Physical ecosystem engineering by emergent aquatic vegetation: the importance of biomechanical traits

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I hereby declare that the work presented in this thesis is my own and has not been submitted elsewhere for any award.

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Abstract

This thesis explores the potential of the emergent macrophyte *Sparganium erectum* to act as a physical ecosystem engineer and delivers an understanding of the vegetative processes that enable it to function in such a capacity. An ecosystem engineer is an organism that creates or modifies habitat; the habitats in question are rivers, particularly low energy sections, the modification relates to the capacity of the species to trigger geomorphological change via a process of flow velocity reduction, sediment accumulation, and reinforcement by underground biomass.

The influence of *S. erectum*, and other aquatic species, on flow and sediment accumulation has been demonstrated before, but its changeable influence at different energy conditions and a detailed understanding of how its morphology influences physical processes has yet to be revealed. To address these gaps in understanding, the research conducted within this thesis is divided into three distinct results chapters; Chapter 4 investigates the influence of *S. erectum* on patterns of flow and sediment at three reaches of the River Blackwater, Surrey, UK; Chapter 5 explores the capacity of the species to resist mimicked hydraulic stress, and the biomechanical traits that underpin its influence on physical processes; Chapter 6 measures the changing belowground architecture and biomass of the species.

The research demonstrates that growth of *S. erectum* significantly alters river habitats and physical processes, but the nature of its influence varies substantially at the three study reaches, which are indicative of different energy conditions. The species demonstrates a number of subtle biomechanical and morphological traits that cause it to function so efficiently as an ecosystem engineer; these include its long growth cycle, high resistance to uprooting, and tendency for underground mass to occupy surficial layers of sediment. The study concludes by assessing the management implications of the results, which include the potential of the species as a restoration tool, given its ability to create a diversity of river habitats.
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# Table of Contents

Abstract ........................................................................................................................................... 3  
Acknowledgements .......................................................................................................................... 4  
Table of Contents ............................................................................................................................ 5  
List of Figures .................................................................................................................................. 9  
List of Tables .................................................................................................................................. 13  
Chapter 1: Introduction .................................................................................................................... 16  
Chapter 2: Literature Review ............................................................................................................. 19  
  2.1 Introduction ............................................................................................................................. 19  
  2.2 Interactions between macrophytes, flow and sediment .......................................................... 20  
    2.2.1 Aquatic plant morphotypes .............................................................................................. 20  
    2.2.2 Interactions between submerged plants and river flows ............................................... 21  
    2.2.3 Interactions between emergent plants and river flows ................................................. 22  
    2.2.4 Morphological adaptations of aquatic plants exposed to hydraulic stress .................... 23  
    2.2.5 Sedimentation and aquatic vegetation ............................................................................ 23  
    2.2.6 Sparganium erectum – a model emergent macrophyte species? ................................. 24  
  2.3 Physical ecosystem engineering by riparian and aquatic vegetation ....................................... 26  
    2.3.1 Erosion control and sediment reinforcement by vegetation ........................................ 26  
    2.3.2 Measuring the underground biomass of vegetation ...................................................... 27  
    2.3.3 Vegetation induced fluvial landform development ....................................................... 29  
    2.3.4 Assessing physical ecosystem engineering by vegetation ............................................. 30  
  2.4 Research gaps and thesis research questions .......................................................................... 32  
Chapter 3: Research Design ........................................................................................................... 35  
  3.1 Introduction ............................................................................................................................. 35  
    3.1.1 Conceptual background ................................................................................................. 35  
  3.2 Site selection rationale and site descriptions .......................................................................... 36  
    3.2.1 Space-time rationale underpinning the field research design ....................................... 36  
    3.2.2 National survey sites ..................................................................................................... 39  
    3.2.3 Study sites on the River Blackwater, Surrey .................................................................. 41  
  3.3 Investigative design .................................................................................................................. 46
Chapter 4: Reach scale interactions between river flows, aquatic macrophytes and sediment in the headwaters of a lowland river

Chapter summary

4.1 Introduction
4.2 Investigative design
   4.2.1 Study reaches
   4.2.2 Field measurements
   4.2.3 Data analysis
4.3 Results
   4.3.1 Reach average properties
   4.3.2 Hierarchical agglomerative cluster analysis of streamwise flow velocity observations
   4.3.3 Hierarchical agglomerative cluster analysis of cross-stream flow velocity observations
   4.3.4 Hierarchical agglomerative cluster analysis of the Sparganium erectum abundance index
   4.3.5 Bed sediment depth and calibre
4.4 Discussion
   4.4.1 Associations between flow velocity, vegetation and sediment
   4.4.2 Contrasts in flow velocity, vegetation and sediment between study reaches
   4.4.3 Management implications
4.5 Synthesis

Chapter 5: Linking the morphology and strength of Sparganium erectum

Chapter summary

5.1 Introduction
5.2 Investigative Design
   5.2.1 Field measurements
   5.2.2 Laboratory measurements
   5.2.3 Data analysis
5.3 Results ........................................................................................................................................114
  5.3.1 National Survey ........................................................................................................114
  5.3.2 River Blackwater, Reach 4: Field Measurements ...............................................................118
  5.3.3 Laboratory Measurements ..................................................................................................129
  5.3.4 Associations between the morphology and strength of *S. erectum* ...................................133
5.4 Discussion .....................................................................................................................................149
5.5 Synthesis .......................................................................................................................................154

Chapter 6: Structural changes in the below ground biomass of
*Sparganium erectum* .........................................................................................................................157

Chapter summary .................................................................................................................................157
6.1 Introduction .....................................................................................................................................158
6.2 Investigative design ........................................................................................................................159
  6.2.1 Ingrowth Core Design .........................................................................................................159
  6.2.2 Field Installation ..................................................................................................................161
  6.2.3 Timing and frequency of core retrieval .................................................................................163
  6.2.4 Laboratory analysis ...............................................................................................................164
  6.2.5 Data Analysis .......................................................................................................................165
6.3 Results ............................................................................................................................................167
  6.3.1 Changes in plant biomass ......................................................................................................167
  6.3.2 Estimating net primary production .......................................................................................175
6.4 Discussion .......................................................................................................................................175
6.5 Synthesis .......................................................................................................................................177

Chapter 7: Conclusions .........................................................................................................................181
7.1 Introduction .....................................................................................................................................181
7.2 Key findings ....................................................................................................................................181
  7.2.1 To what extent does the seasonal growth and senescence of
       *S. erectum* affect the hydraulic performance and sediment
       dynamics of contrasting river reaches? .......................................................................................182
  7.2.2 How do the growth traits and biomechanical properties of *S. erectum*
       vary spatially and temporally; both between reaches along the
       same river and nationally between rivers? ...............................................................................184
  7.2.3 How does *S. erectum* root and rhizome architecture vary through
       the annual cycle of canopy growth and senescence? ............................................................185
7.2.4 What are the underlying biomechanical and morphological properties that enable *S. erectum* to act as an ecosystem engineer?  186

7.3 Methodological contributions and considerations  ........................................  187

7.3.1 Biomechanical measurements  ....................................................................  188

7.3.2 Underground biomass  ..................................................................................  188

7.4 Opportunities for future research  .................................................................  189

7.4.1 Developing an integrated study of ecosystem engineering by aquatic macrophytes  .................................................................................................................  189

7.4.2 Spatiotemporal considerations  ....................................................................  191

7.4.3 Exploring other species and habitats ............................................................  192

7.5 Implications for river management  .................................................................  193

7.6 Research summary  ..........................................................................................  196

7.6.1 Physical ecosystem engineering by *S. erectum*: a conceptual overview  196

7.6.2 How might ecosystem engineers such as *S. erectum* be incorporated into general river ecosystem models? .................................................................  197

References  ............................................................................................................  200

Appendix I  .............................................................................................................  215

Appendix II  .............................................................................................................  218
List of Figures

Figure 3.1: Conceptual model of reciprocal interactions between *S. erectum*, water flow and sediment dynamics that drive fluvial landform development .................................................................36

Figure 3.2: A plan of how the different field investigations fit within a framework of space and time scales .................................................................38

Figure 3.3: National survey site locations ..............................................................................41

Figure 3.4: The catchment of the River Blackwater and the location of the four study reaches .............................................................................................................44

Figure 3.5: Images of the four reaches during spring 2009 .................................................45

Figure 3.6: An uprooting experiment being conducted at reach 4 of the River Blackwater ..............................................................................................................49

Figure 3.7: In-growth core tubes placed on adjacent banks of reach 2 of the River Blackwater ..............................................................................................................51

Figure 4.1: The 4-stage biogeomorphological sequence contributing to bank aggradation / migration .........................................................................................55

Figure 4.2: The River Blackwater catchment and the position of the three study reaches ..............................................................................................................57

Figure 4.3: The three study reaches at minimum and peak aquatic macrophyte growth .......................................................................................................................58

Figure 4.4: The timings of the seven hydraulic/macrophyte survey recording periods .......................................................................................................................64

Figure 4.5: Downstream changes in reach and time average values of fine sediment depth, the proportion of the riverbed covered in fine material, and flow velocity .................................................................64

Figure 4.6: Temporal changes in the reach average flow velocity, Manning’s n, and bed material index in reaches 1 to 3 ........................................................................66

Figure 4.7: Downstream changes in reach and time average values of percentage cover of *S. erectum*, other macrophytes, and the percentage of the total cover of macrophytes composed of submerged species ..........68

Figure 4.8: Temporal changes in the coverage of *S. erectum*, other macrophytes, and the proportion of the total macrophyte community that consisted of submerged species in reaches 1-3 ..............................................69
Figure 4.9: Maximum leaf length of *S. erectum* observed for samples of 10 plants within the most developed stand in each cross section at reaches 1-3 over recording periods 1 to 5 ........................................71
Figure 4.10: The stem densities of *S. erectum* within the most developed stand in each cross section at reaches 1-3 over recording periods 1 to 5 ..73
Figure 4.11: Temporal patterns in average flow velocity, bed sediment calibre index, *S. erectum* abundance index and other macrophyte abundance index of survey points falling within each of the four velocity classes during each of the recording periods........................................76
Figure 4.12: The spatial distribution of measurement points falling into streamwise velocity classes 1-4..................................................80
Figure 4.13: Temporal changes in the average cross-stream velocity for the survey points within each of the three velocity classes during each of the recording periods..................................................81
Figure 4.14: Temporal changes in the average *S. erectum* abundance index for the survey points within each of the four growth classes during each of the recording periods..................................................86
Figure 4.15: The spatial distribution of measurement points falling into *S. erectum* abundance classes 1-4 ........................................89
Figure 4.16: The spatial distribution of sand and finer or gravel and larger bed material at reach 1, in recoding periods 1 and 7.........................90
Figure 4.17: The spatial distribution of sand and finer or gravel and larger bed material at reach 2, in recoding periods 1 and 7.........................91
Figure 4.18: The spatial distribution of sand and finer or gravel and larger bed material at reach 3, in recoding periods 1 and 7.........................92
Figure 4.19: *Nasturtium officinale* using senescent shoots of *S. erectum* and associated fine sediments as a substrate for growth.................95
Figure 4.20: The average path of highest velocity in relation to the *S. erectum* growth clusters .................................................................99
Figure 4.21: Ecosystem engineering by emergent vegetation: a conceptual development of distinct habitats........................................102
Figure 4.22: A conceptual model of the annually created habitats induced by the growth of emergent vegetation in lowland rivers...............103
Figure 5.1: The plant puller, front and side........................................108
Figure 5.2: The distribution of biomechanical measurement recording periods throughout the two seasons .........................................................109

Figure 5.3: An uprooted plant from June 2010 prior to washing and dissection.111

Figure 5.4: A hypothetical relationship between stem strength and leaf length ..112

Figure 5.5: Measurements of the aboveground standing crop at the national survey reaches with statistically significantly different groupings identified using Kruskal Wallis tests........................................116

Figure 5.6: Measurements of the belowground standing crop at the national survey reaches with statistically significantly different groupings identified using Kruskal Wallis tests.................................117

Figure 5.7: Measurements of strength measurements at the national survey reaches with statistically significantly different groupings identified using Kruskal Wallis tests..................................................118

Figure 5.8: Temporal changes in measures of the above ground standing crop during 2009 and 2010.........................................................120

Figure 5.9: Temporal changes in measures of the below ground standing crop during 2009 and 2010..........................................................122

Figure 5.10: Temporal changes in the force required to cause failure during 2009 and 2010.................................................................124

Figure 5.11: Temporal changes in the proportion of plants suffering stem failures rather than uprooting in 2009 and 2010 ..................125

Figure 5.12: Temporal changes in the plant slenderness ratio of sampled plants during 2009 and 2010.........................................................128

Figure 5.13: Temporal changes in the biomass of S. erectum, and its separate organs, during 2010..............................................................131

Figure 5.14: Scatter plots of individual recording period relationships derived from the multiple regression models relating plant failure to stem cross sectional area and maximum leaf length measured in 2009 ....139

Figure 5.15: Scatter plots of individual recording period relationships derived from the multiple regression models relating measures of plant failure and uprooting resistance to all measures of the standing crop measured in 2010 ......................................................147

Figure 5.16: Changes in the structure of leaves and rhizomes in S. erectum over the period of growth and senescence ..............................152
Figure 5.17: The potential fates for clonal macrophytes exposed to increased hydraulic stress .............................................. 154
Figure 5.18: A theoretical link between unit stream power and the fate of emergent vegetation ...................................................... 155
Figure 6.1: From left to right: an ingrowth core tube, sleeve and cap .......... 161
Figure 6.2: The location of the five ingrowth core patches at reach 2 ............. 162
Figure 6.3: In situ ingrowth cores, reach 2 of the River Blackwater, March 2010 ........................................................................ 163
Figure 6.4: Laboratory dissection of ingrowth cores ................................ 165
Figure 6.5: The timing and distribution of the seven recording periods used to measure underground biomass ........................................ 167
Figure 6.6: The changing proportion of underground biomass within each recording period .......................................................... 168
Figure 6.7: (A) Box and whisker plots showing total above ground and below ground biomass observed in the core samples. (B) Box and whisker plots showing the ratio of above ground to below ground biomass... 169
Figure 6.8: Box and whisker plots showing variations in total below ground (roots and rhizomes), root, and rhizome biomass at different depths and recording periods ............................................................. 171
Figure 6.9: Estimates of total below ground, root and rhizome biomass from the models summarised in Table 6.3 ....................................... 174
Figure 6.10: Young S. erectum shoots trapping sediment and reinforcing a depositional bench on its inner margin and downstream end ........... 178
Figure 6.11: Rhizomes trail in the winter flow but remain anchored within the bed ........................................................................... 179
Figure 6.12: The annual growth cycle and sediment retention strategies of Sparganium erectum .................................................................. 180
Figure 7.1: A conceptual overview of ecosystem engineering by S. erectum. .... 197
List of Tables

Table 3.1: Locations, bankfull width and gradient of river reaches investigated .41
Table 3.2: The study reaches used to answer the research questions......................46
Table 4.1: Key management and morphological features of reaches 1-3 of the
River Blackwater........................................................................................................56
Table 4.2: Survey dates of the seven recording periods, and discharge and
wetted channel dimensions at the time of each survey.................................59
Table 4.3: Measurements taken at fixed cross sections in the three study
reaches .............................................................................................................................61
Table 4.4: Results of Kruskal Wallis tests applied to sampled streamwise
velocity and bed material index values in reaches 1-3 during each
recording period..............................................................................................................67
Table 4.5: Results of Kruskal Wallis tests applied to reach coverages of
S. erectum, other macrophytes and submerged macrophytes in
reaches 1 -3 during each recording period.........................................................70
Table 4.6: Results of Kruskal Wallis tests applied to observations of S. erectum
maximum leaf length in reaches 1 -3 during recording periods 1 to 5..72
Table 4.7: Description of the temporal patterns in average velocity within the
four velocity classes identified using hierarchical agglomerative
cluster analysis..................................................................................................................74
Table 4.8: Results of Kruskal Wallis tests applied to streamwise flow velocities
observed at measurement points falling within velocity classes 1 to 4
during each of the recording periods ...............................................................75
Table 4.9: Results of Kruskal Wallis tests comparing values of the S. erectum
abundance index, other macrophyte abundance index and bed material
calibre index observed at measurement points falling within streamwise
velocity classes 1 to 4 during each of the recording periods...............77
Table 4.10: The proportional (and absolute) streamwise velocity cluster
membership of observation points within the three reaches....................79
Table 4.11: Description of cross-stream velocity classes identified using
hierarchical cluster analysis.......................................................................................81
Table 4.12: Results of Kruskal Wallis tests comparing cross-stream flow
velocities observed at measurement points falling within classes 1
to 3 during each of the recording periods .......................................................82
Table 4.13: Results of Kruskal Wallis tests comparing values of the *S. erectum* abundance index, submerged macrophyte abundance index and bed material calibre index observed at measurement points falling within cross stream velocity classes 1 to 3 during each of the recording periods .................................................................83

Table 4.14: Description of the *S. erectum* abundance classes used to describe the seasonal growth pattern of *S. erectum* in reaches 1-3......................86

Table 4.15: Results of Kruskal Wallis tests comparing the *S. erectum* abundance index observed at measurement points falling within growth classes 1 to 4 during each of the recording periods ...............................................87

Table 4.16: The proportional and absolute growth cluster membership values for the three reaches.................................................................................................88

Table 4.17: Four habitats derived from analysis of interactions between flow, sediment and macrophytes, and commonly observed on the River Blackwater........................................................................................................101

Table 5.1: Sampling dates of uprooting experiments.................................................109

Table 5.2: Descriptions of measurements taken during uprooting measurements ..............................................................................................................................110

Table 5.3: The location and timings of national survey river reach investigations .................................................................115

Table 5.4: Statistically significant differences in measures of the above and below ground standing crop of sampled *Sparganium erectum* plants assessed using Kruskal Wallis tests, applied separately to the 2009 and 2010 data......................................................................................123

Table 5.5: Statistically significant differences in measures of the biomechanical properties of *Sparganium erectum* plants assessed using Kruskal Wallis tests, applied separately to the 2009 and 2010 data ..............127

Table 5.6: Statistically significant differences in component measures of plant biomass assessed using Kruskal Wallis tests.................................132

Table 5.7: Spearman rank correlations between field and laboratory measurements of plant structure/biomass.........................................................133

Table 5.8: Spearman rank correlations between field measurements of plant strength and the standing crop in 2009.........................................................134
Table 5.9: Spearman rank correlations between rhizome strength and rhizome diameter in 2009 .................................................................135

Table 5.10: Multiple regression models relating 2009 measurements of biomechanical strength to measures of the standing crop ..................136

Table 5.11: Multiple regression models relating 2009 measurements of plant failure as the dependent variable to recording period dummy variables, two measures of the standing crop and interactions between the dummy variables and the two measures of the standing crop .................................................................138

Table 5.12: Spearman rank correlations between measurements of biomechanical strength and the standing crop 2010 .......................142

Table 5.13: Spearman rank correlations between uprooting resistance and measurements of plant biomass .................................................142

Table 5.14: Spearman’s rank correlations between rhizome diameter and strength in each of the recording periods in 2010 .......................143

Table 5.15: Multiple regression models relating 2010 measurements of uprooting resistance to measures of the standing crop .................144

Table 5.16: Multiple regression models relating 2010 measurements of plant failure and uprooting resistance as the dependent variables to recording period dummy variables, four measures of the standing crop and interactions between the dummy variables and the two measures of the standing .................................................................145

Table 6.1: Core extraction dates (recording periods) .........................................................164

Table 6.2: Statistically significant differences in total above ground and total below ground biomass between recording periods investigated using one way, parametric ANOVA followed by Tukey pairwise comparisons ...........................................................................170

Table 6.3: Regression models estimated for total below ground, root and rhizome biomass .......................................................................173
Chapter 1

Introduction

Until recently, vegetation was considered a passive element in the structural development of rivers, and its spatial pattern and development was thought to be controlled by hydrogeomorphological processes (Knighton & Nanson, 1993; Corenblit et al. 2007). Whilst hydrologeomorphological processes are highly influential in determining the abundance, distribution and species composition of vegetation communities (Roberts & Ludwig, 1991; van der Nat et al. 2001; Steiger et al. 2001; Riis & Biggs, 2003; Gilvear & Willby, 2006), there is a growing understanding of how plants can control geomorphological processes (Tabacchi et al. 2000; Gurnell et al. 2001), due to their ability to resist the hydraulic forces acting upon them. This understanding has developed largely from research conducted on riparian trees, which has demonstrated their ability to control sediment erosion and in many circumstances to stimulate sediment accretion and landform development in natural and managed scenarios (Gurnell et al. 2001; Gurnell & Petts, 2002; Simon et al. 2004). This is achieved primarily by (1) the flow resistance of the canopy which reduces flow velocities and shear stresses at the ground surface, protecting the latter from erosion and allowing the settlement of transported sediments, and (2) the reinforcing effects of root systems, which allow the deposited sediments to be retained and to further accumulate into erosion resistant landforms (Millar, 2000; Corenblit et al. 2007).

Studies that have explored interactions between vegetation and channel dynamics have focused mostly on riparian trees, however recent research has demonstrated that a range of plant species can trigger fluvial landform development (e.g. Sand-Jensen, 1998; Hupp & Rinaldi, 2007; Asaeda et al. 2009; Rominger et al. 2010). These studies provide evidence of river engineering by aquatic plants (i.e. acting as ‘physical ecosystem engineers’ sensu Jones et al. 1997), indicating that in-channel aquatic vegetation may also be capable of triggering profound, long-term structural changes to river channels.

Therefore, just as understanding in fluvial geomorphology has progressed from a perception of vegetation as a passive element, to recognition and understanding of how riparian trees influence geomorphological processes, it is now timely to explore the function of aquatic plants in a similar context.
Of the various aquatic plant morphotypes, linear emergent macrophytes, and particularly the species *Sparganium erectum*, have been identified as having the greatest potential influence on channel structure due to their high flow resistance and tendency to rapidly accumulate fine sediments (Gurnell et al. 2006a; Naden et al. 2006; Asaeda et al. 2009). Additionally, *Sparganium erectum* is the most commonly occurring vascular aquatic species in Great Britain, based on an analysis of 1,200 aquatic plant (Mean Trophic Rank) surveys (Gurnell et al. 2010). Therefore, in this thesis, *Sparganium erectum* is chosen as a model species for investigating interactions between aquatic plants, fluvial processes and sediment retention at a range of spatial and temporal scales, and the implications of these interactions for river environments and their management.

Following a literature review (Chapter 2), the investigative design of the research is outlined in Chapter 3. The aim of this chapter is to introduce the research sites and methods, and how these underpin the specific research studies that were undertaken at different space and time scales and are reported in subsequent chapters. Thus Chapter 3 provides a broad overview of sites and methods, which are developed in much greater detail in later chapters. The results of the research are then reported in three chapters (4, 5 and 6), which are written as free-standing reports, using a style similar to an academic paper, with introduction, methods, results and discussion sections.

Chapter 4 provides an analysis of associations between aquatic plants, flow velocity, and bed sediment associations through an annual cycle of plant growth and senescence in three reaches located at increasing distances from the source of a single river: the River Blackwater, Surrey, England. The analysis demonstrates the central role of emergent aquatic macrophytes, specifically *S. erectum*, in controlling spatial patterns of flow velocity and fine sediment retention in this low energy gravel-bed river, and the way in which these spatial patterns change downstream with increasing discharge, flow velocity and flow depth through the three reaches. This reach scale analysis is followed in Chapter 5 by detailed observations of the strength of *S. erectum*, particularly its resistance to uprooting, and how this varies through the annual cycle of growth and senescence, and is controlled by the size of the stem, rhizomes and roots of the plant. The national transferability of this detailed research, undertaken on the River Blackwater, is assessed using data collected at the peak of annual growth from 14 sites spread across England and southern Scotland. Following the observations of the
remarkable strength of the belowground organs of the species, Chapter 6 explores the changing architecture and distribution of root and rhizome biomass through the annual growth and senescence of the species within the upper 25 cm of fine sediment. This illustrates how the majority of the belowground biomass is located within the top 10 cm of sediment and how the rhizomes persist within this layer throughout the year, providing sediment reinforcement through the winter when no above ground biomass is present.

Finally, Chapter 7 draws together the results presented in chapters 4, 5 and 6, to summarise how a number of subtle biomechanical and morphological traits enable *S. erectum* to function so efficiently as an ecosystem engineer, including its long growth cycle, high resistance to uprooting, and tendency for underground mass to occupy surficial layers of sediment. Chapter 7 then assesses the management implications of these results, including the potential of the species as a restoration tool, given its ability to contribute to the diversity of river habitats.
Chapter 2

Literature Review

2.1 Introduction

The research presented in this thesis concerns (i) the physical role of aquatic plants, particularly the emergent species, *Sparganium erectum*, in modifying flow patterns, trapping and reinforcing sediments, and subsequently influencing the morphology of river channels and (ii) the biomechanical properties of the plant that underpin this ability to physically modify river ecosystems.

This literature review provides a context for the research reported in this thesis and is split into two main parts. The first part (section 2.2) explores interactions between macrophytes, flow velocity and fine sediment. Focus is given to how different plant morphotypes affect flow velocity and patterns, and sedimentation. There is also a discussion of how physical stress can induce morphological adaptations in aquatic plants. The purpose of exploring these interactions is to identify which species, or set of morphological traits, has the greatest influence on physical parameters; essentially, which aquatic plants demonstrate the greatest ability to alter the physical environment.

Having identified a set of morphotypes that operate as ecosystem engineers, the second part (section 2.3) explores the reasons for the profound effects of certain aquatic plants on hydraulic and sedimentary processes. Analogies are drawn, and understanding gained, from research that has described ecosystem engineering by riparian trees; namely their ability to generate new landforms and their reinforcement of sediment via the growth of below ground mass. Therefore, section 2.2 is concerned with the immediate effects macrophytes have on the physical environment, whilst section 2.3 assesses the potential long term consequences of those effects, how multi-seasonal geomorphological changes induced by aquatic plants can be gauged, and the biophysical traits that cause changes.

Research gaps are identified, which are used to inform a set of research questions that are addressed in the following chapters (section 2.4).
2.2 Interactions between macrophytes, flow and sediment

The principal effects of aquatic plants on the physical environment are to act as an obstruction to flow, which reduces average streamwise flow velocity, increases water depth, induces complex flow patterns in and around plant stands and, as a result, often causes deposition of sediment within plant stands. Early studies of the effects of macrophytes on flow velocity considered the gross impact of seasonal plant growth on average water depth, flow velocity and flow resistance, usually represented by Manning’s roughness coefficient ‘n’ (e.g. Watson, 1987; Gurnell & Midgley, 1994).

More recently, research has considered the detailed, local, hydraulic effects of individual plants and stands of different species (e.g. Sand-Jensen & Mebus, 1996; Sand Jensen & Pedersen, 1999; Sand Jensen, 2003; Green, 2005a,b; Cotton et al., 2006; Statzner et al., 2006), and their impacts on flow patterns at the cross section to reach scales (e.g. Gurnell et al., 2006a; Naden et al., 2006), with changing discharge and seasonal growth. These impacts vary greatly with plant/species morphology.

2.2.1 Aquatic plant morphotypes

The extent of local effects on flow velocity patterns by aquatic macrophytes are highly species specific, but a plant’s effect on flow is primarily driven by its morphology, flexibility and tendency to occupy different channel locations (Green, 2005a; Gurnell et al. 2006a). Green (2005a) describes four aquatic plant morphotypes that each have a different hydrodynamic effect; emergents, plants with surface floating leaves, submergents, and free-floating plants. Although relationships between flow velocity and macrophytes are not explicitly measured, the study by Gurnell et al. (2010) provides an alternative classification of five aquatic plant morphotypes: Mosses, submerged linear macrophytes, submerged patch-forming macrophytes, linear emergent macrophytes, branched emergent macrophytes. It is stated that ‘within the submerged and emergent types, the linear forms are more open and streamlined and less bushy than the patch submerged and branched emergent forms’ (Gurnell et al., 2010, p 136). The distinction between patch submerged (e.g. Ranunculus and Callitriche sp.) and linear submerged species (e.g. Sparganium emersum) also relates to the fact that the latter tend to cover a large area of the bed but have a relatively low stem density. The distinctions between patch submerged and linear submerged species and between linear and branched emergent species are used hereafter, because they are both more readily interpretable in the discussion of the hydrodynamic effects of aquatic vegetation.
2.2.2 Interactions between submerged plants and river flows

The distinction between patch and linear submerged species is particularly important because submerged species have been the primary focus of research that has investigated the effects of macrophytes on flow velocity patterns, which has shown these two morphotypes to have profoundly different effects. Patch submerged species typically cause a sharp reduction in flow velocity shortly within the boundaries of the plant’s canopy (Sand-Jensen & Mebus 1996; Sand-Jensen, 1998; Green, 2005b). Conversely, linear submerged species often have a negligible effect on the flow velocity profile (Sand-Jensen, 1998) due to their highly flexible morphology and comparatively low shoot densities (Sand-Jensen & Pedersen, 1999). Thus the local presence and distribution of these two morphotypes will have major implications for flow velocity patterns in a given river reach; ‘meadow’ forming linear species such as *S. emersum* (Green 2005b) generate a relatively homogenous hydraulic environment, due to the small changes in flow velocity found inside/outside their physical boundaries (Sand-Jensen & Mebus, 1996; Sand-Jensen & Pedersen, 1999), unlike patch submerged species such as *Ranunculus* spp., which induce large bodies of slow flowing water within their canopies, adjacent to threads of high velocity between plant stands (Sand-Jensen, 1998; Green, 2005b; Cotton et al, 2006; Gurnell et al. 2006a; Warren et al. 2009). The strong reduction in flow velocity within the stands of patch submerged species provides a depositional environment within which significant sedimentation can occur (Sand-Jensen, 1998; Heppell et al. 2009; Nuriminen & Horppila, 2009). However, the availability of transported sediment is also a crucial ingredient for sediment deposition within submerged macrophyte stands. Therefore, sedimentation can occur wherever hydraulic conditions and sediment supply permit, including within submerged macrophyte stands regardless of their morphotype (Schulz et al. 2003).

Morphological adaptations have been made by a number of submerged species to minimise the effects of hydraulic stress, which in turn affect their relative ability to trap transported sediment particles. Individual leaves of linear submerged species, such as *S. emersum*, have a streamlined shape that minimises drag and therefore their susceptibility to removal or damage during high velocity flow events (Sand-Jensen, 2003; O’Hare et al. 2007). In cases of damage or removal, loss of fitness is mitigated by an additional growth trait; these species develop rhizomes (underground stem structures) within the bed sediments from which relatively small sets of leaves (in terms of their biomass) develop (Pollux et al. 2007) and as a result, leaf detachment does not
constitute a significant loss. This trait, of shedding the leaves under stress, is common in submerged aquatic plants and is termed a ‘mechanical fuse’ (Usherwood et al. 1997; Schutten & Davy, 2000; Miler et al. 2010). However, the loss of above-ground biomass would be more significant for many patch submerged species, because they produce a dense plume of foliage from a single stem. Consequently, certain patch submerged plants (including *Ranunculus* spp.) have an alternative means of minimising their drag, whereby they reconfigure their canopy in a horizontal layer parallel to the riverbed during higher flow velocities so that water can pass freely above their canopy (Sand-Jensen & Mebus, 1996; Sand-Jensen & Pedersen, 1999). This adjustment protects the plant from critical drag forces, bed scour and uprooting (Sand-Jensen, 1997).

### 2.2.3 Interactions between emergent plants and river flows

The hydraulic and sedimentary influences of emergent species have been studied far less than submerged species, and general distinctions in the impacts of different sub-morphologies (linear/branched) have yet to be ascertained. Nevertheless, a group of studies have investigated the influence of linear emergent species upon flow resistance and flow velocities at the patch and reach scale. Many of these studies have demonstrated the overall resistance effect of *Sparganium erectum* in particular. This probably reflects the widespread occurrence of this species and its ability to develop large stands in low energy river environments (Cook, 1962), leading to a more significant increase in flow depth (and thus reduction in average flow velocity) with respect to discharge (Naden et al. 2006). The local hydraulic effect of linear emergent species is similar to patch submerged species, in that flow velocities are dramatically reduced within the area of flow occupied by their canopies (Gurnell et al. 2006a; Naden et al. 2006; Asaeda et al. 2009; Bal et al. 2010), but because of their emergent form, this reduction in velocity occurs throughout the entire water profile and at higher flow rates because plants are unable to reconfigure. The broader hydraulic consequences of this flow blocking effect is to squeeze flow into a narrower portion of the channel, causing increased velocities and water depths in the channel areas that are not occupied by emergent macrophyte stands (Gurnell et al. 2006a; Naden et al. 2006). Because of the tendency for emergent species to grow along the river channel margins, the flow is funnelled into central areas of the channel dominated by submerged species, which provide additional flow resistance / blockage, further increasing water depth and confining narrow threads of high flow velocity to areas of the channel between the submerged plant stands (Sand Jensen, 1998; Gurnell et al., 2006a; Naden et al. 2006).
2.2.4 Morphological adaptations of aquatic plants exposed to hydraulic stress

The body of literature summarised in sections 2.2.2 and 2.2.3 that has investigated the effects of macrophytes on flow is now being complimented by a smaller but expanding body of research that explores how aquatic plants alter their morphology in response to environmental factors. Specifically, macrophytes exhibit adaptive traits in response to mechanical (hydrodynamic) stress that significantly reduce the forces experienced by the plants (Puijalon & Bornette, 2004, 2006; Asaeda et al. 2005; Peralta et al. 2006; Puijalon et al. 2008a; Kotschy & Rodgers, 2008). There appear to be four principal morphological adaptations made by aquatic macrophytes under stress: 1) Increased patch density, generated by reduced internodal length and increased branching of rhizomes (Jensen & Bell, 1999; Asaeda et al. 2005); 2) Improved anchorage via altered traits such as increased biomass or proportional mass of below ground organs (Puijalon & Bornette, 2006; Lui et al. 2007); 3) Alterations to above ground structure, such as dwarfed stem and leaf sizes (Doyle, 2001), to minimise drag; 4) Escape strategies whereby the plant seeks more sheltered areas for growth, which is achieved through reduced branching and increased internodal length of rhizomes (Puijalon et al. 2008b; also exhibited by terrestrial plant exposed to increased wind velocities: de Kroon et al. 1994; Dong and de Kroon, 1994; de Kroon and Hutchings, 1995).

Thus the relationship between aquatic vegetation and flow hydraulics is a complicated and dynamic one. Fluvial vegetation mosaics can adapt to changes in their environment so that they can persist throughout space and time, and there is a growing body of evidence that suggests that, even in undesirable growing conditions, plants are able to move into new areas of the channel or adjust their morphology so that they can survive.

2.2.5 Sedimentation and aquatic vegetation

Studies that have specifically measured sedimentation within stands of aquatic vegetation are few. However, those that measure hydrodynamic effects often refer anecdotally to sedimentation as a by-product of the altered hydrodynamics. Sedimentation rates within stands of submerged macrophytes have been observed to exhibit a pattern that mimics the growth and decay of foliage (Sand-Jensen et al. 1989; Sand-Jensen, 1998; Madsen et al. 2001; Schulz et al. 2003; Cotton et al. 2006; Heppell et al. 2009) supporting previous evidence that submerged macrophytes both induce sediment deposition and also protect accumulations as a result of adjustments in their
canopy shape during high flow velocities (Sand-Jensen, 1997). As with flow velocity, sedimentation is inherently linked to the morphology of the plant, with patch submerged species inducing greater sedimentation rates than linear submerged species (Sand-Jensen, 1998). Patch submerged species are therefore credited with generating heterogeneous physical habitats, which encourage the presence of a diverse biota (Gregg & Rose, 1985; Quinn & Hickey, 1994).

The limited number of studies that have investigated seasonal changes in fine sediment depths within stands of emergent vegetation have revealed an almost inverse pattern to those seen within patch submerged vegetation. Studies by Gurnell et al. (2006a) and Asaeda et al. (2009) showed greater sediment depths at the beginning and end of the growth season, and markedly reduced depths throughout summer. In areas associated with S. erectum, Asaeda et al. (2009) proposed that the pattern of sedimentation is linked to the life cycle of the species; Spring: young, submerged shoots trap large amounts of fine sediment, despite their small biomass; Summer: surficial sediment layers are eroded during peak growth due to the low efficiency of emergent shoots in settling fine sediments; Autumn/winter: the collapsed emergent shoots trap additional suspended sediments, whilst, at the same time, inhibiting bottom sediment resuspension and erosion. However, such a theory should be subject to further scrutiny, given that (1) the initial submerged growth form of S. erectum is morphologically very similar to S. emersum, which has been shown to generate very low sedimentation rates (Sand-Jensen, 1998), (2) sedimentation is known to be strongly linked to biomass (Hovarth, 2004; Cotton et al. 2006), (3) emergent shoots certainly offer protection to underlying sediments, but their ability to trap floating sediments must be questioned given that they overlay the bed and often protrude from the water surface (pers. obs.). Alternative explanations for lower sediment depths during summer months could be settlement and compaction, in part due to the significant addition of overlying biomass, and subsequent raised water levels, or alternatively, increased uptake of organic matter caused by the vigorous growth of the species (Howard-Williams, 1985; Clarke & Wharton, 2001).

2.2.6 Sparganium erectum – a model emergent macrophyte species?

The studies by Gurnell et al. (2006a), Naden et al. (2006), Asaeda et al. (2009) and Bal et al. (2010) demonstrate that S. erectum is an influential species in terms of its capacity to alter flow hydraulics and sediment dynamics. Areas associated with its growth are those that exhibit the lowest flow velocities and highest sedimentation rates (Gurnell et
al. 2006a; Naden et al. 2006; Asaeda et al. 2009). Its profound effects on physical parameters are perhaps influenced by its ability to produce large quantities of biomass, including secondary or even tertiary daughter plants in a single season (Asaeda et al. 2009), which can exceed other highly productive and common linear emergent macrophytes, including *Phragmites australis, Phalaris arundaciea, Typha latifolia* (Mason and Bryant, 1975; Klopatek and Stearns, 1978) and *Spartina alterniflora* (Darby and Turner, 2008). Its ability to generate numerous new rhizomes during the growing season, which exceed other linear emergent macrophytes in terms of their mass and length (Sculthorpe, 1967), extending up to two meters beyond the shoot in a single season (Cook, 1962), allow it to grow into new channel areas and generate new sets of leaves that will affect the aforementioned processes. Its aggressive growth habit has been acknowledged for some time, and was perhaps first recorded by Charles Darwin (1880: p189) who described its rhizomes, which ‘grow out horizontally in the soil to a considerable length’¹. It is also the most widely occurring emergent macrophyte in the UK (O’Hare et al. 2010). It is found in the margins of rivers and lakes of the British Isles and in many other northern temperate regions (Cook, 1961), and it is also present as an exotic species in North America, where it has been identified as a ‘noxious weed’ in many US states (USDA, 2010).

Thus, due to its growth habits, morphology, widespread distribution, environmental preferences and a recent, growing body of research exploring its effect on river environments, *S. erectum* is a species that provides an appropriate subject for exploring potential ecosystem engineering functions of emergent macrophytes. The role of vegetation in engineering landforms is explored more fully in section 2.3. Although the species has been studied in several rivers, over a wide geographical area, its effects upon hydraulic and sedimentary processes haven’t been explicitly tested across a range of river reaches of different energy conditions. Given that emergent vegetation can be severely limited by flow velocity and depth (Cook, 1962; Sculthorpe, 1967; Haslam, 2006; Bornette & Puijalon, 2011) a study that reveals the hydraulic and sediment retention impact of emergent species under different energy conditions will support a fuller understanding of the potential effects of this morphotype on its environment. In the UK, and elsewhere in the northern temperate zone, aquatic plant communities shift from bryophyte-dominated in steep, high-energy streams, through a mixed community

¹ The text refers to *Sparganium ramosum* but, due to some taxonomic confusion, the species now classified as *Sparganium erectum* was referred to *Sparganium ramosum* in the 19th century (Cook, 1961).
in medium-energy streams, to domination by vascular plants in lowland, low-energy streams (Gurnell et al. 2010). This indicates that flow conditions can preclude or restrict the growth of vascular plants in many locations. Whilst the changing abundance of different plant morphotypes throughout the temperate river continuum has been defined, the spatial extent and vigour of the growth that is required to generate fluvial habitat complexity has not been demonstrated, and thus the threshold conditions under which emergent macrophytes, in particular, can impact on river morphology have yet to be identified. Because of its wide occurrence and tolerance of a wide spectrum of hydrochemical conditions, *S. erectum*, provides an ideal species for investigating whether such physical threshold conditions exist and how these relate to river energy and other physical properties of colonised river reaches.

2.3 Physical ecosystem engineering by riparian and aquatic vegetation

Physical ecosystem engineering is the process whereby organisms cause a physical modification, maintenance or creation of new habitats (Jones et al. 1994, 1997). Studies that have investigated physical ecosystem engineering by vegetation within the riparian zone have focussed primarily on riparian trees, their capacity to generate new landforms in natural systems and also their application as an erosion control technique in the reinforcement of vulnerable stream banks in human-impacted river systems. These are discussed separately in sections 2.3.1 and 2.3.3, and linked to a hypothesized function of aquatic vegetation as a physical ecosystem engineer.

2.3.1 Erosion control and sediment reinforcement by vegetation

The bioengineering application of vegetation is principally to minimise hydraulic erosion and mass movement, and thus manage sediment entrainment and soil stability on hillslopes and river margins (e.g. Morgan & Rickson, 1995; Gray & Sotir, 1996). Recently, there has been a strengthening research focus on detailed quantification of the reinforcing effects of riparian trees on streambanks (Abernathy & Rutherford, 1998, 2000; Easson & Yarbrough 2002; Simon & Collison, 2002; Pollen et al. 2004), where tree planting represents a softer engineering strategy compared to traditional erosion control techniques of bank reinforcement using concrete and rip-rap. Such a strategy also has a number of positive ecological benefits; vegetated riparian zones are often areas of high biodiversity and are used as migratory pathways by many animal species.
Vegetation principally limits erosion in two ways: (1) Above ground mass has the effect of deflecting and reducing flow velocities and shear stresses at the ground surface, and hence the potential to disturb and resuspend sediment particles (Hickin, 1984); (2) Below ground biomass increases soil strength through the production of a root–soil matrix (Thorne, 1990) whereby shear stresses in the soil are transferred to tensile stresses in roots (Grey & Sotir, 1996; Pollen et al. 2004).

Thus, research has, for some time, acknowledged the importance of roots in limiting soil erosion and failure. A number of recent studies have attempted to quantify the reinforcing effect attributable to roots of many different types of vegetation, including riparian trees (Simon & Collinson, 2002; Pollen & Simon, 2005; Pollen, 2007; Pollen-Bankhead & Simon, 2010), mature temperate trees (Mickovski & Ennos, 2003; Nicoll et al. 2006) and grasses (Ennos et al. 1993; Mickovski et al. 2003; Stokes et al. 2007). The specific geotechnical improvements made by roots include increased soil shear strength, binding soil particles, increasing bulk density, modifying the matric suction within the soil profile and the addition of organic matter (Gyssels et al. 2005; Pollen-Bankhead & Simon, 2010). However, no studies have directly measured the contribution made by aquatic plants to the stability of fluvial sediments (Grabowski et al. 2011).

2.3.2 Measuring the below ground biomass of vegetation

The presently unmeasured contribution made by the below ground biomass of aquatic vegetation to sediment stability is perhaps, in part, due to measurement difficulties. Whilst a method has been established that measures the strength of the roots of riparian and terrestrial plants, which can then be used to model their reinforcement of streambanks (Abernathy & Rutherford, 2000; Pollen, 2007), this method is highly destructive, because it involves observations in deep trenches cut through the root profile. It is also heavily reliant on visual observations and mechanical measurements of roots and their architecture, and therefore cannot be directly transferred to submerged sediments or exposed saturated sediments that can be easily displaced. Whilst there are no studies that have explicitly measured the contribution made by the below ground biomass of aquatic vegetation to sediment stability, it can be assumed that some of the soil modifications found in association with terrestrial vegetation are comparable to those imposed by aquatic vegetation; these may include increased shear strength, binding of soil particles and the addition of organic matter.
There are few empirical studies that quantify the below ground biomass of aquatic plants, though Haslam (2006) has provided qualitative classifications of the rooting depth and structure of several aquatic plants commonly found in the UK. These range from species that commonly inhabit faster flowing areas within river channels and have short, curled roots that wrap around the larger bed substrate particles to anchor the plant to the bed (several patch submerged species e.g. Callitriche spp, Ranunculus spp.), to species that typically grow in areas of low flow velocity, and produce deep, relatively straight roots that penetrate finer sediments (many linear emergent species e.g. Sparganium erectum and Phragmites australis). Haslam (2006) also noted that Sparganium erectum varied its rooting depth as material aggraded, suggesting it may provide reinforcement to newly deposited, unconsolidated sediment material, which is most susceptible to erosion.

Sophisticated methods have been devised to measure the below ground growth and dynamics of terrestrial vegetation, including (1) Root windows: a Perspex sheet embedded in the soil to observe and mark changes in root length; (2) Wall excavations: digging a trench to observe the depth and abundance of below ground biomass; (3) Minirhizotron cameras: a specialized digital camera that can slide inside an underground tube to capture images of the tube-soil interface (Metcalfe et al. 2009). In addition, ingrowth core methods, involving the placement of root penetrable core tubes into sediments and subsequent removal following a period of root development, have been used for assessing root production and architecture in forested (Steele et al. 1996; Cheng & Bledsoe, 2002) and riparian areas (Kiley & Schneider, 2005; Boyd & Svejcar, 2009). However, none of these methods are entirely suitable for observing root growth in aquatic sediments because water limits visual observations and causes sediments to be highly unstable.

Alternative, less sophisticated means of assessing below ground biomass have been devised to investigate aquatic plants, which mainly involve excavation of sediment blocks to determine the dry biomass they contain (Klopatek & Stearns, 1978; Klimes et al. 1999; Asaeda et al. 2006a,b, 2009; League et al. 2006). This type of approach allows total mass to be accurately quantified but gives little information on its distribution within the sampled sediment. However, Darby and Turner (2008) devised a method for investigating root profiles in relatively cohesive estuarine sediments, which involved cutting and extracting a core using 11cm x 30cm stainless steel tubes with sharpened edges and then dissecting 10cm depth increments for analysis. This revealed that over
50% of root biomass was found in the upper 10cm of sediment, suggesting a lateral spread of roots within surficial soil layers. A near-equal proportion of rhizome material was found between 10-20cm of sediment depth, perhaps being a trait that offers protection from erosion.

Therefore, there presently exist no empirical studies that measure, in detail, the below ground architecture of aquatic vegetation. Such an effort would perhaps be less appropriate for those species identified by Haslam (2006: 64) as rooting in coarse substrates, as these are shallow rooted, and can be removed and observed with relative ease and minimal disturbance. Additionally, above ground biomass is thought to be more influential in the acquisition and retention of fine sediments for these species (Sand-Jensen, 1998). However, an investigation into the rooting architecture of emergent species could be highly revealing; specifically an understanding of the depth, abundance and seasonality of below ground biomass would usefully inform an assessment of the ecosystem engineering potential of these morphotypes. It is presently unknown if the highly seasonal nature of above ground biomass production in linear emergents (Haslam, 2006: 161) mean that their profound hydrodynamic and sedimentary effects are negated by remobilisation of retained sediments during dormancy when above ground biomass is absent. Understanding seasonal changes in the depth and abundance of below ground mass would inform hypotheses about its effect on sediment stability and retention during periods when above ground biomass is present and absent.

2.3.3 Vegetation induced fluvial landform development

Whilst knowledge of the reinforcing effect of vegetation has been widely adopted in management scenarios, the principles of that knowledge are also being applied to understand natural geomorphological processes in rivers. Riparian tree species influence channel structure by reducing near surface velocities, inducing sediment deposition and reinforcing sediment with their roots (Corenblit et al. 2007; Erskine et al. 2009; Francis et al. 2009; Moggridge & Gurnell, 2009). These processes can generate landforms in many locations, across a variety of channel types and, where growth is in marginal areas (where emergent macrophytes commonly grow), reinforcement of existing as well as newly-trapped sediment can occur, allowing extension of the bank-toe into the active channel (Gurnell et al. 2001; Simon et al. 2004; Rominger et al. 2010). Research from the River Tagliamento in Italy has demonstrated that vegetative elements drive the
development of fluvial landforms, essentially through a sequence of deposition, growth, hydraulic obstruction, sediment aggradation and reinforcement (Gurnell et al. 2001; Francis & Gurnell, 2006). Such a process is potentially analogous to the development of aquatic plant stands and their associated sediment accumulations, which can become established in new locations following the dispersal of viable fragments from upstream (Cook, 1962; Miler et al. 2011). Aquatic plants have been studied far less in this context, perhaps because it has been assumed that any effects they have on channel structure will be time limited to the period when above ground biomass is present. Such a theory is probably applicable to submerged species, where the tendency for sediment accumulations to remobilise following the dieback of foliage in winter has been noted (Heppell et al. 2009), and is likely to prevent longer term changes in channel structure. However, it has been shown by Bennett et al. (2007) that channel narrowing and thalweg meandering are possible products of discrete plantings of rigid, emergent, marginal vegetation mimics in flumes, whilst such planting in river channels can also be used to reinforce existing geomorphological features (Rominger et al. 2010). Thus, just as riparian trees are now recognised for their ability to function as ecosystem engineers, under certain conditions, in-channel vegetation may also constitute an important element in the structural development of rivers.

2.3.4 Assessing physical ecosystem engineering by vegetation

Monitoring and quantifying physical ecosystem engineering is a difficult task, the methodologies for which are dependent on the type of environments and processes being studied. Unless a highly dynamic environment is being observed, a frequent problem appears to be that the processes of change exceed the length of the study period. In these situations, alternative measurements, which are unlikely to alter significantly between seasons, are commonly used to infer probable long-term changes in the physical environment. For example, hydraulic measurements are commonly used as a proxy for sedimentation in discrete vegetated, unvegetated and species-specific areas (Bouma et al. 2005; Gurnell et al. 2006a; Asaeda et al. 2009; Bouma et al. 2010). This is because hydraulic measurements (flow velocity and wave intensity in these examples) relate to sediment trapping capability, which in turn is associated with ecosystem engineering capability (Bouma et al. 2010). In situations where erosion is the hypothesized physical change, simulated scour in vegetated/unvegetated areas can be used to assess the susceptibility of sediment to erosion. This may involve a concentrated jet of water being applied to the sediment surface, and the rate or depth of scour used to
inform the erodibility of the sediment (Hanson 1990; Hanson 1991; Hanson & Simon, 2001; Simon & Thomas, 2002). Thus, measurements that mimic an accelerated process or those that are considered to be seasonally invariant are common means of assessing ecosystem engineering. In rivers, these measurements usually relate to the ability to resist hydrodynamic forces, as these are the principal forces that can redistribute sediments. However, it is noteworthy that there are studies that have demonstrated vegetation controlled spatiotemporal geomorphological changes in rivers (e.g. Gurnell et al. 2001; Gurnell et al. 2006b, Bertoldi et al. 2011).

There is a growing body of research that uses biomechanical measurements as a means of assessing ecosystem engineering potential. The study of plant biomechanics involves the application of mechanical measurements to the structural components of plants. Measurements are typically concerned with the response of physical structures to force or displacement (Taylor, 2007), and the subsequent effect of these on the plant and its environment.

Just as hydrodynamic measurements have been used as a proxy for sedimentation (e.g. Bouma et al. 2010), it has been argued that certain biomechanical measurements, such as uprooting resistance, stem strength and root strength, can be used as a surrogate for erodibility (Burylo et al. 2009) or a component in the modelling of sediment stability (Schutten & Davy 2000; Schutten et al. 2005). Biomechanical measurements have been applied to several studies that explore interactions between vegetation, sediment and water movements, including lake bottom sediments (Schutten & Davy 2000; Schutten et al. 2005), river banks and margins (Abernethy & Rutherford, 2000; Simon & Collinson, 2002; Pollen & Simon, 2005; Pollen, 2007) and hill slopes (Burylo et al. 2007; De Baets et al. 2005).

The long standing recognition of the reinforcing effect roots have on sediment (Hickin, 1984; Thorne, 1990) and existing geotechnical measurements such a shear strength, bulk density and porosity are now being complimented by biomechanical measurements. In situations where many geotechnical measurements cannot be applied (i.e. in highly saturated or submerged sediments), biomechanical measurements may represent the only means of inferring the erosion resistance of plants and their associated sediments. Furthermore, it has been suggested that vegetation is so crucial to the retention and reinforcement of sediment in many environments that measures of
uprooting resistance and sediment cohesion are of equal importance (Corenblit et al. 2007).

An additional advantage of biomechanical measurements is that their study allows for the incorporation of additional morphological measurements, which can further reveal the ways in which vegetation affects its environment (Schutten & Davy, 2000; Karrenburg et al. 2003; Miler et al. 2010) and can provide practitioners with simple methods of judging erosion resistance (Burylo et al. 2009; Stokes et al. 2009). At present, there are no studies that have measured the biomechanical strength of emergent aquatic plants or the geotechnical properties of the sediments they accumulate, despite there being several studies that describe their ecosystem engineering effects (Gurnell et al. 2006a; Naden et al. 2006; Bennett et al. 2007; Asaeda et al. 2009; Rominger et al. 2010). Biomechanical classifications of these plants would be particularly useful because geotechnical measurements used to assess erodibility cannot be easily applied in the highly saturated sediments they typically occupy. Furthermore, whilst several of those studies explored the seasonal influence of emergent vegetation upon flow velocity and sedimentation patterns (Gurnell et al. 2006a; Naden et al. 2006; Asaeda et al. 2009) a temporally extensive study of biomechanical properties, particularly the strength of underground organs, would more usefully inform any seasonality in their reinforcing effect, which is thought to be crucial to their ability to generate new landforms.

2.4 Research gaps and thesis research questions

This review has identified the following research gaps that are relevant to the ecosystem engineering potential of linear emergent macrophytes:

1. The influence of emergent vegetation upon flow hydraulics and sediment dynamics has only been conducted in areas where it is thought to have a profound effect (Naden et al. 2006; Asaeda et al. 2009), has been observed incidentally (Gurnell et al. 2006a), or has been artificially tested (Bal et al. 2010). A study that reveals the hydraulic/sedimentary impact of varying spatial distributions of emergent species across a range of energy conditions is required to more fully understand the effects this morphotype has on its environment.
2. There presently exist no studies that have measured, in detail, the depth, abundance and seasonality of the below ground biomass of emergent aquatic vegetation. Such a study is required to inform hypotheses about the protection these below ground components offer to fluvial sediment accumulations.

3. Biomechanical measurements have been deemed a useful way of gauging the ecosystem engineering capacity of linear emergent species. However, there is no published research that has measured the biomechanical properties of linear emergent macrophytes, specifically their resistance to uprooting and the breaking strength of above/below ground components. The undertaking of biomechanical measurements would also make a useful contribution to a growing body of literature that is revealing the strength of different plant species, and how their morphologies and growth strategies affect their surroundings.

In order to reduce the inherent variability that may exist between different emergent aquatic species, particularly in their response to different environmental conditions other than those that are flow and sediment related, it is useful to focus on one species. In this study, *S. erectum* was selected because of its widespread occurrence and recognised tolerance of a wide range of environmental conditions. Therefore, *S. erectum* is used in the present research to investigate a set of research questions. These are listed below, along with the corresponding result chapter(s) that address them:

(i) To what extent does the seasonal growth and senescence of *S. erectum* affect the hydraulic performance and sediment dynamics of contrasting river reaches? Chapter 4.

(ii) How do the growth traits and biomechanical properties of *S. erectum* vary spatially and temporally; both between reaches along the same river, and nationally between rivers? Chapter 5.

(iii) How does *S. erectum* root and rhizome architecture vary through the annual cycle of canopy growth and senescence? Chapter 6.

(iv) What are the underlying biomechanical and morphological properties that enable *S. erectum* to act as a physical ecosystem engineer? All results chapters.
The methods used to address these questions are given generally in Chapter 3 and in detail in Chapters 4, 5 and 6. The results obtained build to provide a picture of the biomechanical niche of *Sparganium erectum*, which is described in chapter 7.
Chapter 3
Research Design

3.1 Introduction

Following from the research aims and questions stated at the end of Chapter 2, this chapter introduces the overall design adopted to address those aims and questions. Whilst Chapters 4, 5 and 6 are written as semi-independent papers, this chapter provides integrated details of the field areas where the research was undertaken (section 3.2) and the methods that were used in combination at each site (section 3.3) to deliver the research results discussed in Chapters 4, 5 and 6.

3.1.1 Conceptual background

Corenblit et al. (2007) proposed a conceptual model detailing the interactions between flow, sediment and vegetation that are fundamental to the structural development of new riparian landforms. The model lists the principal effects of vegetation upon sediment dynamics (erosion, transport and deposition), which are influenced by the vegetation’s resistance to flow and the capacity of underground biomass to alter substrate cohesion. Whilst the original model was principally concerned with riparian plant species, the interactions remain applicable to in-channel vegetation, and an adapted version of this model, presented in Figure 3.1, provides a useful means of visualising the way in which *S. erectum* is hypothesized to function as an ecosystem engineer.

At present, many of the model components have yet to be proven and measured. Chapters 4, 5 and 6 therefore present observations relevant to the components of the model that are poorly understood in the context of aquatic vegetation (though in several cases they are thoroughly studied for riparian vegetation). The numbers 4-6 in Figure 3.1 correspond with the adjacent elements of the model that are addressed in the Chapters 4-6 of this thesis; corresponding outlines of the methods used are discussed in sections 3.3.1 – 3.3.3 of this chapter.
Figure 3.1: Conceptual model of reciprocal interactions between *S. erectum*, water flow and sediment dynamics that drive fluvial landform development. Grey arrows indicate the contribution of vegetation to morphogenesis processes (adapted from Corenblit et al. 2007).

3.2 Site selection rationale and site descriptions

3.2.1 Space-time rationale underpinning the field research design

Gaining an understanding of the processes detailed in Figure 3.1 required a combination of methodological approaches, which varied in terms of their spatial extent and sampling intensity. An element of the survey design that incorporated sampling across a large geographic area was considered particularly important given that *S. erectum* is the most widely-occurring macrophyte in Britain, occurring abundantly across many river environments (O’Hare et al. 2010). It is therefore subject to a huge range of environmental conditions that are likely to be limited in localised experimental areas and could potentially influence its functionality as an ecosystem engineer. A spatially extensive study of the species was therefore undertaken to provide a national impression.
of its biomechanical properties, which could be used to infer the broader application of results acquired from in-depth, local investigations.

Richards (1996) has argued that a combination of extensive and intensive methodological approaches produce the most revealing outcomes in environmental science. In such a situation, it is often the case that extensive, empirical studies, with high sample numbers, are undertaken initially, the results of which are later understood using intensive examination of a small number of locations and samples (Yatsu, 1992). This thesis attempts to adopt such an approach, however, the combination of intensive and extensive approaches must be considered in the context of spatial distribution and sampling frequency. Although intensive research is traditionally conducted within a single location (Richards, 1996) such an approach is not usefully applicable where evaluation of spatial variability and seasonality are key requirements of the investigation. In the present research it is argued that, when seeking to understand the spatiotemporal variation of measurements, time and space should provide the context for intensive versus extensive sampling strategies. The thesis therefore employs temporally extensive measurements of *S. erectum*’s biomechanical properties on a single river, which are contextualised using a temporally limited but spatially extensive study, to provide evidence of the theoretical influence of the species through time and space. Where measured physical or macrophyte properties are the focus of investigation, the thesis uses the traditional method of using intensive site-specific measurements to infer the properties of a larger population. For example, associations between plants and fine sediment were observed across all investigated sites and inferences were drawn concerning the growth properties of below ground biomass. However, detailed measurements of below ground biomass were investigated at only one site.

Thus, in order to balance a broad national perspective with in-depth scientific investigations, a range of temporal and spatial scales were adopted to address the research questions (section 2.4). The geographical distribution and temporal frequency of the research elements ranged from monthly stand-scale experiments in a single reach over two years, to single site visits at fourteen rivers that stretched from the southern counties to the Scottish borders. The application of different methods ranged from those that focussed on individual plants, through plant stands, up to reach-scale studies. By varying the scale and resolution of measurements across space and time, the aim was to
gain a deep understanding of the biomechanical strategies and performance of *S. erectum* that underpin its potential role as a river ecosystem engineer (Chapter 7).

A plan of how the different field investigations fit within a framework of extensive/intensive spatiotemporal sampling is presented in Figure 3.2. It shows how the different elements of the research fit into a collective research design. The methods employed within each of the research elements are described (as indicated in Figure 3.2), in sections 3.3.1, 3.3.2 and 3.3.3 of this chapter. The location of the different field sites at which the research was undertaken, the frequency and timings of measurements, and the rationale for site selection are discussed in sections 3.2.2 and 3.2.3.

Figure 3.2: A plan of how the different field investigations fit within a framework of space and time scales.
3.2.2 National survey sites

The most spatially extensive element of the research was conducted across 14 rivers in the UK, extending from the southern counties to the Scottish borders (Figure 3.3, Table 3.1). These sites were subjected to a single stand-scale survey in 2009 during the period of peak *S. erectum* biomass (July - August). The sites were selected using Mean Trophic Rank (MTR) surveys conducted by the Centre for Ecology and Hydrology (CEH) and Environment Agency to ensure that *S. erectum* was present. Measures of the standing crop and biomechanical properties of *S. erectum* at these sites provided information on the degree to which these properties varied according to geographical location (particularly latitude). Measurements from these 14 sites provided a national context against which more detailed spatiotemporal investigations within a single river system (Site 11, Figure 3.1: River Blackwater, Surrey) could be placed.
Figure 3.3: National survey site locations.
Table 3.1: Locations, bankfull width and gradient of river reaches investigated.

<table>
<thead>
<tr>
<th>River name</th>
<th>Easting</th>
<th>Northing</th>
<th>Bankfull Width (m)</th>
<th>Slope (cm/m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aln</td>
<td>411950</td>
<td>613750</td>
<td>6.49</td>
<td>0.87</td>
</tr>
<tr>
<td>Blackadder</td>
<td>370965</td>
<td>645760</td>
<td>10.0</td>
<td>0.61</td>
</tr>
<tr>
<td>Blackwater - 1</td>
<td>488550</td>
<td>152750</td>
<td>5.40</td>
<td>0.84</td>
</tr>
<tr>
<td>Blackwater - 2</td>
<td>488250</td>
<td>155150</td>
<td>6.20</td>
<td>0.66</td>
</tr>
<tr>
<td>Blackwater - 3</td>
<td>486202</td>
<td>158957</td>
<td>5.30</td>
<td>0.29</td>
</tr>
<tr>
<td>Blackwater - 4</td>
<td>486070</td>
<td>159082</td>
<td>ca. 6.00</td>
<td>ca. 0.30</td>
</tr>
<tr>
<td>Bourne</td>
<td>415755</td>
<td>131255</td>
<td>8.00</td>
<td>0.46</td>
</tr>
<tr>
<td>Eye Brook</td>
<td>483850</td>
<td>298380</td>
<td>4.00</td>
<td>3.37</td>
</tr>
<tr>
<td>Leet</td>
<td>378750</td>
<td>643950</td>
<td>2.95</td>
<td>2.44</td>
</tr>
<tr>
<td>Mease</td>
<td>426275</td>
<td>311380</td>
<td>5.00</td>
<td>0.81</td>
</tr>
<tr>
<td>Pont</td>
<td>416885</td>
<td>573195</td>
<td>5.50</td>
<td>0.71</td>
</tr>
<tr>
<td>Rother</td>
<td>480715</td>
<td>122905</td>
<td>7.00</td>
<td>0.88</td>
</tr>
<tr>
<td>Sence</td>
<td>435050</td>
<td>303050</td>
<td>5.00</td>
<td>2.30</td>
</tr>
<tr>
<td>Skern</td>
<td>430500</td>
<td>527000</td>
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</tr>
<tr>
<td>Tove</td>
<td>467880</td>
<td>249175</td>
<td>5.00</td>
<td>0.78</td>
</tr>
<tr>
<td>Warren Burn</td>
<td>415400</td>
<td>631200</td>
<td>2.92</td>
<td>0.87</td>
</tr>
<tr>
<td>Wey</td>
<td>482254</td>
<td>145385</td>
<td>5.70</td>
<td>1.69</td>
</tr>
</tbody>
</table>

3.2.3 Study sites on the River Blackwater, Surrey

Research at all other space and timescales was conducted along the River Blackwater, Surrey. This lowland river was selected because it supports extensive growth of *S. erectum*, in addition to many other macrophyte species, throughout its course. It was therefore possible to identify reaches for study with different discharge, slope, channel dimensions and morphology that also contained extensive stands of *S. erectum*. The River Blackwater is similar to many lowland, low energy, rivers in the UK in that it supports abundant growth of macrophytes and has been subject to significant management (Gurnell, 2010). It is typical of the group A British rivers (Lowland rivers with shallow gradients and rich geology) specified by Holmes et al. (1999), particularly sub-types I (lowland, low-gradient rivers) and IV (base rich / neutral impoverished rivers), both of which are particularly common in the south and east of England.
The Blackwater is a tributary of the River Loddon, which subsequently feeds into the River Thames. The catchment (Figure 3.4) is dominated by urban and industrial activity, containing the towns of Aldershot, Farnborough, Frimley and Camberley. Gravel is found throughout the Blackwater Valley, and post-war demand for building materials has seen its almost continuous extraction since the 1950s. Thus, industrial, residential and transport pressures have lead to the natural vegetation of the river valley being constrained to a narrow strip surrounding the river. This strip, and the river itself, are now highly valued by the local community and protected by various public and charitable bodies (notably the Blackwater Valley Countryside Partnership and local Environment Agency office), who provided access and support for the research conducted in this thesis. There is a Blackwater Valley Site of Special Scientific Interest (SSSI) in addition to three nature reserves within the catchment. Although the river has been heavily altered, most notably large sections were moved to accommodate the building of the Blackwater Valley road (A331), there are sections that have been restored and others that have been subjected to very little interference. Thus the river is morphologically diverse, containing managed, restored and semi natural sections, and represents an appropriate river system for the purposes and scope of this study.

Three reaches of the River Blackwater were selected for detailed study. They were spaced at approximately 8, 11 and 15 km from the river’s source to give a distinct gradient in river discharge, slope and river channel dimensions, and were all subject to extensive growth of *S. erectum*. A fourth reach was located a short distance downstream of reach 3 and was used for destructive measurements to complement non-destructive investigations in the other three reaches. A description of the reaches follows, their location is shown in Figure 3.4 and images of the reaches during spring fieldwork are shown in Figure 3.5

Reach 1 (51° 15’ 59” N, 0° 43’ 54” W) is 7.7 km from the source, 38m in length, with a slope of 0.00084 m/m, and an average baseflow flow water width of 5.4m. It has a smooth, slightly sinuous planform and trapezoidal cross profile, indicating that it is a realigned channel, which appears to be over-widened. The bed material is predominantly organic-rich silt overlying fine to medium gravel, which is exposed in some small areas of the bed. The channel is dominated by *S. erectum*, almost to the complete exclusion of other aquatic plants.
Reach 2 (51° 17’ 16” N, 0° 44’ 11” W) is 11.4 km from the source, 25m in length, with a slope of 0.00066 m/m, and an average baseflow water width of 6.2m. This reach is located on private land and appears to be relatively unmanaged, at least in recent years, with clear evidence of bank accretion and erosion and a higher morphological complexity than reaches 1 and 3. Like reach 1, the bed material is predominantly silt overlying fine to medium gravel, which is exposed in larger patches than in reach 1.

Reach 3 (51° 19’ 14” N, 0° 45’ 48” W) is 14.9 km from the source, 63m in length, with a slope of 0.00029 and has an average baseflow water width of 5.3m. This reach is straight and has been realigned. The right bank has been artificially reinforced using stone filled gabions, producing a steep channel margin. The left hand bank is not reinforced and shows evidence of significant morphological adjustment with both marginal benches and sections of eroding bank. The bed material is predominantly medium to coarse gravel with relatively small marginal areas overlain by silt.

Reach 4 (51° 19’ 26” N, 0° 45’ 59”W) is located 15.2 km from the source and contains large, marginal patches of *S. erectum* that were easily accessible for field experiments and were used for destructive measurements. The reach is within a restored section that was originally designed by Professor Robert Selling from the University of Bristol. It was designed specifically with ecological considerations in mind, and contains areas of suitable habitat for plants and wildlife.

Being a predominantly urban catchment, general and local management priorities of the River Blackwater have been to prevent flooding of the settlements and infrastructure that border the river (Figure 3.4). Therefore, to increase conveyance, many sections have been channelized to accommodate flood events. This strategy causes reduced velocity at baseflow, increased siltation and the growth of aquatic plants; other influences such as nutrient availability and the removal of riparian trees are also likely to contribute to the abundant growth of in-channel vegetation. The combination of siltation and aquatic plant growth has complicated long-term assessment of the river’s hydrological regime, as they interfere with discharge measurements made by the electromagnetic gauging station situated shortly downstream of reach 2. The poor quality of data provided by this gauging station and the large distance downstream to the next station mean that multi-year discharge records are not included in this thesis.
Figure 3.4: The catchment of the River Blackwater and the location of the four study reaches.
Figure 3.5: Images of the four reaches of the River Blackwater (as denoted by numbers 1-4) during spring 2009. All photographs are taken looking upstream, with the exception of reach 4.
3.3 Investigative design

Field and laboratory work aimed to investigate the following specific research questions, previously given in section 2.4:

(i) To what extent does the seasonal growth and senescence of *S. erectum* affect the hydraulic performance and sediment dynamics of contrasting river reaches?

(ii) How do the growth traits and biomechanical properties of *S. erectum* vary spatially and temporally; both between reaches along the same river, and nationally between rivers?

(iii) How does *S. erectum* root and rhizome architecture vary through the annual cycle of canopy growth and senescence?

(iv) What are the underlying biomechanical and morphological properties that enable *S. erectum* to act as an ecosystem engineer?

The field sites described in section 3.2 were used to investigate each of these research questions as summarised in Table 3.2. An outline of the methods used to address these questions follows in sections 3.3.1, 3.3.2 and 3.3.3.

Table 3.2: The study reaches used to answer the research questions.

<table>
<thead>
<tr>
<th>Research Question</th>
<th>i</th>
<th>ii</th>
<th>iii</th>
<th>iv</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reach 1</td>
<td>✓</td>
<td>✓</td>
<td></td>
<td>✓</td>
</tr>
<tr>
<td>Reach 2</td>
<td>✓</td>
<td>✓</td>
<td></td>
<td>✓</td>
</tr>
<tr>
<td>Reach 3</td>
<td>✓</td>
<td>✓</td>
<td></td>
<td>✓</td>
</tr>
<tr>
<td>Reach 4</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>National sites 1-14</td>
<td>✓</td>
<td></td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

3.3.1 Hydraulic surveys

It has previously been shown at varying scales that macrophyte growth has a significant effect on flow velocities and sediment dynamics (e.g. Sand-Jensen, 1998; Gurnell et al. 2006a). In this thesis, it is hypothesized that *S. erectum*, and perhaps other macrophytes of a similar morphology, could profoundly influence the physical properties of certain
rivers because of their effect on the hydraulic environment. Specifically, it is hypothesized that *S. erectum* can often be the cause of a sharp decrease in velocities, causing the accumulation of fine sediment within its stands, which may be stabilised and protected from erosion by the growth of below ground biomass. This process may ultimately lead to a change in channel morphology, and given its abundance and broad spatial extent, the species may be an important element in the structure, function and evolution of river channels.

To assess the influence of *S. erectum* on reach hydraulics through growth, senescence and dormant seasons, this study adopted a repeat cross section survey methodology, similar to that used by Gurnell et al. (2006a). Respectively 10, 7 and 10 fixed cross-sections were established at reaches 1-3 of the River Blackwater; The priorities when selecting reaches were: (1) that they were relatively straight, which reduces the influence of channel morphology on sedimentary processes and highlights the role of aquatic vegetation; (2) an absence of overhanging riparian trees that would prevent the growth of aquatic plants. Reach 2 therefore contained fewer cross sections because it was significantly shorter than the other two reaches; this was principally because it occupied a comparatively unmanaged section of the river and was therefore more sinuous and showed a greater occurrence of riparian trees. Ten cross sections could have been included in this shorter reach, but this would have meant it had a higher resolution of measurement points and surveying would have caused greater disturbance of vegetation and sediment accumulations. Selecting seven cross sections meant that the distances between them were similar between reaches. The survey tapes installed at the cross section sites at reaches 1-3 can be seen in Figure 3.5.

The reach scale/cross section method was chosen because it gives a high resolution of hydraulic, physical and macrophyte measurements within the necessary timeframe, thereby giving an accurate reflection of the river’s hydraulic performance and other attributes. Cross-sections also generally include discrete patches of macrophytes, allowing for direct comparison between vegetated/unvegetated areas. This research element was explicitly designed to address research question (i), but repeat measurements in identical locations also enabled detailed recordings of plant growth and spread, which help to address research question (ii) by giving reach-scale measurements of the standing crop. The reach scale investigations also sample a reasonably broad channel area, which is likely to encompass properties that are representative of other reaches of the river. It also has the potential to capture larger
physical processes, such as bench development, which constitute a substantial focus of this thesis.

Details of the specific field measurements undertaken within the cross sections are fully described in Chapter 4, but in summary, they captured information on flow velocity, water depth, substrate calibre, macrophyte species and coverage at approximately six-week intervals through the growth and senescence seasons of 2009, and once during dormancy in early 2010, and supported an analysis of changes in the velocity and bed sediment environment in response to the phases of macrophyte growth and decay.

3.3.2 Uprooting experiments

If the plant is to function as an ecosystem engineer, it must be able to withstand hydraulic stress, and so its ability to withstand breakage and uprooting must exceed the force exerted by river flows. While the reach scale studies assess the effect of the presence and growth of macrophytes on the hydraulic environment, the objective of the uprooting experiments was to quantify and describe the seasonal strength of the plant and the growth traits that underpin its strength and enable it to function as an ecosystem engineer. To assess these biomechanical properties, this research element used mimicked hydraulic stress (Figure 3.6) to determine the threshold up to which the plants can resist damage or uprooting, and then related this to measurements of various physical properties of the damaged/uprooted plant.
Figure 3.6: An uprooting experiment being conducted at reach 4 of the River Blackwater.

Uprooting experiments were conducted throughout the growing seasons of 2009 and 2010. Destructive measurements that recorded the force required to induce failure of the plant, and measures of their growth structure, were conducted at reach 4 of the River Blackwater at approximately 5 week intervals between April – October 2009 and 2010. These were purposefully conducted downstream of reaches 1-3 to prevent the risk of plant removal affecting the hydraulic and other measurements conducted within these three reaches. The experiments were designed to answer research questions (iii) and (iv), and the same methods were used to assess the spatial variability of the growth and biomechanical properties of *S. erectum* at peak growth (July – August) 2009, in the National survey across sites 1 – 14 (Figure 3.1). Full details of the specific field measurements undertaken during the uprooting experiments are provided in Chapter 5.

### 3.3.3 Below ground biomass measurements

The purpose of this research component was to assess the temporal development, and vertical distribution in the below ground biomass of *S. erectum* through the annual phases of plant growth, senescence and, to a lesser extent, dormancy. Belowground biomass is crucial to the longevity and stability of aquatic plants, and usually constitutes
the majority of total biomass for a single plant or in a given site (Sculthorpe, 1967; Darby & Turner, 2008), whilst it is also an important factor in the stability of sediment (Gyssels et al. 2005). Despite the importance of the below ground organs for both the resistance of the plant to uprooting and the resistance of the penetrated sediment to erosion, there are few studies that have investigated the belowground dynamics of plants occupying saturated soils, perhaps due to the complications that arise from sampling in such an environment.

A number of studies have investigated fine root distributions using ingrowth cores in forested and other terrestrial areas (e.g. Steele et al. 1997, Cheng & Bledsoe 2002) and a limited number of studies have investigated riparian areas (Kiley & Schneider 2005; Boyd and Svejcar 2009), which might expect closer proximity to the water table and seasonal inundation. This study used an adapted ingrowth core method from the aforementioned studies to investigate the belowground portions of *S. erectum*. The method was designed following observations of plants uprooted during 2009 fieldwork. Complicated growth patterns of the substantial below ground biomass were apparent, but the depth and distribution of roots and rhizomes could only be speculated upon once the plants were uprooted. This method was designed to address research question (iii) by establishing the depth at which *S. erectum* occupies its sediment, and potentially the temporal extent to which its rhizomes and roots offer protection and reinforcement to those sediments, particularly the surficial layers, which are exposed to high shear stresses during winter when above-ground biomass is absent.

The ingrowth core method involves the placement of a penetrable core into a location where plant growth is predicted (Figure 3.7). The core must contain a large number of holes through which roots/rhizomes can grow, so that restriction of their growth is minimal and the contents of the core remains a near-accurate reflection of local below ground biomass. A total of 50 in-growth cores were placed into fine sediment patches within reach 2 on the River Blackwater in February 2010, before the onset of growth. Between 6-8 cores were extracted at approximately 5 weekly intervals from May 2010 – November 2010 and again once more in January 2011. The captured sediment profiles were analysed in the laboratory to establish the changing vertical distribution of root and rhizome biomass. Full details of these field and laboratory measurements are provided in Chapter 6.
3.4 Summary

This chapter has provided a broad overview of the field locations and field and laboratory measurements conducted to address the research questions posed following the literature review in section 2.4. The aim was to provide a context upon which the detailed research elements reported in Chapters 4 to 6 could be placed. Full descriptions of all research methods are given in the relevant chapters (4, 5 and 6), which have been deliberately written as free-standing research reports.

Figure 3.7: In-growth core tubes placed on adjacent banks of reach 2 of the River Blackwater. Photograph taken March 2010.
Chapter 4

Reach scale interactions between river flows, aquatic macrophytes and sediment in the headwaters of a lowland river

Chapter Summary

This chapter investigates interactions between flow velocities, fine sediment and aquatic macrophyte growth, particularly growth of the emergent macrophyte *Sparganium erectum*, within three reaches of a single river but at different distances from the source. In particular the chapter investigates the degree to which *S. erectum* may be able to actively engineer river environments, and potentially enhance hydraulic and physical habitat diversity through river bed and bank adjustment.

The investigated reaches vary considerably in terms of their morphology, ranging from an upstream reach where the plant widely colonises and almost ‘chokes’ the channel, to the most downstream reach where growth of the species is limited by water depth and flow velocity, and an intervening reach, where the plant generates greater hydraulic diversity.

Cluster analysis was applied to measurements of flow velocity taken at a network of fixed points within the three reaches on seven sampling occasions between March 2009 and February 2010. The analyses revealed four distinct classes (clusters) of velocity behaviour across the three reaches, which were associated with statistically significantly different values of macrophyte type and abundance, and bed sediment calibre. Linear emergent macrophytes, particularly *S. erectum*, were strongly associated with the slowest velocity class and fine sediment, which persisted throughout the year despite the winter dieback of foliage. The results of the analysis of streamwise flow velocities were supported by cluster analysis of cross-stream velocities and *S. erectum* abundance. This allowed inferences to be drawn concerning the capacity of *S. erectum* to function as an ecosystem engineer by causing profound changes in flow conditions at local and reach scales.

The strong associations between the velocity classes, physical and macrophyte measurements were used to classify four distinct habitats that existed commonly
throughout the three reaches. These were incorporated into a conceptual model of the development of these habitats, which are triggered by the growth of emergent vegetation.

4.1 Introduction

There is an intimate relationship between vegetation and landforms, and recent research has demonstrated that under many circumstances and across rivers of all sizes, a range of plant species are associated with fluvial landforms (Bendix & Hupp, 2000; Hupp & Bornette, 2003; Hupp & Rinaldi, 2007) and can influence river form and dynamics (Gurnell et al., 2006 a,b) by acting as ‘physical ecosystem engineers’ (sensu Jones et al., 1997). As a consequence, interactions between fluvial processes and vegetation are a central component of ecosystem function, inducing both structural and functional changes across time and space.

Just as riparian trees are now recognised for their ability to function as ecosystem engineers (Gurnell et al. 2001; Corenblit et al. 2007; Erskine et al. 2009; Francis et al. 2009), under certain conditions, in-channel vegetation may also constitute an important element in the structural development of rivers. Aquatic plants have been studied less in this context, but it is hypothesized that the structure, growth cycle and habitat preferences of certain emergent species allow them to function in such a capacity.

The principle hydrodynamic effect of all aquatic plants is to reduce flow velocity, which can result in accretion of sediment within and around plant stands. However, profound changes in channel structure will only occur as a result of this process where accumulated sediment persists from one year to the next. The seasonal tendency for sediments associated with submerged species to remobilise (Heppell et al. 2009) may prevent them from inducing significant changes in channel structure. However, the potential of sediment accretion around emergent aquatic vegetation to support more persistent sediment retention remains to be investigated. Gurnell et al. (2012) have recently proposed a biogeomorphological sequence of landform development initiated by sediment and seed retention within emergent macrophyte stands (Figure 4.1). This model is based on an analysis of the seed banks and sediment characteristics of different vegetated and unvegetated patches found on the bed of three low energy river reaches.
(Gurnell et al., 2007a), and describes a sequence of initial seed and sediment retention by an emergent macrophyte stand, which aggrades to the low flow water level. At this point, the emergent macrophytes are displaced laterally and wetland species germinate from the seedbank to support continued sediment aggradation, terrestrialisation and extension of the bank profile through marginal bench development. The key to this process is that sediment is retained from one year to the next with a sufficient diversity of seed species to drive the transition from aquatic through wetland to terrestrial vegetation. Whilst the species richness of elevated fluvial landforms has been previously demonstrated (Gilvear & Willby, 2006) and the seedbank aspect of this model explored by Gurnell et al. (2007b, 2008), the hydrodynamic processes and spatial application of the model require investigation.

This chapter explores interactions between flow velocity, aquatic vegetation and bed sediment characteristics within reaches 1-3 of the River Blackwater, Surrey, UK to investigate how these interactions vary through the cycle of annual macrophyte growth and senescence. It seeks to establish whether fine sediment accretion in this low energy river is associated with this cycle, and the degree to which particular plant morphotypes are linked to characteristic behaviour in flow velocity and bed sediment calibre. In particular, the collected data sets will be explored for evidence of the biogeomorphical sequence of landform development proposed by Gurnell et al. (2012) Figure 4.1.
4.2 Investigative design

4.2.1 Study reaches

The research was carried out at reaches 1-3 on the River Blackwater, Surrey, UK (Figure 4.2). The River Blackwater is 32 km long and is a tributary to the River Loddon, which in turn drains into the River Thames. The three study reaches were located in the headwaters and were 38, 25, 63 m in length with an average water width at low-flow of 5.4, 6.2 and 5.3 m, respectively. The reaches were different lengths to avoid influence of shading by riparian trees, which significantly limit the growth of aquatic plants (Gurnell et al. 2006a). Figure 4.3 illustrates the three reaches at minimum and peak annual macrophyte growth and Table 4.1 summarises the key reach characteristics. Despite their headwater location, reach slopes were very low in this low energy lowland river,
but showed a reduction in gradient downstream from reach 1 (0.00084) through reach 2 (0.00066) to reach 3 (0.00029) (Table 4.2).

Table 4.1: Key management and morphological features of reaches 1-3 of the River Blackwater.

<table>
<thead>
<tr>
<th>Reach no.</th>
<th>Management and morphological features</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>o A realigned and widened channel</td>
</tr>
<tr>
<td></td>
<td>o Extensive superficial deposits of silt and finer sediment across much of the channel</td>
</tr>
<tr>
<td></td>
<td>o Very limited exposure of the underlying gravel</td>
</tr>
<tr>
<td>2</td>
<td>o A semi-natural, irregular planform with clear evidence of both bank toe extension and erosion associated with active channel migration</td>
</tr>
<tr>
<td></td>
<td>o Much of the river bed was covered by superficial silt and finer sediment deposits, but with relatively larger patches of the underlying gravel exposed than in reach 1</td>
</tr>
<tr>
<td></td>
<td>o Some evidence of past channel management, with soil heaps on the bank tops (now heavily vegetated)</td>
</tr>
<tr>
<td>3</td>
<td>o Realigned and the right bank had been reinforced with gabions, which were buried within the bank profile</td>
</tr>
<tr>
<td></td>
<td>o The left bank showed channel narrowing through the development of a pronounced bench that had been colonised by emergent macrophytes, predominantly <em>Typha latifolia</em>, above the low flow water level and <em>Sparganium erectum</em> on the submerged section of the bench</td>
</tr>
<tr>
<td></td>
<td>o In this reach, superficial deposits of silt and finer sediment were largely confined to the left margin with gravel exposed across the majority of the channel bed</td>
</tr>
</tbody>
</table>
Figure 4.2: The River Blackwater catchment and the position of the three study reaches.
Figure 4.3: The three study reaches at minimum and peak aquatic macrophyte growth 2009. Pictures of reaches 1 and 2 are facing upstream, reach 3 faces downstream.

4.2.2 Field measurements

Measurements of water width, water depth (using measuring tapes and rigid graduated rules), flow velocity (streamwise and cross-stream using an ADV), and visual indices of macrophyte distribution and density, and riverbed sediment calibre were collected on the three reaches on seven occasions between March 2009 and February 2010 (Table 4.2). Fine sediment depth to the underlying gravel was also measured using a thin steel rod on the first and last survey date. These measurements, were obtained from the same measurement points arranged along fixed cross-profiles within the study reaches, and captured changes in flow velocity at baseflow and sedimentation patterns before, during
and after the growth of aquatic macrophytes. In addition, metal stage rods inserted in the channel bed at the upstream and downstream ends of each reach provided datums against which water surface elevation could be recorded and from which water surface slope could be estimated.

Table 4.2: Survey dates of the seven recording periods, and discharge and wetted channel dimensions at the time of each survey.

<table>
<thead>
<tr>
<th>Survey dates</th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>01/04/09</td>
<td>31/03/09</td>
<td>30/03/09</td>
</tr>
<tr>
<td>2</td>
<td>06/05/09</td>
<td>05/05/07</td>
<td>07/05/09</td>
</tr>
<tr>
<td>3</td>
<td>15/06/09</td>
<td>11/06/09</td>
<td>12/06/09</td>
</tr>
<tr>
<td>4</td>
<td>28/07/09</td>
<td>30/07/09</td>
<td>29/07/09</td>
</tr>
<tr>
<td>5</td>
<td>03/09/09</td>
<td>04/09/09</td>
<td>02/09/09</td>
</tr>
<tr>
<td>6</td>
<td>14/10/09</td>
<td>16/10/09</td>
<td>15/10/09</td>
</tr>
<tr>
<td>7</td>
<td>12/02/10</td>
<td>15/02/10</td>
<td>11/02/10</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mean Discharge during survey (m$^3$/s)</th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.11</td>
<td>0.21</td>
<td>0.28</td>
</tr>
<tr>
<td>2</td>
<td>0.11</td>
<td>0.11</td>
<td>0.20</td>
</tr>
<tr>
<td>3</td>
<td>0.07</td>
<td>0.17</td>
<td>0.27</td>
</tr>
<tr>
<td>4</td>
<td>0.07</td>
<td>0.18</td>
<td>0.22</td>
</tr>
<tr>
<td>5</td>
<td>0.28</td>
<td>0.21</td>
<td>0.17</td>
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</tr>
<tr>
<td>7</td>
<td>0.17</td>
<td>0.28</td>
<td>0.45</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Average water surface slope during surveys (m/m)</th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.000842</td>
<td>0.000656</td>
<td>0.000291</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Reach length (m)</th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>38</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>63</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Average water width during surveys (m)</th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Ten, seven and ten fixed cross-sections were established at reaches 1, 2 and 3, respectively, to ensure that measurements were taken at the same locations during each
of the seven surveys. Topographic surveys undertaken using a TopCon differential GPS and surveying level recorded the positions and profiles of the 27 cross sections and also the positions and levels of the 6 stage rods. Maps of the three reaches generated using the DGPS are given in Appendix I. Condensed reach images are presented throughout this chapter to provide an effective visual representation of patterns in measurements across the three reaches.

Recordings of water depth, streamwise and cross-stream flow velocity, bed sediment calibre, proximity to vegetation, and vegetation type and density were taken at 0.5m intervals across each cross section on each survey date (Table 4.3). Average 30 second flow velocities were sampled at 0.6 of the water depth from the surface using a Sontek ADV. Bed sediment calibre and vegetation density were given index values (detailed in Table 4.3) based on visual observations. In addition, water width and the proportion of the water width occupied by each of the main macrophyte species were recorded at each cross-section. The number of *S. erectum* stems were recorded in a 0.5 m x 0.5 m quadrat centred on the most developed stand of *S. erectum* within each cross section and the maximum leaf length of 10 randomly selected individuals within the same quadrat were also recorded.

Measurements along the cross sections were mainly gathered during baseflow, although the falling limb of a storm hydrograph was captured during the fifth recording period, affecting flow velocities and water depths during the survey at reach 1 and, to a lesser extent, reach 2.
Table 4.3: Measurements taken at fixed cross sections in the three study reaches.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Single measurements on each cross section</strong></td>
<td></td>
</tr>
<tr>
<td>Water width</td>
<td>Width of the wetted channel to nearest 0.1m</td>
</tr>
<tr>
<td>Extent of aquatic macrophyte species</td>
<td>Width of channel occupied by each of the main macrophyte species present to nearest 0.1m</td>
</tr>
<tr>
<td>S. erectum stem density</td>
<td>Number of stems in a 0.5 m x 0.5 m quadrat centred on the most developed S. erectum stand within the cross section</td>
</tr>
<tr>
<td>S. erectum leaf length</td>
<td>Maximum leaf length of 10 plants randomly selected within a 0.5 m x 0.5 m quadrat centred on the most developed S. erectum stand within the cross section</td>
</tr>
<tr>
<td><strong>Measurements taken at 0.5 m intervals across each cross section</strong></td>
<td></td>
</tr>
<tr>
<td>Water depth</td>
<td>Depth of water to nearest cm</td>
</tr>
<tr>
<td>Velocity</td>
<td>Streamwise and cross-stream 30 second average velocity in m/s (taken at 0.6 depth from water surface using a Sontek ADV with velocity sampled at 1 second intervals)</td>
</tr>
<tr>
<td>S. erectum abundance</td>
<td>An index of relative abundance for Sparganium erectum: (0 = none, 1= light, 2 = intermediate, 3 = heavy)</td>
</tr>
<tr>
<td>Other macrophyte types and abundance</td>
<td>An index of abundance for other macrophyte species: (0 = none, 1= light, 2 = intermediate, 3 = heavy)</td>
</tr>
<tr>
<td>Riverbed sediment class</td>
<td>An index of bed material calibre:</td>
</tr>
<tr>
<td></td>
<td>1, Silt/clay (&lt;0.06mm); 2, Sand (0.06-2mm); 3, pebbles (2mm – 1.6cm); 4, cobbles (1.6 - 6.4 cm); 5, boulders (&gt;6.4 cm)</td>
</tr>
<tr>
<td>Depth of fine sediment (only measured in recording periods 1 and 7 to minimise disturbance of accumulating finer sediment)</td>
<td>Depth of superficial sand and finer sediment, measured using a thin steel rod to the nearest cm</td>
</tr>
</tbody>
</table>
4.2.3 Data analysis

The data were analysed in three main ways:

(1) Aggregate reach properties: Averages of several of the measured properties were calculated for each of the reaches and recording periods to summarise graphically the broad changes over time. Average bed material index and average streamwise velocity were estimated for each reach and recording period from the point measurements collected along the cross-section profiles. The average velocity was combined with average water cross-section dimensions in each reach and the water surface slope to estimate the reach average Manning’s ‘n’ (a measure of flow resistance) for each reach during each of the seven recording periods. Calculated as follows:

\[
    n = \frac{\text{hydraulic radius}^{0.66} \times \text{slope}^{0.5}}{\text{flow velocity}}
\]

For vegetation, the percentage of survey points recording the presence of *S. erectum*, and the percentage of survey points recording the presence of other macrophytes, as well as the proportion of the total macrophyte community recorded as submerged/emergent species were estimated for each reach and recording period. Box and whisker plots summarise the maximum *S. erectum* leaf length and stem density as a further indicator of macrophyte abundance and biomass.

(2) Hierarchical cluster analysis: The calculation of reach average properties was followed by further analysis of the spatiotemporal behaviour and structure of macrophyte and physical properties within each reach for each of the 0.5m interval observation points. This was achieved using a similar analytical approach to that adopted by Emery et al. (2003) and Gurnell et al. (2006a). Hierarchical agglomerative cluster analysis was applied to all time and space point observations of flow velocity and *S. erectum* abundance measurements. Agglomerative hierarchical cluster analysis assigns observations to subgroups of data based on their plotted ‘distance’ from one and other, with similar observations being brought together to generate groups that share similar values. These subgroups are called clusters (or classes). The aim was to identify areas of the three reaches that behaved in a similar manner in relation to particular variables (streamwise velocity, cross-stream velocity and *S. erectum* abundance)
through time so that the patterns described by these different physical and vegetation variables could be compared and interpreted.

In all cases, following Gurnell et al. (2006a), the distance measure selected was Euclidean distance and the linkage algorithm was Ward’s. The data were not standardised prior to clustering since space and time measures of only a single variable were clustered in each analysis. The most effective number of clusters for each subject variable was initially selected by observing the cluster dendrogram and agglomeration schedule plot, particularly the strongest change of slope on the latter. A range of cluster numbers centring on the number indicated by the cluster dendrogram and agglomeration schedule plot were investigated to select the smallest number of clusters that characterised spatio-temporal variations in the variables effectively.

(3) Statistical significance of differences between reaches and clusters: Finally, Kruskal Wallis tests (a non-parametric equivalent of analysis of variance) were used to identify the degree to which the selected clusters exhibited statistically significantly different properties of each analysed variable within each of the seven recording periods, and also to assess whether other measured properties showed statistically significant discrimination when grouped using the same spatiotemporal clusters. This non-parametric test was used because of the ordinal scale on which some of the variables were recorded. Where Kruskal Wallis tests indicated a significant difference in a particular measurement/index, multiple pairwise comparisons were performed using Dunn’s procedure with Bonferroni correction to identify those clusters that exhibited significantly different values. Kruskal Wallis tests were also used to assess the degree to which the point measurements underlying the reach average estimates and the quadrat-based measurements of leaf length were statistically significantly different between reaches and recording periods.
4.3 Results

4.3.1 Reach average properties

Despite the relatively short distance between the reaches, they exhibited pronounced gradients in the measured physical and macrophyte properties from upstream (reach 1) to downstream (reach 3). For reference, the temporal distribution of the seven recording periods are shown in Figure 4.4 and the months during which they were undertaken are given in figures hereafter. A table detailing the averages of all point observation measurements within each recording period at the three reaches can be found in Appendix II.

Figure 4.4: The timings of the seven hydraulic/macrophyte survey recording periods.

4.2.1.1 Physical properties

Average values of key physical measurements for the three reaches are illustrated in Figure 4.5 to provide a broad understanding of how the reaches differ. More detailed description of these, and their seasonal patterns, are then presented.

Figure 4.5: Downstream changes in reach and time average values of (a) fine sediment depth, (b) the proportion of the riverbed covered in fine material, and (c) flow velocity.

The depth of surficial sand and finer sediment deposits on the channel bed, measured at every measurement point during recording periods 1 and 7, showed a marked decline in average depth from reach 1 through to reach 3, as did the proportion of the channel bed covered by finer sediment. The average depth (standard error) and proportion of the bed...
affected by superficial sand and finer deposits changed from 26.9 cm (2.2 cm) and 70% cover at reach 1, through 13.4 cm (1.9 cm) and 60% cover at reach 2, to 8.5 cm (1.3 cm) and 40% cover at reach 3. Average water depth, flow velocity and bed sediment calibre index increased downstream from 0.39 m, 7.03 cm.s\(^{-1}\) and 1.59, respectively, at reach 1, through 0.50 m, 7.59 cm.s\(^{-1}\) and 1.65 at reach 2 to 0.63 m, 10.43 cm.s\(^{-1}\) and 2.31 at reach 3.

Figure 4.6 illustrates changes in reach average values of physical parameters between recording periods in the three study reaches. In general, the reaches show increased average flow velocities with distance downstream (Figure 4.6a). Kruskal Wallis tests (Table 4.4) applied to the sample of flow velocities obtained in the three reaches show that reach 3 supported significantly higher (p < 0.05) flow velocities during all recording periods than reaches 1 and 2, except recording period 5, when the survey conducted at reach 1 and, to a lesser extent, reach 2 coincided with the falling limb of a storm hydrograph. Velocities observed in reach 2 were also significantly higher (p < 0.05) than in reach 1 in recording period 7 (Table 4.4). The bed material index was significantly higher (p < 0.05) in reach 3 than reaches 1 and 2 throughout all recording periods (Table 4.4, Figure 4.6c).
Estimates of reach average Manning’s n were derived from reach average flow velocity, water depth and water width at the time of survey, and are shown in Figure 4.6b. The very low water surface slopes varied little between recording periods but were very susceptible to small manual measurement errors at the stage rods and so the average low flow water surface slope was used in all calculations (Table 4.2). Although the components of the Manning equation changed consistently downstream with hydraulic radius (a function of water width and depth) and flow velocity increasing and water surface slope decreasing, estimates of Manning’s n values at reach 2 were generally higher than at reaches 1 and 3. This mainly reflects the fact that the water surface slope at reach 2 was only slightly lower that at reach 1, whereas the hydraulic radius at reach 2 was only slightly lower than that at reach 3. The high Manning’s n estimates at reach 2 may also be a consequence of the high S. erectum cover and abundance index, which are only slightly lower than reach 1 (Figure 4.8) coupled with the higher morphological complexity of unmanaged reach 2, which has a more sinuous planform with more complex bed and bank profiles than the modified channels found at reaches 1 and 3.
Table 4.4: Results of Kruskal Wallis tests applied to sampled streamwise velocity and bed material index values in reaches 1-3 during each recording period. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons were undertaken using Dunn’s procedure with Bonferroni correction to identify which reaches possessed statistically significantly different values (p < 0.05)

<table>
<thead>
<tr>
<th>Variable and recording period</th>
<th>Kruskal Wallis test probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Significant differences between reaches 1-3 (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Point observations of streamwise Velocity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.032</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>2</td>
<td>0.003</td>
<td>2</td>
<td>3 &gt; 2</td>
</tr>
<tr>
<td>3</td>
<td>0.012</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>4</td>
<td>0.001</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>5</td>
<td>0.435</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>6</td>
<td>0.012</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>7</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>Point observations of the bed material index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>2</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>3</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>4</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>5</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>6</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>7</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
</tbody>
</table>

4.3.1.2 Macrophyte properties

As with the measurements of physical parameters, there were clear downstream shifts in the average measured properties of in-channel vegetation between reaches 1 to 3 (Figure 4.7).
Figure 4.7: Downstream changes in reach and time average values of percentage cover of (a) *S. erectum*, (b) other macrophytes, and (c) the percentage of the total cover of macrophytes composed of submerged species.

Figure 4.7 illustrates a particularly noticeable shift in the average percentage cover of *S. erectum* from reach 1 to 3, which was accompanied by a change in the average abundance index. *S. erectum* showed a reduction in percentage cover from reach 1 to 2 to 3 of 48.4%, 45.4% and 12.1%, respectively, and a reduction in average abundance index of 1.02 to 0.96 to 0.21. The average abundance index and cover of other macrophytes was highest at reach 3 (0.86, 47.4%, respectively), followed by reach 1 (0.45, 22%) with the lowest values at reach 2 (0.36, 16.8%). Considering the total cover of macrophytes, there was also a transition downstream from reach 1 where on average 85.4% were emergent species and 14.6% were submerged species through 83.0% emergent and 17.0% submerged at reach 2 to 45.0% emergent and 55.0% submerged at reach 3.

The temporal pattern in the reach average macrophyte indices also demonstrate strong contrasts between reaches, with further upstream to downstream trends clearly evident. Figure 4.8 shows that reaches 1 and 2 are dominated by the species *S. erectum*, whilst reach 3 showed a higher average percentage cover of other macrophytes and particularly submerged macrophytes. Kruskal Wallis tests (Table 4.5) indicate that either or both of reaches 1 and 2 contained a significantly greater (*p < 0.05*) cover of *S. erectum* than reach 3 in every recording period. All three reaches exhibited an increase in *S. erectum* coverage between recording periods 1 and 2 (Figure 4.8a), followed by an approximately constant coverage throughout the following recording periods until recording period 5 (recording period 6 in reach 1), after which cover declined rapidly during senescence.
Figure 4.8: Temporal changes in the coverage of (a) *S. erectum*, (b) other macrophytes, and (c) the proportion of the total macrophyte community that consisted of submerged species in reaches 1-3 (based on point observations across the monitored cross sections).

The cover of other macrophytes in the study reaches developed more slowly than *S. erectum*, peaking twice at reaches 1 and 2 in recording periods 3 and 6, and 4 and 6 respectively (Figure 4.8b). Reach 3 supported a significantly greater cover of other macrophytes than reaches 1 and 2 in recording periods 1-4, and also a significantly greater cover than reach 2 in recording periods 5 and 7 (Kruskal Wallis tests, p < 0.05, Table 4.5). Reach 3 consistently had the highest coverage of submerged species (Figure 4.8c), with significantly higher cover than reaches 1 and 2 in recording periods 1-4, and then reach 1 in recording periods 5 and 7 (Kruskal Wallis tests, p < 0.05, Table 4.5).
Table 4.5: Results of Kruskal Wallis tests applied to reach coverages of *S. erectum*, other macrophytes and submerged macrophytes in reaches 1-3 during each recording period. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons were undertaken using Dunn’s procedure with Bonferroni correction to identify which reaches possessed statistically significantly different values (p < 0.05)

<table>
<thead>
<tr>
<th>Variable and recording period</th>
<th>Kruskal Wallis test probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Significant differences between reaches 1-3 (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Point observations containing S. erectum</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.015</td>
<td>2</td>
<td>2 &gt; 3</td>
</tr>
<tr>
<td>2</td>
<td>0.013</td>
<td>2</td>
<td>1 &gt; 3</td>
</tr>
<tr>
<td>3</td>
<td>0.002</td>
<td>2</td>
<td>1, 2 &gt; 3</td>
</tr>
<tr>
<td>4</td>
<td>0.007</td>
<td>2</td>
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<td>0.014</td>
<td>2</td>
<td>1, 2 &gt; 3</td>
</tr>
<tr>
<td>6</td>
<td>0.003</td>
<td>2</td>
<td>1 &gt; 3</td>
</tr>
<tr>
<td>7</td>
<td>&lt;0.001</td>
<td>2</td>
<td>1 &gt; 3</td>
</tr>
<tr>
<td><strong>Point observations containing other macrophytes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>2</td>
<td>0.003</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
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<tr>
<td>3</td>
<td>0.002</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>4</td>
<td>0.001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>5</td>
<td>0.025</td>
<td>2</td>
<td>3 &gt; 2</td>
</tr>
<tr>
<td>6</td>
<td>0.5</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>7</td>
<td>0.031</td>
<td>2</td>
<td>3 &gt; 2</td>
</tr>
<tr>
<td><strong>Point observation containing submerged species</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.002</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>2</td>
<td>0.005</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>3</td>
<td>0.002</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>4</td>
<td>0.001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>5</td>
<td>0.005</td>
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</tr>
<tr>
<td>6</td>
<td>0.104</td>
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</tr>
<tr>
<td>7</td>
<td>0.022</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
</tbody>
</table>
The maximum leaf length of 10 plants at each cross section (where *S. erectum* was present) was measured throughout recording periods 1 to 5; no measurements are available for recording period 6, because the shoots had completely collapsed/degraded, or 7, because the leaves had yet to emerge. The purpose of this was to assess whether reach conditions not only affected the abundance, longevity and spatial extent of plant stands, but also the relative size of plants within the reach. Shoot length may also offer a partial indication of the plants’ resistance to flow. Box and whisker plots illustrate changes in the maximum leaf length over time at the three reaches (Figure 4.9), and Kruskall-Wallis tests indicated statistically significant differences in maximum leaf length between the reaches (Table 4.6).

Figure 4.9: Maximum leaf length of *S. erectum* observed for samples of 10 plants within the most developed stand in each cross section at reaches 1-3 over recording periods 1 to 5.
Table 4.6: Results of Kruskal Wallis tests applied to observations of *S. erectum* maximum leaf length (illustrated in Figure 4.9) in reaches 1-3 during recording periods 1 to 5. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons were undertaken using Dunn’s procedure with Bonferroni correction to identify which reaches possessed statistically significantly different values (p < 0.05).

<table>
<thead>
<tr>
<th>Overall probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Differences between reaches (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&lt; 0.0001</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>&lt; 0.0001</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>&lt; 0.0001</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>&lt; 0.0001</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>0.001</td>
<td>2</td>
</tr>
</tbody>
</table>

Figure 4.9 shows that there were similar seasonal patterns of leaf growth at each site, with the longest leaves occurring at all three reaches during recording period 4. Throughout all recording periods, the leaves of *S. erectum* at reach 3 were significantly shorter than those at either reach 1, 2 or both (Kruskal Wallis tests, p < 0.05, Table 4.6).

The number of *S. erectum* stems per m² was measured on the most developed area of each cross section. In all reaches, there was a noticeable increase in stem density in recording period 4 (Figure 4.10), which was indicative of the emergence of secondary growth plants. Prior to this (recording periods 1-3), stem density was relatively constant, albeit with a slight downward trend, in reaches 1 and 2. Reach 3 demonstrated a more erratic pattern, probably due to the small number of cross sections that contained the species. All reaches showed a decline in stem density between recording periods 4 and 5.
Figure 4.10: The stem densities of *S. erectum* within the most developed stand in each cross section at reaches 1-3 over recording periods 1 to 5.

4.3.2 Hierarchical agglomerative cluster analysis of streamwise flow velocity observations

Hierarchical agglomerative cluster analysis was applied to streamwise velocity measurements obtained at all measurement points in all recording periods across the three reaches. Four distinct classes (clusters) were found to describe the spatiotemporal velocity patterns within the three reaches most effectively. Figure 4.11a illustrates average velocities within each of the four classes in each recording period and Table 4.7 describes the patterns revealed by these average velocities. Table 4.8 reports the results of Kruskal Wallis tests applied to the velocities observed within the four clusters in each recording period, confirming that all of the classes are statistically significant different from one another across several recording periods. There are areas of the three reaches that display consistently low (class 1) and high (class 4) streamwise velocities throughout all recording periods, although the class 4 velocity values are markedly subdued in summer by comparison to their winter values. There are also areas of the channel displaying intermediate velocities, with some areas having relatively higher velocities during winter and relatively lower velocities in summer (class 3), whilst others have a complementary pattern of relatively higher velocities in summer and lower velocities in winter (class 2).
Table 4.7: Description of the temporal patterns in average velocity within the four velocity classes identified using hierarchical agglomerative cluster analysis.

<table>
<thead>
<tr>
<th>Class</th>
<th>Flow Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>The lowest average velocities throughout all recording periods with very low velocities recorded in recording periods 7 and 1, reducing to near zero in all other recording periods.</td>
</tr>
<tr>
<td>2</td>
<td>Second lowest average velocities overall, but showing an inverse temporal pattern of velocity to all other velocity clusters with lowest average velocities in recording periods 1 and 6 and maximum average velocity in recording period 3.</td>
</tr>
<tr>
<td>3</td>
<td>Second highest average velocities overall and largest difference between maximum and minimum velocity of all clusters. Velocity is highest in recording period 7, with moderately high velocities in recording periods 1 and 6 and relatively low velocities (below those observed in cluster 2) in recording periods 2 to 5, reaching a minimum in recording period 4.</td>
</tr>
<tr>
<td>4</td>
<td>Highest average velocities in all recording periods. Moderate to high velocities maintained throughout recording periods 1 to 7 but with the lowest values observed during recording periods 2 to 4.</td>
</tr>
</tbody>
</table>
Table 4.8: Results of Kruskal Wallis tests applied to streamwise flow velocities observed at measurement points falling within velocity classes 1 to 4 during each of the recording periods. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons were undertaken using Dunn’s procedure with Bonferroni correction to identify which classes possessed statistically significantly different velocities (p < 0.05).

<table>
<thead>
<tr>
<th>Recording period</th>
<th>Kruskal Wallis test probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Significant differences between velocities observed at measurement points within the 4 velocity clusters (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4, 3, 2 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4, 3 &gt; 2</td>
</tr>
<tr>
<td>2</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4, 3, 2 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4 &gt; 3, 2</td>
</tr>
<tr>
<td>3</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4, 3, 2 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4 &gt; 3, 2</td>
</tr>
<tr>
<td>4</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4, 3, 2 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4 &gt; 3, 2</td>
</tr>
<tr>
<td>5</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4, 3, 2 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4 &gt; 3, 2</td>
</tr>
<tr>
<td>6</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4 &gt; 3 &gt; 2 &gt; 1</td>
</tr>
<tr>
<td>7</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4, 3, 2 &gt; 1</td>
</tr>
</tbody>
</table>

The average values for the bed material index, *S. erectum* abundance index and other macrophyte abundance index observed at sampling points within the four velocity classes during each recording period are displayed in Figures 4.11b, c and d, respectively. Table 4.9 applies Kruskal Wallis tests to the same three indices grouped according the velocity class in which they fall, and shows the degree to which statistically significantly different values of the indices are found within areas of the channel affected by the four velocity classes.
Figure 4.11: Temporal patterns in average (a) flow velocity, (b) bed sediment calibre index, (c) *S. erectum* abundance index and (d) other macrophyte abundance index of point observations falling within each of the four velocity classes during each of the recording periods.
Table 4.9: Results of Kruskal Wallis tests comparing values of the *S. erectum* abundance index, other macrophyte abundance index and bed material calibre index observed at point observations falling within streamwise velocity classes 1 to 4 during each of the recording periods. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons of the four classes were undertaken using Dunn’s procedure with Bonferroni correction to identify which classes possessed statistically significantly different values of the indices (p < 0.05).

<table>
<thead>
<tr>
<th>Variable and recording period</th>
<th>Kruskal Wallis test probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Significant differences between index values observed at measurement points within the 4 velocity clusters (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. erectum</em> abundance index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.002</td>
<td>3</td>
<td>1 &gt; 3, 4</td>
</tr>
<tr>
<td>2</td>
<td>&lt;0.001</td>
<td>3</td>
<td>1 &gt; 3, 4</td>
</tr>
<tr>
<td>3</td>
<td>&lt;0.001</td>
<td>3</td>
<td>1, 2 &gt; 3, 4</td>
</tr>
<tr>
<td>4</td>
<td>&lt;0.001</td>
<td>3</td>
<td>1, 2 &gt; 3, 4</td>
</tr>
<tr>
<td>5</td>
<td>&lt;0.001</td>
<td>3</td>
<td>1 &gt; 3, 4, 2</td>
</tr>
<tr>
<td>6</td>
<td>&lt;0.001</td>
<td>3</td>
<td>1 &gt; 3, 4, 2</td>
</tr>
<tr>
<td>7</td>
<td>&lt;0.001</td>
<td>3</td>
<td>1 &gt; 3, 4</td>
</tr>
<tr>
<td>Other macrophyte abundance index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.905</td>
<td>3</td>
<td>NS</td>
</tr>
<tr>
<td>2</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3, 4 &gt; 2, 1</td>
</tr>
<tr>
<td>3</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3, 4 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3 &gt; 2</td>
</tr>
<tr>
<td>4</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3 &gt; 1, 2, 4</td>
</tr>
<tr>
<td>5</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3 &gt; 1, 4, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 &gt; 4</td>
</tr>
<tr>
<td>6</td>
<td>0.001</td>
<td>3</td>
<td>2 &gt; 3, 4</td>
</tr>
<tr>
<td>7</td>
<td>0.722</td>
<td>3</td>
<td>NS</td>
</tr>
</tbody>
</table>
In every recording period, *S. erectum* is significantly more abundant in areas affected by the lowest velocities (class 1) than classes 3 and 4, showing a strong association with channel areas subject to consistently low velocities (Table 4.9). In recording periods 3-6, *S. erectum* is also abundant in channel areas affected by the second lowest velocities (class 2), showing a significantly greater extent than in areas of the channel affected by velocity classes 3 and 4. Channel areas in velocity classes 3 and 4 show a very subdued increase in *S. erectum* extent up to recording period 4 followed by a consistent decline (Figure 4.11c).

There is no significant difference in the abundance index of other macrophytes between velocity classes during recording periods 1 and 7 but marked contrasts develop between the areas under different velocity classes during recording periods 2-6 (Table 4.9, Figure 4.11d). During recording period 2, channel areas falling within velocity classes 3 and 4 show a clear increase in the abundance of other macrophytes (Figure 4.11d), with statistically significantly greater values than areas under classes 1 and 2 (Table 4.9). Thereafter, other macrophytes decline consistently in their abundance in class 4 areas of the channel through to recording period 7, whereas areas under class 3 show significantly larger amounts of other macrophytes than areas of the channels under any other velocity classes through recording periods 3-5. Areas of the channel under velocity classes 1 and 2 have a significantly lower abundance of other macrophytes than areas under classes 3 and 4 during recording periods 2 and 3, and also lower than areas under class 3 during recording periods 4 and 5. However, other macrophytes clearly extend into channel areas under classes 1 and 2 late in the summer, reaching their maximum abundance index values during recording periods 4 to 6, with areas under
velocity class 2 showing significantly larger values than the fast flowing class 4 areas in recording periods 5 and 6.

Bed material calibre shows a consistent gradient from relatively coarse to relatively fine across velocity classes 4 to 1 (Figure 4.11b), with the calibre in class 3 and 4 being statistically significantly coarser than class 2, which in turn was significantly coarser than class 1 in all recording periods (Table 4.9).

Finally, Figure 4.12 shows the spatial distribution of the velocity classes within each of the three reaches. Overall, areas of the channel falling within velocity classes 1 and 2 become more restricted in spatial extent from reach 1 through to reach 3, whereas areas within velocity classes 3 and 4 occupy a relatively larger area of the channel. Areas under classes 2 and 3 often form spatial transition zones between classes 1 and 4.

Reach 1 has a narrow linear thread of relatively high velocities (class 4) adjacent to the left bank, fringed by small areas under velocity class 3, with the majority of the channel area under velocity classes 1 and 2. Reach 2 shows a more complex spatial pattern, with a sinuous thread of observation points falling into class 4, bordered by points falling into class 3 and the remainder of the channel bed showing a patchy pattern of points falling into classes 2 and 1. Finally, reach 3 is dominated by the two highest velocity classes (3 and 4), with zones of measuring points falling into classes 1 and 2 largely confined to the left margin of the channel. The cluster membership for the three reaches is given in Table 4.10 below:

Table 4.10: The proportional (and absolute) streamwise velocity cluster membership of observation points within the three reaches.

<table>
<thead>
<tr>
<th>Class</th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class 1</td>
<td>43% (43)</td>
<td>37% (29)</td>
<td>28% (32)</td>
</tr>
<tr>
<td>Class 2</td>
<td>32% (32)</td>
<td>26% (20)</td>
<td>14% (16)</td>
</tr>
<tr>
<td>Class 3</td>
<td>8% (8)</td>
<td>24% (19)</td>
<td>41% (46)</td>
</tr>
<tr>
<td>Class 4</td>
<td>17% (17)</td>
<td>13% (10)</td>
<td>17% (19)</td>
</tr>
</tbody>
</table>
Figure 4.12: The spatial distribution of measurement points falling into streamwise velocity classes 1-4.
4.3.3 Hierarchical agglomerative cluster analysis of cross-stream flow velocity observations

Cross stream velocities were all ascribed a positive value (i.e. there was no differentiation in direction only in strength of cross-stream velocity). Three classes were found to effectively describe cross-stream velocities measured in the three reaches. These are described in Table 4.11, average values of cross stream velocity within each class and recording period are illustrated in Figure 4.13, and the statistical significance of differences in cross stream velocity between the classes in each recording period is assessed using Kruskal Wallis tests in Table 4.12.

Table 4.11: Description of cross-stream velocity classes identified using hierarchical cluster analysis

<table>
<thead>
<tr>
<th>Class</th>
<th>Flow Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Low cross-stream flow velocity in all recording periods.</td>
</tr>
<tr>
<td>2</td>
<td>Low-moderate cross stream flow velocities, showing an approximately inverse pattern to class 3, being relatively higher in summer (recording period 3) and lower in Autumn (recording periods 6-7).</td>
</tr>
<tr>
<td>3</td>
<td>High cross-stream velocities in recording periods 1 and 7, moderate in recording periods 2, 3, 5 and 6, low in recording period 4.</td>
</tr>
</tbody>
</table>

Figure 4.13: Temporal changes in the average cross-stream velocity for the survey points within each of the three velocity classes during each of the recording periods.
Table 4.12: Results of Kruskal Wallis tests comparing cross-stream flow velocities observed at measurement points falling within classes 1 to 3 during each of the recording periods. Where the Kruskal Wallis test was statistically significant ($p < 0.05$), multiple pairwise comparisons were undertaken using Dunn’s procedure with Bonferroni correction to identify which classes possessed statistically significantly different velocities ($p < 0.05$).

<table>
<thead>
<tr>
<th>Recording Period</th>
<th>Overall probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Differences between classes ($p &lt; 0.05$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>2</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>3</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2 &gt; 3 &gt; 1</td>
</tr>
<tr>
<td>4</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>5</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>6</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>7</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
</tbody>
</table>

There are areas of the three reaches with negligible cross stream velocity (class 1) in all recording periods, where the velocity is significantly lower ($p<0.05$) than areas occupied by one or both of classes 2 and 3. In the areas occupied by classes 2 and 3, cross stream velocity is significantly higher in class 3 than class 2 zones during recording periods 1, 5, 6 and 7, lower in recording period 3, and there is no statistically significant difference in cross stream velocity between zones 2 and 3 during recording periods 2 and 4 (Table 4.12). Overall this indicates a switching in the strength of cross stream velocity between classes 3 and 2 in summer.

Table 4.13 reports the results of Kruskal Wallis tests comparing values of streamwise velocity, *S. erectum* abundance index, submerged macrophyte abundance index and bed material calibre index observed at measurement points falling within cross-stream velocity classes 1 to 3 during each of the recording periods.
Table 4.13: Results of Kruskal Wallis tests comparing values of the streamwise flow velocity, *S. erectum* abundance index, submerged macrophyte abundance index and bed material calibre index observed at measurement points falling within cross stream velocity classes 1 to 3 during each of the recording periods. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons of the four classes were undertaken using Dunn’s procedure with Bonferroni correction to identify which classes possessed statistically significantly different values of the indices (p < 0.05).

<table>
<thead>
<tr>
<th>Variable and recording period</th>
<th>Overall probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Differences between classes (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Streamwise Flow velocity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>2</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>3</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>4</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>5</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>6</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>7</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td><em>S. erectum</em> abundance index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.995</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>2</td>
<td>0.201</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>3</td>
<td>0.042</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>4</td>
<td>0.030</td>
<td>2</td>
<td>1 &gt; 3</td>
</tr>
<tr>
<td>5</td>
<td>0.299</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>6</td>
<td>0.406</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>7</td>
<td>0.407</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>Submerged macrophyte index</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------------------------</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>1</td>
<td>0.045</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>2</td>
<td>&lt;0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>3</td>
<td>0.003</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>4</td>
<td>0.029</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>5</td>
<td>0.335</td>
<td>2</td>
<td>NS</td>
</tr>
<tr>
<td>6</td>
<td>0.006</td>
<td>2</td>
<td>1 &gt; 3</td>
</tr>
<tr>
<td>7</td>
<td>0.294</td>
<td>2</td>
<td>NS</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Bed material calibre index</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>2</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>3</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>4</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1</td>
</tr>
<tr>
<td>5</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>3 &gt; 1, 2</td>
</tr>
<tr>
<td>6</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>7</td>
<td>&lt; 0.0001</td>
<td>2</td>
<td>2, 3 &gt; 1</td>
</tr>
</tbody>
</table>

Kruskall-Wallis tests (Table 4.13) indicate a relationship between cross and streamwise flow velocity, as the streamwise velocities occurring in class 3 are significantly higher (p < 0.05) than those in class 1 during all recording periods. The velocities in class 2 are significantly smaller than those observed in areas of the channel in cross stream velocity class 3 in recording periods 1, 6 and 7, whilst they exceed those in class 1 during recording periods 2 and 3.

There was no significant difference in *S. erectum* abundance between the cross-stream flow velocity classes apart from in recording period 4 and there were only 3 recording periods when a significant difference in submerged macrophyte abundance was found between any of the cross stream velocity classes. However, significantly coarser substrates occurred in the areas of fastest cross-stream flow velocity (classes 2 and 3), and throughout all the recording periods the average bed material index was coarser in areas of the channel within cross stream velocity class 3 than class 1. Due to the relatively few statistical associations between cross stream velocity and vegetation, and...
the lack of distinguishable patterns within the reaches, images showing the cluster membership for the three reaches have not been included.

4.3.4 Hierarchical agglomerative cluster analysis of the Sparganium erectum abundance index

Hierarchical agglomerative cluster analysis was also used to investigate the growth patterns of *S. erectum* in the three reaches, and to further explore any relationships between plant growth and flow conditions. Four clusters were found to describe the different growth trends experienced within the three reaches. These are described in Table 4.14 and Table 4.15 presents the results of Kruskal Wallis tests, which assess the degree to which *S. erectum* abundance varies significantly between the four classes in each recording period.

The clusters in *S. erectum* growth behaviour (Tables 4.14 and 4.15, Figure 4.14) illustrate a tendency for the species to grow in relatively low density (class 2) or abundantly (classes 3 and 4) in distinct areas of the channel, with the denser areas of growth distinguished by a relatively longer seasonal growth cycle in class 4 compared to 3. There are also areas of the channel that exhibit little or no growth (class 1). The small temporal distinctions in abundance within the four classes reflects the fact that relative rather than absolute abundance scales were used within each recording period. However, it is apparent from the Kruskal Wallis tests reported in Table 4.15 that the highest abundance of *S. erectum* is exhibited by class 4 from recording period 4 onwards, that class 3 supports an equally high abundance to class 4 in the early recording periods but then persists as the second most abundant class from recording period 4 onwards, and that the abundance in class 2 although the third highest in the early recording periods is similar to class 3 from recording period 4 onwards (p < 0.05, Table 4.15).
Table 4.14: Description of the *S. erectum* abundance classes used to describe the seasonal growth pattern of *S. erectum* in reaches 1-3.

<table>
<thead>
<tr>
<th>Class</th>
<th>Temporal pattern in <em>S. erectum</em> abundance across the recording periods</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Little or no growth of <em>S. erectum</em>.</td>
</tr>
<tr>
<td>2</td>
<td>Light cover of <em>S. erectum</em> in recording periods 1-3, increasing substantially in recording period 4 and declining thereafter.</td>
</tr>
<tr>
<td>3</td>
<td>Dense cover of <em>S. erectum</em> in recording periods 2-4, declining suddenly thereafter.</td>
</tr>
<tr>
<td>4</td>
<td>Dense cover of <em>S. erectum</em> in recording periods 2-6, being relatively less prior to emergence and following senescence in recording periods 1 and 7.</td>
</tr>
</tbody>
</table>

Figure 4.14: Temporal changes in the average *S. erectum* abundance index for the survey points within each of the four growth classes during each of the recording periods.
Table 4.15: Results of Kruskal Wallis tests comparing the *S. erectum* abundance index observed at measurement points falling within growth classes 1 to 4 during each of the recording periods. Where the Kruskal Wallis test was statistically significant (p < 0.05), multiple pairwise comparisons were undertaken using Dunn’s procedure with Bonferroni correction to identify which classes possessed statistically significantly different growth index values (p < 0.05).

<table>
<thead>
<tr>
<th>Recording period</th>
<th>Kruskal Wallis test probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Significant differences between abundance observed at measurement points within the 4 growth clusters (p &lt; 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3,4 &gt; 1, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 &gt; 1</td>
</tr>
<tr>
<td>2</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3,4 &gt; 1, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 &gt; 1</td>
</tr>
<tr>
<td>3</td>
<td>&lt;0.001</td>
<td>3</td>
<td>3,4 &gt; 1, 2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 &gt; 1</td>
</tr>
<tr>
<td>4</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4 &gt; 1, 2, 3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>5</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4 &gt; 1, 2, 3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2 &gt; 1</td>
</tr>
<tr>
<td>6</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4 &gt; 1, 2, 3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2, 3 &gt; 1</td>
</tr>
<tr>
<td>7</td>
<td>&lt;0.001</td>
<td>3</td>
<td>4 &gt; 1, 2, 3</td>
</tr>
</tbody>
</table>

Figure 4.15 shows the spatial distribution of the *S. erectum* growth clusters within the three reaches. The percentage (number) of measurement points attributed to classes 3 and 4 diminishes from reaches 1 to 3, whilst class 1 occupies a large proportion of the channel in reach 3 (Table 4.16). Class 2 is generally located close to the bank and at the margins of areas of the channel belonging to classes 3 or 4. It is rare throughout all reaches for there to be an abundance class greater than 2 immediately adjacent to the bank, suggesting reduced availability of water or shading limits its growth there.

Reach 1 shows an increased abundance and spread of the plant from upstream to downstream. The narrow linear thread of flow described in the streamwise velocity analysis is mimicked by the constant presence of abundance class 1 adjacent to the left
bank. Reach 2 shows a more heterogeneous abundance pattern with the proportion and arrangement of classes varying substantially between cross-sections. At upstream and downstream areas of the reach, there are open cross sections that exhibit minimal cover of *S. erectum* (cross sections 1 and 6 from upstream to downstream) consisting entirely of classes 1 and 2. Between these, *S. erectum* is abundant but patchy. There is perhaps a slightly greater abundance and longevity (class 4) of plants situated towards the left bank of the channel. Reach 3 is largely dominated by abundance class 1. There are small upstream and downstream patches of the plant that, despite their small size, exhibit the similar pattern of areas of high abundance being bordered by areas of lower abundance.

Table 4.16: The proportional and absolute growth cluster membership values for the three reaches.

<table>
<thead>
<tr>
<th></th>
<th>Reach 1</th>
<th>Reach 2</th>
<th>Reach 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Class 1</td>
<td>30% (30)</td>
<td>35% (27)</td>
<td>80% (91)</td>
</tr>
<tr>
<td>Class 2</td>
<td>22% (22)</td>
<td>23% (18)</td>
<td>11% (12)</td>
</tr>
<tr>
<td>Class 3</td>
<td>7% (7)</td>
<td>21% (16)</td>
<td>4 % (4)</td>
</tr>
<tr>
<td>Class 4</td>
<td>41% (41)</td>
<td>22% (17)</td>
<td>5% (6)</td>
</tr>
</tbody>
</table>
Figure 4.15: The spatial distribution of measurement points falling into *S.erectum* abundance classes 1-4.
4.3.5 Bed sediment depth and calibre

Figures 4.16-4.18 illustrate the distribution of patches of sand and finer bed sediment and exposures of the gravel in the underlying river bed at the start and end of the study, providing an indication of the degree to which the former persisted from one year to the next.

Figure 4.16: The spatial distribution of sand and finer or gravel and larger bed material at reach 1, in recoding periods 1 and 7.
Figure 4.17: The spatial distribution of sand and finer or gravel and larger bed material at reach 2, in recording periods 1 and 7.
The three reaches generally showed stable patches of sand or finer sediment accumulations, and larger areas of finer sediment accumulations showed greater persistence than smaller ones. When the total number of observation points under each sediment class within each reach were considered, there were changes in bed sediment calibre between recording periods 1 and 7 in 5%, 19% and 14% of observation points in reaches 1-3 respectively. However, when the proportion of observation points consisting of the two defined different bed material types in the reaches were considered, there was a net change of only a single point in reach 1, changing from coarse to fine material. Reach 2 showed a large increase in the proportion of...
observation points that had fine bed material, with seven more in recording period 7 in comparison with recording period 1. Reach 3, like reach 1 showed a change in only a single observation point and this was the only reach to show net erosion of fine material to expose the underlying gravel.

The fine sediment depth was measured at each observation point throughout the three reaches in recording periods 1 and 7 to compare net seasonal changes in deposition and erosion. It was not measured during the five other recording periods to minimise interference with the sediment accumulations. The average change in sediment depth (standard error) and percentage of the bed that showed net accumulation:erosion changed from +1.3 cm (1.3 cm) 43%:33% at reach 1, through -0.1 cm (0.9 cm) and 35%:30% at reach 2, to 3.3 cm (1.1 cm) and 31%:16% at reach 3.

4.4 Discussion

4.4.1 Associations between flow velocity, vegetation and sediment

Spatial and temporal classifications of velocity, macrophyte abundance and sediment calibre data all reveal clear complementary patterns that are most readily discussed through interpretation of the analysis of streamwise velocity classes, since streamwise velocity influences the mobilisation and deposition of sediment and is influenced by vegetation roughness. Four distinct streamwise velocity classes were identified across the three reaches during the monitoring period and these show strong associations with macrophyte type, abundance and sediment calibre (Figure 4.6 and 4.8).

Areas of the channel that show consistently low streamwise velocities (velocity class 1) are associated with the highest abundance of S. erectum, the accumulation of fine, silty sediment and a late season peak in the abundance of other macrophytes. This interaction between plants, velocities and sediment reflects the high flow resistance of S. erectum, enabling the trapping of fine sediments followed by a late summer encroachment of other marginal macrophyte species such as Myosotis scorpiodes and Nasturtium officinale across the emerging fine sediment surface as S. erectum senesces and is weakened by the exposure of the aggrading river bed (Figure 4.19).
Areas of the channel that show slightly higher, but still relatively low velocities (velocity class 2), also contain a fairly high abundance of *S. erectum*. This lower relative abundance of *S. erectum* is associated with slightly coarser bed sediment calibre (on average intermediate between silt and sand). As well as being less abundant than in class 1, *S. erectum* shows a slightly delayed seasonal development, which follows an initial increase in average flow velocity, and then accompanies a fall in average flow velocity. Other macrophytes increase in abundance in class 2 towards the end of the summer growth period, and slightly later than in class 1 areas of the channel. The increase and decline in velocity and delayed development of *S. erectum* reflects spatial expansion of its stands from channel areas falling into class 1, which explains the juxtaposition of these two velocity classes in the study reaches. The later encroachment by other macrophytes through the same mechanism described for class 1 (Figure 4.19) is also a result of the relative position of class 2 patches with respect to class 1 patches, and the probably delayed cycle of fine sediment aggradation.

The areas of the channel affected by the growth of *S. erectum* extended from velocity class 1 into velocity class 2 as the plant developed, causing the funnelling of flow described by Naden et al. (2006) and supporting the concept of sediment scavenging and trapping described by Gurnell et al. (2006a), whereby the plant is able to obtain fine sediment from areas of adjacent flow, and subsequently expand its habitat.

Areas of the channel that showed relatively high flow velocities in the early and late growing season but with notably low flow velocities at the height of the growing season (velocity class 3) show a low abundance of *S. erectum* but the highest abundance of other macrophytes and relatively coarse bed sediment calibre (average in the range sand to pebbles). In this case, the other macrophytes are typically linear submerged morphotypes, with by far the most abundant and widespread species being *Sparganium emersum*, although *Potamogeton natans* was also quite abundant and other *Potamogeton* and *Callitriche* spp. were also observed occasionally. The areas of the channel falling within velocity class 3 occupied much of the central part of the channel in reach 3 and were arranged along the interface between classes 1 and 2 and class 4 in reaches 1 and 2. The submerged macrophyte growth in these areas would cause the increase in drag described by Naden et al. (2006) but their impact on flow velocity is not as severe as the studied emergent species due to their having a flexible morphology.
that allows water to pass over/around their leaves (Sand-Jensen & Mebus, 1996).

Overall the increased drag attributable to the submerged species within the areas of the channel attributable to velocity class 3 coupled with the funnelling by *S. erectum* within areas under velocity classes 1 and 2, induce the deeper water depths observed during the baseflow surveys at the height of the growing season (Appendix II).

Finally, the areas of the channel that fell within velocity class 4 supported the highest flow velocities during all recording periods, the coarsest bed sediments, the lowest abundance of *S. erectum*, and, following an early increase in abundance, a rapid decline and low cover of other macrophytes during most of the growing season. As with velocity class 3, the macrophytes were submerged and dominated by *S. emersum*, and the decline in macrophyte abundance probably reflects the increasing flow velocities in these areas of the channel as flow was gradually squeezed into the area occupied by this velocity class by the growth and extension of emergent and submerged macrophytes in all other areas of the channel (velocity classes 1 to 3).

![Image](image1)

Figure 4.19: *Nasturtium officinale* using senescent shoots of *S. erectum* and associated fine sediments as a substrate for growth.

The stability of the finer sediments that accumulate around the aquatic macrophytes, particularly *S. erectum*, is indicated by the limited adjustment in the spatial extent of sand and finer sediments between recording periods 1 and 7 in the study reaches. This was further supported by measurements of fine sediment depth, which were stable or increasing across all three reaches. Additionally, reaches 1-3 all had a higher proportion of recording points that demonstrated accumulation compared to erosion.
4.4.2 Contrasts in flow velocity, vegetation and sediment between study reaches

Despite the relatively short distance between the studied reaches, they exhibited pronounced differences in the measured properties, such as macrophyte type and abundance, bed sediment calibre and velocity, throughout the seven recording periods, which provide a local illustration of national scale associations between river channel physical properties and macrophyte abundance identified by Gurnell et al. (2010) and O’Hare et al. (2010).

There was a noticeable downstream shift in the peak cover of *S. erectum*, from 58.5% and 57.7% to 18.9% at reaches 1, 2 and 3 respectively. This was accompanied by an increase in both discharge and average streamwise flow velocity. All three sites showed a plateau in the coverage of *S. erectum* that remained fairly consistent throughout the summer recording periods until the plants’ senescence in late summer - autumn. This suggests that the plants that successfully emerged at the beginning of the season were not removed by hydraulic forces or competition with other aquatic or marginal species during the growing season. The data also suggest that *S. erectum* is larger, has a longer season and a greater spatial extent in the upstream reach 1, where it shows a less pronounced and later onset of senescence, with no obvious decline in *S. erectum* occurrence by recording period 6, unlike in reaches 2 and 3. Reach 1 also showed a gradual decline in the abundance and coverage of submerged macrophytes once the majority of the *S. erectum* leaves had emerged, suggesting that their canopy is detrimental to the growth of submerged species.

Reach 3 had the lowest cover of emergent macrophytes and as a result supported the highest flow velocities. These prevented fine sediment from depositing and settling in much of the channel and, as a result, the reach had a relatively coarse and invariant average bed material index with sandy gravel dominating much of the channel and finer material only being trapped on the channel margin that supported the growth of emergent macrophytes. Ten of the sixteen changes in bed material type (changing from gravel to silt) within reach 3 (Figure 4.18) occurred on the five cross sections where *S. erectum* was present, perhaps being an indication of the species’ ability to modify flow velocities and trap sediment.
In terms of flow velocity conditions, bed material calibre and macrophyte community, reach 1 presented an almost opposite pattern to reach 3: in reach 1, most of the channel was dominated by a thick layer of fine sediment supporting abundant growth of *S. erectum*, and the majority of the flow was concentrated down a narrow thread of channel adjacent to the left bank, which is the only portion of the channel that had a coarser substrate.

Reach 2 was the only reach to show clear temporal changes in its average bed material index, which is perhaps an indication of the complexity of its macrophyte community, and the resulting complexity of flow velocity patterns and associated movement and trapping of sediment through the growing season.

Overall, there was a clear and close association between fine sediment retention and the presence of *S. erectum*, which suggests that, whilst fine sediment movements undoubtedly occur, fine sediment accumulations associated with the growth of *S. erectum* are able to persist throughout the year, including through winter and despite the lack of foliage.

### 4.4.3 Evidence of ecosystem engineering and management implications

It has been observed that emergent species (Haslam, 2006) and particularly *S. erectum* (Watson, 1987) can represent a significant flood risk, particularly when they are able to occupy a high proportion of the channel width (Green, 2005a). The very high reach-average Manning’s *n* values and increasing summer water depths observed at low flows in this study provide some support for this claim, particularly in reaches 1 and 2 where *S. erectum* extends over nearly 60% of the observation points in mid-summer. However, observations at bank full conditions would be required to fully assess the effect of seasonal growth of the species on flow resistance, velocities and water depth.

This study has also illustrated (in reach 1) that the ecosystem engineering capacity of this species is so profound, that the intended conveyance benefits of deliberate channel enlargement have been short-lived. Reach 1 is dominated by *S. erectum* abundance class 4, the most abundant and seasonally persistent of the abundance classes identified, which provides the maximum opportunity for trapping the high supply of fine sediments passing through this over-widened reach in space and time. This has caused *S. erectum* to induce significant ecosystem engineering by gradually narrowing the active channel.
through the building of fine sediment benches. The narrow band of exposed gravel on the river bed indicates a transition to a width more suitable for conveying the river’s discharge at this point in the catchment. If this plant engineering were allowed to continue, the channel edges would become terrestrialised leaving a narrower and thus more efficient channel cross profile that would support higher flow velocities and a coarser substrate.

Reach 3 has also been channelised. Most notably the channel has been straightened and reinforced on one bank in association with the development of the nearby Blackwater valley road. Here there has also been channel adjustment, which has progressed to the point where a bench of finer sediment now exists above the low flow water level and is encroaching into the channel from the left bank. This bench supports a band of *S. erectum* of varying width on its leading edge, which appears to be contributing to the extension of the bench into the channel, particularly at its upstream end.

In both reaches 1 and 3, the modified channel has provided space for channel adjustment involving sediment trapping by *S. erectum*, which has helped to funnel a distinct thread of high velocity flow along these reaches.

Although *S. erectum* is indisputably the dominant species in reach 2, its patchy growth creates a greater range of flow velocities (whilst reducing extreme localised flow conditions), open areas for growth of other macrophytes, and a more irregular bed topography; all of which produce a greater physical habitat complexity as well as contributing to patchy marginal bench development and in some cases erosion of the opposite bank (as seen in and around reach 2), leading to channel migration. Just as the simple flow pattern in reach 1 can be attributed in part to the simplicity of its plant community, there appears a more dynamic relationship between flow and the growth of *S. erectum* in reach 2. The plant grows abundantly, but there are almost equal numbers of observation points that exhibit growth classes 2, 3 and 4 (18:16:17 respectively). To illustrate the effect of *S. erectum* growth on flow in this reach, Figure 4.20 below traces an approximate thread of highest velocity through the *S. erectum* abundance clusters, based on the path of velocity class 4 (Figure 4.12). The image shows that at no point does the hypothesized route of highest velocity come into contact with *S. erectum* abundance class 4, and generally passes through or adjacent to class 1.
The interactions between flow and macrophyte growth at reach 2 generate a more sinuous flow pattern within the reach, which may be an indication or trigger of channel movement. This contrasts with the hydraulic environment shown at reach 1, which is unlikely to alter significantly between seasons. Flume experiments have indicated that discrete planting of rigid emergent vegetation can alter channel hydraulics and subsequently induce positive geomorphological changes, such as channel adjustment and thalweg meandering (Bennett et al., 2007). When the results are considered at the reach scale, elements of these benefits can be observed, and further inferences can be made about the capacity and potential of *S. erectum* to act as a physical ecosystem engineer in several contexts:

- It has the effect of narrowing over-widened sections to dimensions more suited to the discharges passing through the channel (reach 1);

- It acts as a dynamic component in the creation of a number of interesting geomorphological features, including a sinuous thalweg and varied bed topography that result from patchy and unconstrained growth of the plant (reach 2);
- It continues to be associated with low flow velocities and fine sediment accumulations in higher energy sections of the river (reach 3), contributing to bench development along the channel margins.

4.5 Synthesis

1) This study has shown that aquatic plant growth, particularly S. erectum, has a significant localised effect on flow velocities and is strongly associated with fine sediment accumulations. Only minimal growth is required for the plant to cause a sharp reduction in flow velocities, and these reductions exist until late in the year, when collapsed senescent leaves constitute a hydraulic impediment and protect sediment accumulations (Asaeda et al, 2009). There is evidence to suggest that sediment accumulated by large stands of S. erectum is semi-permanent, and the growth of the plant can cause changes in channel structure.

2) Although the local hydrodynamic effects of growth are similar in all reaches, reach scale implications are most pronounced in upstream reaches of the river, where the plant has created large areas of wetland environment that experience negligible flow velocities. Across the study reaches, the spatial extent, density and size of the species diminishes with distance downstream, and at reach 3 its growth is limited to two relatively small marginal patches. The greatest diversity of flow and growth patterns was exhibited in reach 2, where a number of interesting geomorphological features, including a sinuous thalweg and varied bed topography, are associated with patchy growth of the plant.

3) The four streamwise velocity classes derived from agglomerative hierarchical cluster analysis each have strong associations with several other measured properties. Each cluster can therefore be described as a distinct ‘habitat’ in terms of its relationship to measured physical and macrophyte properties (Table 4.17).
Table 4.17: Four habitats derived from analysis of interactions between flow, sediment and macrophytes, and commonly observed on the River Blackwater.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Key habitat features</th>
</tr>
</thead>
</table>
| Habitat 1 | • Dense growth of *S. erectum*, which demonstrates a long growth cycle and quickly out-competes other species.  
|           | • Low or negligible flow velocity throughout the year.                                |
|           | • A substrate consisting of thick layers of fine material.                           |
| Habitat 2 | • Thinner but abundant growth of *S. erectum*, which has a shorter growth cycle and competes actively with other species towards the end of the season.  
|           | • Low to moderate flow velocities throughout the year.                              |
|           | • A mixed substrate containing much silt, but also a significant amount of sand and gravel. |
| Habitat 3 | • Significant growth of submerged species.                                           |
|           | • Relatively high flow velocities during winter that reduce to low velocities during spring and summer.  
|           | • A coarse substrate dominated by gravel.                                           |
| Habitat 4 | • No *S. erectum* present.                                                           |
|           | • Consistently high velocities throughout the year.                                 |
|           | • A coarse substrate consisting of gravel and pebbles                               |

These habitats interact and adjust throughout the season, and their relative abundance is likely to alter considerably under different aggregate energy conditions. However, within the low energy river environment explored in this chapter, the growth of emergent vegetation is the driving force in the sequential generation of these habitats on a seasonal basis. The development and turnover these habitats are consequences of the profound effect linear emergent macrophytes have on flow velocity and sediment retention. It is hypothesized that these habitats, which constitute diverse and dynamic hydraulic channel areas, will trigger physical ecosystem engineering in the form of changes in channel structure (Figure 4.21).
Figure 4.21: Ecosystem engineering by emergent vegetation: a conceptual development of distinct habitats.

The sequential development of the four habitats is best conceived by initially picturing an unvegetated cross-section, which has a homogenous flow character and bed sediment size. Once pioneer emergent species colonise a marginal area, they are generally able to grow rapidly, causing a sharp reduction in flow velocity locally, an accumulation of fine bed sediment material, and the generation of Habitat 1. Shortly thereafter, the extent of this influence is expanded, due to the rapid growth habit of this morphotype. In this new, expansive area of growth, which is classified as Habitat 2, flow velocities are likely to be slightly higher, whilst fine sediment depth and plant density will be lower. The expanding growth of marginal vegetation across the breadth of the channel causes a funnelling of flow, increasing velocities that prevent the growth of additional emergent plants, but are highly suitable for submerged species (Haslam, 2006; Naden et al. 2006; O’Hare et al. 2007). This portion of the channel, Habitat 3, perhaps experiences the
greatest seasonal variation in flow velocities, which are initially high, due to the
funnelling effect, but are then reduced due to the growth of submerged plants, before
increasing again towards the end of the year when all vegetation senesces. Finally, the
extensive growth of vegetation, both submerged and emergent, generates narrow linear
threads of high velocity through which much of the discharge is conveyed. These
passages have enough energy to remove existing vegetation and erode river banks, and
are classified as Habitat 4.

These processes, which start and end with the growth and senescence of emergent
macrophytes, are summarised in Figure 4.22, which provides a broad conceptualisation
of the habitats, and the impacts of their sequential development, observed on the River
Blackwater.

Figure 4.22: A conceptual model of the annually created habitats induced by the growth
of emergent vegetation in lowland rivers.
Chapter 5

Linking the morphology and strength of *Sparganium erectum*

Chapter Summary

Results from the previous chapter have indicated the pronounced effect *Sparganium erectum* has on flow velocity, fine sediment retention and the growth of other macrophytes at the reach scale. However, the study provided only a snapshot of the effects *S. erectum* has on its surrounding environment based on observed spatiotemporal correlations between the measured factors. Direct biomechanical measurements of the plant’s strength are required to underpin interpretation of these correlations and provide mechanistic understanding of how the species may interact with its environment. Biomechanical measurements characterise plant strength, and therefore its ability to control or resist external forces (e.g. hydraulic stress). Variations in these measurements during the plant’s annual cycle of growth and senescence provide insights into the way in which the plant may interact differentially with its environment, particularly in terms of its ability to slow flow velocities, induce fine sediment deposition and provide reinforcement for the deposited sediment. Overall, this chapter seeks to determine the biomechanical strength and growth traits of *S. erectum* across time and space, which facilitate its role as an ecosystem engineer and allow it to be such a pervasive species.

Biomechanical properties, specifically plant uprooting resistance, stem strength and rhizome strength, were measured over two years at reach 4 of the River Blackwater. In addition, the same measurements were made during the period of peak biomass (July/August) at thirteen additional sites located between the Scottish borders and southern counties to provide an indication of the degree to which the single site measurements might be transferable across Britain. The national survey results indicated that biomechanical strength was largely independent of geographical location, despite plants in southern locations generally being larger in size. Experiments conducted on the River Blackwater revealed large seasonal variations in the uprooting resistance of the species, which increased rapidly from spring and peaked in June, before declining steadily thereafter. Due to the highly changeable structure of the species throughout the season, linking strength to morphology was complicated.
However, larger plants were generally stronger and relatively simple measures of plant size, such as stem cross-sectional area, were useful indicators of strength. Multiple regression analysis incorporating dummy variables for the time periods when measurements were taken provided a method of untangling shifts in plant growth and biomechanical properties and their interrelationships through time. It was particularly useful in identifying the importance of both root length and the number of rhizomes in influencing the resistance of *S. erectum* to uprooting.

The plant demonstrated a number of interesting biomechanical and growth traits that enhance its function as an ecosystem engineer. Of particular note was the tendency for leaves to shear at the beginning and end of the season, preserving undisturbed below ground biomass and ensuring future viability at the expense of seasonal growth. Rhizomes also performed an important function, as they retained a consistent strength throughout all recording periods. Additionally, their growth cycle differed from the rest of the plant, and their tendency to expand rapidly in length and number towards the end of the season may reinforce associated sediment, particularly given that it was the only component of plant biomass to overwinter.

The likelihood of successful plant growth at the range of stream energy conditions is presented in the form of a conceptual model, which integrates the changeable propensity of the plant for generating new physical habitats.

The results acquired from 2009 field experiments have been published in the journal *Ecological Engineering* (Liffen et al. 2011) and used to underpin a modelling study that explored the flow forces required to uproot *S. erectum* in the River Blackwater (Bankhead et al. in press).

### 5.1 Introduction

The biomechanical strength of aquatic macrophyte species are receiving increasing research attention, and their relationships with physical parameters such as flow velocity (Miler et al. 2010) and sediment stability (Schutten & Davy, 2000; Schutten et al. 2005) have been explored. To date, these studies have made a limited but useful contribution to the understanding of aquatic plants and their influence on their surrounding physical
environment, particularly in relation to the assessment of sediment stability because the application of traditional geotechnical measurements is very challenging in submerged sediments.

The importance of root strength and abundance in root-soil mechanics is recognised and well studied for terrestrial vegetation, including riparian tree species (Gray and Barker, 2004; Pollen et al. 2004; Stokes et al. 2007), whilst soil properties such as shear strength and bulk density can make important contributions to the stability of vegetation (Burylo et al. 2009). However, it has been argued that the uprooting resistance of vegetation can also be a useful measure of soil erodibility and it is hypothesized that in fine, saturated sediments, biomechanical strength makes a relatively larger contribution to overall vegetation and sediment stability than in more terrestrial contexts (Corenblit et al. 2007).

The uprooting resistance of certain terrestrial and submerged macrophytes has been studied to some extent (Scutten & Davy 2000; Scutten et al. 2005; Burylo et al. 2009), and has shown that strength is highly species dependent, but intra-species morphological measurements can provide a useful means of predicting the strength of plants. Of those measurements, underground biomass is perhaps most commonly associated with anchorage in several types of vegetation; these range from mature temperate trees (Mickovski & Ennos, 2003; Nicoll et al. 2006) to grasses (Ennos et al. 1993a; Mickovski et al. 2005; Stokes et al. 2007) and aquatics (Schutten & Davy, 2000; Schutten et al. 2005). However, due to the difficulties associated with sampling these sub-surface properties within fluvial environments, there is little field based evidence that links the structure and biomechanical strengths of aquatic plants. Thus, although below ground components of vegetation are thought to improve sediment stability (Gyssels et al. 2005) whilst anchoring plants of many varieties, the contribution they make to aquatic plants and associated sediments has yet to be explored.

It is hypothesised that the above and below ground components of aquatic macrophytes have considerable potential to influence river morphology, and by measuring the strength of the plant, it is possible to gain an indication of its strength/resistance to erosion and thus the sediment which the plant occupies. Therefore, this study uses biomechanical strength to measure the plant’s ability to affect the surrounding environment in terms of flow resistance, erosion resistance and sediment reinforcement.
through time and space. These functions, inferred in the previous chapter, are necessary if the species is to act as an ecosystem engineer. Biomechanical measurements linked to the annual cycle of macrophyte growth and senescence are likely to be consistent between years, and can therefore be used as a proxy for multi-year data, which would be necessary to measurably influence the development of fluvial landforms.

5.2 Investigative Design

5.2.1 Field measurements

Field measurements were conducted in reach 4 (Figure 3.4) of the River Balckwater during 12 field visits distributed through the 2009 and 2010 growing seasons (Table 5.1). Similar measurements were also obtained on a single occasion at the time of peak Sparganium erectum development at each of 14 sites distributed from the southern England to southern Scotland (Figure 3.3). This was to assess the degree to which measurements on the Blackwater were transferable more generally across Britain and thus assess the degree to which the former were representative of a national pattern or whether there were significant spatial variations. To ensure comparability between sites, measurements were conducted at the peak of the growth season during the summer of 2009, starting with a group of southern sites (sites 7-14) followed by more northerly sites (sites 1-6, see Figure 3.3).

Three widely-spaced 0.5 m x 0.5 m quadrats (one quadrat for the national survey sites) were selected at random within well-developed stands of S. erectum. Ten plants were selected at random within the quadrat for detailed study, giving a total of thirty plants investigated within each recording period (ten plants for each national survey site). Maximum leaf length and maximum and minimum stem diameter were measured before the plant was attached to the plant-pulling device (Figure 5.1) to measure uprooting resistance (note that stem diameter was measured at a slightly different position in 2009 and 2010, giving smaller diameters relative to other measures in 2010, Table 5.2). The plant-puller was based on a design by Abernethy and Rutherford (2001) and is similar to the device used by Pollen-Bankhead et al. (2009) to measure the root strength of riparian trees. It was built and supplied by the United States Department of Agriculture, Agricultural Research Service (USDA, ARS).
Figure 5.1: The plant puller, front and side.

The plant-puller consists of a winch mounted on a metal frame that was placed on the river bank adjacent to the patch of *S. erectum* to be investigated. A load cell, which measures the resistance, was attached to a cable that ran from the winch to the plant. The cable was attached to the plant using a U-bolt clamp. The winch was then cranked to apply a tensile stress to the plant (measured as a force, in Newtons [N]) that was increased until the plant uprooted or the stem snapped. Data were recorded using a SSI load cell display and logger. To simulate the action of river flows on plant breakage or uprooting, the device was set up to pull plants at an angle of between 10 and 20 degrees from the horizontal. Once each plant was uprooted or the stem had snapped, one of the plant’s rhizomes was either excavated in the river bed sediment and attached to the cable using a smaller U-bolt clamp (method used in 2009) or the clamp was attached to a rhizome that had been uprooted with the plant and was pulled by the winch until failure (method used in 2010). The diameter of the rhizome at the point of failure was then recorded. Table 5.2 details the measurements obtained for each plant. Maximum root length (commencing in recording period 3 2009) and the number of rhizomes (commencing in recording period 4 2009) were also recorded for each uprooted plant. During 2010, the full set of measurements adopted by mid-season 2009 (number of rhizomes and maximum root length) were collected from the beginning of the season.
Figure 5.2 shows the distribution of the recording periods, both national and at reach 4, throughout the two seasons. The specific dates of the recording periods are given in Table 5.1. To aid interpretation, the months during which the reach experiments were conducted are included underneath the recording periods in the results section.

Figure 5.2: The distribution of uprooting experiment recording periods throughout the two seasons. Grey shadings refer to experiments at reach 4 of the River Blackwater, black shadings are the experiments undertaken at 14 sites in the North (N) and South (S).

Table 5.1: Sampling dates of uprooting experiments.

<table>
<thead>
<tr>
<th>Recording periods</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td>08/04</td>
<td>20/05</td>
<td>23/06</td>
<td>10/08</td>
<td>14/09</td>
<td>18/11</td>
</tr>
<tr>
<td>2010</td>
<td>14/04</td>
<td>15/05</td>
<td>16/06</td>
<td>02/08</td>
<td>15/09</td>
<td>14/10</td>
</tr>
</tbody>
</table>
Table 5.2: Descriptions of measurements taken during uprooting measurements

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum stem diameter / Stem basal diameter (1 &amp; 2)</td>
<td>The bunched leaves of <em>S. erectum</em> are oval shaped in cross section, therefore, two diameters were measured to give a maximum and minimum from which stem cross-sectional area could be estimated. In 2009, these measurements were taken approximately 10cm above the stem base, whereas in 2010, they were measured at the stem base.</td>
</tr>
<tr>
<td>Maximum leaf length</td>
<td>The length of the longest leaf of the plant measured from the leaf base.</td>
</tr>
<tr>
<td>Number of rhizomes</td>
<td>Total number of rhizomes attached to the uprooted plant (measured from recording period 4 2009 onwards).</td>
</tr>
<tr>
<td>Maximum root length</td>
<td>The length of the longest root measured from the root base (measured from recording period 3 2009 onwards).</td>
</tr>
<tr>
<td>Strength at point of uprooting/stem snapping</td>
<td>The resistance posed by the plant to uprooting/stem breakage. Measured in Newtons (N).</td>
</tr>
<tr>
<td>Strength at point of rhizome breakage</td>
<td>The resistance posed by the rhizome to breakage. Measured in Newtons (N).</td>
</tr>
<tr>
<td>Rhizome diameter</td>
<td>The diameter of the rhizome at the point of breakage. Measured in mm.</td>
</tr>
<tr>
<td>Dry weight (of separate organs)</td>
<td>The dry weight of separate plant organs (stem, roots, corm and rhizomes). Measured in grams from April 2010 onwards.</td>
</tr>
</tbody>
</table>

5.2.2 *Laboratory measurements*

It has previously been shown that large physical size of plants can improve their resistance to uprooting, particularly the size, structure and biomass of their underground portions (e.g. Ennos et al. 1993b; Bailey et al. 2002; Schutten et al. 2005; Burylo et al. 2009). Therefore, during 2010, a sub-sample of approximately 15 plants uprooted during field experiments were brought back to the laboratory for dissection and analysis of dry weight (Figure 5.3) to test whether this was the case for *S. erectum.*
Each plant that was returned to the laboratory was thoroughly washed free of sediment. Once clean, each plant was cut into four separate parts: stem/leaves, corm, roots and rhizomes (though sometimes there were no rhizomes present). This material was then dried for 72 h at 85°C, weighed and dried for a further 4h to ensure a constant weight, following Asaeda et al. (2005, 2009).

5.2.3 Data analysis

Box and whisker plots and scatter plots were used to display variations in each of the measures of the standing crop, plant biomass and mechanical properties between recording periods. Because some of the measured properties showed differences in variances between recording periods, the non-parametric Kruskal Wallis test was used to assess whether differences between recording periods were statistically significant. Also, because of slight changes in the method of measurement of stem diameters and rhizome diameters between 2009 and 2010, data for the two years have been analysed separately. Where Kruskal Wallis tests indicated a significant difference between reaches or recording periods, they were followed by multiple comparisons using Dunn’s procedure with Bonferroni correction to identify those recording periods that showed significantly different values of the measured properties. The strength and statistical
significance of associations between different plant properties were estimated using Spearman’s rank correlation coefficients.

Associations between measures of standing crop, biomass and strength were explored using correlation and multiple linear regression analysis. Exploration of changes in relationships between strength and morphology were explored using multiple regression analysis including dummy variables in a manner similar to Gurnell and Midgley (1994). In regression analysis, a dummy variable is a variable assigned the value of 0 or 1 to indicate the presence or absence of a subgroup of data that may influence the outcome. In this case, dummy variables were used to represent the recording periods, due to the changeable seasonal influence morphological measurements had on plant strength. The value of dummy variables in regression analysis is best conveyed with a hypothetical example:

The relationship between stem strength and leaf length is to be analysed based on two field experiments; one conducted in April (Figure 5.4a), the other in August (Figure 5.4b).

![Image](image-url)

**Figure 5.4:** A hypothetical relationship between stem strength and leaf length.

The two recording periods have independently very strong relationships between the two variables, however, the equations that best describes the relationships for the two separate recording periods are very different. When the data is grouped, the equation that best describes the relationship between the two variables is influenced by data from both recording periods, the line of this equation is a poorer reflection of that relationship, and the independent variable cannot be accurately predicted.
The inclusion of a dummy variable allows for the interpretation of time effects in the regression. One recording period is used as a base (dummy = 0) and for the second recording period dummy = 1. The dummy variable (allocated values of 0/1 as appropriate) is introduced into the regression analysis as an independent variable and also as a product with the independent variable ‘leaf length’. This allows the following multiple regression equation to be estimated:

\[ \text{Stem strength} = b_1 + b_2 \times \text{dummy} + b_3 \times \text{leaf length} + b_4 \times \text{dummy} \times \text{leaf length} \]

By assessing whether the constants \(b_1, b_2, b_3, b_4\) are significantly different from 0, it is possible to identify whether there is:

(i) a single relationship regardless of recording period:

\[ \text{Stem strength} = b_1 + b_3 \times \text{leaf length} \text{ (i.e. } b_2 \text{ and } b_4 \text{ are not significantly different from zero)} \]

(ii) a different intercept but similar slope:

\[ \text{Stem strength} = b_1 + b_2 \times \text{dummy} + b_3 \times \text{leaf length} \text{ (i.e. intercept is } b_1 \text{ in recording period 1 and } b_1+b_2 \text{ in recording period 2)} \]

(iii) a different slope but similar intercept:

\[ \text{Stem strength} = b_1 + b_3 \times \text{leaf length} + b_4 \times \text{dummy} \times \text{leaf length} \text{ (i.e. slope is } b_3 \text{ in recording period 1 and } b_3+b_4 \text{ in recording period 2)} \]

(iv) a completely different relationship in the two recording periods:

\[ \text{Stem strength} = b_1 + b_2 \times \text{dummy} + b_3 \times \text{leaf length} + b_4 \times \text{dummy} \times \text{leaf length} \text{ (i.e. in recording period 1 intercept = } b_1 \text{ and slope = } b_3, \text{ in recording period 2 intercept = } b_1+b_2 \text{ and slope = } b_3+b_4) \]

Of course in (i), (ii) and (iii) the regression would be rerun without the variables that showed a non-significant slope to re-estimate the appropriate values of \(b_1, b_2, b_3\) or \(b_4\).

This approach can be applied with numerous dummy variables, all taking on the value 0 or 1 to represent whether or not data refers to a particular recording period (one recording period is always used as a base against which other periods are compared and
so has no dummy variable associated with it). In this way, one multiple regression model can be estimated for all recording periods, highlighting different recording periods only when they behave in a statistically significantly different way from the base recording period included in the model. This allows shifts in the relationship between measures of plant strength and biomass to be assessed from an analysis of data drawn from all recording periods.

5.3 Results

5.3.1 National Survey

Measurements of the standing crop and plant strength were obtained at 14 rivers during summer 2009 (Figure 3.3). The sites could be broadly grouped into northern sites (rivers 1 to 6, Figure 3.3) and southern sites (rivers 7 to 14, Figure 3.3), giving a northern sample of 6 reaches (60 plants) and a southern sample of 8 reaches (80 plants). The dates of the surveys (Table 5.3) were timed so that southern sites were sampled before northern sites to allow time for peak growth to be achieved at all sampled sites. The measured properties for each reach are compared using Kruskal-Wallis tests to assess statistically significant differences (p < 0.05) between them. Histograms, ordered by average values, with standard error bars and different statistically significant groupings (using Kruskal-Wallis tests and identified as A, B, C etc.), are presented to illustrate the differences between reaches and the distribution of north-south sites relative to one and other (Figures 5.5, 5.6, 5.7). The location of the site (north or south) is shown for each reach in brackets along the x-axis, to provide an indication of the tendency of northern or southern sites to be located towards the extremes of measurements. For ease of comparison, the reach numbers for southern sites have been highlighted in bold in the discussion of statistical differences. Where samples sizes were low (n<5), due to low occurrence of a particular form of failure (e.g. stem breakage or plant uprooting), sites were omitted from Kruskal-Wallis tests.
Table 5.3: The location and timings of national survey river reach investigations.

<table>
<thead>
<tr>
<th>Reach number</th>
<th>River name</th>
<th>Survey date</th>
<th>Easting</th>
<th>Northing</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Blackadder</td>
<td>17/8/09</td>
<td>370965</td>
<td>645760</td>
</tr>
<tr>
<td>2</td>
<td>Leet Water</td>
<td>18/8/09</td>
<td>378750</td>
<td>643950</td>
</tr>
<tr>
<td>3</td>
<td>Warren Burn</td>
<td>19/8/09</td>
<td>415400</td>
<td>631200</td>
</tr>
<tr>
<td>4</td>
<td>Aln</td>
<td>20/8/09</td>
<td>411950</td>
<td>613750</td>
</tr>
<tr>
<td>5</td>
<td>Pont</td>
<td>21/8/09</td>
<td>416885</td>
<td>573195</td>
</tr>
<tr>
<td>6</td>
<td>Skern</td>
<td>24/8/09</td>
<td>430500</td>
<td>527000</td>
</tr>
<tr>
<td>7</td>
<td>Mease</td>
<td>8/7/09</td>
<td>426275</td>
<td>311380</td>
</tr>
<tr>
<td>8</td>
<td>Sence</td>
<td>9/7/09</td>
<td>435050</td>
<td>303050</td>
</tr>
<tr>
<td>9</td>
<td>Eye Brook</td>
<td>7/7/09</td>
<td>483850</td>
<td>298380</td>
</tr>
<tr>
<td>10</td>
<td>Tove</td>
<td>6/7/09</td>
<td>467880</td>
<td>249175</td>
</tr>
<tr>
<td>11</td>
<td>Blackwater</td>
<td>16/7/09</td>
<td>486070</td>
<td>159082</td>
</tr>
<tr>
<td>12</td>
<td>Wey</td>
<td>14/7/09</td>
<td>482254</td>
<td>145385</td>
</tr>
<tr>
<td>13</td>
<td>Bourne</td>
<td>15/7/09</td>
<td>415755</td>
<td>131255</td>
</tr>
<tr>
<td>14</td>
<td>Rother</td>
<td>13/7/09</td>
<td>480715</td>
<td>122905</td>
</tr>
</tbody>
</table>

Maximum leaf length (Figure 5.5) showed a number of statistically significant differences between reaches and a greater tendency for plants with larger leaves to occur in southern sites. Of the statistical differences, there were only instances of reaches from the southern grouping exhibiting larger leaves than the northern grouping, whilst there were some statistically significant differences within the southern group: Plants from reach 7 had longer leaves than reaches 1, 3, 4, 5, 6, 9 and 10; those in reaches 11 and 13 had longer leaves than 1, 3, 4, 5, 9 and 10; plants in reach 12 had longer leaves than reaches 3, 4 and 10.

There were fewer statistically significant differences in the stem cross sectional area between sites (Figure 5.5). However, as with the maximum leaf length, there were only instances of reaches from the southern grouping exhibiting larger stems than the northern grouping, whilst there were some statistically significant differences within both the southern and northern groups. Reaches 2, 4, 5, 7, 9, 12, 13 and 14 had thicker stems than reach 1; furthermore, plants from reaches 13 and 14 were thicker than reach 10, whilst those at reach 13 were also thicker than reach 6.
Figure 5.5: Average and one standard error measurements of the above ground standing crop at the national survey reaches with statistically significantly different groupings identified using Kruskal Wallis tests (p < 0.05).

All three measures of the below ground standing crop (maximum root length, number of rhizomes and rhizome diameter: Figure 5.6) showed few statistically significant differences between sites. The maximum root length of plants measured in reach 2 were larger than reaches 3 and 10; plants from reach 3 had more rhizomes than reaches 1 and 10; the diameters of rhizomes from reach 12 were thicker than reach 10. The sites were relatively mixed in their distribution along the x axis in relation to measurements of maximum root length and thickness of rhizomes, whilst there was seemingly a tendency for plants in northern sites to have more rhizomes since the four highest average number of rhizomes came from northern sites.
Figure 5.6: Average and one standard error measurements of the below ground standing crop at the national survey reaches with statistically significantly different groupings identified using Kruskal Wallis tests (p < 0.05). Note: when a site does not have a letter group, it’s sample size was less than 5.

Analysis of measurements of plant strength showed that there were very few significant differences in the biomechanical strength between northern and southern sites (Figure 5.7). Rhizome failure and uprooting resistance exhibited no statistically significant differences between sites. There was a single statistically significant difference in the values for plant and stem failure; plants from reach 2 showed a greater resistance to failure than reach 6; the force required to induce stem failure in reach 6 was greater than reach 5.
Figure 5.7: Average and one standard error measurements of strength at the national survey reaches with statistically significantly different groupings identified using Kruskal Wallis tests (p < 0.05). Note: when a site does not have a letter group, it’s sample size was less than 5.

The very few statistical differences in the morphological and biomechanical properties of *S. erectum* measured during the national survey give confidence that the results obtained at the River Blackwater are reflective of the species at a broad spatial scale.

### 5.3.2 River Blackwater, Reach 4: Field Measurements

#### 5.3.2.1 Measures of the standing crop

The following overview of observed changes in measures of the standing crop of *S. erectum* in reach 4 of the River Blackwater, refers to patterns revealed in box and whisker plots (Figures 5.8 and 5.9) and the statistical significance of differences in observed properties between recording periods assessed using Kruskal Wallis tests (Table 5.4).

There was a similar seasonal pattern of leaf growth and decay in 2009 and 2010 (Figure 5.8). Statistical analysis of the 2009 experiments showed that leaves were statistically significantly longer in recording periods 4 and 5 than all other recording periods. Leaf
lengths measured in recording periods 3 and 6 also exceeded lengths observed in recording period 1 (all p<0.05, Table 5.4). The pattern of leaf growth was similar in 2010 and recording periods 4 and 5 also had the longest leaves, but the changes in leaf length between recording periods were slightly less pronounced than in 2009. Leaves in recording period 1 were significantly smaller than in all other recording periods.

The seasonal pattern of stem cross-sectional area was broadly similar between the two seasons, although the cross sectional area estimates for most recording periods in 2010 were smaller than in 2009, due to the slight alteration in measurement location (Table 5.2, Figure 5.8). In 2009, stem thickness peaked in recording period 3, perhaps partially due to the emergence of secondary growth plants by recording period 4 (see section 5.3.1.3). Stem cross sectional areas were smallest at the beginning and end of the growing season; being significantly larger in recording periods 2-5 than in recording periods 1 and 6, and significantly larger in recording period 3 than recording period 2 (all p<0.05, Table 5.4). The decline in stem thickness by recording period 6 was likely due to decay and the greater likelihood of pulling secondary growth plants at this time.

The 2010 data showed stem cross sectional area followed a very similar pattern to that of leaf growth, with the peak occurring during recording period 4, which showed significantly greater values than recording periods 2 and 6, whilst 5 also showed significantly greater values than 2. As in 2009, recording period 1 in 2010 had the smallest stem diameters, being significantly smaller than all other recording periods (p<0.05, Table 5.4).
Figure 5.8: Temporal changes in measures of the above ground standing crop during 2009 and 2010.

In 2009 maximum root length and total number of rhizomes were only measured in recording periods 3-6 and 4-6 respectively (Figure 5.9). However, interesting changes in the underground portions of plants were observed and there were distinct similarities between observations in 2009 and 2010. Maximum root length appeared to decline from recording period 3 during both seasons, long before other plant organs. In 2009, roots in recording period 6 were significantly shorter than 3, 4 and 5, whilst those measured in recording period 3 were significantly longer than those in recording period 4 (p<0.05, Table 5.4). In 2010, the maximum root length of plants was also greatest in recording period 3, growing to an average length of 45cm and being greater than 60cm in one exceptional case. Root lengths declined rapidly thereafter, reducing to average lengths of 29, 17 and 12cm in recording periods 4, 5 and 6 respectively. Root lengths in recording periods 1-4 were significantly longer than in 6; lengths in recording periods 2-4 were significantly longer than in 5; lengths in recording periods 2 and 3 were longer than in 1; and lengths in recording period 3 were longer than in 4 (all p<0.05, Table 5.4); indicating that roots measured in the first three recording periods were generally longer than those measured in the last three recording periods.

Both seasons showed an increase in the number of rhizomes per plant towards the end of the season (Figure 5.9). In 2009, the number of rhizomes per plant in recording periods 5 and 6 were significantly greater than in recording period 4 (P<0.05). In 2010,
the average number of rhizomes per plant increased during every recording period (Figure 5.9), with numbers in recording periods 3, 4, 5, 6 being significantly larger than in recording period 1, and recording periods 5 and 6 being significantly larger than in recording periods 2, 3 and 4 ($p<0.05$, Table 5.4). The extremes in the average number of rhizomes per plant were 0.5 and 9 (recording periods 1 and 6 respectively), illustrating the striking underground rhizomatous growth of the plant throughout the season. Most variation was seen in recording periods 3, 4 and 6, perhaps associated with sampling some secondary growth plants with fewer rhizomes than more mature plants and, in the case of recording period 6, the effects of detachment from the mother plant (section 5.3.1.3).

Because of the change in measurement method between 2009 and 2010, the breakage point at which the rhizome diameter was measured tended to be closer to the parent plant in 2010 and thus the rhizome diameters measured in 2010 tended to be larger than in 2009 (Figure 5.9). However, rhizome diameter showed a general tendency to increase throughout both seasons. In 2009, rhizomes measured in recording periods 2, 4, 5 and 6 were significantly thicker than in recording period 1, and in 2010 those measured in recording periods 5 and 6 were significantly thicker than in recording period 1 (all $p<0.05$, Table 5.4).
Figure 5.9: Temporal changes in measures of the below ground standing crop during 2009 and 2010.
Table 5.4: Statistically significant differences in measures of the above and below ground standing crop of sampled *Sparganium erectum* plants assessed using Kruskal Wallis tests, applied separately to the 2009 and 2010 data.

<table>
<thead>
<tr>
<th></th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kruskal Wallis overall probability (adj. for tied ranks)</td>
<td>Kruskal Wallis overall probability (adj. for tied ranks)</td>
</tr>
<tr>
<td>Maximum leaf length (cm)</td>
<td>&lt; 0.0001 5 3, 4, 5, 6 &gt; 1 4, 5 &gt; 2, 3, 6</td>
<td>&lt;0.0001 5 4, 5 &gt; 2 4, 5 &gt; 3 4 &gt; 6</td>
</tr>
<tr>
<td>Stem Cross Sectional Area (cm$^2$)</td>
<td>&lt; 0.0001 5 2, 3, 4, 5 &gt; 1, 6 3 &gt; 2</td>
<td>&lt;0.0001 5 4, 5 &gt; 2 4 &gt; 6</td>
</tr>
<tr>
<td>Maximum root length (cm)</td>
<td>&lt; 0.0001 5 3, 4, 5 &gt; 6 3 &gt; 4</td>
<td>&lt;0.0001 5 2, 3, 4 &gt; 5 2, 3 &gt; 1 3 &gt; 4</td>
</tr>
<tr>
<td>Number of rhizomes</td>
<td>&lt; 0.0001 5 5, 6 &gt; 4</td>
<td>&lt;0.0001 5 3, 4, 5, 6 &gt; 1 5, 6 &gt; 2, 3, 4</td>
</tr>
<tr>
<td>Rhizome diameters (mm)</td>
<td>&lt; 0.0001 5 2, 4, 5, 6 &gt; 1 0.001 5 5, 6 &gt; 1</td>
<td></td>
</tr>
</tbody>
</table>
resistance are grouped (indicating plant failure through either mechanism), both seasons showed the highest strength measurements in recording period 3, and plants were shown to be weakest at the beginning and end of the growth season. In 2009, resistance to failure was significantly greater in recording periods 3, 4 and 5 than recording periods 1 and 6, and was significantly greater in recording period 2 than in recording period 1. In 2010, resistance to failure was significantly greater in recording periods 3 and 4 than in recording periods 1, 5 and 6, and was significantly greater during recording period 4 than recording period 2 (p<0.05, Table 5.5).

Figure 5.10: Temporal changes in the force required to cause failure during 2009 and 2010.
Throughout the recording periods, there were marked differences in the proportion of sampled plants that were uprooted or experienced stem breakage. The proportion of total measurements reflecting stem breakage changed from 0.94, 0.74, 0.13, 0.17, 0.27, 0.37 through recording periods 1-6 in 2009, and 0.60, 0.33, 0.27, 0.13, 0.30 and 0.43 in 2010 (Figure 5.11).

Figure 5.11: Temporal changes in the proportion of plants suffering stem failures rather than uprooting in 2009 and 2010.

When the plant failure measurements were separated into different forms of failure, some recording periods were omitted from statistical analysis due to low sample sizes (Table 5.5). The pattern of uprooting resistance was similar for the two study years, although there appeared to be a more gradual decline in uprooting resistance following recording period 3 in 2010 compared to 2009 (Figure 5.10). In 2009, uprooting resistance was significantly greater in recording periods 3, 4 and 5 than in recording period 6, and was significantly greater in recording period 3 than recording period 2 (p<0.05, Table 5.5). In 2010 the pattern of uprooting resistance mimicked the pattern shown for plant failure due to the greater overall propensity for plants to uproot instead of break at the stem (uprooted plants = 118, stem failures = 62). In 2010, uprooting resistance in recording periods 3 and 4 was significantly greater than in recording
periods 1 and 6, and also greater in recording period 3 than in recording period 5 (p<0.05, Table 5.5).

The force required to induce stem failure increased from recording period 1 until recording periods 5 and 4 in 2009 and 2010 respectively; though the values in 2010 may not be a true reflection of the population due to the low number of plants that suffered stem failure in recording period 4 (Figure 5.11). In 2009, stems showed a greater propensity for snapping early in the season, with the force required to cause snapping being significantly greater in recording periods 2, 5 and 6 than in recording period 1 (p<0.05, Table 5.5, recording periods 3 and 4 were omitted because of low sample sizes, caused by the greater propensity for plants to uproot). In 2010, the force required to induce stem failure was significantly greater in recording period 3 than in recording periods 1 and 6 (p<0.05, Table 5.5).

Whilst the stem strength and uprooting resistance of *S. erectum* corresponded broadly with measures of plant growth, rhizome strength varied little between recording periods. There were no statistically significant differences in rhizome strength between recording periods in either 2009 or 2010 (Table 5.5).
Table 5.5: Statistically significant differences in measures of the biomechanical properties of *Sparganium erectum* plants assessed using Kruskal Wallis tests, applied separately to the 2009 and 2010 data.

<table>
<thead>
<tr>
<th></th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kruskal Wallis overall</td>
<td>Significant</td>
</tr>
<tr>
<td></td>
<td>probability (adj. for tied</td>
<td>differences between</td>
</tr>
<tr>
<td></td>
<td>ranks) df</td>
<td>recording periods</td>
</tr>
<tr>
<td>Plant failure (N)</td>
<td>&lt;0.0001 5</td>
<td>2, 3, 4, 5 &gt; 1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3, 4, 5 &gt; 6</td>
</tr>
<tr>
<td>Uprooting resistance</td>
<td>&lt;0.0001 4</td>
<td>3, 4, 5 &gt; 6*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3 &gt; 2</td>
</tr>
<tr>
<td>Stem failure (N)</td>
<td>&lt;0.0001 3</td>
<td>2, 5, 6 &gt; 1**</td>
</tr>
<tr>
<td>Rhizome failure (N)</td>
<td>0.059 5</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Results from recording period 1 omitted due to low sample size (n=2)

** Results from recording periods 3 & 4 omitted due to low sample sizes (n=4 & 5)

*** Results from recording period 4 omitted due to low sample size (n=4)

5.3.2.3 Secondary growth plants

Although the likelihood of a plant being a primary or secondary plant was not recorded in the field, because any such recording would have been to some extent subjective, the development of secondary plants from rhizomes during the growing season would inevitably influence measures of the standing crop and plant strength based on random samples of plants. It is difficult to determine when a sampled plant emerged, given the rapid rate at which secondary plants grow leaves to a height similar to their mother plants, but it is hypothesized that an estimate of the proportion of secondary growth plants within a sample can be based on their slenderness. Primary plants sprout from a corm, whilst secondary plants grow from a rhizomatous node, which generally result in
narrower stems during their first season. Thus a slenderness ratio (leaf height/stem cross-sectional area) could provide an indication of when secondary growth plants emerge. Seasonal changes in this plant slenderness ratio are illustrated in Figure 5.12.

Figure 5.12: Temporal changes in the plant slenderness ratio of sampled plants during 2009 and 2010.

The slenderness ratios for 2009 and 2010 cannot be directly compared because of differences in the method used to measure the stem diameters. However, the temporal patterns described within each year are similar. Figure 5.12 shows an increasing slenderness of plants and higher variation within samples of plants taken towards the end of the growing season (note that larger values indicate more slender plants). In 2009, there were significant differences in slenderness between recording periods (Kruskal Wallis test), with plants measured in recording periods 5 and 6 being significantly more slender than in recording periods 1-4 (p<0.05). Recording periods 1 and 4 also showed more slender plants than in recording period 3 (p<0.05). These results suggest that secondary plants began to emerge (or to be more specific, were being measured) by recording period 4 in 2009. The high variability in recording period 6 might be explained by the decay of outer leaves from both primary and secondary plants, which resulted in some very narrow stems supporting long leaves. These results
suggest that some of the measurements of stems, roots and strength from recording period 4 onwards in 2009 are attributable to the sampling of secondary growth plants.

In 2010, there were also significant differences in slenderness between recording periods (Kruskal Wallis test: p <0.0001). Plants were significantly more slender in recording period 1 than in recording periods 4 and 5. The ratios suggest there was a reduced presence of secondary growth plants because the slenderness ratio continued to decrease until recording period 5. This suggests that the diminishing values for maximum root length that were observed in both years from recording period 3 are likely to be due to decay rather than the measurement of secondary growth plants. The upturn in slenderness towards the end of the growing season in 2010 mimics that of 2009.

5.3.3 Laboratory Measurements

5.3.3.1 Biomass Measurements

As with previous sections, this overview of observed changes in laboratory measurements of plant biomass refers to temporal patterns revealed by box and whisker plots (Figure 5.13) and testing of the statistical significance of differences in biomass measures between recording periods using Kruskal Wallis tests (Table 5.6).

Analysis of plant biomass showed distinct changes throughout the growing season. Although total plant biomass appeared to increase through the growing season (Figure 5.13), the only statistically significant change was that biomass in recording periods 2, 4, 5, and 6 was significantly greater than in recording period 1 (p<0.05, Table 5.6). The below ground biomass was significantly greater in recording periods 2, 5, 6 than in recording period 1, and was significantly greater in recording period 6 than in recording periods 3 and 4 (p<0.05, Table 5.6). The high value of underground biomass recorded in recording period 2 is attributable to both rhizome and root growth (Figure 5.13).

The vegetative organs, stems (leaves) and roots, showed almost inverse patterns in biomass allocation through the growing season (Figure 5.13). The stem biomass increased steadily until recording period 4, following which there are signs of decline, probably due to decay, but these are not statistically significant. Stem biomass values for recording periods 3 to 6 were significantly greater than for recording period 1, whilst
stem biomass values in recording periods 4 to 6 were significantly greater than for recording period 2 (p>0.05, Table 5.6). Root biomass showed a dramatic increase between recording periods 1 and 2, was significantly greater in recording periods 2, 3 and 4 than in recording periods 1 and 6, and biomass in recording period 2 was also significantly greater than in recording period 5 (p<0.05, Table 5.6).

The reproductive organs of the plants, corms and rhizomes, showed a similar seasonal trend, whereby their mass increased markedly towards the end of the season (Figure 5.13). Furthermore, rhizomes exhibited a sharp increase in biomass during recording period 2. Corm biomass was significantly greater in recording periods 2 - 6 than in recording period 1, significantly greater in recording periods 5 and 6 than recording period 3 and significantly greater in recording period 6 than recording period 4 (p<0.05, Table 5.6). The very low corm biomass values in recording period 1 may be due to the plant having nearly exhausted its nutritional reserves through overwintering. Rhizome biomass was significantly greater in recording periods 5 and 6 than in recording periods 1, 3 and 4 (p<0.05, Table 5.6).
Figure 5.13: Temporal changes in the biomass of *S. erectum*, and its separate organs, during 2010.
Table 5.6: Statistically significant differences in component measures of plant biomass assessed using Kruskal Wallis tests.

<table>
<thead>
<tr>
<th>Component</th>
<th>Kruskal Wallis overall probability (adjusted for tied ranks)</th>
<th>df</th>
<th>Significant differences between recording periods ($p &lt; 0.05$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total Biomass (g)</strong></td>
<td>$&lt;0.0001$</td>
<td>5</td>
<td>2, 4, 5, 6 &gt; 1</td>
</tr>
<tr>
<td><strong>Below ground Biomass (g)</strong></td>
<td>$&lt;0.0001$</td>
<td>5</td>
<td>2, 5, 6 &gt; 1, 6 &gt; 3, 4</td>
</tr>
<tr>
<td><strong>Stem (g)</strong></td>
<td>$&lt;0.0001$</td>
<td>5</td>
<td>3, 4, 5, 6 &gt; 1, 4, 5, 6 &gt; 2</td>
</tr>
<tr>
<td><strong>Corm (g)</strong></td>
<td>$&lt;0.0001$</td>
<td>5</td>
<td>2, 4, 5, 6 &gt; 1, 5, 6 &gt; 3</td>
</tr>
<tr>
<td><strong>Roots (g)</strong></td>
<td>$&lt;0.0001$</td>
<td>5</td>
<td>2, 3, 4 &gt; 1, 6 &gt; 2</td>
</tr>
<tr>
<td><strong>Rhizome (g)</strong></td>
<td>$&lt;0.0001$</td>
<td>5</td>
<td>5, 6 &gt; 1, 3, 4</td>
</tr>
</tbody>
</table>

5.3.3.2 Associations between field and laboratory measurements

Table 5.7 illustrates significant correlations between field measurements of the standing crop and laboratory measurements of biomass assessed using Spearman’s rank correlation coefficient. Significant correlations between laboratory measures of dry weight and direct field measures of the standing crop suggest that the latter non-destructive field measurements provide a good indication of plant biomass. For example, stem cross sectional area (CSA) and maximum leaf length correlate well with stem dry weight, producing correlations of 0.80 and 0.82 respectively. Weaker, but still statistically significant relationships exist between maximum root length and root dry weight ($R = 0.69$), and rhizome dry weight and number ($R= 0.76$). There appear to be particularly strong associations between the corm dry weight and the number of rhizomes ($R = 0.83$) and also rhizome dry weight ($R = 0.84$, not shown in table 5.7). It is plausible that the corm weight is indicative of the plants nutritional reserves and thus capacity to produce new underground biomass.
Table 5.7: Spearman rank correlations between field and laboratory measurements of plant structure/biomass.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Stem cross sectional area</th>
<th>Maximum leaf length</th>
<th>Maximum root length</th>
<th>Number of rhizomes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem dry weight</td>
<td>0.80</td>
<td>0.82</td>
<td>-0.04</td>
<td>0.80</td>
</tr>
<tr>
<td>Corm dry weight</td>
<td>0.47</td>
<td>0.62</td>
<td>-0.33</td>
<td>0.83</td>
</tr>
<tr>
<td>Roots dry weight</td>
<td>0.39</td>
<td>0.26</td>
<td>0.69</td>
<td>0.09</td>
</tr>
<tr>
<td>Rhizome dry weight</td>
<td>0.33</td>
<td>0.42</td>
<td>-0.35</td>
<td>0.76</td>
</tr>
</tbody>
</table>

Note: Values in bold are different from 0 with a significance level of p < 0.05

5.3.4 Associations between the morphology and strength of *S. erectum*

Due to slight differences in some measurement techniques, associations between the measures of plant morphology (standing crop) and strength were explored separately for 2009 and 2010. Analysis of both seasons is structured in the following way: (i) Spearman’s rank correlations are estimated between measures of the standing crop and biomechanical strength to assess whether statistically significant associations are present. Rank correlations were used to avoid the necessity for data transformation to satisfy the bivariate normality assumption underpinning significance testing of product moment correlation coefficients; (ii) Multiple regression models were estimated between each biomechanical variable (dependent variable) and all possible standing crop variables (independent variables) using a stepwise procedure to determine which combination of standing crop measurements provide the best indication of plant strength. In most cases the explanatory power of the ‘best’ model increased notably in comparison with models including only one independent variable, but in both cases the residual normality / homogeneity of variance assumptions of regression were not met because of temporal shifts in the relationship between the dependent and independent variables. Therefore, this analysis was followed by (iii) estimation of multiple regression models between each biomechanical variable (dependent variable) and each individual standing crop variable (independent variable) coupled with a set of dummy variables representing the recording periods and their interactions with the independent variable. Again, the ‘best’ model was estimated using a stepwise procedure and the resultant models described the seasonal pattern in the dependence of plant...
biomechanical properties on measures of the standing crop. These dummy variable regression models provided distributions in residuals that more closely met the assumptions of normality and homogeneity of variance and they had a higher explanatory power than the multiple regression models estimated using method (ii). Sample sizes were insufficient to combine approaches (ii) and (iii) with confidence.

5.3.4.1 Experiments conducted in 2009

(i) Spearman’s Rank correlations between field measures of the standing crop and biomechanical strength: Three of the four in-situ measures of the standing crop showed positive, significant and relatively strong associations with various measures of biomechanical strength (Table 5.8). The strength of association between stem cross-sectional area (CSA) and the force required to induce failure was approximately equal for uprooted plants and those which experienced stem failure (R=0.75 and 0.77 respectively). Maximum leaf length showed a stronger association with stem failure (R=0.64) than uprooting resistance (R=0.35). Maximum root length had a strong association with uprooting resistance (R=0.69).

Table 5.8: Spearman rank correlations between field measurements of plant strength and the standing crop in 2009

<table>
<thead>
<tr>
<th>Variables</th>
<th>Plant failure</th>
<th></th>
<th>Uprooting resistance</th>
<th></th>
<th>Stem failure</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>p</td>
<td>R</td>
<td>p</td>
<td>R</td>
<td>p</td>
</tr>
<tr>
<td>Stem Cross Sectional Area (cm²)</td>
<td>0.77</td>
<td>&lt; 0.0001</td>
<td>0.75</td>
<td>&lt; 0.0001</td>
<td>0.77</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Max Leaf Length (cm)</td>
<td>0.54</td>
<td>&lt; 0.0001</td>
<td>0.35</td>
<td>&lt; 0.0001</td>
<td>0.64</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Max Root Length (cm)*</td>
<td>n/a</td>
<td></td>
<td>0.69</td>
<td>&lt; 0.0001</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>Number of Rhizomes**</td>
<td>n/a</td>
<td></td>
<td>0.19</td>
<td>0.137</td>
<td>n/a</td>
<td></td>
</tr>
</tbody>
</table>

* Recording periods 3-6
** Recording periods 4-6

There was an apparently inconsistent relationship between rhizome diameter and strength. When all data points were incorporated, the relationship was not statistically
significant, but statistically significant correlations were estimated for several individual recording periods (Table 5.9).

Table 5.9: Spearman rank correlations between rhizome strength and rhizome diameter in 2009.

<table>
<thead>
<tr>
<th>Recording period</th>
<th>R</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.06</td>
<td>0.786</td>
</tr>
<tr>
<td>2</td>
<td>-0.17</td>
<td>0.535</td>
</tr>
<tr>
<td>3</td>
<td>0.70</td>
<td>0.001</td>
</tr>
<tr>
<td>4</td>
<td>0.57</td>
<td>0.007</td>
</tr>
<tr>
<td>5</td>
<td>0.36</td>
<td>0.132</td>
</tr>
<tr>
<td>6</td>
<td>0.66</td>
<td>0.042</td>
</tr>
</tbody>
</table>

(ii) Stepwise multiple regression analysis was used to select regression models relating measures of plant strength to field measures of plant size and structure (Table 5.10). Depending on the type of failure, up to four independent variables were included in the analysis (steam cross-sectional area, maximum leaf length, maximum root length, number of rhizomes) and following a forward and backward selection procedure, regression equations were selected that predicted a measure of plant strength with the highest coefficient of determination from a combination of field measures that all exhibited slope coefficients that were significantly different from zero.

Using the entire dataset collected in 2009, only stem cross-sectional area and maximum leaf length were statistically significant predictor variables for plant failure (Table 5.10), and they jointly explained 61% of the variation in the plant failure (a combination of uprooted plants and stem failures) measurements. The same two variables also explained 77% of the variance in measures of stem failure, although it should be noted that this regression model is predominantly estimated from early recording periods when stem failure dominated. Finally, uprooting resistance was best predicted using three measurements; stem cross-sectional area, maximum root length and maximum leaf length. This combination of variables explained 56% of the variation in plant uprooting resistance, though samples could only be taken from recording periods 3-6 when maximum root length was measured. For the final three recording periods, when the number of rhizomes was recorded (recording periods 4-6), inclusion of number of
rhizomes in addition to stem cross-sectional area and maximum leaf length in the regression model explained 54% of the variation in uprooting resistance (p = <0.0001, n=60).

Table 5.10: Multiple regression models relating 2009 measurements of biomechanical strength (dependent variable: plant failure, stem failure and uprooting resistance) to measures of the standing crop (independent variables: maximum leaf length (cm), stem cross-sectional area (cm$^2$), maximum root length (cm), number of rhizomes) selected following forward and backward stepwise selection. The listed models provided the highest coefficients of determination whilst only including independent variables whose slope coefficient was significantly different from zero (p<0.05)

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Independent Variables</th>
<th>Intercept</th>
<th>Slope Coefficients</th>
<th>$R^2$ (adj.)</th>
<th>F</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant failure (N)</td>
<td>Maximum leaf length (cm)</td>
<td>-0.51</td>
<td>1.20</td>
<td>0.61</td>
<td>137.6</td>
<td>&lt; 0.0001</td>
<td>2, 174</td>
</tr>
<tr>
<td></td>
<td>Stem cross sectional area (cm$^2$)</td>
<td></td>
<td>0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uprooting resistance (N)</td>
<td>Stem cross sectional area (cm$^2$)</td>
<td>-12.72</td>
<td>0.85</td>
<td>0.56</td>
<td>36.8</td>
<td>&lt; 0.0001</td>
<td>3, 85</td>
</tr>
<tr>
<td></td>
<td>Maximum root length (cm)</td>
<td></td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maximum leaf length (cm)</td>
<td></td>
<td>0.54</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stem failure (N)</td>
<td>Maximum leaf length (cm)</td>
<td>-3.25</td>
<td>1.32</td>
<td>0.77</td>
<td>128.0</td>
<td>&lt; 0.0001</td>
<td>2, 74</td>
</tr>
<tr>
<td></td>
<td>Stem cross sectional area (cm$^2$)</td>
<td></td>
<td>0.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The multiple regression analysis generated statistically significant models relating plant strength to measurements of the standing crop. However, given that (1) the distribution of the residuals from the models were not always normal with equal variance and (2) some models are based primarily on data acquired from early/mid season (e.g. stem failure, from which much of the data relates to recording period 1), it was decided that an alternative approach that modelled time variations in the associations between biomechanical properties and measurements of the standing crop was required.

(iii) Stepwise multiple regression analysis incorporating dummy variables: Using recording period 1 as a basis for comparison, dummy variables were introduced for the other recording periods to allow temporal changes in the relationship between biomechanical strength (dependent variable) and field measures of the standing crop (independent variables) to be assessed. The results of these analyses are presented in Table 5.11, where only values for plant failure (uprooted plants and stem failures combined) have been used as the independent variable to maximise the size of the data set and ensure data from all recording periods were analysed. Plots of these data and equations are shown in Figure 5.14. Of the four field measurements of the standing crop only stem cross-sectional area and maximum leaf length were used as predictor variables since both were measured throughout all recording periods in 2009.
Table 5.11: Multiple regression models relating 2009 measurements of plant failure (N) as the dependent variable to recording period dummy variables, two measures of the standing crop (stem cross sectional area (cm^2) and maximum leaf length (cm)) and interactions between the dummy variables and the two measures of the standing crop (all independent variables).

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Standing Crop Independent variable</th>
<th>Degrees of freedom</th>
<th>F (p)</th>
<th>R^2 (adj.)</th>
<th>Multiple Regression Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant failure (N)</td>
<td>Stem cross-sectional area (CSA)</td>
<td>6, 170</td>
<td>44.6  (&lt;0.0001)</td>
<td>0.598</td>
<td>Plant Failure = 32.2 (+34.3<em>D3 +100</em>D5+27.3<em>D6) + 6.7(D2</em>CSA) +5.1(D3<em>CSA) +7.2(D4</em>CSA)</td>
</tr>
<tr>
<td>Plant failure (N)</td>
<td>Maximum leaf length (MLL)</td>
<td>8, 166</td>
<td>33.4  (&lt;0.0001)</td>
<td>0.598</td>
<td>Plant Failure = 28.6 (-136.0<em>D2 -136.4</em>D3-235.8<em>D4 +28.4</em>D6) +2.0(D2<em>MLL) +1.7(D3</em>MLL) +1.7(D4<em>MLL) +0.5(D5</em>MLL)</td>
</tr>
</tbody>
</table>

Notes:

i. D2, D3, D4, D5, D6 are dummy variables taking on the value of 1 for data values recorded in recording periods 2, 3, 4, 5, 6 respectively and 0 for data values from all other recording periods.

ii. Separate models were estimated using the two standing crop measures as independent variables following forward and backward stepwise selection. The listed models provided the highest coefficients of determination whilst only including independent variables whose slope coefficient was significantly different from zero (p<0.05).
Figure 5.14: Scatter plots of individual recording period relationships derived from the multiple regression models relating plant failure (N) to stem cross sectional area (cm²) and maximum leaf length (cm), measured in 2009.

The multiple regression model estimated using stem cross sectional area (CSA) as the independent variable, shows a significant shift in the intercept term in recording periods 3, 5 and 6 and a significant positive shift in the slope term in recording periods 2, 3 and 4 relative to recording period 1. This indicates the strength at plant failure increases more rapidly with changes in CSA during recording periods 2, 3 and 4 (thicker stems...
become relatively stronger in recording periods 2, 3 and 4 relative to recording periods 1, 5 and 6) and there is also an increase in the resistance to failure of plants with a CSA of a given size in recording periods 3, 5 and 6 in comparison with recording period 1 (which increases the intercept term).

The scatter plot and statistically significant different seasonal regression relationships (Figure 5.14, A) suggest that the data for recording periods 2-4 are grouped closely, showing a similar response of plant failure to changing CSA in these recording periods. Although recording period 5 does not have a significantly different slope to recording period 1, its extremely high intercept value means that the data occupy a similar position on the graph to recording periods 2-4, though stem CSA does not significantly affect plant failure during this recording period. Thus, the most prominent observations are that (1) the contributory strength of stems develops and disappears rapidly with growth and senescence; (2) established stems show a relatively consistent relationship between their strength and cross sectional area through the main part of the growing season; (3) when decay of the stem commences (recording period 5), plants remain relatively strong, but weaken rapidly as decay progresses (recording period 6).

A linear regression model relating plant failure to CSA without including dummy variables gave an $R^2 = 0.50$. When the dummy variables were added, the $R^2$ value (adjusted for degrees of freedom and thus the addition of the dummy variable terms) increased to 0.60 because it incorporated significant temporal shifts in the relationship as plant strength for the same CSA increased (recording periods 2-4) and then declined (recording periods 5 and 6).

The multiple regression model estimated using maximum leaf length (MLL) as the independent variable, shows a significant negative shift in the intercept term in recording periods 2, 3, 4 and a positive shift in recording period 6 relative to recording period 1. The slope term shows a steeper relationship between MLL and plant strength in recording periods 2, 3, 4 and 5 relative to recording periods 1 and 6. Observation of the scatter plot (Figure 5.14, B) provides a useful visualisation of the results and reveals the highly changeable size in leaves between recording periods and the pronounced positive relationship between plant strength and MLL during mid-season (recording periods 2-5) relative to the beginning and end of the season (recording periods 1 and 6).
Recording periods 2 and 3 are grouped closely and the steeper slope term for recording period 2 indicates that stems of a similar length have greater strength than recording period 3. Recording periods 4 and 5 are also grouped closely, but the larger slope coefficient for recording period 4 is offset by the much lower intercept, and the scatter plot suggests that smaller plants are weaker and larger plants stronger in recording period 4 relative to 5. The sudden growth in leaves between recording periods 3 and 4 means that data between these groups cannot easily be compared; one might judge, from the scatter plot, that a plant with a leaf length of 150cm would be significantly stronger in either recording periods 2 or 3 than 4 or 5, but this is 20cm shorter than any leaves measured in either recording period 4 or 5 and therefore is an assumption not based on recorded data. It is plausible that after plants reach a certain size, further growth of their leaves has less influence on their strength. Recording periods 1 and 6 show no significant increases in strength with MLL (overall plants are weakest in these recording periods), although the slightly higher intercept term for recording period 6 suggests a slightly higher strength for a given MLL in this recording period in comparison with recording period 1.

A simple linear regression model estimated between plant strength and MLL gave an $R^2 = 0.37$. When the dummy variables were added, the $R^2$ value (adjusted for degrees of freedom) increased to 0.60 because it incorporated significant temporal shifts in the relationship through the growing season.

5.3.4.2 Experiments conducted in 2010

(i) Spearman’s rank correlations between field measurements of the standing crop and biomechanical strength: As in 2009, stem cross-sectional area and maximum leaf length showed significant positive associations with measures of plant failure in 2010 (Table 5.12). The strength of the associations between uprooting resistance and measures of the standing crop were very similar to the previous year; the same three measures of stem cross sectional area, maximum leaf length and maximum root length were positively associated with uprooting resistance, generating $R$ values of 0.70, 0.53 and 0.63 respectively. Compared to 2009, stem cross-sectional area showed a weaker positive association with stem failure ($R=0.32$) whilst there was no significant association between maximum leaf length and stem failure.
Table 5.12: Spearman rank correlations between measurements of biomechanical strength and the standing crop 2010

<table>
<thead>
<tr>
<th>Variables</th>
<th>Plant failure</th>
<th>Uprooting resistance</th>
<th>Stem failure</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>p</td>
<td>R</td>
</tr>
<tr>
<td>Stem Cross Sectional Area (cm²)</td>
<td>0.59</td>
<td>&lt; 0.0001</td>
<td>0.70</td>
</tr>
<tr>
<td>Max Leaf Length (cm)</td>
<td>0.44</td>
<td>&lt; 0.0001</td>
<td>0.53</td>
</tr>
<tr>
<td>Max Root Length (cm)</td>
<td>n/a</td>
<td>0.63</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Number of Rhizomes</td>
<td>n/a</td>
<td>0.17</td>
<td>0.075</td>
</tr>
</tbody>
</table>

Spearman’s rank correlations between measures of plant biomass and uprooting resistance (Table 5.13) were similar to those of the standing crop, in that measurements relating to the vegetative organs (stem and root dry weight) showed significant correlations with uprooting resistance, while the reproductive organs showed no such associations.

Table 5.13: Spearman rank correlations between plant uprooting resistance and measurements of plant biomass

<table>
<thead>
<tr>
<th>Biomass measurements</th>
<th>R</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem dry weight</td>
<td>0.40</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Corm dry weight</td>
<td>0.01</td>
<td>0.94</td>
</tr>
<tr>
<td>Roots dry weight</td>
<td>0.55</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Rhizome dry weight</td>
<td>-0.03</td>
<td>0.83</td>
</tr>
<tr>
<td>Underground dry weight</td>
<td>0.13</td>
<td>0.28</td>
</tr>
<tr>
<td>Total dry weight</td>
<td>0.35</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Aggregate rhizome measurements (dry weight, number of rhizomes) did not show any significant correlations with measures of uprooting resistance. However, rhizomes have previously been shown to be consistently strong individually (Figure 5.10) and 2010 data revealed their strength was strongly correlated with their diameter during each
recording period (Table 5.14), although the strength weakens slightly in recording period 6.

Table 5.14: Spearman’s rank correlations between rhizome strength and diameter in 2010.

<table>
<thead>
<tr>
<th>Recording period</th>
<th>R</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.80</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>2</td>
<td>0.85</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>3</td>
<td>0.86</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>4</td>
<td>0.92</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>5</td>
<td>0.80</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>6</td>
<td>0.75</td>
<td>0.002</td>
</tr>
</tbody>
</table>

(ii) Stepwise multiple regression analysis was used to select regression models relating measures of plant strength to field measures of the standing crop using the same methodology adopted in 2009. In the case of plant failure, predictions could not be improved using a stepwise regression over relationships based on a single independent variable, stem cross-sectional area ($R^2 = 0.36$). Statistically significant predictions of stem failure could not be made using measurements of the standing crop, perhaps partially due to the smaller amount of stem failures in early recording periods.

For uprooted plants, a stepwise regression provided a useful means of improving the prediction of uprooting resistance. As with the 2009 data, stem cross-sectional area, maximum leaf length and maximum root length provided statistically significant predictors of a plant’s resistance to uprooting ($R^2 = 0.61$, Table 5.15).
Table 5.15: Multiple regression models relating 2010 measurements of uprooting resistance to measures of the standing crop (independent variables: maximum leaf length (cm), stem cross-sectional area (cm$^2$), maximum root length (cm), number of rhizomes) selected following forward and backward stepwise selection. The listed model provided the highest coefficients of determination whilst only including independent variables whose slope coefficient was significantly different from zero (p<0.05)

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Independent Variables</th>
<th>Intercept</th>
<th>Slope</th>
<th>R$^2$</th>
<th>F</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uprooting resistance (N)</td>
<td>Stem cross-sectional area</td>
<td>-11.60</td>
<td>0.63</td>
<td>0.61</td>
<td>61.3</td>
<td>&lt; 0.0001</td>
<td>3, 113</td>
</tr>
<tr>
<td></td>
<td>Maximum root length (cm)</td>
<td>0.08</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maximum leaf length (cm)</td>
<td>0.32</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(iii) Stepwise multiple regression analysis incorporating dummy variables: During the 2010 season, maximum leaf length, stem cross-sectional area, maximum root length and number of rhizomes were measured throughout all recording periods. Since maximum root length and the number of rhizomes were only measured for plants that were fully removed (uprooted) from the substrate, they can only be used as predictor variables for uprooting resistance (Table 5.16). The influence of maximum leaf length and stem cross-sectional area were investigated in relation to the complete set of plant strength estimates (Table 5.16). Plots of these data and equations are shown in Figure 5.15.
Table 5.16: Multiple regression models relating 2010 measurements of plant failure (N) and uprooting resistance (N) as the dependent variables to recording period dummy variables, two measures of the standing crop (for plant failure: stem cross sectional area (cm$^2$), maximum leaf length (cm); for uprooting resistance: maximum root length (cm), and number of rhizomes) and interactions between the dummy variables and the two measures of the standing crop (all independent variables).

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Predictor variable</th>
<th>Degrees of freedom</th>
<th>F (p)</th>
<th>R$^2$ (adj.)</th>
<th>Multiple Regression Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant failure (N)</td>
<td>Stem cross-sectional area (CSA)</td>
<td>5, 173</td>
<td>61.0 (&lt;0.0001)</td>
<td>0.589</td>
<td>Plant failure = (53.2-31.6<em>D2) +17.5(D2</em>CSA) +15.7(D3<em>CSA) +6.7(D4</em>CSA) +3.1(D5*CSA)</td>
</tr>
<tr>
<td>Plant failure (N)</td>
<td>Maximum leaf length (MLL)</td>
<td>7, 171</td>
<td>24.9 (&lt;0.0001)</td>
<td>0.485</td>
<td>Plant failure = (53.2-136.9<em>D2-345.3</em>D3-120.8<em>D4) +1.5(D2</em>MLL) +3.2(D3<em>MLL) +1.0(D4</em>MLL) +0.1(D5*MLL)</td>
</tr>
<tr>
<td>Uprooting resistance (N)</td>
<td>Maximum root length (MRL)</td>
<td>6, 153</td>
<td>60.6 (&lt;0.0001)</td>
<td>0.700</td>
<td>Uprooting resistance = (51.6 -133.3<em>D2-368.0</em>D3) +4.7(D2<em>MRL) +10.5(D3</em>MRL) +1.9(D4<em>MRL) +1.3(D5</em>MRL)</td>
</tr>
<tr>
<td>Uprooting resistance (N)</td>
<td>Number of rhizomes (NR)</td>
<td>10, 143</td>
<td>19.6 (&lt;0.0001)</td>
<td>0.549</td>
<td>Uprooting resistance = (55.7+3.6<em>D2+3.3</em>D3-9.6<em>D4-40.0</em>D5-41.2<em>D6) +10.3(D2</em>NR) +22.7(D3<em>NR) +10.8(D4</em>NR) +6.7(D5<em>NR) +4.0(D6</em>NR)</td>
</tr>
</tbody>
</table>

Note:

i. D2, D3, D4, D5, D6 are dummy variables taking on the value of 1 for data values recorded in recording periods 2, 3, 4, 5, 6 respectively and 0 for for data values from all other recording periods.
ii. Separate models were estimated using the four standing crop measures as independent variables following forward and backward stepwise selection. The listed models provided the highest coefficients of determination whilst only including independent variables whose slope coefficient was significantly different from zero (p<0.05).
Figure 5.15: Scatter plots of individual recording period relationships derived from the multiple regression models relating measures of plant failure (N) and uprooting resistance (N) to all measures of the standing crop measured in 2010.
The multiple regression model estimated between plant failure (dependent variable) and stem cross sectional area (CSA) as the standing crop independent variable, shows a significant shift in the slope term between recording periods with the steepest slope in recording period 2, declining through recording periods 3, 4 and 5, but all showing steeper slopes than recording periods 1 and 6 (Figure 5.15, A). These changes in slope are related to the same intercept in all recording periods apart from 2. Thus in recording period 2 there is the strongest increase in plant strength with CSA but from a lower intercept than the other recording periods. Thereafter, there is a progressive decrease in slope from the same intercept through recording periods 3, 4 and 5, indicating decreasing plant strength for a particular stem cross sectional area and no significant variation in strength with cross sectional area in recording periods 1 and 6. The model explains 59% of the variation in plant failure – a major increase over the 36% explanation provided by a simple linear regression model.

The multiple regression model estimated between plant failure (dependent variable) and maximum leaf length (MLL) as the standing crop independent variable, shows a more complex picture. Plant strength increases most rapidly with an increase in MLL in recording period 3, followed by recording periods 2, 4 and 5, with the model suggesting there are no significant changes in plant strength with increases in MLL during recording periods 1 and 6 (Figure 5.15, B). Although the $R^2$ value of 0.49 associated with the dummy variable equation suggests maximum leaf length is a less effective predictor of plant failure compared to stem cross-sectional area, it is substantially larger than the very low value of $R^2$ (0.08) obtained when a simple linear regression relationship is estimated, indicating that the strength of MLL as an indicator of plant strength varies enormously through time.

The multiple regression model estimated between uprooting resistance (dependent variable) and maximum root length (MRL) as the standing crop independent variable, is very powerful, providing a 70% explanation of variation in the dependent variable. Uprooting resistance increases very sharply with rooting length in recording period 3, followed by recording periods 2, 4 and 5, which all show steeper relationships between the two variables than recording periods 1 and 6 (Figure 5.15, C). This model indicates the extreme importance of early root development in influencing uprooting resistance in recording periods 2 and 3, and the weakening relationships found in recording periods.
4, 5 and finally 1 and 6, which coincide with the reduction in rooting length after recording period 3 and the smaller root network found early and late in the growth season.

Finally, the multiple regression model estimated between uprooting resistance (dependent variable) and the number of rhizomes (NR) as the standing crop independent variable, shows a strong explanatory power in this simple independent variable. The slope of the relationship between these two variables reaches a maximum in recording period 3, followed by recording periods 4 and 2, 5, 6 and finally 1 (Figure 5.15, D). The increased intercept term suggests that plants with more rhizomes have greater strength in recording periods 2 and 3, but the reduction in the intercept during recording periods 5 and 6 counteracts the slope term, and observation of Figure 5.15, D reveals that there is probably little difference in the relationship between rhizome number and uprooting resistance during recording periods 5 and 6 to 1. The strength (slope) of the relationship mimics the trend in uprooting resistance in general; rising between recording periods 2-3, then declining steadily thereafter. The relatively high $R^2$ value of 0.55 illustrates how important it is to incorporate temporal changes in plant properties, given the very low associations between rhizomes and overall biomechanical strength revealed in previous time-aggregated analyses.

Particularly concerning the 2010 data, these time-related multiple regression models have been shown to have a higher explanatory power than the multiple regression analyses based on temporally grouped data.

5.4 Discussion

The results presented in this chapter show complex changes in the above and below ground components of $S. \textit{erectum}$, which are reflected in the remarkable (yet changeable) strength of this species, and its high resistance to uprooting despite occupying generally soft and silty sediments.

The national survey revealed that, at peak growth, there was surprisingly little spatial variation in the biomechanical strength of $S. \textit{erectum}$ across England and southern Scotland. There was some indication that plants make slight morphological adaptations
depending on their geographical location, with plants in southern sites having larger leaves, but those in northern sites growing more rhizomes. The lack of spatial variation found in this national survey provides confidence that the detailed results obtained from the River Blackwater are most likely to be applicable nationally.

When the reach-scale results were separated into different forms of failure, clear patterns relating to the strength of the plant and its propensity for different types of failure at different times of the year were apparent in both seasons. In both seasons uprooting resistance increased until recording period 3 before showing a gradual decline. Strength at stem failure continued to increase for an additional one and two recording periods in years 2010 and 2009 respectively. However, this was sometimes difficult to support statistically, given the greater tendency for plants to uproot rather than suffer stem failure during the middle of the growing season. These results show that plants can become very strong and well anchored during summer but, whilst achieving that strength takes several months, it generally diminishes quite suddenly towards the end of the season. Thus, autumn might be considered the most vulnerable time in the plant’s survival; uprooting resistance reduces but leaves remain long and begin to collapse, potentially causing a larger drag on the plant as a whole. Furthermore, there remains a strong tendency for plants to uproot rather than suffer stem failure, occurring on 73% and 70% of pulling tests, during recording period 5 of 2009 and 2010 respectively.

Explaining a plant’s strength using morphological measurements was not always simple, and varied with the type of failure. Multiple regression analysis of the 2009 data showed that whilst the measured variables can be used to make predictions about the force required to induce failure, the combination of those variables giving the highest predictive power changes throughout the season, and their usefulness in predicting the plants resistance seems to diminish towards the end of its growth cycle. As found in studies on other plants (Ennos, 1993b; Schutten et al. 2005; Burylo, 2008), stem cross-sectional area and maximum leaf length were the most useful indicators of a plant’s resistance to failure, with both collectively and individually showing strong positive relationships between their size and different forms of failure. The leaves therefore provide a good indication of plant fitness; a plant capable of producing large
leaves is well equipped to extract nutrition from both the atmosphere and the substrate, and therefore develop a large, strong and well connected physical structure.

The multiple regression dummy variable analysis further demonstrated that associations between plant morphology and strength vary through the growing season. This was perhaps best exemplified by root length. The maximum root length of plants showed a reasonably strong association with uprooting resistance in both field seasons, and a strong visual comparison of the patterns of uprooting resistance and maximum root length could be made using Figures 5.8 and 5.10. However, the strength of the relationship was only fully revealed once seasonal differences were accounted for, which attributed much of the increasing uprooting resistance of plants during early recording periods to the growth of roots. Unlike rhizomes, roots were never observed to break during field measurements and there always occurred a rotational slip failure of the root bole (an observation also made by Schutten (2000) on submerged macrophytes). These results and observations suggest that roots collectively make a substantial contribution to plant stability, which is probably limited by the low shear strength of surrounding sediment.

The dummy variable regression analysis also revealed that relatively simple measures of the standing crop could provide useful indications of a plant’s strength, provided that seasonality was accounted for. Stem cross-sectional area and maximum leaf length were consistently useful indicators of a plant’s resistance to failure, suggesting that easily applied measurements or even visual observations may be a legitimate means of estimating a patch’s susceptibility to removal. Perhaps the most surprising revelation of dummy variable regression analysis was the relatively strong influence that rhizome number had on uprooting resistance. This was surprising because previous analyses that did not allow for temporal variations failed to reveal a statistically significant contribution of rhizomes to the strength of the plant. Whilst it was plausible they did not perform this function, it was considered unlikely given that when experiments were conducted a progressive breaking of rhizomes was often felt and often coincided with peaks in uprooting resistance. Previous studies have also suggested that the rhizomes are the principal anchoring devices for upright culms (Speck and Spatz, 2003), more so than roots in _S. erectum_ (Sand-Jensen, 2008). In this study, the pattern of the association between rhizomes and uprooting resistance suggests that the contribution made by
rhizomes to the uprooting resistance of the plant is a significant one, with more rhizomes having the effect of stabilising plants during peak growth. Thereafter, this association declines, despite rhizome numbers increasing, further suggesting that their expansive growth during autumn is an adaptive growth trait (discussed below).

The seasonally invariant strength of individual rhizomes was shown during both field seasons. Rhizome strength showed a strong positive relationship with rhizome diameter throughout the 2010 season, although the strength of the relationship was slightly diminished towards the end of the season as rhizome diameter increased. The number of rhizomes per plant also increased steadily throughout the growing season, and their reduced strength during the latter recording periods could be an indication of their tendency to become more brittle and break up throughout winter, or a physiological change whereby the plant generates more nutritional mass relative to its structural tissue, as a means of overwintering. These traits of consistent strength and increasing mass until winter may have important implications for sediment stability, with fine material being protected from winter flows by strong and abundant rhizomes that partially mitigate the dieback of roots and foliage.

Although the dry biomass measurements were not able to improve the prediction of uprooting resistance, they gave further evidence of the importance of vegetative organs (roots and leaves), which all showed statistically significant positive relationships with uprooting resistance. However, biomass measurements helped to reveal the changing morphology of the plant, illustrated by Figure 5.16.

Figure 5.16: Changes in the structure of leaves and rhizomes in *S. erectum* over the period of growth and senescence.
It is thought that the elevated values for rhizome biomass in recording period 2 are due to their ‘creeping’; exhibiting an initial growth spurt similar to the leaves, before sprouting secondary shoots that were pulled independently later in the season.

Measurements of the total plant biomass (Figure 5.13) and the ratio of above-below ground mass also suggest that, towards the end of the growth season and the onset of senescence, plants invest heavily in the growth of their underground portions, which are more protected from decay, damage or desiccation in the sediment. This increase in mass is almost entirely rhizome material and is remarkable given that roots show decay from recording periods 4 onwards. This could also be regarded as a vegetative strategy, as rhizome fragments are detached and dispersed throughout winter (Cook, 1962), and by increasing their biomass the amount available for transport also increases. So whilst the plant seemingly grows roots early to stabilise itself, rhizomes grow more gradually as a method of dispersal and survival as well as stability.

When compared to similar experiments conducted on different types of plants, these results show that, at its peak, \( S. \) erectum’s resistance to uprooting is similar to many of the juvenile trees and shrub species studied by Burylo et al (2009), despite generally growing in unstable sediments. Even in its weakest state, the uprooting resistance of \( S. \) erectum was far greater than other (submerged) aquatic species (Brewer & Parker 1990; Usherwood et al. 1997) including the nine tested by Schutten et al. (2005) which ranged in average uprooting resistance from 0.25–12 N; the latter is approximately 1/3 the average uprooting resistance of \( S. \) erectum during recording period 1. These papers also cite soil shear strength as being of key influence in a plant’s ability to resist uprooting. These results argue that biomechanical traits, and the dense web of underground organs produced by \( S. \) erectum, are principally responsible for the stability of the species, and subsequently provide reinforcement to the loose, highly saturated sediment that it commonly traps and occupies.

These factors contribute to the species ability to act as an ecosystem engineer, largely as a function of (1) underground structural organs, which are important for plant stability, and it is therefore reasonable to assume that they have implications for sediment stability, and (2) leaf size and structure, which are a dense and strong impediment to flow during the growing season. These factors make a significant contribution to understanding the ability of stands of \( S. \) erectum to withstand hydraulic stresses and
form an effective trap for fine sediments.

5.5 Synthesis

The observations collected by this study have shown that *S. erectum* is a strong plant, which helps explain its broad distribution throughout the UK, and that strength is not consistently associated with one feature or organ. Given the typical environment in which it grows, it has a great resistance to removal, which indicates its ability to survive extreme flow events. Figure 5.17, summarises the range of potential responses of *S. erectum*, and other clonal macrophytes, to an increase in hydraulic stress and their implications for the fate of the plant.

![Diagram](image_url)

**Figure 5.17**: The potential fates for clonal macrophytes exposed to increased hydraulic stress.

The patterns of stem size, structure and strength, and plant uprooting resistance through the growth season result in a propensity for plant stems to break before the plant is uprooted at the beginning and end of the growth season (scenario 3), but for the stems to have sufficient strength in mid-season for plant uprooting to dominate, though this is thought to be a rare outcome due to the strength of the plant and limited energy of the
river (scenario 4 or 5). The occurrence of a plant shedding its leaves to protect the root system has been termed a 'mechanical fuse' (Usherwood et al. 1997) and has also been observed in submerged macrophytes (Schutten et al. 2005). The pattern of seasonal stem breakage versus uprooting seen in *S. erectum* may be an advantageous one; it is reasonable to assume that exposure to the largest hydraulic stresses will occur more frequently towards the beginning and end of the growth season (spring and autumn), when river discharges are generally higher than in summer. Thus, whilst the plant is growing and decaying, it may frequently lose its leaves or become damaged, but remains viable for future growth.

The most common outcome at the reach scale in this study was successful anchorage, whereby the plant remains relatively undisturbed throughout the season. At broader scales, there is likely to be a large spatial heterogeneity in the proportion of plants that attain successful anchorage, and indeed across the breadth of the channel. At a national scale, the proportion of the species suffering uprooting may increase with increasing river energy, as described by Gurnell et al. (2010). Within low energy systems, such as the River Blackwater, the fate of individual plants and stands may also vary with stream energy (Figure 5.18), with outcome 5 being prevalent but with a proportional shift towards outcome 1 as unit stream power increases.

![Figure 5.18: A theoretical link between unit stream power and the fate of emergent vegetation.](image)

The overall propensity for a given *S. erectum* community to suffer different fates will have important implications when considering the ability of the species to function as an ecosystem engineer. It is argued that, where patches are relatively stable (scenario 4), *S. erectum* will have the greatest potential to positively influence the long-term dynamics
of channel structure. These patches will allow the gradual aggradation of new sediment material, which will in time lead to the marginal adjustments described in Figure 4.1, and potentially the generation in channel habitats described at the end of Chapter 4 and new riparian habitats. In expanding patches (scenario 5), profound changes are likely to occur, but these may result in conditions such as those seen in reach 1 of the River Blackwater, where habitat diversity is low and vegetation dominates channel structure.
Chapter 6

Structural changes in the below ground biomass of

*Sparganium erectum*

Chapter Summary

In Chapter 5, strong associations were found between simple measures of the below ground biomass of *Sparganium erectum* and its resistance to uprooting. The reinforcing and stabilising effect of root systems in unsaturated soils is well established, however there does not currently exist research that has fully quantified the contribution made by aquatic plant roots/rhizomes to sediment reinforcement. This study begins to address this research gap, and provides a far more detailed appraisal of the architecture of below ground organs than was provided in Chapter 5, by quantifying the depth, seasonality and abundance of the below ground biomass of *S. erectum*. These observations have significant implications for the reinforcement and stability of fine sediment associated with the species.

The study uses a modified ingrowth core method to sample below ground biomass, and finds *S. erectum* to be a highly productive species, with a staggered development of roots, foliage and rhizomes. Roots develop quickly between May and August, before declining rapidly thereafter. Increases in rhizome mass are modest by comparison and remain relatively constant throughout the year. Analysis of the depth of the root and rhizome mass show it to be highly concentrated in the upper layers of sediment; typically over 70% of total underground mass was contained within the top 10cm of sediment from the surface throughout all recording periods.

The results show *S. erectum* to be a shallow rooted species, which differs from previous assumptions. The shallowness of its underground mass is likely to have a protective effect on surficial layers of fine sediment, including that which is being regularly deposited within and between the dense foliage of the species. It is hypothesized that the growth cycles of *S. erectum*’s various organs engineer preferable substrate conditions, whereby they facilitate the accumulation, reinforcement and protection of fine sediment.
6.1 Introduction

In order to function as an ecosystem engineer and remain viable for future growth, aquatic vegetation must be capable of retaining trapped sediment and resisting hydraulic forces exerted upon it. Studies that explore interactions between vegetation and sediment in rivers, including those reported in the fourth chapter of this thesis, generally attribute sediment accumulation to the growth and presence of above ground biomass (e.g. Gurnell et al. 2006a; Asaeda et al. 2009). Whilst above ground biomass is highly influential in the initial accumulation of sediment, below ground biomass is arguably more influential in the retention of fine sediment, principally by increasing its resistance to erosion. Root reinforcement of aquatic sediments is important given the dieback of above ground biomass during autumn and winter, and thus the exposure of accumulated sediments at a time when flood disturbance is likely to be particularly high. Conversely, sediment reinforcement is important for the vegetation itself, as it will prevent damage to and dispersal of the underground mass. This is particularly relevant for species such as *Sparganium erectum*, that typically grow in fine, easily-eroded sediments, and is perhaps less important for species that root in coarser river bed material e.g. *Ranunculus* spp.

Below ground biomass of terrestrial vegetation has been shown to make a significant contribution to the erosion resistance of soils by reinforcing and binding sediment particles in surficial layers (Thornes, 1990; Gray & Sotir, 1996; De Baets et al. 2005), resulting in increased shear strength and reduced surface scour compared to unvegetated soils (Styczen & Morgan, 1995). Research conducted along river margins has demonstrated the potential of riparian vegetation to stabilise streambanks (Simon & Collison, 2002), with root systems being particularly important for bank-toe stabilisation during seasons when above ground biomass is limited (Pollen-Bankhead & Simon, 2010).

Below ground biomass is crucial to the longevity and stability of in-channel vegetation (Sand-Jensen 2008), and often constitutes the majority of total biomass in linear emergent species (Sculthorpe, 1967), but there are few studies that have investigated the dynamics of the below ground biomass of aquatic plants. Methods exist for determining underground biomass, and a number of studies have explicitly studied root distribution, depth and biomass in forested and other terrestrial areas (e.g. Steele et al. 1996; Cheng
and a limited number of studies have investigated species occupying riparian areas (Kiley & Schneider, 2005, Boyd and Svejcar, 2009). A small number of studies conducted in saturated sediments have determined total underground biomass by excavating entire soil blocks (e.g. Asaeda et al. 2006a,b, 2009; League et al. 2006), and a single study by Darby and Turner (2008) used a stainless steel coring cylinder to determine the below ground biomass of salt marsh vegetation at 10cm depth increments.

This study adapts the ingrowth core method that was developed to assess the underground dynamics of terrestrial vegetation (Gray & Sotir, 1996) to investigate the structure and biomass of roots and rhizomes of aquatic vegetation. The research aims to quantify seasonal changes in the biomass and depth distribution of roots and rhizomes of *Sparganium erectum*, from which implications for sediment stability and landform development can be interpreted.

### 6.2. Investigative design

#### 6.2.1 Ingrowth Core Design

The principal objective of this study was to determine the changing below ground biomass and depth of the roots and rhizomes of *S. erectum*. To achieve this, a modified ingrowth core tube suitable for investigations in submerged river beds composed of fine sediment was designed and constructed. In order to minimise any physical or chemical impact on surrounding vegetation or sediment, the core tubes were designed with the following specifications:

- Each tube was 50cm in length and had an inner diameter of 11cm. These dimensions were chosen because (1) the fine sediment accumulations within large *S. erectum* stands at the River Blackwater study reaches were generally less than 50cm depth, thus all material could be captured and recorded using the tubes, including that which aggraded; (2) 11cm was deemed sufficiently wide for a large *S. erectum* plant to emerge unrestricted from the top of the contained core.

- It was important that the core tubes were predominantly permeable structures that allowed plants to grow in/out of their boundaries, yet the core needed to remain a strong and rigid structure. Therefore, holes were drilled in the walls of the core tubes
in a honeycomb arrangement to minimise the distance between them without compromising the strength of the core tube.

- Each hole was 2.6cm in diameter; twice the diameter of the largest rhizomes measured during uprooting investigations in 2009.

- The prototype was initially made using polyvinyl chloride (PVC), but this was subsequently changed to polypropylene due to concerns about the possibility of chlorinated compounds affecting plant growth (Fyfield et al. 1984).

Given the differences between those environments previously sampled using the ingrowth core method and that of the bed of the River Blackwater (or fine, saturated, submerged bed sediments in general), some adaptations had to be made to ensure that a representative root/soil sample could be successfully extruded. Two specific problems previously encountered during core tube use were (i) saturated soils often fall out of the bottom of the core when extraction is attempted and (ii) roots ‘slide’ out of the core holes when it is removed (Boyd and Svejcar, 2009). To minimise the displacement of roots, plant material was cut flush to the edge of the core in the field using a sleeve with a sharpened edge 1mm larger in diameter than the core tube itself. The sleeve was forced directly over the core immediately prior to extraction. To prevent the loss of material from the bottom, the core was leveraged slightly before a cap was placed underneath its base. The core could then be removed as a single, undisturbed profile of sediment. The core was retained within the tube, sleeve and cap during transport back to the laboratory. Figure 6.1 shows the components of the ingrowth cores used in this research.
Figure 6.1: From left to right: an ingrowth core tube, sleeve and cap.

6.2.2 Field Installation

The ingrowth core tubes were installed within reach 2 of the River Blackwater during February 2010 and were retrieved at intervals throughout the 2010 period of growth and senescence of *S. erectum*, and once in January 2011. Reach 2 was selected for this research because it is located on private land and so was thought to be less susceptible than the other Blackwater study reaches to human interference; this was a concern given the very obvious nature of the cores prior to the emergence of above ground mass (Figure 6.3). The detailed distribution of *S. erectum* within the channel had been observed during hydraulic surveys conducted in 2009, and so it was possible to locate areas of probable *S. erectum* growth prior to the emergence of the vegetation. Portions of the reach that had sediment accumulations of substantial depth were prioritised, because it was deemed preferable to have cores in areas where the underlying gravel riverbed would not limit the growth of roots and rhizomes, allowing the maximum depth of growth to be determined. Five 1.5m x 1.5m plots (hereafter referred to as patches) were marked within reach 2. These were each located on a channel cross-section studied during the previous year’s hydraulic surveys and at sites where dense seasonal growth of *S. erectum* and retention of fine sediment throughout the winter had previously been observed (Figure 6.2).
Figure 6.2: The location of the five ingrowth core patches at reach 2.

Within the five patches, 8-12 ingrowth core tubes were forced into the fine superficial bed sediment to a sufficient depth to support the core and prevent its upheaval by
hydraulic drag, but with some bed surface clearance to allow for sediment surface aggradation during the growing season. Cores were installed early in February 2010 to minimise damage and interference with the initial seasonal growth of vegetation. Figure 6.3 shows installed cores shortly after the initial emergence of vegetation.

Figure 6.3: In situ ingrowth cores, reach 2 of the River Blackwater, March 2010. (1) a young S. erectum plant emerges inside a core; (2) a group of 9 cores situated inside a stand of S. erectum; (3) patches 2 and 3 adjacent to opposite banks of the reach; (4) leaves beginning to emerge in and around the cores.

6.2.3 Timing and frequency of core retrieval

The timing and frequency of core retrieval was based upon the following observations of S. erectum development during uprooting experiments in 2009:

20\textsuperscript{th} May: First signs of significant development of both roots and rhizomes.

23\textsuperscript{rd} June: The emergence of secondary growth plants and substantial development of root bole; some roots exceeding 40cm and most containing secondary root hairs.
10th August: Secondary plants develop their own roots and rhizomes.

14th September: Significant proportional change in underground organs as roots show significant decay whilst rhizomes continue to sprout.

Core retrieval was conducted within two weeks of these dates during 2010 (Table 6.1) and continued through winter to investigate the underground biomass during senescence and dormancy. Fifty core tubes were placed in reach 2 during February 2010 and 6 to 8 cores were removed on seven occasions, producing a total of 49 retrieved cores. The stem density within each patch was also recorded during each core retrieval period using a 0.5m x 0.5m quadrat.

Table 6.1: Core extraction dates (recording periods)

<table>
<thead>
<tr>
<th>Recording periods</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date of removal</td>
<td>23/5/10</td>
<td>30/6/10</td>
<td>5/8/10</td>
<td>3/9/10</td>
<td>8/10/10</td>
<td>23/11/10</td>
<td>14/1/11</td>
</tr>
<tr>
<td>Number of cores removed</td>
<td>6</td>
<td>7</td>
<td>7</td>
<td>6</td>
<td>8</td>
<td>7</td>
<td>8</td>
</tr>
</tbody>
</table>

6.2.4 Laboratory analysis

The ingrowth cores were transported directly from reach 2 to the laboratory, where they were frozen to minimize decay of plant material prior to analysis. When a core was to be analysed, it was removed from the freezer and allowed to thaw for approximately 1h, at which point the outer sleeve was removed and the core tube placed horizontally on the workbench (Image 1, Figure 6.4). The total depth of the sediment was then measured and the sediment was extruded from the core and cut into 5 cm depth increments (Images 2 and 3, Figure 6.4). If the total depth was not divisible by five, the final few centimetres of sediment at the base of the core were analysed separately. All cores were dissected within 72h of retrieval from the field. An advantage of freezing was that the core could be easily extruded as a single profile avoiding mixing and collapse of the saturated soil when laid horizontally.
Following Darby and Turner (2008), each 5cm increment was washed in a 2mm sieve over a 0.5mm sieve to prevent the loss of dead and fine root material. The collected plant material was then separated into roots and rhizomes and dried for 72 h at 85°C to measure the dry weight of *S.erectum* biomass, following Asaeda et al (2009). The plant material was then weighed before being placed back in the oven for a further 4h and weighed again to ensure no additional moisture was being lost. The dry weight of the above ground biomass was analysed using the same drying procedure.

Figure 6.4: Laboratory dissection of ingrowth cores.

6.2.5 Data Analysis

Data are presented in the form of multiple box and whisker plots and bar charts.

Variations in the total above ground and total below ground biomass between recording periods were analysed using one way parametric analysis of variance (ANOVA). The observations of total above ground and total below ground biomass were square root transformed to ensure a normal, homoscedastic error distribution following ANOVA. In the case of above ground biomass, a few growth tubes showed no biomass during
recording periods 1, 2, 3, 4 and 5, although they were located within stands of well-developed *S. erectum*. Observations of above ground biomass from these tubes were omitted from the ANOVA, since they were not representative of the biomass in the surrounding stand. During recording period 7, no above ground *S. erectum* biomass was present in the study reach and so this recording period was omitted from the ANOVA. Following ANOVA, Tukey pair-wise comparisons established the degree to which there was a statistically significant difference (p<0.05) in biomass between recording periods.

When 5 cm depth increments of total below ground biomass (roots plus rhizomes), root biomass, and rhizome biomass were investigated, these response variables were log10 transformed to ensure a normal, homoscedastic error distribution following multiple regression analysis. Because these biomass data sets included zero values, where zero represented a genuine absence of biomass at a particular depth within a particular recording period, a two step analysis similar to that described by Polce et al. (2011) was adapted. The first step was conducted on biomass presence-absence data (1 or 0) and established the probability of biomass being present at specific time and depth. The threshold probability at which biomass observations were removed from further analysis was 0.2, where this was equivalent to only one positive value in the smallest samples (i.e. number of cores = 6). The second step only analysed biomass observations that were greater than zero. The three response variables (total below ground biomass, root biomass, rhizome biomass) were introduced as the dependent variable in multiple linear regression analyses, where the independent variables were dummy variables representing recording period, depth increment and the interaction between recording period and depth increment. In each case recording period 1 and depth 0-5 cm were retained as the base against which the impact of changes in recording period and depth could be assessed. The multiple regression models were estimated using a stepwise procedure to derive the regression model with the highest coefficient of variation (adjusted for degrees of freedom), which also contained independent variables with slope coefficients that were significantly different from zero (p<0.05). Predictions from the multiple regression model were set to zero where the probability of biomass being present was less than 0.05.

Net primary production (NPP) was estimated using different methods depending on the type of plant material. Given that the above ground biomass was observed to decay
entirely, the dry weight of individual stems at peak growth indicated the amount of newly generated biomass within a season (Singh et al. 1975; Long et al. 1989) expressed as g m$^{-2}$ yr$^{-1}$. The same method was possible for roots, whilst values for rhizomes, which overwinter, were derived by subtracting the minimum from maximum observed values. An additional measure of above ground NPP that multiplies the above ground biomass for the individual stems sampled in the cores by the quadrat stem density recorded for the relevant patch (Mason & Bryant, 1975) was also estimated to overcome any bias caused by interference of the core tubes with shoot development. Biomass values for the various types of plant material for a set of cores extracted during each recording period is expressed as g m$^{-2}$.

6.3 Results

For ease of interpretation, Figure 6.5 provides a visual reference of when sampling was undertaken. The months that correspond with the seven recording periods are also shown in graphs depicting seasonal trends.

Figure 6.5: The timing and distribution of the seven recording periods used to measure underground biomass.

6.3.1 Changes in plant biomass

Figure 6.6 illustrates the proportion of biomass contained within the various depth increments. It shows that the vast majority of below ground biomass was contained within the upper 15cm of sediment throughout the year. The proportion of total below ground biomass contained within the top 15cm generally exceeded 90% until the final recording period (7) where it constituted 100% of the underground biomass. With the exception of recording period 3, there seems to be an increase in the proportion of
biomass contained in the uppermost 10cm, which generally exceeds 70% and rises to 88% in recording period 7.

Figure 6.6: The changing proportion of underground biomass within each recording period.

There were strong variations in above and below ground biomass between recording periods (Figure 6.7, A), and also the ratio between the two. Both showed a strong seasonal cycle of growth and senescence and there was a greater below ground than above ground biomass in all recording periods (Figure 6.7, B), though some individual samples showed a higher proportion of above ground to below ground biomass.
Figure 6.7: (A) Box and whisker plots showing total above ground biomass (foliage) and below ground biomass (roots + rhizomes) observed in the core samples across the seven recording periods. Note that observations of no biomass are excluded from the above ground biomass box and whisker plots. (B) Box and whisker plots showing the ratio of above ground to below ground biomass across the seven recording periods in cores which contained above ground biomass.
When these data sets were square root transformed and subjected to one way parametric ANOVA, statistically significant changes in biomass were found between recording periods (Table 6.2). Below ground biomass was greatest during recording periods 2 and 3, whereas above ground biomass was greatest in recording periods 2, 3 and 4.

Table 6.2: Statistically significant differences in total above ground and total below ground biomass between recording periods investigated using one way, parametric ANOVA followed by Tukey pairwise comparisons.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>df</th>
<th>F (p)</th>
<th>$R^2$ (adj.)</th>
<th>Recording periods with significantly different biomass (p&lt;0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SQRT (total above ground biomass, g.m$^{-2}$)</td>
<td>5, 19</td>
<td>10.58 (&lt;0.001)</td>
<td>0.664</td>
<td>2, 3, 4 &gt; 1, 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5 &gt; 6</td>
</tr>
<tr>
<td>SQRT (total below ground biomass, g.m$^{-2}$)</td>
<td>6, 42</td>
<td>17.7 (&lt;0.001)</td>
<td>0.676</td>
<td>1, 2, 3, 4, 5 &gt; 7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2, 3, 4 &gt; 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2, 3 &gt; 5</td>
</tr>
</tbody>
</table>

When the below ground biomass was investigated within five depth classes (class 1=0-5, class 2=5-10, class 3=10-15, class 4=15-20 and class 5=20-25 cm depth below the fine sediment surface), strong variations between recording periods were again observed, with different behaviour exhibited by rhizomes and roots (Figure 6.8). Root biomass developed strongly from recording periods 1 to 3, showing an increase in biomass through time and with depth. Thereafter, root biomass showed a rapid decline through recording periods 4 to 6, with no detectable root biomass in recording period 7. In contrast, rhizome biomass showed far less variation through time or with depth. Rhizome biomass was observed in all recording periods, and, although rhizomes were found at some time within all depths sampled, the majority of the rhizome biomass was confined to the 0-5 and 5-10 cm depth layers.
Figure 6.8: Box and whisker plots showing variations in total below ground (roots and rhizomes), root, and rhizome biomass at different depths and recording periods. (Note all zero observations are excluded)

The multiple regression models summarised in Table 6.3 and predictions from the models illustrated in Figure 6.9 show that most of the below ground biomass is confined to the 0-5 and 5-10 cm layers below the river bed. There is a significant expansion in the biomass within the 5-10 cm layer between recording periods 1 and 2, which is a combination of root and rhizome development. Thereafter root development accounts
for the increasing quantity and depth of total below ground biomass to recording period 3. From recording period 3, root biomass decreases in all depth layers until it disappears completely in recording period 7. At the same time, rhizome biomass is sustained at depths 0-5 and 5-10 cm and shows some increases within deeper layers until recording period 6. In recording period 7, rhizomes disappear below 15 cm, but are sustained in shallower soil layers. Thus, from recording periods 3 to 6, root biomass declines whereas rhizome biomass is stable or increasing. Recording period 7 showed no root biomass but a substantial rhizome biomass in the shallower soil layers (0-15 cm).
<table>
<thead>
<tr>
<th>Response Variable</th>
<th>df</th>
<th>F</th>
<th>$R^2$ (adj.)</th>
<th>Multiple Regression Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log10 (Total below ground biomass in g.m$^{-2}$)</td>
<td>12,168</td>
<td>28.5</td>
<td>0.647</td>
<td>Log10(TBG) = 2.86 (-0.14Period4 - 0.21Period5 - 0.30Period6 - 0.75Period7 - 0.29Depth3 - 0.76Depth4 - 1.06Depth5 - 0.31(Period1<em>Depth2) + 0.44(Period4</em>Depth4) - 0.32(Period6<em>Depth1) - 0.38(Period6</em>Depth3) + 0.36(Period7*Depth1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(&lt;0.0001)</td>
<td>For period 5, depth 5 and period 7, depths 4 and 5, total below ground biomass estimated as 0</td>
</tr>
<tr>
<td>Log10 (Root biomass in g.m$^{-2}$)</td>
<td>7, 148</td>
<td>47.5</td>
<td>0.677</td>
<td>Log10(roots) = 2.49 (+0.22Period3 - 0.41Period5 - 0.78Period6 - 0.32Depth3 - 0.63Depth4 - 0.72Depth5 + 0.28(Period2*Depth1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(&lt;0.0001)</td>
<td>For period 5, depth 5 and period 7, all depths, root biomass estimated as 0</td>
</tr>
<tr>
<td>Log10 (Rhizome biomass in g.m$^{-2}$)</td>
<td>8, 151</td>
<td>13.6</td>
<td>0.39</td>
<td>Log10(rhizomes) = 2.42 (-0.49Depth3 - 0.64Depth4 - 0.88Depth5 - 0.34(Period1<em>Depth2) - 0.30(Period2</em>Depth1) + 0.48(Period2<em>Depth3) + 0.34(Period5</em>Depth3) - 0.34(Period7*Depth2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(&lt;0.0001)</td>
<td>For period 2, 3, 4, 5 and 7, depth 5 and period 3 and 7, depth 4, rhizome biomass estimated as 0</td>
</tr>
</tbody>
</table>
Figure 6.9: Estimates of total below ground, root and rhizome biomass from the models summarised in Table 6.3.
6.3.2 Estimating net primary production

If it is assumed that recording period 7 is the time of lowest biomass throughout the year (above ground production of the species has been observed as early as February) then the species demonstrates an average net primary production (NPP) of 3,827 g m\(^{-2}\) yr\(^{-1}\). Of that mass, 50.7\% (1,939 g m\(^{-2}\)) was above ground material and 49.3\% (1,887 g m\(^{-2}\)) was below ground; 41.7\% and 7.6\% roots and rhizomes respectively. The alternative method of calculating NPP of above ground biomass (average stem mass x stem density) gives a value of 2,284 g m\(^{-2}\) yr\(^{-1}\), a difference of 17\% and implying that the former method may underestimate the production of above ground mass.

Thus, of the total mass generated at mid-summer growth, 89.2\% was lost through decay or dispersal. Rhizomes were the only organ not to decay entirely during winter, thus when considered independently, their NPP was 481.6 g m\(^{-2}\) yr\(^{-1}\).

6.4 Discussion

The results show that seasonal variation in the below ground biomass was largely attributable to the growth and decay of roots, which already exceeded the mass of rhizomes by recording period 1 but showed a sudden reduction between recording periods 3 and 4 before gradually decaying until there was no detectable root mass in recording period 7. Although the proportion of material contained in various layers of sediment is relatively consistent, the total biomass of roots changes considerably. However, by recording period 4 when decay commences, plants have generally developed a dense above ground biomass that will reduce flow velocity within stands, perhaps compensating for the dieback of roots and not increasing the susceptibility of surficial sediment to erosion. Prior to their decay (recording periods 2 and 3), it is probable that roots make a significant contribution to the stability of surficial sediment, with 76\% and 78\% of their dry mass (1.16 and 1.25 kg m\(^{-2}\) respectively) being present in the uppermost 10cm of sediment.

Changes in rhizome biomass were relatively invariant, although recording period 4 showed the largest and recording period 7 the smallest values. The modelled values in Figure 6.9 illustrate statistically significant (p<0.05) changes in the distribution of
below ground biomass between recording periods. In relation to the vertical profile of rhizome biomass below the river bed, biomass remained relatively stable in the 0-5 cm layer but increased significantly in the 5-10 cm layer during recording periods 2 to 6, providing a comparable biomass to that present in the 0-5 cm layer. Recording periods 2 and 5 also showed substantial rhizome biomass in the 10-15 cm layers. These results suggest that any contribution the rhizomes make to sediment stability, and its susceptibility to erosion, is likely to be relatively consistent throughout the year. The decline of mass between recording periods 6 and 7 may be attributable to a number of factors, including decay and use of nutritional reserves as a means of overwintering. However, the retention of a similar biomass throughout the year in the 0-5cm layer indicates the potential importance of rhizomes as a web of reinforcement of the surface of fine sediments accumulated during the growing season.

It has been observed by Haslam (2006) that *S. erectum* is a deep rooted species (with ‘*much of its root material contained below 15cm*’) and roots died back slowly in winter. Evidence from the present study in the River Blackwater suggest quite different growth traits, with roots spreading laterally, instead of downwards, and dying back suddenly between August and September (though still being detectable in November).

The results show *S. erectum* to be a species of high productivity. The core biomass values are comparable to those of *S. erectum* measured by Asaeda et al. (2009); although above ground biomass peaked at a higher value in that study (approximately 3,400 g m⁻², as compared to 1,939 g m⁻²) both exhibited sharp declines in mass from July onwards, with a negligible amount of above ground plant material remaining by November. Values of below ground biomass reported by Asaeda et al. (2009) showed a similar pattern, although they peaked later in the growing season and their mass rarely reached that found in the River Blackwater; peaking at approximately 1,500 g m⁻² compared to 2,349 g m⁻² in the present study. Both studies showed similar values of underground biomass during dormancy, being approximately 300-400 g m⁻² in the study by Asaeda et al. (2009) and 461 g m⁻² in the River Blackwater.

Production can be hugely variable in aquatic vegetation, being highly influenced by habitat and seasonal conditions. Furthermore, production by tall emergents is usually higher than any other type of vegetation (Haslam, 2006:161). However, when the above ground biomass of the standing crop is compared to other common emergent species, *S.*
*Sparganium erectum* in this study was shown to exceed other highly productive and common rigid emergent macrophytes, including *Phragmites australis*, *Phalaris arundaciea* and *Typha latifolia* (Mason and Bryant, 1975; Klopatek and Stearns, 1978), and *Spartina alterniflora* (Darby and Turner, 2008).

The NPP of rhizomes may seem relatively modest (481.6 g m\(^{-2}\) yr\(^{-1}\)) especially compared to the leaves and roots, but it constitutes a doubling in mass and therefore a doubling of reproductive biomass from which new material can grow. This may partially explain the ability of the species to rapidly develop dense patches and its widespread geographical distribution.

### 6.5 Synthesis

This study has shown that *Sparganium erectum* is a highly productive species that invests much of its growth in the development of below ground biomass and demonstrates a number of growth traits that enhance its capacity to act as an ecosystem engineer. Of particular importance is the tendency of below ground biomass to occupy the uppermost layers of sediment, which will have the effect of stabilising newly deposited material. Over time and where hydraulic conditions permit, these deposits develop into marginal bench landforms seen frequently on the River Blackwater (Figure 6.10).
Figure 6.10: Young *S. erectum* shoots trapping sediment and reinforcing a depositional bench on its inner margin and downstream end. Meanwhile, a greater stem density of *Typha latifolia* occurs in the upstream and central portions of the bench as it outcompetes *S. erectum* in areas of negligible low flow water depth.

The plant uses its rhizomes as a means of overwintering, and despite its relatively modest production of new rhizome biomass compared to leaves and roots, its ability to retain this mass under difficult conditions is crucial to its survival. The tendency of rhizomes to remain in the upper layers of bed sediment throughout winter suggest they have a reinforcing effect on material close to the surface of the river bed. Their mass throughout the season is relatively constant and whilst there appears to be some loss of material during winter, this may be offset by the accelerated growth during autumn, and transported fragments are a means of plant dispersal and colonisation of new areas (Cook, 1962). There was visual evidence of rhizomes being exposed to flow during winter (Figure 6.11) but they generally had sufficient strength to remain rooted in the substrate, with their presence perhaps also having the effect of reducing bed shear stresses.
Figure 6.11: Rhizomes trail in the winter flow but remain anchored within the bed.

The results from this study suggest that *S. erectum* engineers preferable growth conditions through its cycles of growth and senescence, which facilitate the accumulation, reinforcement and protection of fine sediment. This cycle is illustrated by Figure 6.12.
The rapid growth of roots throughout spring until summer has the effect of stabilising newly deposited sediment associated with the growth of above ground biomass. When these roots decay suddenly in mid-late summer, above ground mass remains, protecting newly deposited material from flow. When senescence commences, foliage takes longer to decay compared to root material, and forms a protective layer that continues to shield fine sediment. During this time, rhizomes exhibit rapid growth, increasing in mass and number but retaining a similar strength. Although undoubtedly less protected from erosion by comparison to summer months, rhizomes remain in the uppermost layers of fine material, reducing the likelihood of scour and ensuring the environment remains suitable for future growth of the plant.
Chapter 7

Conclusions

7.1 Introduction

This chapter summarises the key findings of chapters 4-6, and discusses their implications for physical ecosystem engineering, and more practical areas of river management. The key findings from the results chapters are given, followed by responses to the initial research questions posed in section 2.4, including a discussion of how the results contribute to understanding physical ecosystem engineering by linear emergent macrophytes (section 7.2). There is then a discussion of the relatively new and innovative methods that this research has utilised (7.3). Specific consideration is given to the contribution these have made to the study of aquatic plants and the assessment of ecosystem engineering. This is followed by a discussion of additional research questions that this study has stimulated, and opportunities for these to be incorporated into future research projects (7.4). Consideration of how results from this thesis could be used to inform future river management and restoration strategies is presented in section 7.5. Finally, section 7.6 provides a summary of the research conducted in this thesis in the context of established river ecosystem models. This section also presents a conceptual model of how *S. erectum* operates as an ecosystem engineer in lowland rivers.

7.2 Key findings

The original research questions posed in section 2.4 and the chapters in which they were addressed were as follows:

(1) To what extent does the seasonal growth and senescence of *S. erectum* affect the hydraulic performance and sediment dynamics of contrasting river reaches? Chapter 4.
(2) How do the growth traits and biomechanical properties of *S. erectum* vary spatially and temporally; both between reaches along the same river, and nationally between rivers? Chapter 5.
(3) How does *S. erectum* root and rhizome architecture vary through the annual cycle of
canopy growth and senescence? Chapter 6

(4) What are the underlying biomechanical and morphological properties that enable *S. erectum* to act as an ecosystem engineer? All results chapters.

Responses to these questions are given in sections 7.2.1-7.2.4.

7.2.1 *To what extent does the seasonal growth and senescence of S. erectum affect the hydraulic performance and sediment dynamics of contrasting river reaches?*

The research conducted within Chapter 4 showed that *S. erectum* has a very significant local effect on flow velocities and is strongly associated with fine sediment. Only minimal growth is required for the plant to cause a sharp reduction in flow velocities, and those reductions persist until late in the year, when collapsed senescent leaves constitute a hydraulic impediment and protect sediment accumulations (Asaeda et al., 2009). There is evidence that sediment accumulated by large stands of *S. erectum* is retained throughout winter, as the pattern of bed material calibre changes very little between seasons. The tendency for sediment accumulations to be relatively stable is important if the species is able to induce longer term changes in channel structure.

Whilst the magnitude of flow velocity reduction was consistent throughout all reaches, the spatial distribution of *S. erectum* within the channel, and thus its spatial impact on flow patterns and sediment trapping varies between reaches. In the River Blackwater, the spatial extent of the species diminished with distance downstream and it became increasingly confined to the channel margins. There was visual evidence of the species’ long term effects on channel morphology in all reaches, where it fringed marginal benches that were exposed above the low flow water level and graded into submerged shelves of fine sediment around and within *S. erectum* stands. However, the submerged shelves decreased in area and were increasingly confined to the bank toe with distance downstream.

A further hydraulic effect observed throughout all reaches was that the magnitude of cross-channel flow velocities varied with the magnitude of streamwise velocities. Therefore, areas of low *S. erectum* cover were associated with the strongest cross-channel velocities, providing the potential for fine sediment particles to be transported into areas of negligible flow velocity within the *S. erectum* stands (Gurnell et al. 2006a).
It has previously been shown experimentally that discreet planting of rigid emergent vegetation mimics can account for the hydraulic changes observed in the River Blackwater, inducing thalweg meandering that may result in geomorphological adjustment (Bennett et al. 2007), and such planting can be used to reinforce or develop existing geomorphological features and alter flow patterns (Rominger et al. 2010). When the results are considered at the reach scale, elements of these strategies can be observed, and further inferences can be made about the capacity and potential of *S. erectum* to act as a physical ecosystem engineer in several contexts:

- It has the effect of narrowing over-widened sections to dimensions more suited to the discharges passing through the channel (reach 1);

- It acts as a dynamic component in the creation of a number of interesting geomorphological features, including a sinuous thalweg and varied bed topography that result from patchy and unconstrained growth of the plant (reach 2);

- It continues to be associated with low flow velocities and fine sediment accumulations downstream in relatively higher energy reaches of the river (reach 3), contributing to bench development along the channel margins (all reaches of the River Blackwater).

Therefore, although the growth of the plant becomes much more spatially limited in downstream relative to upstream reaches, it retains a profound yet different influence on its surroundings. Despite being restricted to two marginal patch locations at reach 3, the upstream patch was shown to force the discharge through a narrower channel section, and had the effect of accelerating flow velocities towards the opposing bank. In a natural channel, this would be likely to trigger erosion and meander growth (Rominger et al. 2010), however such an outcome was not possible due to reinforcement of the opposite bank at reach 3.

All three of the study reaches supported stands of *S. erectum* that were actively retaining fine sediment, and so it is not possible to comment on any specific upper limit of channel size or energy at which the species is unable to retain fine sediment or, indeed, grow to form mature stands. However, the observations from the three study reaches do appear to indicate a low energy transition from river channel to wetland. At reach 1, the species is almost completely dominating flow hydraulics and could potentially result in
a total blockage of the channel and its transition from channel to wetland if artificial maintenance was curtailed. In contrast, in reaches 2 and 3 there is a better balance between the effects of the plant’s flow resistance and the forces imposed by river flows, suggesting that the removal of all management would result in the maintenance of a dynamic river channel.

7.2.2 How do the growth traits and biomechanical properties of S. erectum vary spatially and temporally; both between reaches along the same river, and nationally between rivers?

7.2.2.1 Spatial differences

Spatial differences in the biomechanical properties of the species, which were measured at peak growth and in rivers located between the Scottish borders and southern counties, showed little variation. Given that these experiments were conducted over a broad geographical area, across a range of stream environments with widely varying climate, water quality, channel size, gradient and discharge regime, it appears that the species’ strength is relatively uninfluenced by physical stressors and surroundings.

The implications of this are that the effects of the species upon its surroundings, which were measured in Chapter 4, are thought to be relatively consistent throughout the UK, and therefore, the more detailed temporal observations obtained on the River Blackwater are probably also transferable across the wide geographical area that was sampled at the time of maximum plant development.

7.2.2.2 Temporal changes

The detailed observations obtained from the River Blackwater illustrate that S. erectum shows a high degree of temporal variation in biomechanical strength, namely its ability to resist uprooting or damage to its stem, which broadly reflect seasonal changes in its size and structure. A significant discovery has been the remarkable resistance the plant has to uprooting, which exceeds all previously observed values for aquatic plant species (Brewer & Parker, 1990; Usherwood et al. 1997; Schutten et al. 2005) as well as many large terrestrial plants and young trees (Burylo et al. 2009). Measurements of the species’ strength as well as the density of plants found in typical stands help to explain why it is able to present such a high flow resistance and, as a result, reduce flow

184
velocities to almost zero, at least during baseflows. They also provide an indication of why the plant is able to survive bank full and higher events, and therefore why it is has such wide distribution throughout the UK and beyond.

A ongoing question throughout the research has been whether *S. erectum*’s annual cycle of growth and decay prevent it from causing long-term changes in channel structure. Evidence from two years of observations has shown that its rhizomes, which were the only plant material present throughout winter months, retain a consistent strength throughout all recording periods. Their ability to resist damage and to continue to reinforce fine sediment accumulations throughout the year appears to be the key to long term fine sediment retention by this species.

The research has also revealed the significant and complementary contributions made by roots and rhizomes to plant stability during, as well as beyond, the growing season, something that had in part been hypothesized previously but had not been directly observed (Speck & Spatz, 2003; Sand-Jensen, 2008).

A final important finding is that some relatively simple morphological measurements such as leaf length and stem diameter are highly significantly correlated with measures of the plant’s biomechanical strength. This implies that relatively simple non-destructive measurements, or even visual observations, provide the potential to assess the strength of a patch, its susceptibility to erosion and likelihood of expansion.

7.2.3 How does *S. erectum* root and rhizome architecture vary through the annual cycle of canopy growth and senescence?

Contrary to previous assumptions about the species, the long roots of *S. erectum* were shown to predominantly and consistently occupy relatively shallow layers of sediment, with typically 70-80% of the underground mass being contained within the uppermost 10cm of sediment. Given that roots were, on average, 45cm at peak length, and demonstrated extensive lateral branching, the species clearly develops a dense web of underground mass, largely in surficial layers, which must certainly have a reinforcing and protective effect on the loosely consolidated and saturated sediments that the species typically grows in. The fact that the majority of underground biomass is constantly found in surficial sediment suggests that *S. erectum* is able to vary its rooting depth (moving upwards as material aggrades), as previously suggested by Haslam
(2006), meaning that it is able to provide reinforcement to the fine material it rapidly accumulates.

The effects of the remarkable mass and growth habit of the roots could be somewhat negated by their rapid decay. However, the consistent biomass of rhizome material observed throughout all recording periods, and the equal tendency of rhizomes to grow and remain within the top 10cm of sediment, suggest they also reinforce these layers of sediment. The fact that areas of fine material were always associated with the growth of *S. erectum*, whilst coarse underlying bed material was exposed where the species was absent, suggests that rhizome biomass is sufficiently abundant and strong to protect these accumulations of fine sediment throughout winter.

7.2.4 *What are the underlying biomechanical and morphological properties that enable S. erectum to act as an ecosystem engineer?*

Evidence from chapters 4, 5 and 6 is used in this section to identify and interpret a set of biomechanical and morphological traits that make *Sparganium erectum* a rapid and effective ecosystem engineer relative to most other aquatic macrophyte species. These are listed and described below:

1. The long growth-decay cycle of foliage: The foliage of the species began to emerge as early as February along the River Blackwater, though juvenile shoots were not widespread until March and typically had not become emergent until later in the same month. Shoots began to show signs of senescence in September, but did not fully collapse until October or November. The collapsed mass of leaves often represented a significant hydraulic obstacle and was frequently used as a substrate upon which other macrophytes grew. Eventually, following collapse, the foliage decayed and detached, but some trailing dead leaf material was observed throughout all winter months. Therefore, a conservative estimate is that foliage represents some form of hydraulic impediment for over two thirds of the year, and in some channel areas, this occurs throughout the entire year, at least in southern England. The long growth-decay cycle of foliage therefore means that associated sediment accumulations experience reduced shear stresses for a large proportion of the year, reducing their likelihood of erosion.

2. The presence of a mechanical fuse: The presence of a mechanical fuse, whereby the plant sacrifices seasonal growth to preserve its reproductive mass, was clearly apparent.
Throughout both 2009 and 2010, there was a far greater propensity for shoots to break during early growth stages rather than for an entire plant to uproot. Thereafter, stem strength and uprooting resistance became so high that extreme, perhaps unrealistic, flow events would be required to uproot the entire plant (Pollen-Bankhead et al. in press). As shoots emerge early in the season, they increase drag on the plant as a whole (which may be less securely anchored due to a reduction in below ground biomass and some erosion of sediment through winter) but they remain relatively weak. During this early growth, uprooting resistance exceeds stem strength, thus during high velocity flow events the leaves detach and the plant remains viable for growth later in the year or the following year, and the erosion resistance of the sediment is not compromised by the uprooting of below ground material.

(3) Strong and expansive rhizomes: In addition to having a similar strength throughout the study, rhizomes exhibited interesting growth habits that enhance the success of the plant. The number of rhizomes per plant increased substantially throughout the growing season, reaching a maximum during autumn. Additionally, biomass measurements suggest that the plants invest heavily in new rhizome mass towards the end of the growing season, mass that is protected within the sediment from decay, damage or desiccation.

This growth trait may affect ecosystem engineering in two ways: (i) the additional rhizome mass reinforces sediment through the winter; (ii) the amount of viable vegetative fragments available for dispersal throughout winter is increased, therefore incidents of detachment and colonisation of new channel areas are also likely to increase. The increase in rhizome biomass, therefore, offers both sediment reinforcement and a dispersal strategy that increases the influence of the species downstream.

(4) Lateral spread of roots in surficial sediment layers: The distribution of roots through the sediment profile was previously unknown. Research conducted in Chapter 6 revealed that the roots of *S. erectum* spread laterally across the shallow layers of sediment, reinforcing and protecting them from erosion as well as maintaining the stability of the plant during the early stages of annual growth.
7.3 Methodological contributions and considerations

The methods used to conduct the research, particularly those described in Chapters 5 and 6, were derived and adapted from research conducted in very different environments. It is discussed below how this work can be used to inform the future development of suitable research methods that aim to demonstrate and quantify ecosystem engineering by macrophytes over relatively short timescales.

7.3.1 Biomechanical measurements

The biomechanical measurements allowed the broad spatiotemporal susceptibility of *S. erectum* and its associated landforms to be characterised in detail. This strategy was particularly useful because traditional geotechnical methods that measure erodibility often cannot be applied in saturated, submerged sediments. Biomechanical and morphological measurements also informed a number of ecological observations concerning how the plant overwinters, its level of productivity and the development of components of its biomass over its annual growth cycle.

However, to reliably predict the likelihood of plant removal, resistance to hydraulic forces needs to be related to the hydraulic regime of the river i.e. the magnitude of forces the plants are likely to experience. Although the plants were seen to grow in the same locations over three growth season, clear, quantifiable geomorphological change induced by the plant takes a longer time period. Therefore, the ability of plants and their sediments to withstand extreme flow events is crucial if they are to cause major changes in channel structure. Discussion of incorporating different methodological strategies to assess this is given in section 7.4.1.

Although the resistance of *S. erectum* to actual flow events has not been measured, data from this research has been used to model the potential for river flows to remove *S. erectum* from the River Blackwater. This indicated that the resistance of the species was several orders of magnitude larger than the drag forces acting upon it over a typical year’s discharge record (Pollen-Bankhead et al. in press).

7.3.2 Underground biomass

The adapted ingrowth core method represented a useful and efficient means of assessing the depth and abundance of *S. erectum’s* underground biomass. The method was
particularly revealing because it demonstrated seasonal changes in biomass at different depth increments, something which has yet to be recorded in aquatic plant species.

A limitation of the method was that the core itself often represented a hydraulic impediment, protruding slightly from the sediment surface before the growth of vegetation, and therefore potentially influencing initial rates of sediment accumulation. The total sediment depths of cores were measured, but not presented in this thesis for this reason. A useful addition to such a study would be detailed measurements of sediment depths within the same reach, because it would then be possible to ascertain more credibly whether S. erectum varies its rooting depth, moving upwards as sediment aggrades. Further evidence that demonstrates the plants tendency to occupy and consolidate newly deposited material would justify the hypothesis that the species is able to develop new landforms beyond being perennially submerged deposits to substantial and stable features that constitute changes in channel structure.

However, it is important to stress the difficulty of recording sediment depths associated with S. erectum stands. Measurements that involve direct contact with this very fine sediment tends to disturb and remobilise it. This is why only two measurements of sediment depth were taken during the reach scale studies presented in Chapter 4. Measurements of sediment depth need to be obtained in high resolution from small areas that can remain undisturbed (as reported by Asaeda et al. (2009), and measurements would be most accurate if taken as deviations below a fixed datum so that no penetration of the sediment is needed.

7.4 Opportunities for future research

7.4.1 Developing an integrated study of ecosystem engineering by aquatic macrophytes

The focus of this thesis has predominantly been to develop a new understanding of how macrophytes, particularly the rigid, linear emergent species S. erectum, are able to achieve ecosystem engineering; i.e. how do macrophytes as dynamic physical structures influence other physical processes. Therefore, the majority of measurements have been of S. erectum, its strength, structure and growth. These have, in turn, been interpreted in the context of ecosystem engineering. This approach of treating the plant as a physical structure, to which mechanical measurements can be applied, is somewhat different to
other assessments of physical ecosystem engineering, which measure abiotic parameters e.g. flow velocity, wave action, sediment strength and accumulation, but give relatively less attention to biota.

Whilst this study has given greater attention to measurements of vegetation, it is recommended that future studies that aim to demonstrate physical ecosystem engineering in aquatic environments should integrate geotechnical, hydraulic and biomechanical measurements. The processes of geomorphic change described in this thesis require interactions between water, sediment and vegetation, and to neglect the measurement of any of these will leave questions about its tendency to control or be controlled by the other parameters. For example, in this study, although the growth and strength of underground biomass has been measured and assumed to provide reinforcement of sediments, geotechnical measurements that assess the strength of vegetated/unvegetated sediments would be required to directly confirm this hypothesis.

However, whilst these measurements have not been made in this research, it has shown that other studies of ecosystem engineering by aquatic plants are limited by their lack of biomechanical measurements. Without the incorporation of biomechanical measurements, the threshold of a species’ capacity to resist physical stressors acting upon it will remain unknown. For example, if the shear strength of sediments associated with *S. erectum* were found to exceed the typical bed shear stresses in a given location, it might be assumed that, with a consistent sediment supply, landform generation would occur. However, without the incorporation of biomechanical measurements, the plant’s ability to resist the hydraulic stresses exerted upon it remain unknown, and thus whether any reinforcing effect the roots may be negated by the tendency of the plant to uproot. The omission of hydraulic and geotechnical measurements raise similar questions, which are summarised below:
7.4.2 Spatiotemporal considerations

1. Whilst this study has revealed the highly changeable structure and strength of *S. erectum* throughout its growth season (i.e. when above ground biomass is present), relatively little evidence has been gathered which relates to its strength and structure throughout winter. The ingrowth core analysis revealed that rhizomes were the only material to overwinter, and uprooting experiments showed expanding rhizome numbers and biomass in autumn months, but questions remain about the strength of this material through the winter, its reinforcement of sediments and its propensity for decay and dispersal. A useful expansion of the project that would help to address this would be to continue measuring underground biomass architecture in detail throughout winter, whilst uprooting experiments and strength measurements could be conducted on dormant rhizomes.

2. The limited timescale of this study renders it impossible to fully investigate the impact of *S. erectum* engineering on habitat creation and turnover. Although perhaps a difficult challenge, a GIS-based analysis of temporal sequences of air photos would allow quantification of the areal extent and turnover of stands and landforms, and any associated channel margin changes. Such an approach has previously been used to demonstrate channel adjustment (Gilvear, 2004) and worked well with other riparian vegetation types (Zanoni et al. 2008). When conducting such an analysis, it would be important to select relatively unmanaged sites, as artificial channels and banks could prevent the development of landforms and marginal adjustment.
3. The extent of river management in the UK and concerns relating to aquatic macrophytes as flood risk hazards, mean that unmanaged low energy systems with unconstrained macrophyte growth are relatively limited. A study that explicitly targets unmanaged sections would demonstrate the speed of ecosystem engineering and the diversity of habitats that can be generated by allowing rivers to function naturally. Such an investigation could usefully inform restoration projects that seek to restore natural function to low energy reaches.

4. An interesting expansion of the project would be to investigate how the length of the growth cycle affects ecosystem engineering. This study demonstrated that *S. erectum* plants were relatively smaller in Scotland compared to southern England, probably as a result of a shorter growing period at that latitude. Therefore, there remains some uncertainty about how the detailed results acquired from the River Blackwater are best transferred to colder environments where the growth season is shorter. For example, is the rate of ecosystem engineering by aquatic plants slower in Scandinavia because of its cooler climate? Conversely, in climates where productivity is higher, e.g. Mediterranean rivers, is habitat development and turnover more dynamic because vegetation is able to impact channel conditions for a great proportion of the year?

7.4.3 Exploring other species and habitats

1. Whilst *S. erectum* represented an ideal model species due to its morphology, habitat preference and widespread distribution, the ecosystem engineering potential of other species and morphotypes needs to be considered. It would also be pertinent to explore how interactions between species can facilitate ecosystem engineering; for example, watercress has been observed in both this study and in reaches dominated by submerged macrophytes (Hepell et al. 2009) to encroach into the channel later in the growing season, by using other macrophytes as a substrate for growth. Therefore, whilst it is thought that, by comparison to *S. erectum*, submerged species are relatively limited in their capacity to generate changes in channel structure, their interaction with branched emergent species may facilitate the continuing aggradation of fine sediment in marginal areas.
2. *S. erectum* is undoubtedly a robust species, but it is frequently outcompeted by other emergent species, such as *Typha latifolia* (Cook, 1962; Haslam, 2006; personal observations), which has larger above and below ground portions and often retains foliage throughout winter. Whilst *S. erectum* has a preference for growing in submerged areas, *T. latifolia* generally grows just above the baseflow water level, in highly saturated sediments that only become submerged in higher flows. By studying species that exist at the fluvial-riparian interface, it would be interesting to observe how these are able to affect channel structure, as they are anchored in comparatively secure, cohesive sediments, and receive less frequent exposure to hydraulic stress. It was sometimes observed, particularly at reach 3 of the River Blackwater, that *T. latifolia* rhizomes would be grow out of the bank face and into the open channel, suggesting they had the potential to expand their marginal location into the channel, trapping sediment and reducing flow velocities. *T. latifolia* may be representative of a vegetative group that occupies channel margin locations between emergent macrophytes and riparian plants, in terms of their function as ecosystem engineers. Indeed, these species probably represent a sequence of ecosystem engineers that can occupy and reinforce sediments along a hydrological gradient, supporting the development of the same landforms from below low flow water levels up to the level of the floodplain.

7.5 Implications for river management

*Sparganium erectum* has been shown to be a widespread, highly dynamic and active component in river habitats, and its potential uses and influences should therefore be considered in management and restoration schemes. Particular consideration should be given to the design of artificial channels, as it was frequently observed (perhaps most notably at reach 1 but also at several sites throughout the national study) that artificial channels and drainage ditches often become heavily colonised by *S. erectum*. A consistent characteristic of these reaches was that they appeared unnaturally wide, relative to the volume of water being conveyed, which was presumably a flood defence strategy. However, expansive growth of macrophytes, and the channelling effect of *S. erectum*, often causes raised water levels and potentially flooding. Emergent macrophytes are intolerant of very high flow velocities and water depths greater than
approximately 50cm. Therefore, a deep, narrow channel with a tiered margin would perhaps be a more suitable design, as it would minimise macrophyte growth and accommodate floods.

In areas of excessive macrophyte growth, manual removal of plants is sometimes performed to increase conveyance. Evidence from this research could be used to inform the timing of this effort. If attempted early in the season, the plant’s mechanical fuse may lead to a large proportion of the underground biomass remaining within the sediment, and therefore able to grow later in the season or the following year. However, if the plants are left to grow for too long, their strength is such that removal will not be achievable, or will be highly labour intensive. Evidence from this research suggests that removal should be conducted shortly after peak anchorage strength of the S. erectum (September) because stems remain relatively strong, but uprooting resistance diminishes substantially. Additionally, the vast majority of daughter plants will have emerged at this point, and their specific targeted removal may limit growth of the plant in future, given that it does not re-sprout the year after producing flowers. This advice may be especially pertinent in countries where the species is regarded as invasive, such as the USA (USDA, 2010).

Artificially designed channels of poor ecological integrity are often targets for restoration efforts, which frequently include changes to channel structure and planform. It is often an objective that previously straightened channels are given a more sinuous planform, which involves the cutting of a new channel (Gurnell et al. 2006b). In sections where increased channel sinuosity is desired, planting of discrete patches of linear emergent macrophytes, or the creation of marginal sediment shelves for colonisation, would feasibly accelerate this process. Evidence from this and other research (Bennett et al. 2007; Rominger et al. 2010) suggests that the presence of emergent species would induce erosion of the opposing bank, and gradually redirect the river into a more sinuous course. Conversely, to prevent increases in sinuosity, planners could remove emergent vegetation from the inner bank at bends to generate flow over a wider portion of the channel, thus reducing scour of the opposing bank. Alternatively, linear emergent macrophytes could be planted as an ‘erosional buffer’ to prevent channel migration by protecting susceptible or failing banks.
An interesting study that could provide evidence of ecosystem engineering by emergent aquatic plants (assuming they colonise), would be to simply remove restrictive bank structures and allow the river to develop naturally. Such a study would explore the potential of ‘self-recovery’ in river reaches, an area of research that requires active demonstration if it is to be seriously considered in restoration projects. Extensively managed rivers often retain the potential to recover from ecologically degraded circumstances because aquatic and riparian habitats are highly dynamic and subject to extreme natural disturbances (e.g., floods; Kauffman et al. 1995; Hansen & Budy, 2011), which can reset the biological and physical structure of river sections (Corenblit et al. 2007). It has been shown that ‘passive restoration’ (i.e., removal of the source of degradation, or structure that prevents recovery) is sufficient when seeking to restore natural function to rivers (Kauffman et al. 1995; Tullos et al. 2009; Hansen et al. 2011).

In British lowland rivers of the sorts described in this thesis, a consistently observed impediment to natural structure and function was the presence of artificial bank features; these create physically and biologically limited sections by preventing channel migration and the development of marginal habitats, which are areas of high biodiversity (Petts, 1990).

Thus, the condition of marginal areas is highly important when seeking to restore natural function to rivers, either passively or actively. Given that arguably the two most common objectives of river restoration are improvements in ecological integrity and visual appearance, the tendency of linear emergent species such as S. erectum to grow in river margins, trap seeds and sediment, create habitat for aquatic fauna and trigger channel migration, means that they should not be overlooked as a management/restoration tool. This research also suggests that linear emergents should also be considered when seeking to more fully understand the structural development of lowland rivers.

Finally, there appears a strong argument for simply allowing emergent macrophytes to colonise rivers naturally. There is evidence from this research that, in unmanaged river sections, vegetation will engineer a more natural, geomorphologically diverse channel, which is aesthetically pleasing and ecologically more sound. In areas where macrophytes are perceived to cause a significant flood risk, their removal or channel restructuring may be required. However, in many situations, it may be most appropriate
to allow aquatic macrophytes to engineer a natural channel, given that their vigorous growth often undermines the perceived benefits of a greater channel capacity. It is recommended that physical management of the floodplain rather than the channel should be undertaken, so that the floodplain can accommodate extreme flood volumes in certain areas to alleviate pressure in more sensitive / valuable areas such as downstream settlements. Whilst the protection of settlements will almost certainly be the chief consideration when deciding how rivers should be structured, mass-mismanagement of river systems, which compromise their physical and ecological integrity, is no longer an adequate solution, and the unrelenting effects that emergent macrophytes have on flow, sedimentation and channel structure, should be recognised and accounted for in long term management strategies.

7.6 Research summary

The following section provides a summary of the research conducted in this thesis. A conceptual model of how *S. erectum* operates as an ecosystem engineer in lowland rivers is presented, followed by consideration of how this process might be incorporated in to established river ecosystem models.

7.6.1 Physical ecosystem engineering by *S. erectum*: a conceptual overview

Figure 7.1 illustrates the links between *S. erectum* patch growth, sediment dynamics, channel evolution, and habitat creation. Overall the model aims to summarise how *S. erectum* growth and strength (Liffen et al. 2011; Pollen-Bankhead et al. 2011), sediment accumulation (Asaeda et al. 2010), flow alteration (Gurnell et al. 2006a; Naden et al. 2006), seed trapping (Gurnell et al 2007a,b), and channel evolution (Rominger et al. 2010), combine to produce an understanding of ecosystem engineering (Jones et al. 1997).
Figure 7.1: A conceptual overview of ecosystem engineering by *S. erectum*.

7.6.2 How might ecosystem engineers such as *S. erectum* be incorporated into general river ecosystem models?

Drawing analogies between the River Continuum Concept (RCC) (Vannote et al. 1980) and work presented in this thesis is challenging, as much of this work highlights the restorative capacity of *S. erectum*, and management interferes with the longitudinal connectivity associated with the perfect system described by the RCC. However, within the envelope of emergent macrophyte growth of a given river continuum, its fluvial geomorphic influence upon the biota described in the RCC is potentially significant. Specifically, at a smaller, perhaps reach scale, emergent species generate conditions suitable for a range of invertebrate feeding groups; they localise organic matter (O’Hare et al. 2011), such as leaf litter, which can be processed by shredders and grazers, and they also cause a channelling of flow, which generates preferred habitat for collectors that filter fine particulate organic matter from transport. Thus, emergent macrophytes might be considered as geomorphic agents within the RCC, which drive the transition from managed reaches to a more natural state.
The understanding of aquatic plants as ecosystem engineers lends itself more usefully to ecosystem models that interpret rivers as discrete sections. For example, the Nested Heirachy of Habitats conceived by Frissel et al. (1986), and usefully developed by Poole (2002), describes rivers as ‘a patchy discontinuum’ that can be considered at five scales ranging from ‘microhabitat’ to ‘network’. Within these scales, a patch of emergent vegetation would constitute a ‘habitat’, the second smallest of these distinctions. The understanding and use of these scales help demonstrate the profound influence of emergent vegetation as ecosystem engineers, as although their physical mass is limited to a small area, their geomorphic influence extends upwards to the reach and segment scales, when they trigger erosion/deposition and channel migration. Within this framework, the growth of emergent vegetation, and the subsequent geomorphological effects, is described as a ‘bottom-up trans-scale process’ (Poole, 2002). Furthermore, if a keystone species is one that has a disproportionate effect upon its surroundings relative to its biomass (Paine, 1969), then S. erectum must be considered as such; though examples of its capacity to trigger profound channel changes and improve biodiversity need further demonstration and are likely to be limited by management.

The River Ecosystem Synthesis presented by Thorp et al. (2006) is similar to the Nested Hierarchy of Habitats in that it considers rivers as patches. Within these hydrogeomorphic patches, which are determined by catchment geology and flow characteristics, there are ‘functional process zones’ (FPZ), which constitute ecological processes. The envelope of emergent aquatic vegetation growth, which is generally limited at its upper and lower ends by fine sediment availability and unit stream power (Gurnell et al. 2010), could therefore be regarded as a FPZ. Thorp et al. (2006) describe the difficulties associated with understanding lotic biocomplexity across spatiotemporal scales, and the need to assess the importance and distribution of FPZs. This work makes a contribution to the understanding of the distribution of emergent aquatic vegetation as a FPZ, by illustrating its diminishing downstream spatial extent and influence.

Finally, the Shifting Habitats Mosaic described by Stanford et al. (2005) is a useful conceptual tool as it acknowledges the disruptive influence of management upon river habitats and recognises discrete geomorphic features as being dynamic and transitional at longer timescales. The model describes habitats changing over time and being altered
by ‘drivers’; principally these are flooding and channel avulsion, but can also include smaller physical structures such as large woody debris and riparian vegetation. This list of drivers might now be expanded to include emergent aquatic vegetation, as there is a growing body of evidence that demonstrates their influence upon the structural development of rivers.


O'Hare JM, O'Hare MT, Gurnell AM, Dunbar M, Scarlett PD & Laize C (2010) Physical constraints on the distribution of macrophytes linked with flow and sediment dynamics in British rivers. River Research and application. DOI: 10.1002/rra.1379

O'Hare MT, Dunbar M, Scarlett AM, Dunbar M, Scarlett PD & Laize C (2011) Influence of an ecosystem engineer, the emergent macrophyte Sparganium erectum, on seed trapping in lowland rivers and consequences for landform colonisation. Freshwater Biology. doi: 10.1111/j.1365-2427.2011.02701.x


Pollen-Bankhead N, Thomas RE, Gurnell AM, Liffen T, Simon A & O’Hare MT (In press) Quantifying the potential for flow to remove the emergent aquatic macrophyte *Sparganium erectum* from the margins of low energy rivers. *Ecological Engineering*.


Appendix I

Transverse reach and cross-section images generated using a differential GPS
Appendix II. Reach averages of point observation measurements within each recording period.

<table>
<thead>
<tr>
<th>Time Period</th>
<th>Water depth (m)</th>
<th>Streamwise flow velocity (cm/s)</th>
<th>Riverbed material (index)</th>
<th>S. erectum abundance (index)</th>
<th>S. erectum cover (%)</th>
<th>Other macrophyte abundance (index)</th>
<th>Other macrophyte cover (%)</th>
<th>Proportion emergent / submerged (%)</th>
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<tbody>
<tr>
<td>Reach 1</td>
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<td>20.2</td>
<td>71/29</td>
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<td>1.55</td>
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Table 4.3 (ctd.).

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<th>Water depth (m)</th>
<th>Streamwise flow velocity (cm/s)</th>
<th>Riverbed material (index)</th>
<th><em>S. erectum</em> abundance (index)</th>
<th><em>S. erectum</em> cover (%)</th>
<th>Other macrophyte abundance (index)</th>
<th>Other macrophyte cover (%)</th>
<th>Proportion emergent/submerged (%)</th>
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