Light as a first-order control on ecosystem structure in a temperate stream

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ABSTRACT

An emerging issue in ecohydrology is the role of light in fluvial ecosystem dynamics. Here, we investigate how photosynthetically active radiation (PAR) influences the hydrogeomorphology and biogeochemistry of a second-order temperate stream with varying riparian communities from heavily shaded forest sections to unshaded grass sections. First, in-stream PAR was compared to submerged aquatic macrophyte distributions along a 1·2-km reach. The effects of macrophytes on water depth, sediment size, sediment volume, organic matter (OM) accumulation and nutrient uptake were then analysed. Compared with forested sites, non-forested sites had three times more benthic PAR, which resulted in a quadrupling of macrophyte biomass. This greater biomass at non-forested sites increased water depth, sediment accumulation and the uptake of soluble reactive phosphorous (SRP). Bed sediment size and OM were not significantly different between forested and non-forested sites. Finally, we used the above relations to estimate biogeochemical differences between a completely forested reach and a non-forested reach. Compared with a forested reach, the non-forested reach accumulated almost twice as much bed sediment and retained more than four times as much SRP. Thus, changes in riparian conditions may create a cascade through which shading drives changes in stream habitat, which in turn drives changes in hydrogeomorphology and biogeochemical cycles. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS   stream ecology; ecogeomorphology; light regimes; submerged aquatic vegetation; forested versus grassed streams

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INTRODUCTION

Ecosystems are shaped by the interaction of physical and biological drivers. Due to their perceived dominance on stream ecosystem structure (Poff and Ward, 1990; Power and Dietrich, 2002), fluvial studies have mostly focused on physical drivers. Accordingly, biological components have been treated more as responses than drivers of system changes. Fluvial studies that do focus on biological drivers of change tend to treat the physical template as static (Doyle, 2006). The result is relatively few studies that investigate the interplay of physical and biological processes in streams.

Systems in which physical and biological drivers both play considerable roles are typically those that contain organisms which act as 'ecosystem engineers' (Jones *et al.*, 1994). A conspicuous example of ecosystem engineering involves submerged aquatic macrophytes in small streams (Sand-Jensen, 1997; Caraco *et al.*, 2006). Their presence is dictated by physical drivers, but aquatic macrophytes also have the ability to influence physical processes by directly and indirectly altering channel

roughness, velocity patterns and sediment transport (Pitlo and Dawson, 1990; Bunn *et al.*, 1998).

Studies of small lowland streams in the UK have found that macrophytes can increase Manning's roughness coefficient (n) by an order of magnitude, from 0·04 to 0·40 (Dawson, 1978; Watson, 1987; Green, 2006). This increased flow resistance results in a lower mean velocity and consequently greater flow depths for the same discharge (Gurnell, 1994). Accordingly, a dense macrophyte bed can increase flow depth as much as fourfold (or 0·7 m) given the same discharge (Dawson, 1978; Dawson, 1989). In addition to decreasing mean velocity, aquatic vegetation can alter the velocity field vertically, laterally and longitudinally (Sand-Jensen and Mebus, 1996; Nepf, 1999; Sand-Jensen and Pedersen, 1999).

Localized changes in velocity have the potential to influence sediment transport, where the low-energy environment within macrophyte patches mitigates sediment erosion (Dawson, 1978; Sand-Jensen and Mebus, 1996) and promotes sediment deposition (Sand-Jensen, 1998). Aquatic macrophytes also act as filters by trapping bedload, suspended sediment and organic matter (OM) (Sand-Jensen, 1998; Schulz *et al.*, 2003). Once sediment is captured within macrophyte beds, roots and trapped OM increase the cohesion of this material, making it more resistant to erosion (Koetsier and McArthur, 2000; Horvath, 2004).

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In addition to influencing fluvial geomorphology, aquatic macrophytes can affect a range of biological processes, and potentially alter biogeochemical cycles. First, macrophytes trap sediment that can sorb phosphate and ammonium ions, reducing water column nutrient concentrations (Wilcock *et al.*, 2002). Alternatively, macrophyte-trapped sediment can release previously sorbed nutrients, returning nitrogen and/or phosphorus to the water column (Madsen *et al.*, 2001; Wade *et al.*, 2002; Wilcock *et al.*, 2002). Second, aquatic macrophytes influence nutrients via direct uptake of dissolved forms from the water column (Pelton *et al.*, 1998; Meals *et al.*, 1999; Wade *et al.*, 2002). Third, macrophyte beds can strongly affect local redox conditions via depletion or introduction of oxygen within the water column or interstitial environments. The combination of strong redox gradients and an abundance of OM (from either the plant itself or from trapped particles) creates biogeochemical hotspots in many aquatic ecosystems (Caraco *et al.*, 2006). Overall, the presence of aquatic macrophyte beds should increase channel roughness, sediment deposition, OM accumulation and nutrient retention in streams.

Conditions that promote establishment and growth of aquatic vegetation in rivers are plentiful light, sufficient nutrient supply, non-scouring velocities, stable substratum, minimal grazing pressure and suitable water temperature (Hynes, 1970). Of these, photosynthetically active radiation (PAR) is most frequently and strongly correlated with macrophyte coverage (Dodds and Welch, 2000; Hilton *et al.*, 2006; Davies *et al.*, 2008). Thus, the amount of riparian shading is likely to dictate aquatic macrophyte coverage, especially in small streams where channel widths are narrow and light attenuation by the water column is minimal (Julian *et al.*, 2008a). This dependence of macrophytes on light suggests that riparian conditions may create a cascade through which shading drives changes in stream habitat, which in turn drives changes in hydrogeomorphology and biogeochemical cycles.

In this study, we investigate the role of PAR in shaping the ecosystem structure of a second-order temperate stream in Central Wisconsin, USA. First, we compared in-stream PAR measurements with macrophyte distributions. Second, the effects of macrophytes on water depth, sediment size, sediment volume, OM accumulation and nutrient uptake were analysed. Third, we investigated how changes in riparian community composition impact all of the aforementioned variables via changes in shading. Finally, we compared functional ecosystem attributes of forested versus grassed streams. Throughout the paper, we focus on the interplay between physical and biological processes at transect and reach scales.

METHODS

Study site

Big Spring Creek is a second-order spring-fed stream located in the Central Sand Plains of Wisconsin near Big
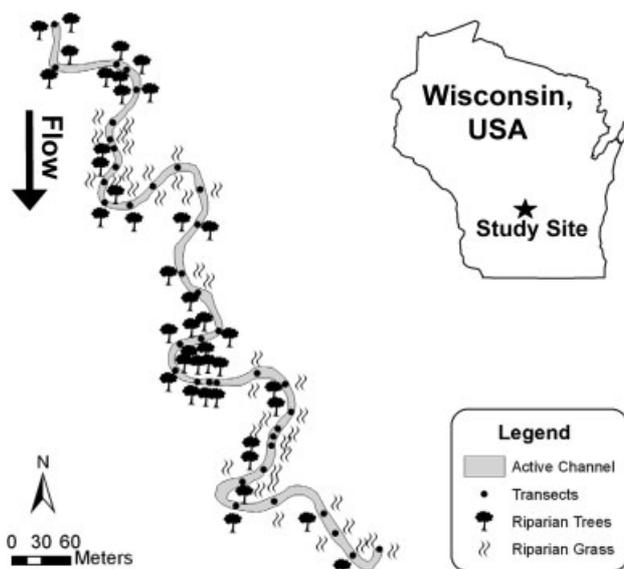

Figure 1. Big Spring Creek study reach. Transects are sequential with #101 being the most upstream and #139 being the most downstream. Riparian type is illustrated for each transect.

Spring, WI, USA (89°38′25″W, 43°40′3″N). This study focused on a 1·2-km reach with no major tributaries and longitudinally consistent optical water quality (Figure 1). Riparian vegetation along this reach was discontinuous, with monocultures of reed canary grass (*Phalaris arundinacea* L.) in some sections, mixed-hardwood forest (predominantly *Acer saccharinum* L., *A. negundo* L., *Fraxinus pennsylvanica* Marsh. and *Celtis occidentalis* L.) in other sections and a blend of reed canary grass and mixed-hardwood forest in remaining sections. Pre-settlement landcover was dominated by oak savanna (characterized by *Quercus macrocarpa* Michx., *Q. alba* L., *Q. bicolor* Willd., *Andropogon gerardii* Vitman and mixed forbs in the ground layer) (Curtis, 1959). Land cover of the 21·1-km^2 watershed in 2000 was mostly agriculture (46%), followed by forest (31%), grassland (21%) and wetland (2%). Fed predominantly by springs, Big Spring Creek's discharge was relatively constant at $0·37 \pm 0·04$ m^3 s^{-1} (mean $\pm$ SD). Spring/summer nutrient concentrations for 2005–2006 were as follows (mg l^{-1}): TN ($2·3 \pm 0·2$), NO$_3$N ($2·0 \pm 0·2$), NH$_4$N ($0·018 \pm 0·014$), TP ($0·027 \pm 0·010$) and soluble reactive phosphorous (SRP) ($0·013 \pm 0·005$) (Powers and Julian, unpublished data). The sand-bed stream was covered irregularly by submerged macrophyte beds. The most common macrophyte species in the river were *Potamogeton crispus* L. (PC), *Potamogeton pusillus/foliosus* L./Raf. (PF), *Zosterella dubia* (Jacq.) Small (ZD), *Elodea canadensis* Michx. (EC) and *Nitella* spp. L. (NS).

Photosynthetically active radiation

We obtained daily above-canopy PAR (E_{can}) from the UV-B Monitoring and Research Program (site WI02; 115 km N of Big Spring, WI), which reported 3-min averages of 20-s readings from a *LI-COR* quantum sensor (USDA, 2007). Methods for characterizing PAR at

the water surface (E_s) and at the streambed (E_{bed}) are described by Julian *et al.* (2008a). Briefly, hemispherical canopy photographs and optical water quality measurements were used with the benthic light availability model (BLAM) to derive estimates of PAR attenuation through the canopy and water column. We used a diffuse attenuation coefficient (K_d) of 0·60 m^{-1} (range: 0·45–0·77 m^{-1}) and a reflection coefficient (r) of 0·88 (range: 0·84–0·96) based on the average of 34 light profiles collected during baseflow during summer months of 2005 and 2006. All PAR values are summer daily averages (15 May to 15 September), reported in mol m^{-2} day^{-1}.

Macrophyte coverage and biomass

We quantified areal coverage of submerged macrophytes in Big Spring Creek approximately monthly from June 2005 to December 2006 at 11 transects from Figure 1: 103–104, 106–108, 123–125 and 129–131. Surveys were not conducted after winter senescence and plant cover was at or near 0% during this time. We estimated percent cover of the five major taxa at four locations per transect (every 20% of channel width) using a 0·25-m^2 gridded quadrat. We did not include periphyton as a cover component because it represented only a small proportion of total autotrophic biomass in the stream. Sediment depth (method described below) was measured at the centre of each quadrat for every vegetation survey we conducted. On 26 June 2006, a longitudinal vegetation survey was conducted where we measured macrophyte cover at all 39 transects (Figure 1).

We converted percent cover to biomass using samples of each plant species collected near the transects during summer of 2005. Eight to eleven samples of each species were collected, with corresponding coverages ranging from 5 to 100%. Plant material was rinsed to remove sediment, epiphytes and macroinvertebrates, then dried for at least 48 h at 60 °C before weighing. Dry-weight biomass (g m^{-2}) was then related to percent cover using linear regression forced through the origin (Table I). Macrophyte biomass and percent cover were obtained for each transect on each date by averaging quadrats within each transect. Total biomass (in kg) for the entire 1·2-km reach was calculated by averaging transect measurements for each riparian type (forested, grassed and mixed) and then multiplying by channel area of the corresponding riparian type.

Table I. Percent cover-biomass regressions for the five major macrophyte species in Big Spring Creek.

Species	Dry biomass (g m^{-2})	r^2
P. crispus	1·56 × cover	0·82
Z. dubia	0·86 × cover	0·89
P. pusillus/foliosis	0·72 × cover	0·86
E. canadensis	2·49 × cover	0·82
Nitella spp.	1·72 × cover	0·81

Channel hydrology and geomorphology

Active channel area (*sensu* Osterkamp and Hedman, 1977), along with a longitudinal profile that included water and sediment depth, was surveyed with a *Trimble 3350DR* total station and graded prism rod. We measured 129 locations along Big Spring Creek on 15 June 2005 with an average interval of 10 m. Survey locations were selected based on changes in channel slope and water depth. For this longitudinal survey and all vegetation surveys, sediment depth was measured as depth to refusal using a pointed rod (diameter = 1 cm). On 26 June 2005, sediment cores (diameter = 2·5 cm) were collected with an *AMS* cross-handle soil recovery probe at each vegetation measurement point ($n = 44$: four locations per transect × 11 transects). Sediments were combusted at 550 °C to determine OM content, then analysed for particle size distributions according to Dane and Topp (2002) using hydrometers and sieves.

A fixed sampling station was established at transect 124 where we monitored water depth, discharge, temperature and turbidity. Water depth and temperature were measured every 15 min by an *Intech WT-HR 2000* stage recorder. Discharge (Q) was calculated using stage-Q rating curves developed with *in situ Q* measurements taken with a *Marsh-McBirney Flo-Mate 2000* current meter. Changes in channel roughness (n) caused by temporal changes in macrophyte biomass were taken into account by using Manning's equation to calculate Q. Turbidity was measured periodically with a *Hach 2100P* turbidimeter.

Phosphorous uptake

Water samples for SRP analysis were collected and field-filtered (0·7 μm glass fibre filter) into 60 ml acid-washed low-density polyethylene plastic bottles at the upstream extent of the study reach (transect 101) approximately biweekly 15 May to 15 September during both 2005 and 2006 ($n = 16$). Samples were kept dark and refrigerated and were analysed within 48 h using the ascorbic acid molybdate photometric reaction (APHA, 1998). Daily SRP loads were calculated by averaging three water samples from across the transect, multiplying by discharge and integrating over 24 h.

We used in-stream mesocosms with nutrient additions to determine macrophyte-associated SRP uptake rates. Mesocosms consisted of thick-walled plastic cylinders that enclosed a streambed area of 0·2 m^2. We drilled two 4-cm diameter holes in each cylinder directly across from each other to allow water flow through the chamber. Cylinders were pushed ca. 20 cm into the bed sediment and left in place overnight, with water flowing through to allow the systems to equilibrate. Mesocosms were placed in locations with similar sediment composition and depth to minimize variation in both substrate sorption and uptake by periphyton. The next day, we closed the holes with rubber stoppers and added a nutrient solution containing phosphate (KH_2PO_4) and a chloride tracer (NaCl). SRP concentrations were raised to approximately two times ambient stream concentrations.

We measured SRP uptake on 8 August 2006 at transect 130. Each experiment consisted of macrophyte present (treatment) and macrophyte absent (control), with the assumption that treatment minus control equalled macrophyte-associated uptake. We used four replicates per experiment, where each replicate was sampled at initial placement of the mesocosms, directly before nutrient addition, and at times t_0, t_2, t_4 and t_6, where subscripts refer to hours after nutrient addition. Water samples were collected from the middle of the mesocosm water column, field-filtered and then analysed for SRP as described above. Chloride samples were frozen and analysed at a later date using a Dionex DX-500 ion chromatograph. We assumed the chloride tracer had no effect on uptake rates.

SRP uptake rates (U, μg m^{-2} h^{-1}) for each experiment were estimated using a first-order nutrient uptake equation (Webster and Valett, 2007). P concentrations were corrected for dilution in the mesocosm using change in concentration of the chloride tracer. However, dilution (leakage) was minimal in most mesocosms. One control replicate from the second experiment was discarded because the mesocosm was dislodged midway through the experiment.

To estimate reach-scale uptake of SRP, we first extrapolated mesocosm uptake rates to a daily value using the average hours of daylight per day from 15 May to 15 September (14·5 h) and assuming SRP uptake only occurred during daylight hours. We then compared the magnitude of macrophyte-associated uptake to daily SRP fluxes for the 1·2-km reach by multiplying area-specific plant uptake rates by reach area. The potential influence of macrophytes on SRP fluxes was expressed as the percent of the daily water column SRP the macrophytes could remove. Average summer reach-scale uptake rates were calculated using vegetation surveys in June to August in both years ($n = 6$) and then averaging for forested transects (103, 104, 123, 124, 125) and grassed transects (106, 107, 129, 130) separately.

RESULTS

Riparian shading

The discontinuous riparian community along the 1218 m reach (Figure 1) was 462 m forested, 399 m grassed and 357 m mixed (one forested bank and one grassed bank). Shading coefficients (s) for forested transects ($n = 15$) ranged 0·15–0·43 and averaged 0·26 ± 0·10 (Figure 2). That is, on average, 26% of incoming PAR (E_{can}) reached the water surface in forested transects. In grassed transects ($n = 13$), s ranged 0·73–0·94 and averaged 0·80 ± 0·07. In mixed transects ($n = 11$), s ranged 0·41–0·62 and averaged 0·52 ± 0·07. Riparian shading among forested, mixed and grassed transects was significantly different (Table II). All the above relationships were similar for benthic PAR (E_{bed}) among transect types (Table II).
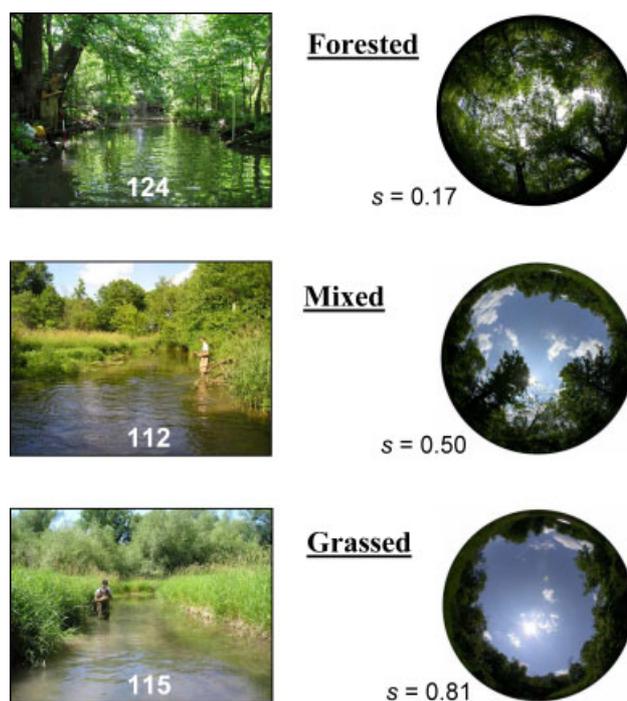

Figure 2. Longitudinal (left) and hemispherical canopy (right) photos of transects in Big Spring Creek with different riparian communities. Transect numbers (Figure 1) are located on the longitudinal photos. Shading coefficients (s—the proportion of above-canopy PAR that reaches the water surface) are located next to the canopy photos from which they were derived. The submerged aquatic macrophyte bed in the grassed transect (bottom left), with ~80% coverage, can be identified by its dark colour contrasted with the light-coloured sand bed of the stream. (This figure is available in colour in the online version of this article).
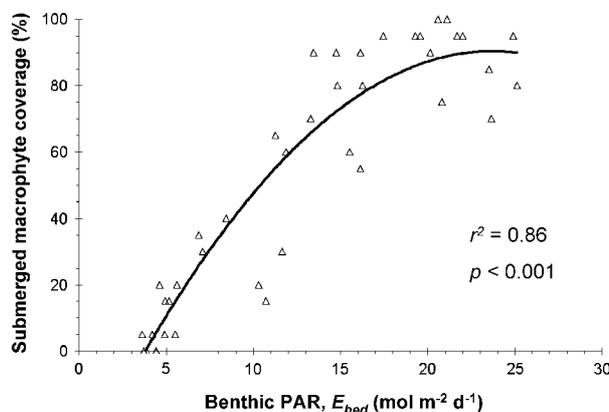

Figure 3. Submerged macrophyte coverage versus benthic PAR in Big Spring Creek on 27 June 2006. The regression equation is:
$$y = -0.23x^2 + 10.83x - 37.88.$$

Submerged aquatic macrophyte distributions

Submerged aquatic macrophytes covered approximately half of Big Spring Creek's 8929-m^2 channel area in mid-summer 2006. Surveys at the 39 transects along the 1·2-km study reach revealed that percent cover of aquatic macrophytes was strongly correlated to E_{bed} (Figure 3). This trend was best characterized by a quadratic polynomial, similar to existing photosynthesis-irradiance curves (Dodds et al., 1999). Above 15 mol m^{-2} day^{-1}, macrophyte coverage began to asymptote to 100%. Macrophyte cover within forested, mixed and grassed transects was

Table II. Habitat characteristics of forested, mixed and grassed transects in Big Spring Creek.

	Forested (mean ± SD)	Mixed (mean ± SD)	Grassed (mean ± SD)	ANOVA (*p*-value)
Transmitted PAR (% of E_{can})	26 ± 10	52 ± 7	80 ± 7	<0·001
Benthic PAR (mol m^{-2} day^{-1})	6·5 ± 3·0	13·5 ± 2·9	21·5 ± 2·3	<0·001
Macrophyte coverage (%)	21 ± 22	62 ± 27	90 ± 10	<0·001
Active channel width (m)	6·8 ± 1·5	7·8 ± 1·3	8·7 ± 1·7	0·007
Baseflow water depth (m)	0·64 ± 0·23	0·59 ± 0·24	0·53 ± 0·17	0·369
Bed sediment depth (cm)	10 ± 8	12 ± 8	22 ± 15	0·014
Bed sediment size, D_{50} (mm)	0·27 ± 0·32	0·17 ± 0·02	0·18 ± 0·03	0·772
Bed sediment OM (%)	2·5 ± 1·3	2·1 ± 1·1	2·1 ± 0·8	0·837
SRP net uptake (μg m^{-2} h^{-1})	−81 ± 291	N/A	322 ± 151	0·032*

Mixed transects have one forested bank and one grassed bank. Forested SRP uptake was derived from sites with 0% macrophyte coverage. Grassed SRP uptake was derived from sites with 80–100% macrophyte coverage.
* *t*-test.

respectively 21% ± 22%, 62% ± 27% and 90% ± 10% and was significantly different among the three transect types (Table II). Two transects had 0% macrophyte coverage (both forested) and two transects had 100% macrophyte coverage (both grassed). The lateral distribution of macrophytes varied greatly among all transects, displaying no obvious pattern.

Macrophyte biomass, as calculated from percent cover (Table I), in Big Spring Creek varied greatly throughout the year with maximum biomass occurring in mid-summer (Figure 4). In forested transects, where PC dominated throughout the year, mean dry biomass ranged 0–41 g m^{-2}. Mean dry biomass in grassed transects ranged 0–91 g m^{-2}, with ZD as the dominant species during mid-summer and PC dominant the rest of the year. In all transects, macrophytes senesced in early winter when water temperatures dropped below 1 °C and reemerged in early-spring when water temperatures consistently exceeded 5 °C.

Channel hydrogeomorphology

The presence of aquatic macrophytes in Big Spring Creek increased Manning's roughness (*n*) from 0·07 during winter (no vegetation) to 0·15 in mid-summer (maximum biomass). This increased roughness was associated with a rise in average baseflow water depth from 0·82 m during February 2006 to 1·15 m during July 2006 (Figure 5). The relationship between channel roughness and flow depth was comparable during floods. On 20 July 2006, a flood of 0·50 m^3 s^{-1} resulted in a flow depth of 1·3 m. On 12 September 2006, a similar flood of 0·53 m^3 s^{-1} resulted in a flow depth of 1·0 m. This 0·3 m difference was important because the July flood overtopped the channel banks, whereas the September flood did not.

The difference in channel geometry among forested, mixed and grassed transects was significant (Table II). Average active channel width for forested transects was 6·8 ± 1·5 m compared with 8·7 ± 1·7 m for grassed transects. This narrower width in forested transects typically led to greater flow depths, 0·64 ± 0·23 m compared with 0·53 ± 0·17 m for grassed transects. Moreover, bed sediment depth significantly increased from

forested (10 ± 8 cm) to mixed (12 ± 8 cm) to grassed (22 ± 15 cm) transects. Neither bed sediment size nor benthic OM content was significantly different among transect types.

Bed sediment depth also varied throughout the year, roughly following the same pattern as biomass (Figure 4). When averaged over all grassed transects, bed sediment depth ranged from 15 cm (23 September 2005) to 24 cm (6 July 2006). Sedimentation patterns at forested and mixed transects were more erratic, likely due to flood effects and changes in sediment supply. Turbidity remained relatively low and constant throughout the year (4·2 ± 2·1 NTU) not varying seasonally except following snow-melt events and in-channel vegetation senescence.

Phosphorus uptake

Mesocosms with macrophytes, which we used to represent grassed transects, had significantly higher uptake rates of SRP than control mesocosms with no macrophytes, representing forested transects (Table II). Macrophyte coverage within vegetated mesocosms ranged 80–100% and averaged 90%. Vegetated mesocosms removed SRP at a net rate of 322 ± 151 μg m^{-2} h^{-1}, whereas non-vegetated mesocosms, on average, actually released SRP at a rate of 81 ± 291 μg m^{-2} h^{-1}. Thus, gross SRP uptake by vegetated mesocosms was 403 μg m^{-2} h^{-1}. For an average summer day with 14·5 h of sunlight, 1 m^2 of macrophytes with 100% coverage would yield net and gross uptake of 0·0052 g day^{-1} and 0·0065 g day^{-1}, respectively; considering P uptake per gram of dry macrophyte biomass and assuming peak macrophyte biomass from this study (91 g m^{-2}) yields gross and net uptake rates of 0·057 mg g^{-1} day^{-1} and 0·071 mg g^{-1} day^{-1}. These values are consistent with a water-macrophyte P flux rate of 0·06 mg g^{-1} day^{-1} estimated by Pelton *et al.* (1998) using ^{32}P under ambient nutrient conditions. The average SRP concentration in Big Spring Creek from 15 May to 15 September was 0·012 ± 0·004 mg l^{-1}, which calculates to an average daily load of 379·7 ± 145·0 g day^{-1}.
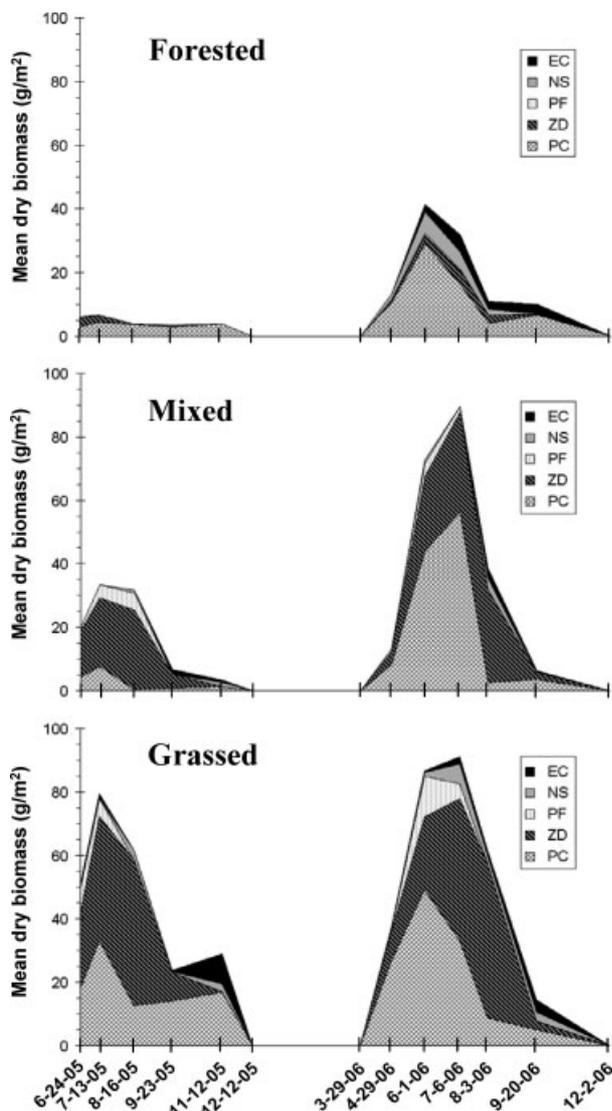
Figure 4. Temporal distribution of species-specific mean dry biomass of submerged macrophytes in Big Spring Creek for (a) forested, (b) mixed and (c) grassed transects. Labels on *x*-axis denote survey dates. Key: *P. crispus* (PC), *Z. dubia* (ZD), *P. pusillus/foliosus* (PF), *Nitella* spp. (NS) and *E. canadensis* (EC).

Reach-scale calculations

Integrating over the entire Big Spring Creek study area allowed us to compare all the above variables at the reach scale for a completely forested channel versus a completely grassed channel (Table III). The first and most obvious difference between the two types of reaches was shading. A forested reach allowed 97 505 mol of PAR per day to reach the water surface, whereas a grassed reach allowed 300 014 mol day^{-1} (208% increase). This increase in PAR was associated with a 328% increase in macrophyte biomass, from 150 to 642 kg.

Increased roughness from in-channel vegetation translated to a water depth 20 cm higher in the grassed reach than the forested reach. Average summer water depth was calculated using linear regression ($r^2 = 0.82$, $p < 0.001$) between water depth and reach-averaged macrophyte biomass from Figure 5 and using a 10-day moving average to minimize storm events. Bed sediment volume was

Table III. Average summer (15 May to 15 September) reach-scale (1212 m) differences between a second-order channel with completely forested versus completely grassed riparian zones.

	Forested	Grassed	Percent increase from forested to grassed
PAR entering reach (mol day^{-1})	97 505	300 014	208
Macrophyte biomass (kg)	150	642	328
Water depth (m)	0.87	1.07	23
Bed sediment volume (m^3)	1080	1933	79
SRP net uptake (% of daily load)	2.6	11.0	323

Reach-scale values were calculated using the transect values from Table II and integrating over the channel area, which was held constant for both forested and grassed reaches.

also much greater in the grassed reach, almost twice as much as the forested reach.

In a completely forested reach with 21% macrophyte coverage, 2·6% of the SRP load would be retained during a typical summer day. A completely grassed reach with 90% macrophyte coverage would retain more than four times as much SRP (11·0% of daily SRP load). These values are net uptake rates. Using gross uptake rates (*U* estimated from mesocosms with macrophytes—uptake from unvegetated mesocosms), macrophyte-associated SRP uptake increased to 3·2% and 13·8% of the daily load for forested and grassed reaches, respectively.

DISCUSSION

Light as a first-order control on fluvial ecosystem dynamics

Based on our observations, the first-order control on Big Spring Creek's summertime ecosystem structure at the reach scale was light (specifically the amount of PAR reaching the riverbed) because it stimulated macrophyte growth, which in turn influenced several key hydrogeomorphic and biogeochemical processes. We measured benthic PAR using the BLAM model (Julian *et al.*, 2008a), which takes into account shading by riparian vegetation and by the water column. From this previous study, we demonstrated that although water column light attenuation is usually the dominant control on benthic PAR in large rivers, riparian shading is the dominant control in smaller systems such as Big Spring Creek. Accordingly, turbidity values in Big Spring Creek were low and changed little over the course of this study. Further, water depths were relatively shallow and also varied minimally either spatially or temporally. Within this context, we assessed how changes in riparian vegetation affected light regimes in the stream.

In completely forested transects, only ∼26% of above-canopy PAR reached the water surface. When only
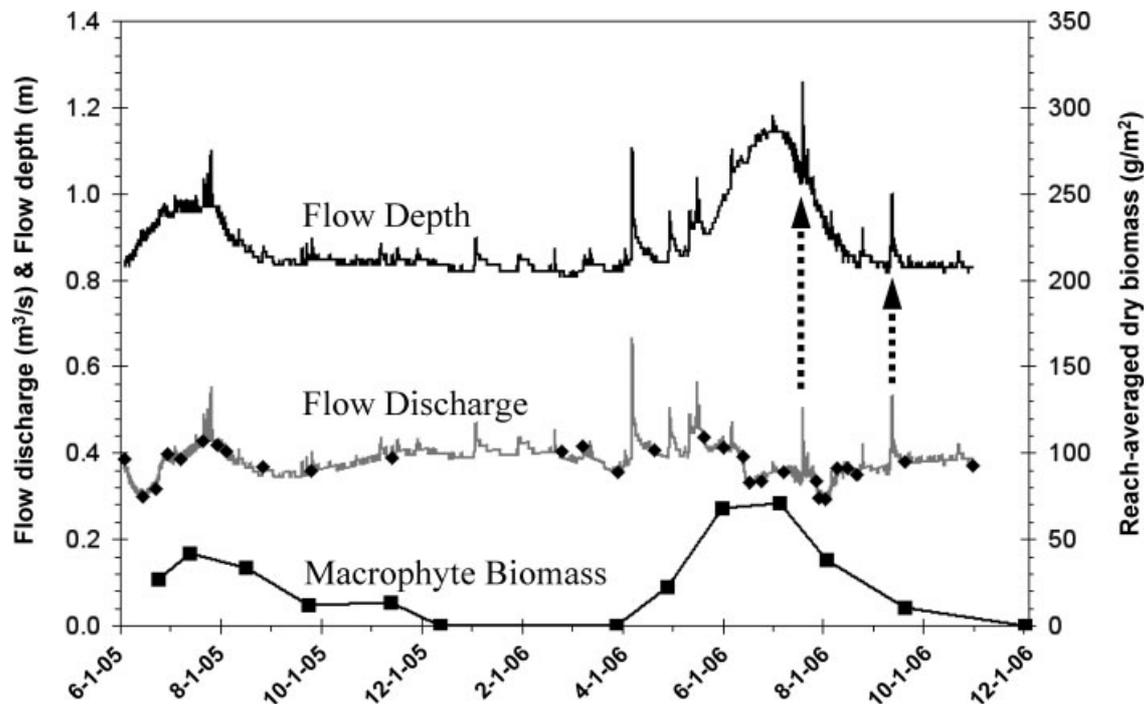
Figure 5. Time-series of macrophyte biomass (bottom), flow discharge (middle) and flow depth (top). Squares denote macrophyte survey dates. Diamonds denote *in situ* discharge measurements. Dashed arrows illustrate how two floods of similar discharge can produce substantially different flow depths in the presence of in-stream vegetation.

one bank was forested (i.e. mixed transects) twice as much PAR reached the water surface. And when neither bank was forested, ∼80% of above-canopy PAR reached the water surface. Thus, the difference in incoming PAR between forested and grassed sites at Big Spring Creek was more than threefold. For other systems, differences in incoming PAR among riparian communities depends on channel width, surrounding topography, canopy structure (height and density) and channel orientation (Davies *et al.*, 2008; Julian *et al.*, 2008b). Compared with north–south channels, east–west channels typically transmit more PAR due to greater canopy openings relative to the sun path (Gomi *et al.*, 2006; Davies *et al.*, 2008; Julian *et al.*, 2008a). Although these factors will be more influential in smaller streams due to their narrow widths, riparian type affects light regimes of all river sizes (Julian *et al.*, 2008b). Most importantly, changes in benthic light availability affect key components of fluvial ecosystems.

Spatiotemporal patterns of aquatic macrophytes

Highly shaded forested sites, such as transect 124 (Figure 2), averaged 21% macrophyte coverage in midsummer, with estimated biomass usually below 40 g m^{-2} (Figure 4). Open sites, such as transect 115, had much greater macrophyte coverage (90% ± 10%), and at some sites had complete coverage. In these grassed transects, macrophyte biomass approached 100 g m^{-2}. In all, we found a strong correlation between macrophyte coverage and benthic PAR (Figure 3), which supports previous evidence that light is generally the best predictor of vegetation growth in streams with favourable conditions (Dodds and Welch, 2000; Hilton *et al.*, 2006; Davies *et al.*, 2008).

Factors other than light that limit aquatic vegetation include grazing pressure, nutrient limitation, flow scour, unsuitable substrate, undesirable water temperature, interspecies competition and anthropogenic disturbances. At Big Spring Creek, the most likely source for the deviations in Figure 3 was unsuitable substrate. Upstream of our study reach was an impoundment that trapped most of the bedload supply, resulting in sections with minimal accumulations of sand in which the macrophytes could take root. Grazing and disruption by crayfish and vertebrates (muskrat, geese, deer) frequently observed at the creek may also have affected macrophyte standing crops. Our finding that PC dominated shaded sites, whereas ZD dominated open sites (Figure 4), suggests possible interspecies competition, which is supported by the evidence of Lacoul and Freedman (2006) of the ability of PC to thrive in shaded conditions.

Factors that were unlikely to affect macrophyte distribution in this system included flooding, nutrient limitation and human disturbance. Big Spring Creek is a lowland spring-fed stream and therefore does not usually experience flows capable of dislodging macrophytes. The few floods that did occur during our study period were not effective at removing vegetation (Figure 5). Located in a predominantly agricultural area, nutrient concentrations in Big Spring Creek were far above those that typically limit macrophyte growth. Indeed, fewer and fewer streams are nutrient limited (Hilton *et al.*, 2006). Similarly, because the creek is situated in a rural area and is almost entirely bordered by private property, in-channel human influences were restricted. We saw little evidence of farming influences on the study reach, as cattle and row

crops were excluded by a buffer at least 30 m, although upstream reaches and tributaries were likely subjected to these influences. Finally, although not a factor spatially, water temperature did dictate seasonal patterns of aquatic vegetation (Figure 4). The biomass peaks in summer and biomass nadirs in winter likely resulted from physiological mechanisms where macrophytes begin to senesce when water temperatures fall below 3 °C (Lacoul and Freedman, 2006).

Hydrogeomorphic feedbacks

The presence of aquatic macrophytes created several hydrogeomorphic feedbacks within Big Spring Creek. The most conspicuous temporal hydrogeomorphic effect was increased flow depths during the summer (Figure 5), resulting from increased channel roughness when the channel was vegetated. These higher flow depths have consequences for velocity patterns (Sand-Jensen and Pedersen, 1999), in-stream ecology (Hynes, 1970) and floodplain ecology (Jones *et al.*, 2008). For example, increased roughness from in-channel vegetation caused overbank flooding during the flood on 20 July 2006. A flood with slightly higher discharge on 12 September 2006, when macrophyte biomass was much lower, did not result in overbank flooding (Figure 5).

The most conspicuous spatial hydrogeomorphic influences of aquatic macrophytes involve bed sediment. Vegetated transects had more than twice the depth of sediment compared with non-vegetated transects (Table II). In addition to influencing biogeochemical processes, this greater sediment depth likely created a positive feedback loop with macrophyte growth (Bunn *et al.*, 1998). Temporal patterns in sediment transport caused by variation in macrophyte coverage are also likely (Schulz *et al.*, 2003). Significant differences in bed sediment size and OM content between vegetated and non-vegetated sites were not found at Big Spring Creek but are possible in other systems (Sand-Jensen, 1998; Horvath, 2004).

In summary, there are numerous hydrogeomorphic feedbacks that occur within vegetated stream channels, with the magnitude of impact dependent on the vegetation's morphology (stem and leaf structure, stiffness, size) and abundance (Sand-Jensen and Pedersen, 1999). For example, large, stiff macrophytes with high stem/leaf density will retard flow and trap more sediment than smaller, flexible vegetation. The spatial scale in which aquatic vegetation influences sediment transport therefore varies with species size and coverage. Due to seasonal changes in light regime, water temperature, discharge and grazer pressure, all the above influences of aquatic vegetation on flow and sediment transport can be temporally variable (Dawson and Robinson, 1984). Further, aquatic vegetation can have considerable indirect effects on channel processes by influencing the abundance of macroinvertebrates, fish, reptiles, amphibians and possibly mammals, which can greatly alter sediment transport within river systems.

Biogeochemical feedbacks

Aquatic vegetation influences numerous biogeochemical processes (Clarke, 2002), but in this study, we focussed on the uptake of SRP because routine monthly sampling revealed that P was likely the nutrient-limiting primary production given low SRP concentrations and N : P ratios consistently >100 (Powers and Julian, unpublished data). Our mesocosm experiments showed that vegetated sites with ~90% macrophyte coverage could take up considerable amounts of SRP, whereas non-vegetated sites actually released SRP. We suspect that SRP release in non-vegetated mesocosms was the result of a container effect where restricted flow throughout the experiment allowed sediment-derived P to accumulate in the water column. The lack of flow in the mesocosms also increased the size of the boundary layer surrounding macrophyte leaves. Because thinner boundary layers make it easier for macrophytes to take up gases and nutrients from the water column (reviewed by Franklin *et al.*, 2008), we likely underestimated the SRP uptake rate of macrophytes in Big Spring Creek. To be conservative in our reach-scale calculations, we did not take into account any releases of P from sediment or compensate for boundary layer effects in mesocosms.

Using the net uptake rate, we estimated that a completely forested 1·2-km reach would retain 2·6% of Big Spring Creek's daily load of SRP, whereas a completely grassed reach would retain 11·0%. If the gross uptake rate is used, forested and grassed reaches would retain 3·2% and 13·8%, respectively. Net and gross rates can be considered as lower and upper bounds on actual macrophyte uptake rates in the creek. Based on these estimates, we conclude that increased light availability (via reduced riparian shading) increases macrophyte standing crops, which in turn facilitates moderate increases in P uptake from the water column in Big Spring Creek. The role of light in controlling nutrient uptake has also been demonstrated for algal-dominated streams following canopy removal (Sabater *et al.*, 2000). Lastly, the increased sediment accumulation we found at vegetated sites likely translates to higher OM and P storage via sediment-associated OM and P. These contrasts in storage and uptake suggest a very different nutrient budget in forested versus grassed stream reaches.

Forested versus grassed channels

Our study illustrates that a completely forested 1·2-km reach in a second-order stream receives ~26% of above-canopy PAR, which results in ~21% aquatic macrophyte coverage. This 150 kg of macrophyte biomass produces an average water depth of 0·87 m, a bed sediment volume of 1080 m^3 and is responsible for the uptake of 2·6% of the stream's daily SRP load (Table III). When this same reach is non-forested, it receives three times more light and has more than four times the biomass of aquatic vegetation. Compared with the shaded forested reach, this unshaded grassed reach has an average water depth that is 20 cm higher, almost twice as much bed
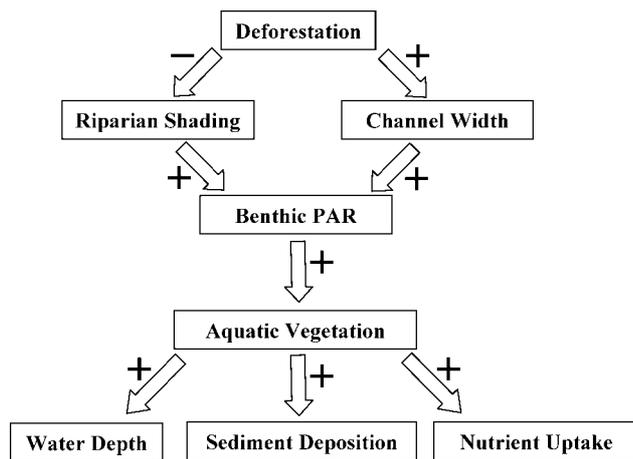
Figure 6. Heuristic diagram of the direct effects of riparian deforestation on stream hydrogeomorphology and biogeochemistry. Indirect effects are not included.

sediment, and a fourfold higher SRP uptake rate. These results can be used to illustrate the consequences of riparian deforestation on stream hydrogeomorphology and biogeochemistry: increased benthic light availability, resulting in a proportional increase in aquatic vegetation, which then increases water depth, sediment accumulation and nutrient uptake (Figure 6).

Another geomorphic difference we found between the two types of channels was that grassed sections were significantly wider (Table II). Our results are similar to DeNicola *et al.* (1992), who found that in a Nebraskan stream with similar characteristics to Big Spring Creek, channel widths decreased with increased riparian cover. In Trimble's (1997) study of the Coon Creek watershed in Wisconsin, however, forested channels were wider than grassed ones. Although in the same state, our study area was in a different environment where channel banks were more cohesive, sediment supply was much lower, and in-channel large woody debris was minimal. Using Trimble's (1997) rationale for the influence of riparian vegetation on channel width, our results likely differ because at Big Spring Creek tree roots increase the cohesion of channel banks; grassed banks do not accumulate large quantities of sediment, and destabilization from large woody debris is minimal. We suggest that the current debate as to whether the riparian community of a river affects its width should be put into this process-based context.

The wider grassed channel in our system was partly responsible for increased benthic PAR by further increasing the canopy opening (Figure 6). Wider channels typically have shallower water depths, which can also increase benthic light availability by reducing aquatic attenuation. Changes in depth did not greatly alter the light regime of Big Spring Creek because of its relatively clear water, but in more turbid streams, channel depth could have a significant impact on benthic light availability (Julian *et al.*, 2008a). In systems where forested streams are wider, opposite outcomes will occur and thus counteract the effect of increased primary productivity in unshaded sites (Bott *et al.*, 2006).

Our experimental design did not allow us to compare influences of riparian vegetation on water temperature, but other studies have found that unshaded reaches can be as much as 8 °C warmer than shaded reaches (Graynoth, 1979; Quinn *et al.*, 1997; Rutherford *et al.*, 2004; Gomi *et al.*, 2006), which is not only due to heating by incident radiation, but also due to evapotranspirational cooling by riparian trees (Gregory *et al.*, 1991). This large difference in water temperature can have substantial chemical and biological consequences in streams (Hynes, 1970). If we consider the trophic consequences of increased primary production (Carpenter and Lodge, 1986; Shupryt and Stelzer, 2009), it is evident that riparian vegetation has the ability to structure river ecosystems.

Applications

The information presented in this study poses various opportunities for future investigations into the interactions between physical and biological drivers, and also has applications for the practice of stream restoration. In many small stream restoration projects, the riparian zone is demolished, the channel is reconfigured and then a new riparian zone is planted. This study suggests that the choice of which vegetation to plant can greatly influence primary productivity, water depth, sediment deposition and nutrient processing by dictating the amount of light that reaches the river. Other studies have shown the choice of riparian vegetation can further dictate the stream's ecological communities (Scarsbrook and Halliday, 1999; Parkyn *et al.*, 2003). Assuming minimal grazing pressure and adequate hydrologic conditions, there exists an ideal light environment for aquatic vegetation in which they will occupy all available space (Kirk, 1994). In this study, the ideal light environment was $\sim$20 mol m^{-2} day^{-1}. By knowing this value or the relationship between E_{bed} and vegetation coverage, restoration plans can be designed according to the desired amount of in-channel vegetation.

The role of light also has implications for the management of streams with aquatic vegetation. Aquatic vegetation can provide valuable ecosystem services (food, habitat, nutrient processing) but can also have undesirable consequences such as overbank flooding (Figure 5). Stream managers have addressed this problem by cutting the vegetation, which is not only extremely time-consuming but also has been proven to be ineffective as cutting often leads to even greater biomass following rapid rejuvenation of the vegetation (Dawson, 1989). Thus, control of in-stream vegetation is limited by our ability to manipulate nutrient availability, grazing pressure, water temperature, flow velocities and light availability. Of these, light availability is the most feasible option by controlling riparian vegetation.

Two emerging issues related to the role of light in stream ecosystems are loss of aquatic vegetation from land-use changes and the introduction of aquatic vegetation in previously unvegetated channels. The clearing of riparian vegetation and increased turbidity associated

with agricultural land-use has considerably altered riverine light regimes and has thus changed spatial and temporal patterns in primary productivity (Julian *et al.*, 2008b). The clearing of riparian vegetation has also created favourable light conditions for the invasion of aquatic macrophytes in previously unvegetated channels, leading to the aforementioned feedbacks (Figure 6). One notable feedback that could have terrestrial consequences is the effect of these newly vegetated channels on hyporheic flow patterns (Jones *et al.*, 2008). Submerged macrophytes have historically been thought of as monospecific patches (Hynes, 1970), but with the increasing introduction of exotic and invasive species (especially from downstream lentic environments) macrophyte beds are likely to consist of numerous species, as demonstrated here (Figure 4). Indeed, the dominant species in Big Spring Creek, especially in shaded sections, was the invasive exotic PC. We expect that invasive and exotic vegetation will continue to inhabit streams, thus altering their ecology and hydrogeomorphology.

CONCLUSIONS

There have been numerous studies that have demonstrated how flow conditions and nutrient levels structure fluvial ecosystems. In this study we have shown that in a typical stream influenced by agriculture, light can be a first-order control on ecosystem dynamics. First, we quantified how much light entered the system, and specifically at the streambed. Second, we surveyed spatial and temporal patterns of in-channel vegetation. Third, we measured a suite of hydrogeomorphic and biogeochemical variables. Finally, we analysed relationships among all the variables, focusing on direct linkages. We found that increased benthic PAR in non-forested sites stimulated the growth of aquatic macrophytes, which in turn increased flow depths, sediment accumulations and P uptake.

This approach of predicting spatiotemporal trends of ecosystem variables using empirical correlations to hydrogeomorphic controls is a relatively recent paradigm in fluvial ecology. Examples include correlating OM and nutrient transport to discharge (Doyle *et al.*, 2005), fish distribution to suspended sediment concentration (Burcher *et al.*, 2007), macroinvertebrate distribution to channel geometry and substrate (Burcher *et al.*, 2007) and mussel distribution to channel gradient (Gangloff and Feminella, 2007). Although this coupling of hydrogeomorphology and fluvial ecology has led to several key contributions in the field, we have only begun to understand how physical and biological processes interact to structure fluvial ecosystems.

REFERENCES

APHA (American Public Health Association). 1998. *Standard Methods for the Examination of Water and Wastewater*, 20th edn. American Public Health Association, American Water Works Association, and Water Environment Federation: Washington, DC.

Bott TL, Newbold JD, Arscott DB. 2006. Ecosystem metabolism in Piedmont streams: reach geomorphology modulates the influence of riparian vegetation. *Ecosystems* **9**: 398–421.

Bunn SE, Davies PM, Kellaway DM, Prosser IP. 1998. Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. *Freshwater Biology* **39**: 171–178.

Burcher CL, Valett HM, Benfield EF. 2007. The land-cover cascade: relationships coupling land and water. *Ecology* **88**(1): 228–242.

Caraco NF, Cole J, Findlay S, Wigand C. 2006. Vascular plants as engineers of oxygen in aquatic systems. *Bioscience* **56**: 219–225.

Carpenter SR, Lodge DM. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany* **26**: 341–370.

Clarke SJ. 2002. Vegetation growth in rivers: influences upon sediment and nutrient dynamics. *Progress in Physical Geography* **26**(2): 159–172.

Curtis JT. 1959. *The Vegetation of Wisconsin*. The University of Wisconsin Press: Madison; 657.

Dane JH, Topp GC. 2002. *Methods of Soil Analysis: Part 4—Physical Methods, 5*. Soil Science Society of America: Madison; 1692.

Davies PM, Bunn SE, Hamilton SK. 2008. Primary production in tropical streams and rivers. In *Tropical Stream Ecology*, Dudgeon D (ed). Elsevier: Amsterdam; 23–42.

Dawson FH. 1978. The seasonal effects of aquatic plant growth on the flow of water in a stream. *Proceedings of the European Weed Research Society 5th Symposium on Aquatic Weeds*, Amsterdam; 71–78.

Dawson FH. 1989. Ecology and management of water plants in lowland streams. *Freshwater Biological Association Report* **57**: 43–60.

Dawson FH, Robinson WN. 1984. Submerged macrophytes and the hydraulic roughness of a lowland chalkstream. *Verhandlungen des Internationalen Verein Limnologie* **22**: 1944–1948.

DeNicola DM, Hoagland KD, Roemer SC. 1992. Influences of canopy cover on spectral irradiance and periphyton assemblages in a prairie stream. *Journal of the North American Benthological Society* **11**(4): 391–404.

Dodds WK, Biggs BJF, Lowe RL. 1999. Photosynthesis-irradiance patterns in benthic microalgae: variations as a function of assemblage thickness and community structure. *Journal of Phycology* **35**(1): 42–53.

Dodds WK, Welch EB. 2000. Establishing nutrient criteria in streams. *Journal of the North American Benthological Society* **19**: 186–196.

Doyle MW. 2006. A heuristic model for potential geomorphic influences on trophic interactions in streams. *Geomorphology* **77**: 235–248.

Doyle MW, Stanley EH, Strayer DL, Jacobson RB, Schmidt JC. 2005. Effective discharge analysis of ecological processes in streams. *Water Resources Research* **41**(W11411): 1–16.

Franklin P, Dunbar M, Whitehead P. 2008. Flow controls on lowland river macrophytes: a review. *Science of the Total Environment* **400**: 369–378.

Gangloff MM, Feminella JW. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, USA. *Freshwater Biology* **52**(1): 64–74.

Gomi T, Moore RD, Dhakal AS. 2006. Headwater stream temperature response to clear-cut harvesting with different riparian treatments, coastal British Columbia, Canada. *Water Resources Research* **42**: W08437, DOI:10.1029/2005WR004162.

Graynoth E. 1979. Effects of logging on stream environments and faunas in Nelson. *New Zealand Journal of Marine and Freshwater Research* **13**(1): 79–109.

Green JC. 2006. Effect of macrophyte spatial variability on channel resistance. *Advances in Water Resources* **29**: 426–438.

Gregory SV, Swanson FJ, McKee WA, Cummins KW. 1991. An ecosystem perspective of riparian zones. *BioScience* **41**(8): 540–551.

Gurnell AM. 1994. Aquatic weed growth and flow resistance—influence on the relationship between discharge and stage over a 25 year river gauging station record. *Hydrological Processes* **8**(1): 63–73.

Hilton J, O'Hare M, Bowes MJ, Jones JI. 2006. How green is my river? A new paradigm of eutrophication in rivers. *Science of the Total Environment* **365**: 66–83.

Horvath TG. 2004. Retention of particulate matter by macrophytes in a first-order stream. *Aquatic Botany* **78**: 27–36.

Hynes HBN. 1970. *The Ecology of Running Waters*. University of Toronto Press: Toronto; 555.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.

Jones KL, Poole GC, Woessner WW, Vitale MV, Boer BR, O'Daniel SJ, Thomas SA, Geffen BA. 2008. Geomorphology, hydrology, and aquatic vegetation drive seasonal hyporheic flow patterns across a gravel-dominated floodplain. *Hydrological Processes* **22**: 2105–2113.

Julian JP, Doyle MW, Stanley EH. 2008a. Empirical modeling of light availability in rivers. *Journal of Geophysical Research—Biogeosciences* **113**: G03022, DOI:10.1029/2007JG000601.

Julian JP, Stanley EH, Doyle MW. 2008b. Basin-scale consequences of agricultural land use on benthic light availability and primary production along a sixth-order temperate river. *Ecosystems* **11**(7): 1091–1105.

Kirk JTO. 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press: New York; 509.

Koetsier P, McArthur JV. 2000. Organic matter retention by macrophyte beds in 2 southeastern USA, low-gradient, headwater streams. *Journal of the North American Benthological Society* **19**(4): 633–647.

Lacoul P, Freedman B. 2006. Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews* **14**: 89–136.

Madsen JD, Chambers PA, James WF, Koch EW, Westlake DF. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**: 71–84.

Meals DW, Levine SN, Wang D, Hoffmann JP, Cassell EA, Drake JC, Pelton DK, Galarneau HM, Brown AB. 1999. Retention of spike additions of soluble phosphorus in a northern eutrophic stream. *Journal of the North American Benthological Society* **18**: 185–198.

Nepf HM. 1999. Drag, turbulence, and diffusion in flow through emergent vegetation. *Water Resources Research* **35**(2): 479–489.

Osterkamp WR, Hedman ER. 1977. Variation of width and discharge for natural high-gradient stream channels. *Water Resources Research* **13**(2): 256–258.

Parkyn SM, Davies-Colley RJ, Halliday NJ, Costley KJ, Croker GF. 2003. Planted riparian buffer zones in New Zealand: do they live up to expectations?. *Restoration Ecology* **11**(4): 436–447.

Pelton DK, Levine SN, Braner M. 1998. Measurements of phosphorus uptake by macrophytes and epiphytes from the LaPlatte River (VT) using ^{32}P in stream microcosms. *Freshwater Biology* **39**: 285–299.

Pitlo RH, Dawson FH. 1990. Flow-resistance of aquatic weeds. In *Aquatic Weeds: The Ecology and Management of Nuisance Aquatic Vegetation*, Pieterse AH Murphy KJ (eds). Oxford University Press: Oxford; 74–85.

Poff NL, Ward JV. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* **14**(5): 629–645.

Power ME, Dietrich WE. 2002. Food webs in river networks. *Ecological Research* **17**: 451–471.

Quinn JM, Cooper AB, Davies-Colley RJ, Rutherford JC, Williamson RB. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. *New Zealand Journal of Marine and Freshwater Research* **31**(5): 579–597.

Rutherford JC, Marsh NA, Davies PM, Bunn SE. 2004. Effects of patchy shade on stream water temperature: how quickly do small streams heat and cool? *Marine and Freshwater Research* **55**: 737–748.

Sabater F, Butturini A, Marti E, Munoz I, Romani A, Wray J, Sabater S. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society* **19**(4): 609–620.

Sand-Jensen K. 1997. Macrophytes as biological engineers in the ecology of Danish streams. In *Freshwater Biology*, Sand-Jensen K, Pedersen O (eds). G.E.C. Gad: Copenhagen; 74–101.

Sand-Jensen K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology* **39**(4): 663–679.

Sand-Jensen K, Mebus JR. 1996. Fine-scale patterns of water velocity within macrophyte patches in streams. *Oikos* **76**: 169–180.

Sand-Jensen K, Pedersen O. 1999. Velocity gradients and turbulence around macrophyte stands in streams. *Freshwater Biology* **42**(2): 315–328.

Scarsbrook MR, Halliday J. 1999. Transition from pasture to native forest land-use along stream continua: effects on stream ecosystems and implications for restoration. *New Zealand Journal of Marine and Freshwater Research* **33**: 293–310.

Schulz M, Kozerski HP, Pluntke T, Rinke K. 2003. The influence of macrophytes on sedimentation and nutrient retention in the lower River Spree (Germany). *Water Research* **37**(3): 569–578.

Shupryt MP, Stelzer RS. 2009. Macrophyte beds contribute disproportionately to benthic invertebrate abundance and biomass in a sand plains stream. *Hydrobiologia* **632**: 329–339.

Trimble SW. 1997. Stream channel erosion and change resulting from riparian forests. *Geology* **25**(5): 467–469.

USDA (US Department of Agriculture). 2007. UV-B Monitoring and Research Program, http://uvb.nrel.colostate.edu/UVB/.

Wade AJ, Whitehead PG, Hornberger GM, Jarvie HP, Flynn N. 2002. On modelling the impacts of phosphorus stripping at sewage works on in-stream phosphorus and macrophyte/epiphyte dynamics: a case study for the River Kennet. *Science of the Total Environment* **282–283**: 395–415.

Watson D. 1987. Hydraulic effects of aquatic weeds in U.K. rivers. *Regulated Rivers: Research & Management* **1**: 211–227.

Webster JR, Valett HM. 2007. Solute dynamics. In *Methods in Stream Ecology*, Hauer FR, Lamberti GA (eds). Academic Press: San Diego; 169–185.

Wilcock RJ, Scarsbrook MR, Costley KJ, Nagels JW. 2002. Controlled release experiments to determine the effects of shade and plants on nutrient retention in a lowland stream. *Hydrobiologia* **485**: 153–162.