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The geomorphological context and impact of the linear emergent macrophyte, *Sparganium erectum* L.: a statistical analysis of observations from British rivers

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ABSTRACT

This paper explores the geomorphological context and impact of the widely-occurring, linear emergent macrophyte, *Sparganium erectum.*

Forty-seven sites across Britain were selected for field investigation, spanning the range of environmental conditions within which *S. erectum* had been found to be present in previous analyses of national data sets. A combination of descriptive graphs and statistics, Principal Components Analysis, and Kruskal Wallis tests were used to explore the large multivariate data set collected at the 47 sites.

The analyses showed that *S. erectum* is present in significant quantities in relatively narrow and shallow (< 18 m wide and < 0.9 m deep to the limit of terrestrial vegetation), low gradient (maximum 0.004) channels of varying bed sediment calibre (cobble to silt). Within these environments, *S. erectum* stands (features) were associated with fine sediment retention, aggradation and submerged landform construction, leading to bench development and so, potentially, to adjustments in channel form and position. Sediment retention and landform construction within *S. erectum* features was most strongly apparent within reaches with a relatively high *S. erectum* cover and the presence of large area *S. erectum* features. It was also associated more weakly with *S. erectum* features that were comprised of relatively higher densities of plants with relatively smaller inter-plant spacing and fewer leaves. The sediment retained in *S. erectum* features and associated bench and bank toe deposits showed larger numbers and species of viable seeds, indicating the potential for colonisation and growth of other species on *S. erectum* features once they aggrade above the low flow water level and are no longer a suitable habitat for *S. erectum*.

KEY WORDS

bench, biogeomorphology, fine sediment, pioneer landform, *Sparganium erectum*

INTRODUCTION

There is increasing evidence to suggest that plants can have a significant impact on river channel size, form and dynamics (see recent reviews by Corenblit et al., 2007, 2009, Osterkamp et al., 2010, 2012, Gurnell et al., 2012; Gurnell, 2013). This is achieved by plant colonisation of the river's bed, banks and riparian margins, the trapping of sediments by the plant canopy, and the stabilisation of the trapped sediments by roots and other underground organs to produce pioneer landforms that can enlarge, coalesce, attach to the channel margins and eventually aggrade to the level of the surrounding floodplain. Indeed, Corenblit et al. (2007) describe a fluvial biogeomorphic succession whereby plants act as 'physical ecosystem engineers' (*sensu* Jones et al., 1997) inducing structural and functional changes to river systems across time and space through the interactions and feedbacks between 'engineering' plant species and fluvial processes. Whilst much research on this theme has been concerned with riparian vegetation, particularly trees and shrubs, aquatic plants may also be capable of modifying river size, form and dynamics.

Abiotic factors, including light, temperature, nutrients, substrate characteristics, typical flow conditions and also flow disturbance characteristics (flood and drought frequency, magnitude, duration) all have an enormous influence on the occurrence of freshwater aquatic macrophyte species and communities (Bornette and Puijalon, 2011). As a result, river ecosystem engineering by these plants can only occur within suitable envelopes of environmental conditions, which vary among plant species and groups (e.g. Bal et al., 2011; Miler et al., 2012). For example, an analysis of information drawn from several national data sets for Great Britain (Gurnell et al., 2010) demonstrated that assemblages of aquatic plants of different morphology were preferentially associated with river channels subject to particular ranges of physical conditions, notably flow energy (a combination of the median annual flood, channel gradient and channel width), bed sediment calibre and altitude. Analysis of the same national data sets by O'Hare et al. (2011) showed that sites with high abundances of particular species of aquatic macrophyte showed different plotting positions with respect to a gradient of increasing bed sediment calibre and decreasing unit stream power, and a gradient of decreasing altitude and channel gradient and increasing median annual flood and channel width. However, although different species and groups of macrophytes varied in their plotting position with respect to these gradients, the cover of aquatic plants was extremely small at sites with a unit stream power in excess of 400 $W.m^{-2}$, and significant abundances rarely occurred above a unit stream power of 100 $W.\ m^{-2}$.

Within an appropriate environmental envelope, the ability of aquatic macrophyte species to persist, retain sediment and build landforms, depends upon their flow resistance and also their ability to resist uprooting and severe damage from the drag, shear stresses, and sedimentation to which they are subjected. There are four broad types of aquatic plant: emergent (leaves protrude above the water surface); submerged (leaves and stems submerged below the water surface); rooted, floating-leaved (leaves float on the water surface, stems are submerged and attached to root systems in the stream bed); and free-floating (leaves usually floating on the water surface with stems and roots suspended in the water column) (Folkard, 2009). However, within each group, the morphology and strength of above-ground and below-ground biomass is highly variable, and thus the flow and erosion / uprooting resistance of different species within each group is also highly variable (Haslam, 2006). The flow resistance of individual species and also their susceptibility to flow damage is governed by leaf properties such as shape, size, serration and roughness (Albayrak et al., 2012); plant / shoot properties such as diameter, density, flexibility, strength and height; stand properties such as areal cover, heterogeneity, shoot density and biomass; and flow properties such as water depth and velocity (Folkard, 2009). The uprooting resistance of aquatic plants reflects the flow resistance of their canopy, and the consequent forces placed on the organs that anchor the plants into the substrate; the architecture, depth and strength of the plants' underground organs; and the nature of the substrate into which the plants are rooted (Bornette and Puijalon, 2011, Liffen et al., 2013a). Nevertheless, within their environmental envelope, individual species can show remarkable architectural plasticity, enabling them to adapt to variations in mechanical stresses (Puijalon et al., 2008, 2011).

This paper focuses on the most widely-occurring aquatic macrophyte species in Great Britain, *Sparganium erectum.* This linear-leaved, emergent species has a wide geographical range, being found in the margins of rivers and lakes across temperate parts of Europe and Asia and, as an introduced species, in North America, where it is viewed as a 'noxious weed' (USDA, 2013). It grows in dense stands (typically 100 stems per m^2 in mid summer) comprised of plants with tall (typically 2m by mid-summer), rigid vertical leaves that show a high uprooting resistance (> 150 N by mid summer) and a complex subsurface architecture of rhizomes (typically penetrating up to 15 cm depth) and dense fine roots (extending to maximum lengths in excess of 40 cm) (Liffen et al., 2011; 2013b). This species grows in a range of substrate and flow energy conditions, but is most frequently found growing from silty sediments in low gradient, low energy rivers (O'Hare et al., 2011), where it appears to trap silt, aggrading the river bed surface and stabilising the accumulated silty sediments with its network of roots and rhizomes. Gurnell et al. (2012) proposed a conceptual model of river bank extension in low-energy rivers colonised by emergent macrophytes such as *S. erectum*, whereby once the surface of the trapped sediment aggrades to the typical low-flow water level, other species start to colonise the sediment, allowing it to aggrade further forming a marginal bench and eventually aggrading to floodplain level (Figure 1).

Based upon analysis of available national data sets and data gathered during a purpose designed field campaign, we explore the physical environment context and the geomorphological role of *S. erectum* (Figure 1). Specifically, the research presented in this paper addresses the following questions:

1. What are the physical conditions under which this species can achieve a high cover and can retain significant quantities of sediment?
2. What are the characteristics of the plant stands at sites where significant quantities of sediment are retained?
3. What are the characteristics of the retained sediment; do these differ significantly from sediment retained elsewhere within the channel bed and banks; and do they provide support for the functioning of *S. erectum* as an ecosystem engineer?

METHODS

Site selection

47 sites were selected across Britain that spanned the range of energy conditions within which *S. erectum* has been found to be present in previous analyses of national data sets (Gurnell et al., 2010; O'Hare et al., 2011). Site selection was also based on information from air photographs and site visits, to ensure that the sites were accessible, unshaded and supported some cover of *S. erectum.* Figure 2 locates the 467 previously investigated sites (hereafter termed the large data set) and the 47 sites (field data set) that were selected for field survey. All sites were visited between early July and early September 2009, a period of the year when the canopy of *S. erectum* is fully developed. Data sets were then assembled to support (i) an investigation of the representativeness of the field sites in the context of the previous national analysis and (ii) to answer the three research questions listed in the introduction to this paper.

Information from national data sets (the large data set)

Information from the large data set was used to describe the environmental conditions under which *S. erectum* is found in river channels across Britain.

Information on six environmental variables was assembled. The median annual flood discharge (Qmed in $m^3.s^{-1}$) was estimated for each site from an equation which incorporates catchment properties (Robson and Reed, 1999), adjusted to take account of the degree to which the equation generated over- or under- estimates for local, similar sites that had a gauged discharge record (Morris, 2003). Valley gradient (in $m.m^{-1}$) was estimated over a 1 km valley length centred on each site from a 50 x 50 x 0.1 m resolution terrain model interpolated from Ordnance Survey of Great Britain contour data (Dawson et al., 2002, Morris and Flavin, 1990). In addition the elevation of each site (altitude in m above sea level), bankfull channel width (m) and observations of the sediment calibre on the river bed were extracted from River Habitat Surveys (Environment Agency, 2003). The ten observations (spot checks) of bed sediment calibre from each 500 m River Habitat Survey reach were combined to estimate a bed sediment calibre index (approximate phi units):

$$\text{Bed sediment calibre} = (-8 \times BO - 7 \times CO - 3.5 \times GP - 1.5 \times SA + 1.5 \times SI + 9 \times CL) / (BO + CO + GP + SA + SI + CL)$$

where BO (boulder), CO (cobble), GP (gravel/pebble), SA (sand), SI (silt) and CL (clay) represent the proportion of the spot checks allocated to each sediment calibre class. Note that because this index approximates a phi scale, it generates positive values for finer bed material and negative values for coarser bed material.

Total stream power ($W.m^{-1}$) was estimated from the Qmed and valley gradient values for each site:

$$\text{Stream power} = 9800 \times \text{Qmed} \times \text{gradient}.$$

The percentage of the channel covered by *S. erectum* was extracted from Mean Trophic Rank surveys (MTR, Dawson et al., 1999) and was converted to four abundance classes (absent, < 5%, 5-25%, > 25%) for the present analyses.

Field measurements (the field data set)

(i) Reach summary information.

Each reach was defined in the field to encompass a fairly uniform channel width and gradient, with *S. erectum* present at a reasonably constant cover and patch (hereafter termed ‘feature’) size. Reaches were up to 300 m in length and contained up to 20 discrete *S. erectum* features. Surveys were conducted during summer baseflow conditions. The reach gradient was estimated from the water surface gradient, surveyed using a level over a downstream distance of at least 40 m (five separate measurements were averaged). Bed material calibre was estimated as part of a River Habitat Survey (Environment Agency, 2003) over the length of each reach, and the bed sediment ‘spot checks’ were used to calculate a reach-scale estimate of bed sediment calibre in the same way as for the large data set.

(ii) *Sparganium erectum* feature characteristics

The overall abundance (percentage cover) and number of discrete *S. erectum* features within each reach was recorded. For each *S. erectum* feature, the length and breadth of the feature (from which the area was subsequently calculated), and the biogeomorphic stage of the feature (1 = no/minimal silt and finer sediment deposited around plants; 2 = small amount of fine sediment around plants; 3 = large amount of fine sediment deposited - sufficient to affect bed elevation; 4 = significant increase in bed elevation relative to surrounding river bed as a result of fine sediment deposition) were recorded.

(iii) Characteristics of a single representative cross-channel transect containing a *S. erectum* feature.

A cross-channel transect was located in a straight section of each reach and containing at least one discrete *S. erectum* feature that was representative of the most advanced biogeomorphic stage present in the reach. The cross profile was accurately surveyed using a level to characterise the bank top breaks of slope, the water’s edge, the limit of riparian vegetation (i.e. typical baseflow water level), water level at the time of survey, key details of bank and bed profile, and the outer limits and form of the *S. erectum* feature(s). These cross-profiles provided information on bankfull channel width and depth; channel width and depth at the lower limit of riparian vegetation; bank height and water depth at the time of survey; bank and bed form; and the form of any sediment accumulation around and within the *S. erectum* feature (Figure 3A).

Properties of the main *S. erectum* feature in the transect were measured, including maximum feature length and width, and properties of the *S. erectum* within a 0.5m x 0.5m quadrat placed in a representative area within the feature (canopy height, canopy cover, stem density, stem diameter, number of leaves per ramet, distance between stems).

Sediment samples were extracted (Figure 3) for laboratory analysis of sediment calibre, organic content, and seed abundance and species richness, from the following locations: 1 -

exposed channel bed sediment in the deepest water part of the transect; 2 - exposed bank toe sediment just below the limit of riparian vegetation and located at the channel margin away from the *S. erectum* feature; 3 - bed sediment at the centre of the *S. erectum* feature; 4 - bank toe sediment just below the limit of riparian vegetation and located at the channel margin adjacent to the *S. erectum* feature (if the feature was associated with marginal bench development this sample was taken at the bench toe); 5 – when present, at the centre of a marginal bench associated with (fringed by) the *S. erectum* feature.

Intact sediment cores were collected from each sampling location. One core was thoroughly mixed and a sub-sample (minimum 40 ml but larger for coarse sediments) was extracted for laboratory analysis of organic material and particle size. The top 2cm of two further cores (sampling area 157 cm^2) were combined to give 314 cm^3 sample volumes for germination trials. The former was frozen and the latter stored in a cold room before laboratory analyses and germination trials commenced.

Laboratory measurements

The samples for particle size and organic material content analysis were dried at 60 ^{o}C for 6 h. The percentage organic content was determined by loss on ignition (550 ^{o}C for 4 h). The particle size distribution was determined by sieving (2000, 1400 and 1000 μm) and then the sub-1000 μm fraction was passed through a laser diffraction particle size analyzer, following which the median particle size (D_{50}), % gravel, % sand, and % silt and % clay were calculated.

For the germination trials, samples were spread in a 1-2 cm layer over 3 cm depth of John Innes No. 2 compost in 22 x 16.5 x 5.5 cm seed trays. The seed trays were arranged randomly in a greenhouse, maintained at 20–22 ^{o}C with 16h daylight, and were watered to keep them moist. Once seedlings germinated, their species and abundance were recorded and they were weeded out to encourage further seed germination. The trials extended over 10 weeks.

Data Analysis

The study generated sizeable multivariate data sets that included observations on ratio and ordinal scales as well as percentages. Furthermore, many variables did not conform to a normal distribution. Therefore, following exploration of the data through scatter plots and summary statistics, statistical analysis employed nonparametric methods.

Principal Components Analysis (PCA) was used to explore several subsets of the data. In each case, PCA was applied to a rank correlation matrix in order (i) to reduce the data to a smaller number of independent dimensions and (ii) to identify the key original variables that were contributing to those dimensions or principal components (PCs). Interpretations focussed on PCs with eigenvalues greater than 1 and variables with loadings > 0.7 on individual PCs. The Kruskal Wallis test was used to establish whether subgroups of sites, samples or *S. erectum* properties were associated with statistically significantly different values of particular environmental variables or indices, or different scores on PCs. Where a significant difference among groups was identified, multiple pairwise comparisons using Dunn's procedure with Bonferroni correction established which subgroups were statistically significantly different from one another. All statistical analyses were conducted using XLSTAT 2011.

RESULTS

Representativeness of the 47 sampled sites in the field data set (Figures 4 and 5)

A first step was to explore the large data set of 467 river reaches using PCA to identify the broad physical characteristics of reaches that supported *S. erectum*. The reaches showed a good range in six environmental variables: altitude (0 to 473 m), valley gradient (<0.0001 to 0.1676), bankfull channel width (0.5 to 89 m), Qmed (0.1 to 576.2 $m^3.s^{-1}$), total stream power (<0.001 to 20545 $W.m^{-1}$) and bed sediment calibre (–8 phi (cobble) to 9 phi (very fine silt)). When Principal Components Analysis (PCA) was applied to this data set (Figure 4A), the first two PCs had eigenvalues greater than 1 and explained 73.4% of the variance (Table 1). Focussing on variables with loadings exceeding 0.7, total stream power had a positive loading on PC1 whereas bed sediment calibre had a negative loading, indicating that PC1 defined an energy gradient from low energy reaches with relatively fine bed sediment to high energy reaches with coarse bed sediment. Altitude and valley gradient both had high positive loadings on PC2, indicating a downstream gradient from steep headwaters to low gradient downstream reaches. Although their loadings were smaller (> 0.55), Qmed and bankfull channel width had positive loadings on PC1 and negative loadings on PC2, supporting the above interpretations of the two PCs. To explore the distribution patterns of *S. erectum,* its percentage cover at the 467 sites was plotted against the first two PCs (Figure 4A). *Sparganium erectum* was absent from steep reaches, located at relatively high altitude (Figure 4A, upper right quadrant of the scatter plot), was sometimes present, but in low abundance, in reaches with a large bankfull channel width and high Qmed and stream power (Figure 4A, lower right quadrant of the scatter plot), and was present with varying abundance in relatively low gradient, lowland reaches of relatively narrow bankfull channel width, low Qmed and stream power, and relatively fine bed material (Figure 4A, left quadrants of the scatter plot). Kruskal Wallis tests followed by multiple pairwise comparisons, identified statistically significant differences among the sites when grouped according their *S. erectum* cover class in relation to both PCs and all six variables apart from Qmed (Table 2). Sites which fell within the 5-25% and >25% *S. erectum* cover classes had a maximum total stream power of 2624 and 652 $W.m^{-1}$, respectively; bed sediment calibre ranging from –6.3 (cobbles) to 3.8 phi (very fine sand) and –4.0 (pebbles) to 1.5 phi (medium sand); a maximum gradient of 0.0099 and 0.0030; a maximum altitude of 100 and 104 m; a maximum bankfull width of 89 and 22 m; and a maximum Qmed of 490 and 369 $m^3.s^{-1}$

A second step was to explore some of the six variables more closely to identify a physical envelope within which the field survey sites fitted. A scatter plot of *S. erectum* abundance from the large data set in relation to Qmed and valley gradient revealed some clustering of sites with *S. erectum* cover in excess of 5% (Figure 4B). A third variable, bankfull channel width, was combined with Qmed and valley gradient into a single index, unit stream power (in $W.m^{-2}$). Analysis of the large data set revealed that low abundances of *S. erectum* could be found in reaches with a unit stream power up to 400 $W.m^{-2}$, but that abundances sufficient to give notable stands of *S. erectum* (> 5% *S. erectum* cover) did not occur at unit stream powers > 185 $W.m^{-2}$. This gave an upper energy criterion for *S. erectum.* It was found that when unit stream power was calculated for the sites in the field data set using the same variables as for the large data set, the maximum unit stream power associated with > 5% *S. erectum* cover was 110 $W.m^{-2}$ and with > 25% cover was 60 $W.m^{-2}$. Thus the field sites appeared to give a reasonable representation of the unit stream power range within which *S. erectum* reached significant abundance in the large data set (Figure 5). The field data set (Figure 5B) covers the range of unit stream power encompassing *S. erectum* cover classes 2 and 3 in the large data set (Figure 5A) and frequency histograms illustrate the range in the percentage channel area covered by *S. erectum* and unit stream power (based on Qmed, valley gradient and bankfull channel width from the large data set) within the field data set (Figure 5 C and D). Moreover, the field sites are centred within an area of the Qmed – gradient scatter plot (Figure 4B, solid line ellipse), where reaches with the highest *S. erectum* cover are found in the large data set.

The field surveys also revealed some limitations of the large data set for characterising the physical environment properties that support *S. erectum.* When the valley gradient (estimated from a national DTM over 1 km) and local channel gradient (estimated by field topographic survey over a 40+ m channel length) were compared, the latter were found to be more varied and smaller on average than the former (mean ratio of local gradient to valley gradient = 0.812). This suggests that the inclusion of a mean gradient over a 1 km valley length in the analysis of the larger data set probably overestimated the gradients in the 500 m River Habitat Survey reaches and the 100 m Mean Trophic Rank survey reaches from which the other data used in the analysis had been extracted (for further details see O'Hare et al., 2011) and that notable *S. erectum* cover may be a feature of local, lower gradient river sub-reaches. Furthermore, when the field survey reaches were overplotted on Figure 4B using local reach gradient rather than valley gradient estimates, they were centred on a slightly different area of the plot (compare areas enclosed by solid and dashed line ellipses, Figure 4B).

Physical properties of river reaches in relation to S. erectum cover

Because of the position of many of the field-surveyed reaches in low gradient rivers (minimum reach gradient = 0.00007, maximum = 0.00390), often in areas of intensive agriculture, it was apparent from site visits that the form of some of the reaches had been modified by anthropogenic interventions. 60% of sites had at least one bank extensively 'resectioned' to create near standard trapezoidal channels with steep banks. In addition at least 11 of the sites were subject to active vegetation management with routine cutting of riparian and/or instream vegetation. Although there was often evidence of geomorphological adjustment following these modifications, it was decided that the channel to the limit of riparian vegetation, which adjusts more quickly to the flow regime than the bankfull channel, was a more geomorphologically meaningful datum from which to compare channel dimensions and capacity among reaches than the bankfull level. Channel dimensions to this level were used with other, mainly field-surveyed, physical properties of the reaches to identify associations with the cover of *S. erectum*. The only variable retained from the large data set was Qmed, since few of the sites were located sufficiently close to flow gauging stations to provide a more site-specific flow analysis.

A PCA was performed on the percentage cover of *S. erectum* and four physical properties (bed sediment calibre: minimum = -8.0, cobble, maximum = 6.0, silt; channel width at riparian vegetation limit: min. = 2.43 m, max. = 17.85 m; channel depth at riparian vegetation limit: min. = 0.03 m, max. = 0.92 m; and stream power calculated from Qmed and local reach gradient: min. = 0.71 $W.m^{-1}$, max. = 707.5 $W.m^{-1}$). This identified two PCs with eigenvalues greater than 1, which explained 60% of the variance in the data set (Table 3). Focussing on variables with loadings greater than 0.7, PC1 identified a gradient of decreasing *S. erectum* cover (negative loading) with increasing channel width (positive loading) and PC2 described a gradient of increasing stream power (positive loading). Thus within the field sites, which represent a much narrower range of physical conditions than the large data set, channel width is most strongly associated with *S. erectum* cover. The maximum *S. erectum* feature stage was taken as an indicator of the ability of the species to act as an ecosystem engineer (by retaining sediment to build landforms) and was used to code the sites on a plot of site scores on PC1 and PC2 (Figure 6). There was a statistically significant difference in site scores on PC1 according to the maximum *S. erectum* feature stage (Kruskal Wallis test: $K = 7.4$, $P = 0.024$). Reaches with a distinct landform associated with the maximum *S. erectum* feature stage had a significantly lower score on PC1 than reaches where a smaller amount of sediment was retained at the maximum *S. erectum* feature stage ($P < 0.05$).

Thus distinct *S. erectum* landforms were found in channels of relatively smaller width (generally less than 10 m). Benches associated with *S. erectum* features were present in channels of all widths, indicating that the process of landform building associated with *S. erectum* occurs in larger channels within the range of channel sizes investigated. Furthermore, 100% of studied reaches that had ‘a distinct landform of fine sediment’ as their maximum feature stage also had an associated bench, whereas in reaches where the maximum feature stage was ‘a large amount of fine sediment’ or ‘a small amount of fine sediment’, 67% and 24% percent, respectively, had associated benches.

Properties of S. erectum

Bivariate scatter plots revealed a negative association between the average biogeomorphic development stage of *S. erectum* features (mean feature stage) and the density of features (features per metre) in the studied reaches (Figure 7A, Spearman correlation = -0.528, P<0.001). In other words features were on average more developed geomorphologically, where they were present in lower density. The average area covered by each feature and the total cover of *S. erectum* in the reaches were positively correlated (Figure 7B, Spearman correlation = 0.750, P<0.0001), indicating that as the cover of *S. erectum* increased, it tended to form larger area features.

PCA was applied to twelve *S. erectum* properties (Table 4). These included the percentage channel cover of *S. erectum* in the reach (min. = 1%, max. = 65%), five properties of the *S. erectum* features (features per metre reach length: min. = 0.003, max. = 0.182; mean feature area: min. = 1.36 m^2, max. = 113.0 m^2; mean feature length: min. = 2.38 m, max. = 29 m; mean feature breadth: min. = 0.5 m, max. = 6 m; mean feature development stage: min. = small amount of fine sediment; max. = distinct landform of fine sediment), and six properties of *S. erectum* plants / stand structure within a representative quadrat in the most developed feature (canopy cover: min. = 5%, max. = 100%; mean canopy height: min. = 0.36 m, max. = 2.43 m; mean stem density: min. = 3 per 0.25 m^2; max. = 33 per 0.25 m^2; mean stem diameter: min. = <0.5 cm, max. = 17 cm; mean number of leaves per ramet: min. = 3, max. = 14; mean distance between stems: min. = 0.01 m, max. = 0.52 m).

Four PCs had an eigenvalue in excess of 1, but the first two PCs were particularly prominent and explained over 50% of the variance in the data set. Focussing on loadings larger than 0.7, PC1 describes a feature size and development gradient, showing that as % *S. erectum* cover increased, so also did all dimensions of feature size (all positive loadings) and their average development stage (positive loading, indicates increasing retention of fine sediment and landform development). PC2 described a gradient in *S. erectum* plant / stand structure with an increase in the size of individual plants (stem diameter has positive loading) being accompanied by a decrease in within-stand *S. erectum* stem density (negative loading) (Figure 7D). When the maximum feature stage was coded onto the scatter plot of site scores with respect to PC1 and PC2 (Figure 7C), it was apparent that the greatest development stages were found at sites with a relatively high percentage channel cover of *S. erectum*, large *S. erectum* features and relatively denser and higher cover of *S. erectum* plants. This was supported by a Kruskal Wallis test (K=10.6, P=0.014), where the scores on PC1 of sites with a maximum development stage involving a distinct landform of fine sediment were significantly greater than sites where only a small amount of sediment was retained. This implies that for landform building, individual plant size is less important than the number / density of plants present within the *S. erectum* features.

Sediment characteristics of S. erectum features

This section briefly summarises the characteristics of sediment samples obtained from the channel margins and bed within transects located in each of the surveyed reaches. For a more detailed analysis of this sediment data set, including discussion of sediment chemistry and seed species present, see O'Hare et al. (2012).

Samples were obtained from five sites both in and around *S. erectum* features, from any associated bench and from the bed and bank toe away from *S. erectum* features (Figure 3). The measured sediment properties all showed a wide range of values (Table 5). The statistical significance of differences in these sediment properties between the five sampling locations were investigated using Kruskal Wallis tests followed by multiple pairwise comparisons (Table 5). The proportion of gravel varied significantly between *S. erectum* -related sampling locations and others, but there was no statistically significant difference in the percentage silt and clay, and percentage organic material only differed significantly between the river bed and other samples. The number of species and abundance of viable propagules was significantly greater in *S. erectum*-related samples than in samples from other locations.

In order to explore the interrelationships between these sediment sample properties, they were included in a PCA. The PCA identified two PCs with eigenvalues greater than 1, which explained 63% of the variance in the data set. Of these first two PCs, loadings of > 0.7 were only found in association with PC1, which described a gradient of increasing particle size (% gravel has a positive loading and D_{50} a negative loading) and decreasing abundance and number of species of seeds. Figure 8 shows the samples plotted according to their scores on PC1 and PC2 and coded according to the five sampling locations. *Sparganium erectum*-related samples show a preferential distribution towards the left of the scatter plot (corresponding to increasing (i.e. fining) D_{50} and increasing abundance and number of species of seeds), particularly towards the lower left quadrant of the plot (corresponding to increasing % organic material), and perpendicular to (i.e. independent of) a particle size gradient that runs diagonally across the plot from high % gravel to high D_{50}. This contrast between *S. erectum*-related and other samples was confirmed when Kruskal Wallis test were applied to sample scores on PC1, grouped according to the five sampling locations. There were significant differences between sampling locations ($K = 51.7$, $P < 0.0001$) with respect to their scores on PC1, with all *S. erectum*-related sample locations (3, 4 and 5) showing significantly lower scores than the other sample locations (1 and 2).

DISCUSSION AND CONCLUSIONS

The results of this research can be considered in relation to the research questions stated in the introduction to this paper.

Research Question 1: What are the physical conditions under which S. erectum can achieve a high cover and can retain significant quantities of sediment?

Analysis of the large data set revealed that British rivers that support more than a 5% cover of *S. erectum* have distinct physical characteristics. They are generally low gradient, low energy lowland systems with relatively fine calibre bed material, and a unit stream power, estimated from the median annual flood, valley gradient and bankfull channel width, that is less than 185 $W.m^{-2}$.

Using the above energy criterion, 47 field locations were investigated where *S. erectum* was present. These river reaches had a wide range in bed sediment calibre (cobble to silt) but their channels were relatively narrow and shallow (< 18 m width and < 0.9 m average depth at the limit of terrestrial vegetation) and of relatively low gradient (maximum 0.004). Within this restricted range, an increase in *S.erectum* cover and the presence of a distinct sediment landform at the maximum feature stage was particularly associated with relatively narrow channels. Nevertheless, benches were found in channels of all widths, with the proportion of reaches supporting benches increasing with the maximum feature stage. In particular, all reaches which showed a distinct sediment landform at the maximum feature stage also supported benches. This supports the biogeomorphic model proposed in the introduction to this paper (Figure 1), whereby sediment trapping by *S. erectum* stands leads to the development of emergent sediment benches that support wetland and riparian vegetation and gradually aggrade to support floodplain extension and channel migration (Gurnell et al., 2012).

Research Question 2: What are the characteristics of the plant stands at sites where significant quantities of sediment are retained?

If *Sparganium erectum* acts as an ecosystem engineer, trapping sediment and supporting landform development, then it is of interest to know what properties of the *S. erectum* stands are most conducive to this landform building process. This theme was explored by considering the subset of stand and plant features that are most associated with reaches where the maximum feature stage incorporates the presence of a distinct sediment landform. Feature stage was found to be strongly associated with feature size and canopy cover within the feature as well as with the cover of *S. erectum* across the reach, and negatively associated with the number of features. The properties of the individual plants were less important, but feature stage was weakly positively associated with relatively higher densities of plants with relatively smaller inter-plant spacing and fewer leaves. This suggests that tightly packed stands of *S. erectum* are more effective in retaining sediment than more open low density stands of larger individual plants, but that the size (length, breadth, area) of the stand is more important than the properties of the individual plants. This is consistent with laboratory studies, which confirm that stand density influences erosion and deposition patterns in and around patches of emergent vegetation (Follett and Nepf, 2012). The importance of stand size is unsurprising, in that edge effects, where scour and remobilisation of sediment can easily occur, are minimised. Moreover, the size of the feature is likely to be important as a protective leading edge for bench development.

Research Question 3: What are the characteristics of the retained sediment, do these differ significantly from sediment retained elsewhere within the channel bed and banks, and do they provide support for the functioning of S. erectum *as an ecosystem engineer?*

The properties of sediment samples obtained from within, around and remote from *S. erectum* features showed a clear impact of *S. erectum* on the character as well as the quantity of the sediment. Whilst channel bed samples were significantly coarser and contained less organic material than other samples, there was no statistically significant difference in silt and organic material content between the *S. erectum*-related samples and those from bank toe locations where *S. erectum* was not present. However, *S. erectum* features and associated bench and bank toe deposits showed larger numbers and species of viable seeds, indicating the potential for colonisation and growth of other species on *S. erectum* features once they aggrade above the low flow water level and are no longer a suitable habitat for *S. erectum*. This confirms the suggestion by Gurnell et al. (2007) that emergent macrophyte stands are key in-channel retention sites for sediments and viable seeds indicative of a potentially important coupling between geomorphological and ecological systems. It also shows that *S. erectum* is an important engineer of the physical properties of low energy river systems, building landforms that can emerge as benches and ultimately contributing to channel planform adjustment, but seed and nutrient trapping coupled with landform development provide a progressively terrestrialising habitat that can support the growth of other plant species, indicating the ecosystem engineering role of the species.

Wider implications

Despite the human modification of many of the lowland river sites included in this study, it was possible to extract meaningful trends from the collected data to answer the research questions. This suggests that *S. erectum* is able to colonise these low energy rivers and to modify them quite rapidly through sediment retention. The process that is highlighted by our analyses is not uniquely associated with aquatic plants. Rhoads and Massey (2012) describe a similar process of bench formation in agricultural ditches in the American Midwest, associated with the strong frictional effects of grasses extending into the flow, and Bennett et al. (2008) report flume experiments to support the in-channel planting of woody vegetation to induce channel narrowing and meander formation in straightened degraded streams. All of these examples illustrate that vegetation extending into the flow or growing on the channel bed is able to induce channel adjustment and, as a result, recovery from channel straightening and widening. The type of vegetation that can achieve this varies across different channel sizes and environments.

While sediment retention in the small lowland rivers investigated in this paper was mainly within *S. erectum* stands located close to the banks, leading to a process of bench development, there is no reason why the same process should not lead to bed aggradation in the middle of the channel and the eventual building of small islands. Indeed, significant sediment retention was observed around stands located away from the banks at some sites. In a recent paper, Schoelynck et al. (2012) present experimental work that illustrates self-organisation and biogeomorphic feedbacks associated with submerged, rooted macrophytes. They found that patch size followed a power law, indicative of spatial self-organisation. By transplanting plants and using mimics within, close to and distant from existing patches, they found that there was a positive feedback in the survival, growth and sedimentation around plants within patches and negative feedback of decreased survival and erosion when transplants were located close to but not within existing macrophyte patches. They also found statistically significant positive correlations between both patch width and patch length, and the height of the aggraded sediment surface within the patch.

The biogeomorphic feedbacks inferred from the analyses presented in this paper not only indicate the potential of *S. erectum* to accelerate channel recovery from human interventions and induce channel dynamics in lowland, low energy river systems (e.g. Figure 9) but also to increase the habitat complexity of the channel bed and margins. Although the focus of this paper is single thread streams, such feedbacks are likely to be important in the development of multi-thread patterns in low energy river environments

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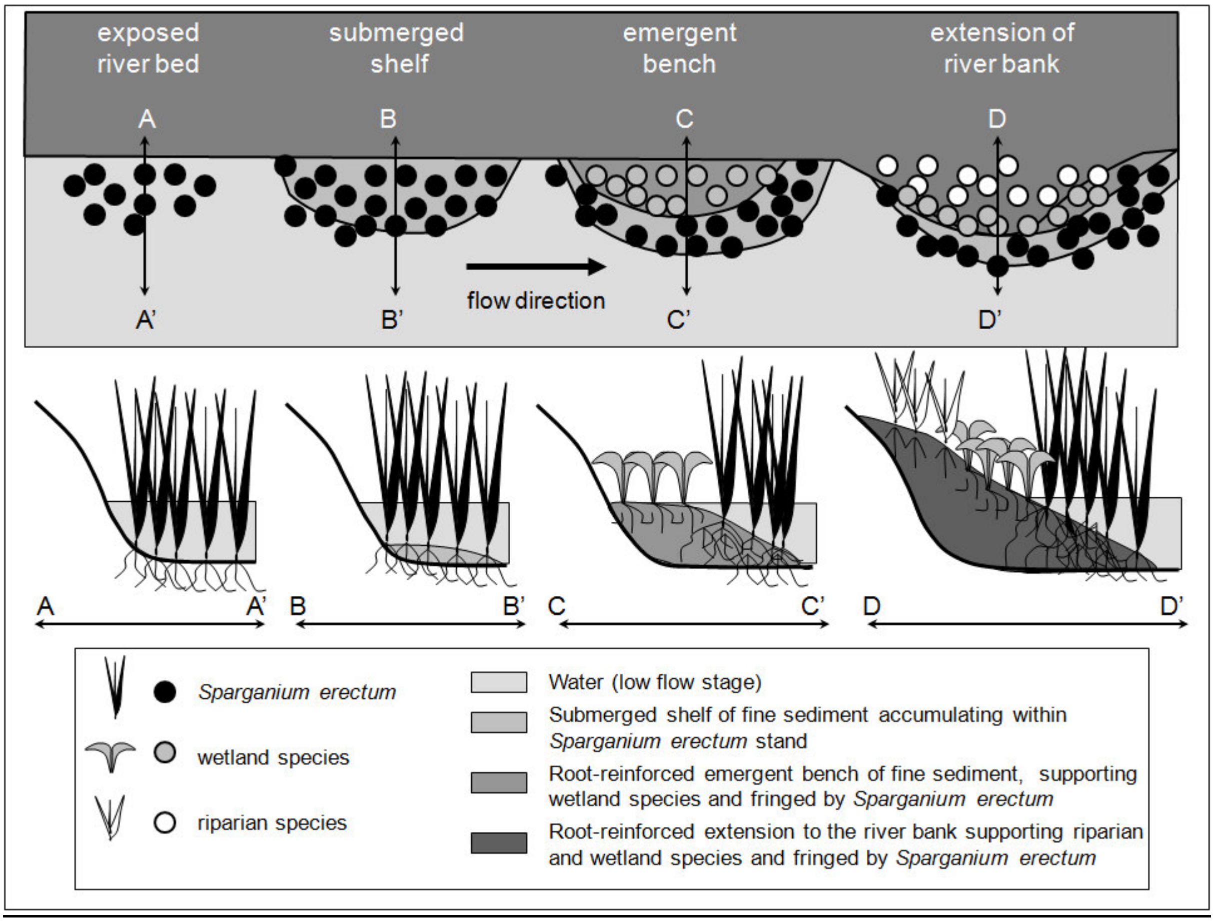

Figure 1: River ecosystem engineering by *Sparganium erectum.*

A. *Sparganium erectum* stand (feature) growing on river bed;
B. Retention of fine sediment to form a submerged shelf;
C. Lateral expansion and aggradation of retained sediment to low flow water level, leading to colonisation of the exposed surface by wetland species to form a bench with *S. erectum* protecting the toe of the feature;
D. Further lateral and vertical extension of the feature to create an extension of the river bank that is reinforced by riparian and wetland plants with the submerged toe protected by *S. erectum.* (Note that plant propagules trapped with the fine sediment are available for germination and growth as the surface of the sediment feature aggrades). (modified after Gurnell et al., 2012).

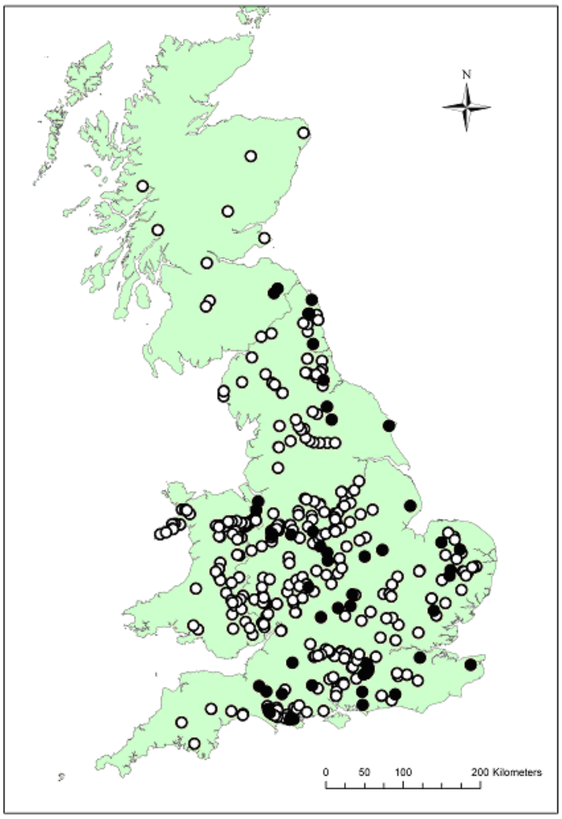

Figure 2 Site locations (white-filled circles: 467 sites for which data from national data sets was analysed previously (the large data set, Gurnell et al., 2010; O'Hare et al. (2011)); black-filled circles - 47 sites for which field survey data is presented and analysed in this paper (the field data set)).

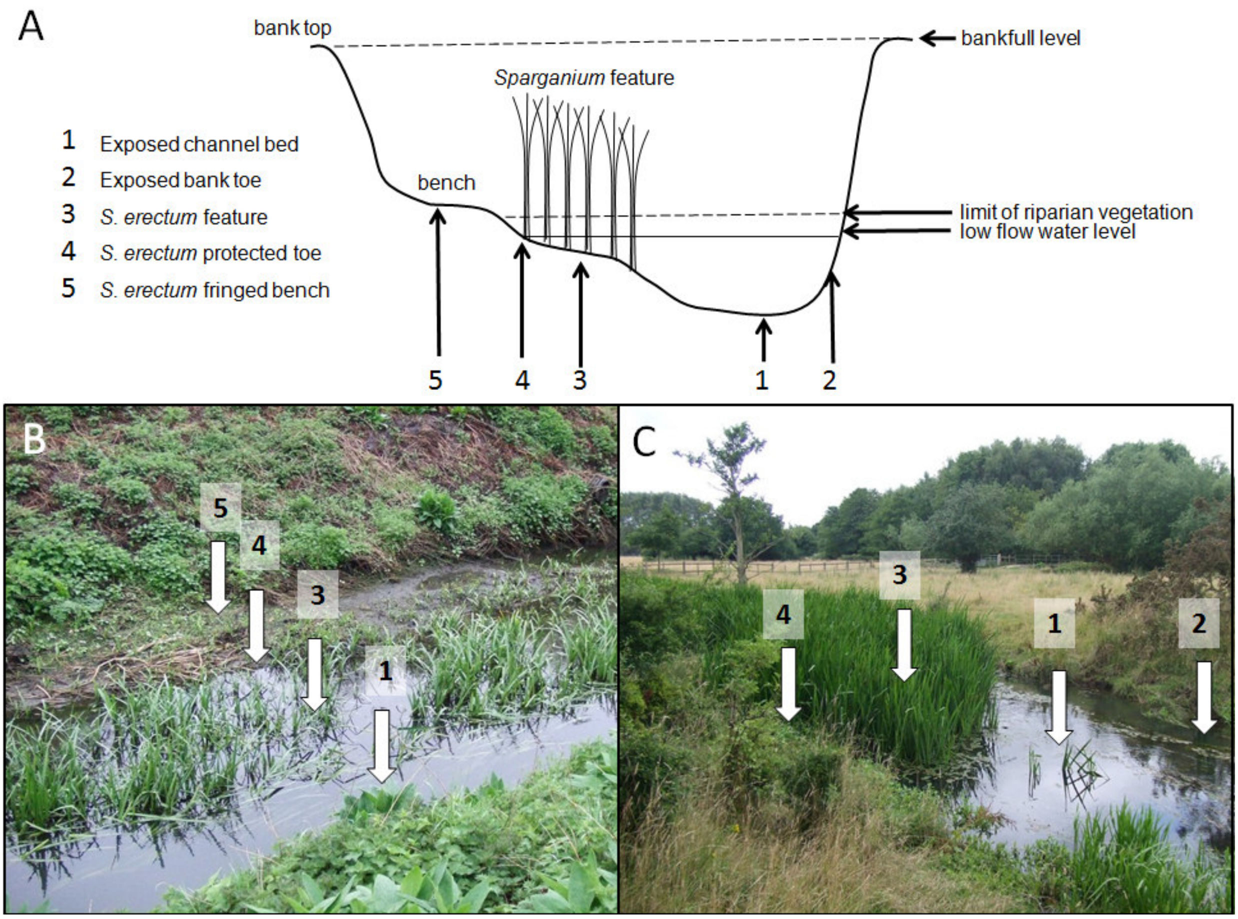

Figure 3 Transect sediment sampling locations

A. A minimum of 4 (locations 1 to 4) and a maximum of 5 (includes location 5) samples were taken, depending upon whether on not the *Sparganium* feature was associated with a marginal bench.
B. A *Sparganium* feature early in the growing season, revealing a small associated bench at the river margin, with sediment sampling sites 1, 3, 4, and 5 indicated
C. A *Sparganium* feature at the peak of the growing season with sediment sampling sites 1, 2, 3, and 4 indicated

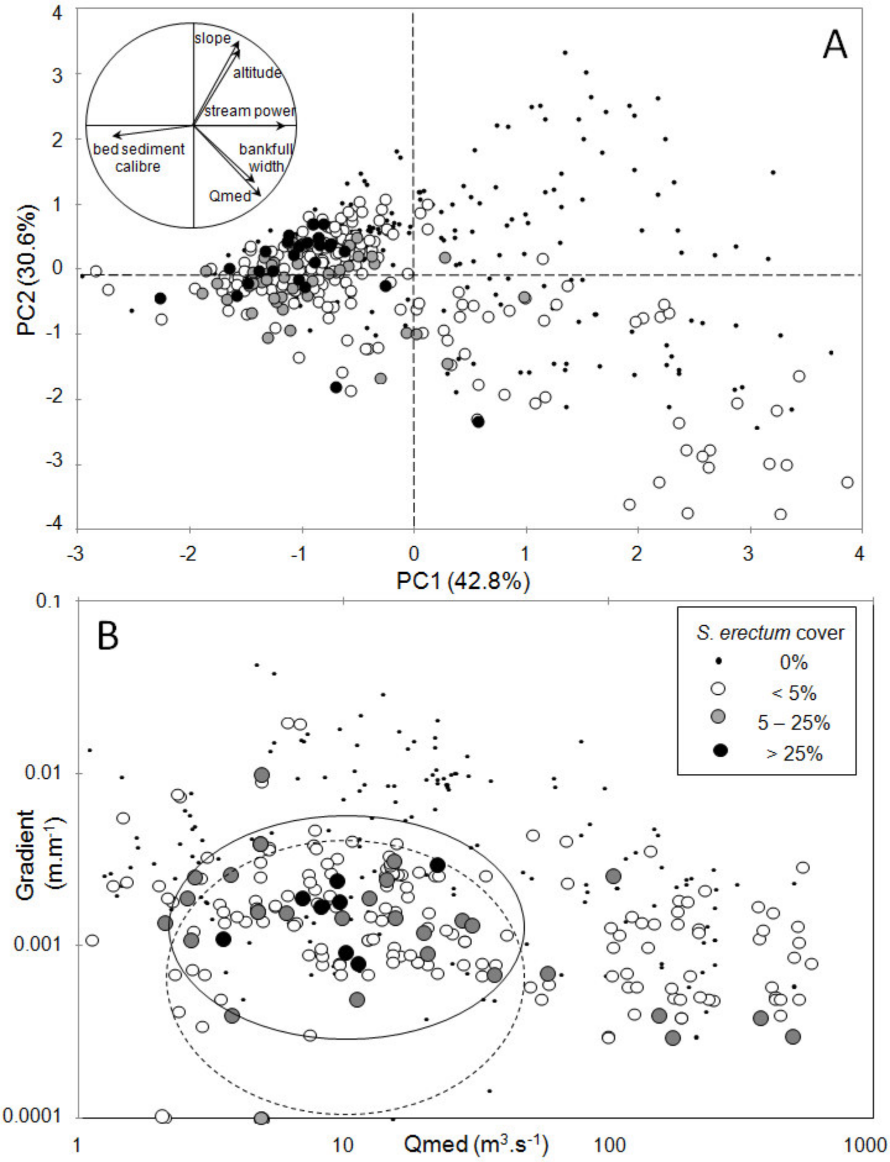

Figure 4

A. The cover of *Sparganium erectum* within the 467 reaches of the large data set in relation to the reach plotting position with respect to the first two components of a PCA. The inset shows the 7 variables that were included in the PCA and their loadings on the first two principal components.

B. The cover of *Sparganium erectum* within reaches of the large data set in relation to gradient and median annual flood (derived, respectively, from field surveys of macrophyte species abundance, a 50×50×0.1 m resolution terrain model interpolated from contour data of the Ordnance Survey of Great Britain, an equation incorporating catchment descriptors and a regional calibration to observed flow records). For explanation of the solid and dashed ellipses, see text.

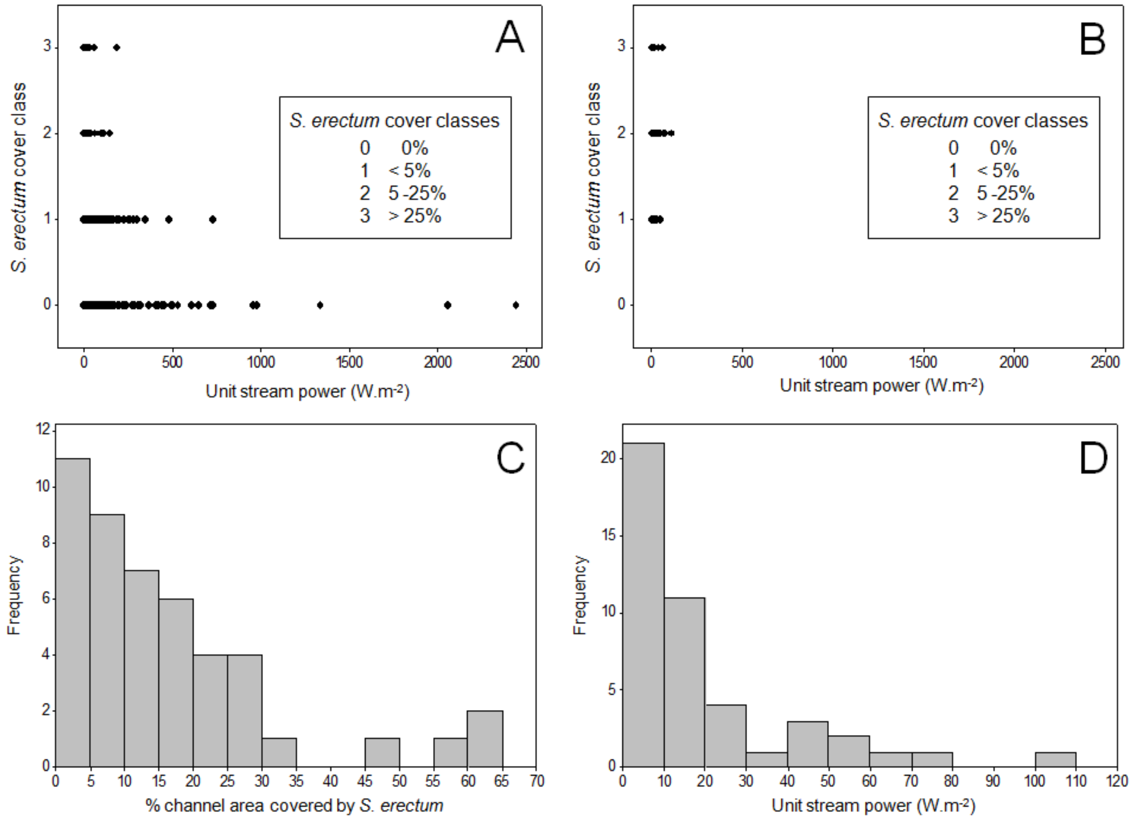

Figure 5

A. The association between *Sparganium erectum* cover and unit stream power across the 467 sites of the large data set.

B. The association between *S.erectum* cover and unit stream power across the 47 sites of the field data set.

C. Frequency distribution of S. erectum cover across the field data set 47 sites.

D. Frequency distribution of unit stream power (based on Qmed, valley gradient and bankfull channel width) across 47 sites of the field data.

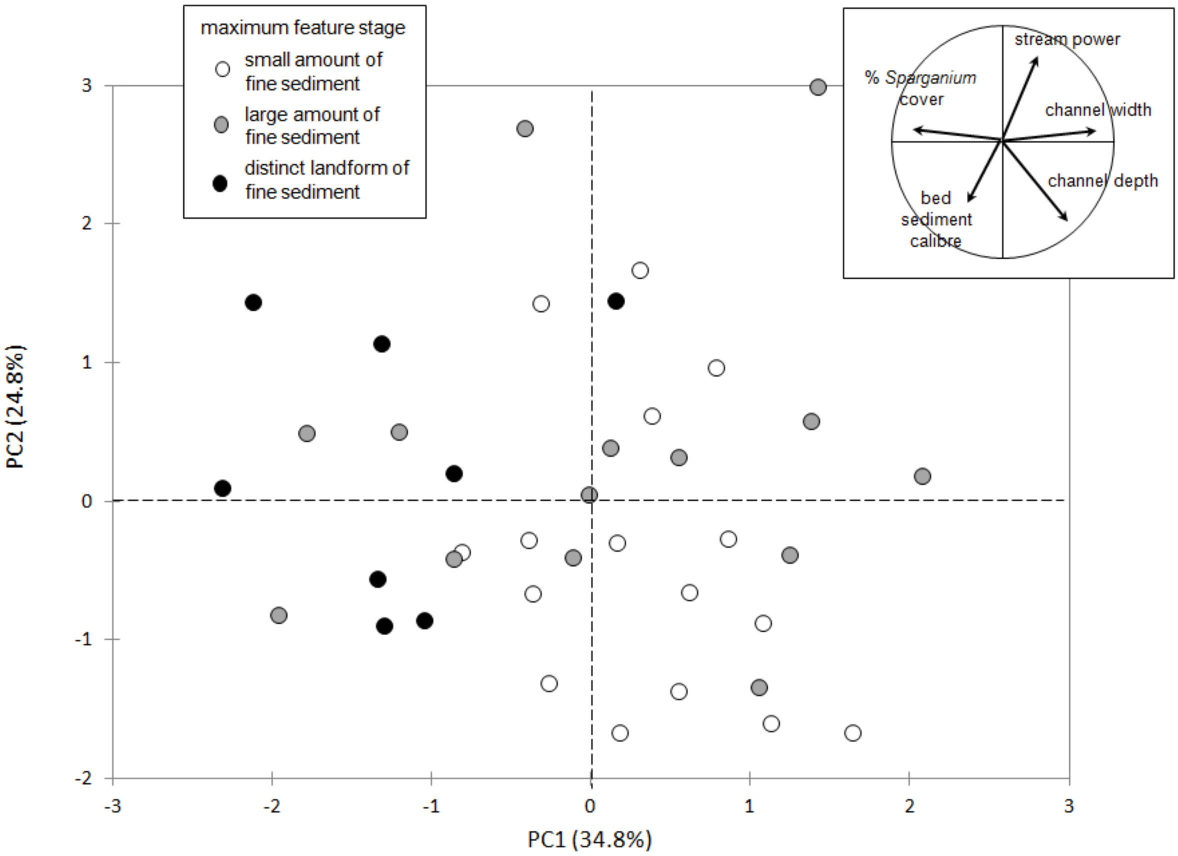

Figure 6. The maximum *Sparganium erectum* feature stage in the 47 river reaches of the field data set in relation to the reach plotting position with respect to the first two components of a PCA. The inset shows the 7 variables that were included in the PCA and their loadings on the first two principal components.

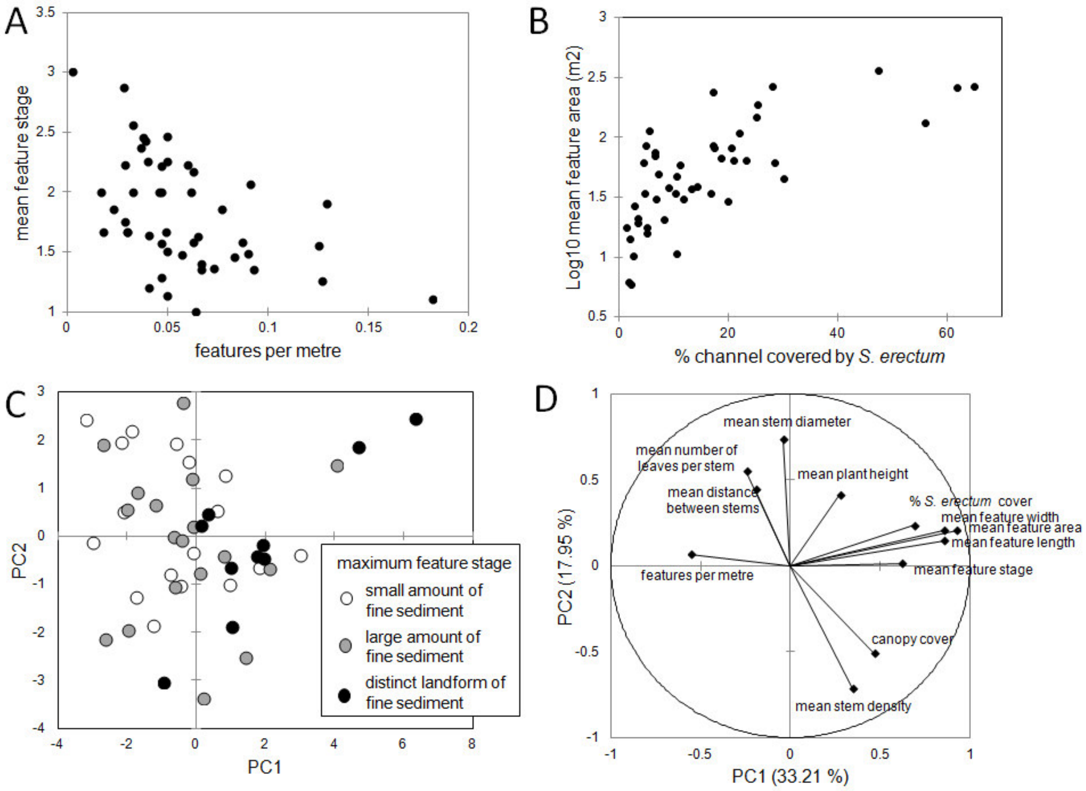

Figure 7 The characteristics of *Sparganium erectum* cover, structure and features and their relationship with sediment retention and landform development at the 47 sites of the field data set.

A. Scatter plot of mean *Sparganium* feature development stage against the number of *Sparganium* features per metre channel length.

B. Scatter plot of the mean area of *Sparganium* features (log10 transformed) against the percentage of the channel covered by *Sparganium erectum*.

C. The 47 sites plotted according to their scores on PC1 and PC2 of the PCA represented by the loading plot in D and coded according to the maximum *Sparganium* feature development stage observed at each site.

D. Plot of the loadings of the 12 variables on PC1 and PC2 of the PCA of *Sparganium* characteristics.

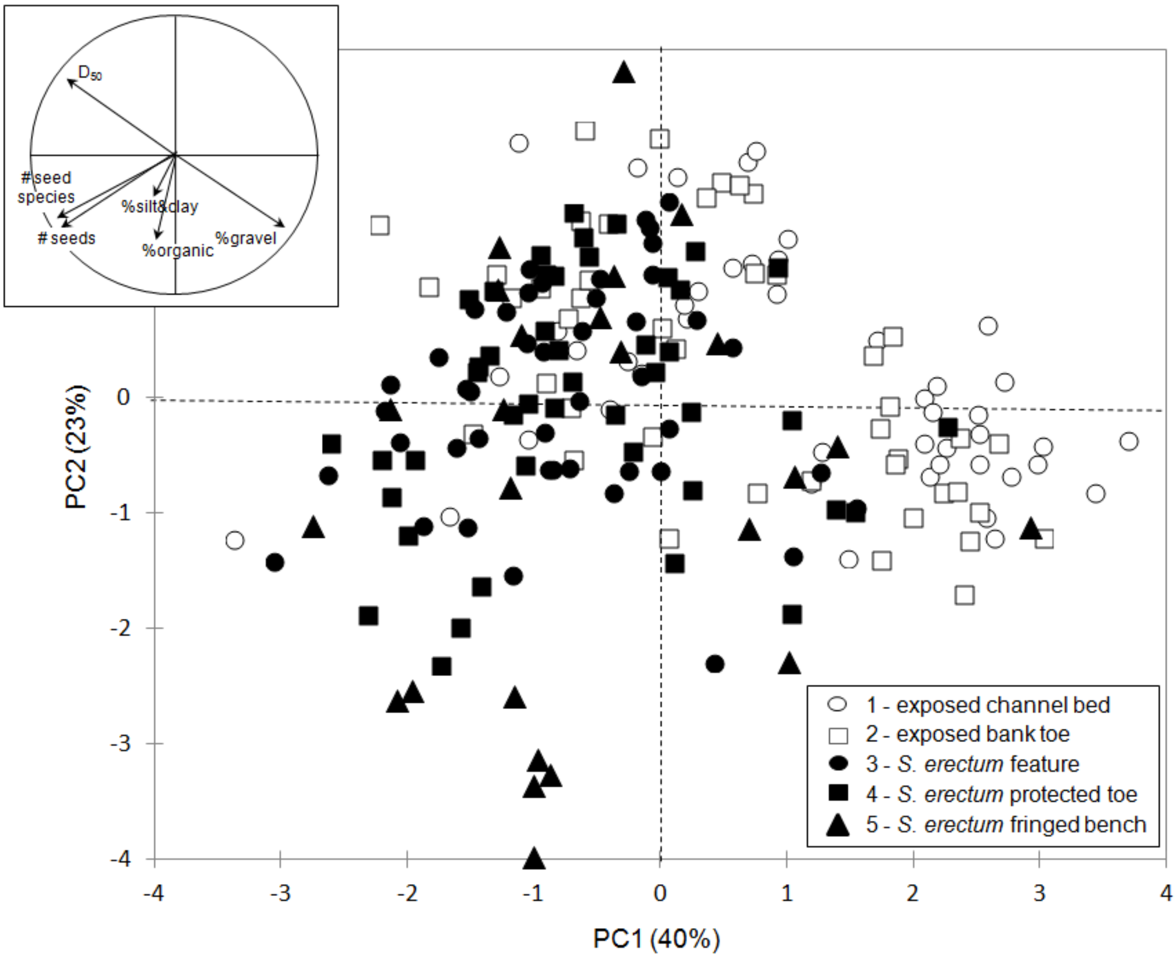

Figure 8 The plotting position of sediment samples obtained from 47 sites and representing exposed locations (exposed channel bed – location 1, exposed bank toe – location 2) and locations within or adjacent to stands of *Sparganium erectum* (within *S.erectum* feature – location 3, bank toe protected by *S.erectum* feature – location 4, *S.erectum* – fringed bench, location 5) plotted according to their scores on the first two axes of a PCA ordination of the sediment's physical and propagule bank characteristics. The inset graph displays the loadings of the 6 variables included in the PCA on the first two principal components.

Figure 9. Channel migration, River Blackwater, UK. *Sparganium erectum* trapping sediment on the river bed, fringes a bench (foreground) that is aggrading above baseflow stage and is sloping upwards towards the channel edge, while undercutting of the opposing bank (below the overhanging shrubs) is resulting in local retreat of the opposite bank. The photograph was taken in April, when the foliage of *S. erectum* is just starting to emerge within the low flow channel and the vegetation on the bench has not yet started to produce leaves (photograph: A. Gurnell)

Table 1 Results of a Principal Components Analysis applied to six environmental variables for the 467 reaches in the large data set.

	PC1	PC2	PC3	PC4
eigenvalue	2.57	1.84	0.58	0.53
variance explained (%)	42.81	30.63	9.62	8.83
cumulative variance %	42.81	73.43	83.06	91.89
loadings				
bed sediment calibre	-0.734	-0.095	0.667	0.076
bankfull width	0.591	-0.550	0.080	0.508
gradient (valley)	0.464	0.779	0.188	-0.139
Qmed	0.650	-0.654	0.133	-0.192
stream power	0.915	0.002	0.260	-0.250
altitude	0.453	0.701	0.067	0.384

Table 2. Results of Kruskal Wallis tests applied to observations from the large data set (467 river reaches) grouped according to their Sparganium abundance class (0 =absent, 1 = <5% cover, 2 = 5-25% cover, 3 => 25% cover) on six physical environment variables and scores on the first two principal components of a PCA on the same six variables. Multiple pairwise comparisons were made using Dunn's procedure with Bonferroni correction.

Variable	K value (3 degrees of freedom in all cases)	Statistical significance of K value	Significant difference among *Sparganium* abundance groups (P<0.05)
bed sediment calibre	92.9	< 0.0001	0 < 1 < 2, 3
bankfull width	14.0	0.003	0, 1 > 3
gradient	65.2	< 0.0001	0 > 1, 2, 3
stream power	35.7	< 0.0001	0 > 1, 2, 3
Qmed	5.3	0.154	NS
altitude	55.4	< 0.0001	0 > 1, 2, 3
PC1	79.1	< 0.0001	0 > 1 > 2, 3
PC2	42.6	<0.001	0 > 1, 2

Table 3 Results of a Principal Components Analysis applied to % *Sparganium erectum* cover and four physical environmental properties of the 47 reaches in the field data set.

	PC1	PC2	PC3	PC4
eigenvalue	1.74	1.24	0.98	0.57
variance explained (%)	34.79	24.83	19.57	11.50
cumulative variance%	34.79	59.62	79.19	90.68
Loadings				
stream power	0.313	0.709	0.531	-0.043
channel width (m)	0.808	0.088	0.270	0.268
channel depth (m)	0.561	-0.678	0.059	0.281
bed sediment calibre	-0.294	-0.514	0.744	-0.290
% *S. erectum* cover	-0.767	0.083	0.258	0.581

Table 4 Results of a Principal Components Analysis applied to twelve *Sparganium erectum* properties of the 47 reaches in the field data set.

	PC1	PC2	PC3	PC4
eigenvalue	3.99	2.15	1.69	1.36
variance explained (%)	33.21	17.95	14.05	11.33
cumulative variance%	33.21	51.16	65.21	76.54
Loadings				
% *S. erectum* cover (entire channel area)	0.689	0.235	0.500	-0.194
features per metre reach length	-0.554	0.067	0.599	-0.100
mean feature area (m)	0.923	0.205	0.117	-0.226
mean feature length (m)	0.855	0.145	0.177	-0.227
mean feature breadth (m)	0.851	0.208	-0.002	-0.181
mean feature stage	0.621	0.016	-0.280	0.443
mean stem density (per $0.25m^2$ quadrat)	0.346	-0.716	0.166	0.332
mean canopy height (m)	0.274	0.413	-0.563	0.352
mean stem diameter (m)	-0.040	0.734	0.195	0.518
mean number of leaves per ramet	-0.248	0.555	0.508	0.424
mean distance between stems (m)	-0.198	0.449	-0.558	-0.266
canopy cover (% in quadrat)	0.464	-0.507	0.052	0.477

Table 5 Results of Kruskal Wallis tests comparing sediment sample properties obtained from the 47 sites in the field data set according to their sampling location. (Identification of significant differences between sample locations was established using Dunn's procedure with Bonferroni correction; the sampling locations were: 1 – exposed channel bed, 2 – exposed bank toe, 3 – in *Sparganium erectum* feature, 4 – bank toe protected by *Sparganium erectum* feature, 5 – bench fringed by *Sparganium erectum* feature).

Sediment property	minimum	maximum	Kruskal Wallis K (degrees of freedom = 4)	Kruskal Wallis P	Significant differences between sample locations (P<0.05)
% gravel	0	96.6	27.4	<0.0001	1, 2 > 3 1 > 4
% silt and clay	0	65.5	2.2	NS	
D_{50} (phi)	-1.48	5.25	28.9	<0.0001	1 < 2, 3, 4, 5
% organic material	0.7	39.5	31.7	<0.0001	1 < 2, 3, 4, 5
number of species	0	16	50.2	<0.0001	1, 2 < 3, 4, 5
number of seedlings	0	204	58.1	<0.0001	1, 2 < 3, 4, 5

Table 6 Results of a Principal Components Analysis applied to the properties of sediment samples obtained from the river bed and margins of the 47 reaches included in the field data set.

	PC1	PC2	PC3
eigenvalue	2.41	1.37	0.98
variance explained (%)	40.08	22.76	16.34
cumulative variance%	40.08	62.84	79.18
Loadings			
% gravel	0.780	-0.514	-0.135
% silt and clay	-0.129	-0.268	0.921
D_{50} (phi)	-0.765	0.548	0.100
% organic material	-0.116	-0.533	0.126
number of species	-0.774	-0.442	-0.251
number of seedlings	-0.762	-0.501	-0.158