated disturbance frequency) is likely to be the primary factor controlling establishment of macrophytes in unshaded streams. Vegetation was absent in streams with more than ~13 flood disturbances per year where the floods exceeded 7 × median flow. Further, vegetation abundance and diversity were significantly negatively related to variations in flood disturbance frequency among streams. We also found that the rate of propagule production was an important trait to cope with flood disturbance, and thus species composition in disturbed streams was strongly dominated by taxa with high rates of propagule production, as previously hypothesized by Riis and Biggs (2001). Second, we found that in our unshaded hydrologically stable study streams, vegetation abundance was related to local hydraulic conditions (i.e., water velocity, depth, and sediment particle size). A significant quadratic relationship between vegetation abundance and vegetation-free velocity showed a peak in abundance of macrophytes at ~0.4 m s^{-1} and the suggestion of an upper velocity threshold for growth into the free stream of ~0.80 m s^{-1}. We also found that our four most common taxa each had different joint velocity/depth/substrate habitat optima, suggesting that these species can potentially coexist in streams containing heterogeneous hydraulic habitat conditions through a process of niche separation.

References

BARRAT-SEGRETAIN, M. H. 1996. Strategies of reproduction, dispersion and competition in river plants: A review. Vegetatio **123:** 13–37.

——, G. BORNETTE, AND A. HERING-VILAS-BÔAS. 1998. Comparative abilities of vegetative regeneration among aquatic plants growing in disturbed habitats. Aquat. Bot. **60:** 201–211.

——, C. P. HENRY, AND G. BORNETTE. 1999. Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats. Arch. Hydrobiol. **145:** 111–127.

BIGGS, B. J. F. 1995. The contribution of disturbance, catchment geology and landuse to the habitat template of periphyton in stream ecosystems. Freshw. Biol. **33:** 419–438.

——. 1996*a*. Hydraulic habitat of plants in streams. Reg. Riv. Res. Manage. **12:** 131–144.

——. 1996*b*. Patterns in benthic algae of streams, p. 31–56. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, [eds.], Algal ecology: Freshwater benthic ecosystems. Academic.

——, AND G. M. PRICE. 1987. A survey of filamentous algal proliferations in New Zealand rivers. N. Z. J. Mar. Freshw. Res. **21:** 175–191.

——, AND H. A. THOMSEN. 1995. Disturbance of stream periphyton by perturbations in shear stress: Time to structural failure and differences in community resistance. J. Phycol. **31:** 233–241.

BILBY, R. 1977. Effects of a spate on the macrophyte vegetation of a stream pool. Hydrobiologia **56:** 109–112.

BORNETTE, G., C. AMOROS, AND D. CHESSEL. 1994. Effect of allogenic processes on successional rates in former river channels. J. Veg. Sci. **5:** 237–246.

BRAUN-BLANQUET, J. 1932. Plant sociology: The study of plant communities. McGraw-Hill.

BURKHOLDER, J. M. 1996. Interactions of benthic algae with their substrate, p. 253–298. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe [eds.], Algal ecology: Freshwater benthic environments. Academic.

BUTCHER, R. W. 1933. Studies on the ecology of rivers I. On the vegetation distribution of macrophytic vegetation in the rivers of Britain. J. Ecol. **21:** 58–91.

CHAMBERS, P. A., E. E. PREPAS, H. R. HAMILTON, AND M. L. BOTHWELL. 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. Ecol. Appl. **1:** 249–257.

CLAUSEN, B., AND B. J. F. BIGGS. 1997. Relationships between benthic biota and hydrological indices in New Zealand streams. Freshw. Biol. **38:** 327–342.

DEATH, R. 2000. Invertebrate-substratum relationships, p. 157–178. *In* K. J. Collier and M. J. Winterbourn [eds.], New Zealand stream invertebrates: Ecology and management. New Zealand Limnological Society.

DODDS, W. K., AND B. J. F. BIGGS. 2002. Water velocity attenuation by stream periphyton and macrophytes in relation to growth form and architecture. J. N. Am. Benthol. Soc. **21:** 2–15.

DOWNES, M. T. 1988. Chemical methods manual. Taupo Research Laboratory Report 102.

FRENCH, T. D., AND P. A. CHAMBERS. 1996. Habitat partitioning in riverine macrophyte communities. Freshw. Biol. **36:** 509–520.

GIBBS, M. M., AND S. E. PICKMERE. 1987. Optimisation of a semi-automated micro Kjeldahl digestion method for the simultaneous determination of nitrogen and phosphorous in seston and sediments. Taupo Research Laboratory Report 96.

GRIME, J. P. 1979. Plant strategies and vegetation processes. Wiley.

HASLAM, S. M. 1978. River plants. Cambridge Univ. Press.

HENRIQUES, J. 1987. Aquatic macrophytes, p. 207–222. *In* P. R. Henriques [ed.], Aquatic biology and hydroelectric power development in New Zealand. Oxford Univ. Press.

HENRY, C. P., G. BORNETTE, AND C. AMOROS. 1994. Differential effects of floods on the aquatic vegetation of braided channels of the Rhone River. J. N. Am. Benthol. Soc. **13:** 439–467.

JOWETT, I. G. 2000. Flow management, p. 289–312. *In* K. J. Collier and M. J. Winterbourn [eds.], New Zealand stream invertebrates: Ecology and management. New Zealand Limnological Society.

——, AND J. RICHARDSON. 1995. Habitat preferences of common, riverine New Zealand native fishes and implications for flow management. N. Z. J. Mar. Freshw. Res. **29:** 13–23.

KENT, M., AND P. COKER. 1992. Vegetation description and analysis. A practical approach. Wiley.

MADSEN, T. V., AND M. SØNDERGÅRD. 1983. The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. Aquat. Bot. **15:** 187–193.

NICHOLS, S. A., AND B. H. SHAW. 1986 Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum, Potamogeton crispus* and *Elodea canadensis.* Hydrobiologia **131:** 3–21.

NIKORA, V. I., D. G. GORING, AND B. J. F. BIGGS. 2002. Some observations of the effects of micro-organisms growing on the bed of an open channel on the turbulence properties. J. Fluid Mech. **450:** 317–341.

——, A. M. SUREN, S. L. R. BROWN, AND B. J. F. BIGGS. 1998. The effects of the moss *Fissidens rigidulus* (Fissidentaceae: Musci) on near-bed flow structure in an experimental cobble bed flume. Limnol. Oceanogr. **43:** 1321–1331.

NILSSON, C. 1987. Distribution of stream-edge vegetation along a gradient of current velocity. J. Ecol. **75:** 513–522.

PETERSON, C. G. 1996. Response of periphyton communities to natural physical disturbance, p. 375–402. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe [eds.], Algal ecology: Freshwater benthic ecosystems. Academic.

RIIS, T., AND B. J. F. BIGGS. 2001. Distribution of macrophytes in New Zealand streams and lakes in relation to disturbance frequency and resource supply—a synthesis and conceptual model. N. Z. J. Mar. Freshw. Res. **35:** 255–267.

SAND-JENSEN, K., AND J. R. MEBUS. 1996. Fine-scale patterns of water velocity within macrophyte patches in streams. Oikos **76:** 169–180.

STEVENSON, R. J. 1996. The stimulation and drag of current, p. 321–340. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, [eds.], Algal ecology: Freshwater benthic environments. Academic.

WESTLAKE, D. F. 1967. Some effect of low-velocity currents on the metabolism of aquatic macrophytes. J. Exp. Bot. **18:** 187–205.

WOLMAN, M. J. 1954. A method for sampling coarse river bed material. Trans. Am. Geophys. Union **35:** 951–956.