LARGE WOOD IN FLUVIAL SYSTEMS: QUANTITY, STRUCTURE AND LANDFORMS; SEDIMENT RETENTION; AND RIPARIAN SEED BANK DEVELOPMENT

by

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A thesis submitted in partial fulfillment of the requirements of the Degree of Doctor of Philosophy in Physical Geography at Queen Mary, University of London

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February 2014

AUTHOR'S DECLARATION

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ABSTRACT

This thesis investigates the characteristics and impacts of large wood accumulations within river reaches of different size and style. Four reaches were studied: (i) a wide, braided, headwater reach, characterised by dead wood (Tagliamento River, Italy); (ii) a lower gradient, wide, braided reach, characterised by resprouting wood (Tagliamento River, Italy); (iii) a low gradient, single thread reach with a natural supply of dead wood (Highland Water, UK), and (iv) a low gradient, single thread reach that has been restored by felling trees into the river (River Bure, UK). In each reach, quantities of wood, types of accumulation and their association with sediment retention, landform and propagule bank development were investigated, generating four main findings:

1. There were marked differences in the size and character of large wood accumulations among the four reaches.

2. Retention of fine sediment and organic matter by wood was observed on all four reaches, giving rise to notable spatial heterogeneity in surface sediments.

3. Sediment retention resulted in the development of different landforms among the four reaches. In the two multi-thread reaches, accretion of finer sediment around large wood led to island development. In the naturally-functioning single-thread reach, wood jams spanned the river channel, accumulating sediment and organic matter to produce unvegetated wood jams, and inducing other landforms, notably pools and bars. Such geomorphic heterogeneity was anticipated in the restored reach, but to date this has not significantly occurred.

4. Spatio-temporal variations were observed in propagule abundance and species richness within different wood-related mesohabitats. Higher abundance and species richness were associated with finer, more organic sediments retained within wood accumulations and related mesohabitats. In the restored reach such associations were not statistically significant, further indicating that responses to wood emplacement take longer than the 4 years since restoration.

Overall, this research has strengthened the evidence concerning the differing nature of wood accumulations in rivers of different size and style, and it has demonstrated the importance of large wood for retaining organic matter and plant propagules, resources essential for riparian vegetation succession and for the success of river restoration efforts.

ACKNOWLEDGEMENTS

First and foremost, I would like to express special thanks to my supervisors, Professor Angela Gurnell and Dr. Gemma Harvey, for their most appreciated time, assistance (both academically and in the field), unwavering support, faith in my abilities and for providing me with valuable research training. I will always be most grateful to you for your enthusiasm, experience, encouragement and guidance throughout. Thank you Angela ('supervisor extraordinaire'), for being there to calm nerves and to help me find the right direction. I could not have asked for a more dedicated principal supervisor.

There are many other people (past and present) within the School of Geography to whom I am extremely grateful. In particular, Dr. Christopher Cockel for his company and botanical expertise in times of joint despair during the germination trials, Dr. Alex Henshaw and Dr. Walter Bertoldi for their informative advice and field assistance, and Simon Dobinson for his useful advice on laboratory procedures and sample analyses. I must also acknowledge Dr. Rob Francis for providing a plant species list of the Tagliamento River that helped in identifying some sampled plant species. The assistance (laboratory and field) of Dr. Matilde Welber, Dr. Tom Liffen, Matthew Cashman and Alejandra Garcia Lugo were also much appreciated. Thanks also to those with whom I have been involved and all the postgrad students whom it has been my pleasure to meet and who have always been such good company. Without knowing all these people, PhD life may otherwise have been a much less enjoyable experience.

Finally, I would like to thank all my friends and my church, and I must convey my deep appreciation to my family for their continued tolerance of an aging student son, and especially my dear wife Ama for putting up with me being away most of the time over the past three years. I would like to thank them all for their encouragement, support and time to talk whenever it was needed.

This thesis is dedicated to my dad, Samuel Kwame Eshun, who always encouraged me to aim high and set ambitious goals but sadly passed away in 2008. I know that dad would be very proud of my achievement.

This research was funded by a Queen Mary, University of London studentship.

TABLE OF CONTENTS

CHAPTER 4: RESPROUTING WOOD AND ISLAND DEVELOPMENT ALONG AN ISLAND-BRAIDED RIVER: THE FLAGOGNA REACH, TAGLIAMENTORIVER, ITALY…………..… 53

CHAPTER 5: DEAD WOOD AND PROPAGULE BANK STRUCTURE ALONG A HILLSLOPE-CONFINED HEADWATER OF A LARGE MULTI-THREADED RIVER: THE FORNI DI SOTTO REACH, TAGLIAMENTO RIVER, ITALY……………… 115

CHAPTER 6: DEAD WOOD JAM AND PROPAGULE BANK STRUCTURE ALONG A SINGLE-THREAD LOWLAND RIVER: THE HIGHLAND WATER, UK…………………………………………. 172

CHAPTER 7: REINTRODUCED WOOD AND PROPAGULE BANK STRUCTURE ALONG A SINGLE-THREAD RESTORED LOWLAND RIVER: THE RIVER BURE, UK..……………………...… 233

LIST OF FIGURES

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 8

.

LIST OF TABLES

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 1

INTRODUCTION

1.1 CONTEXT

River catchments are complex and dynamic physical and ecological systems, which transfer water, sediments, organic material and nutrients from upland areas through river corridors to the river mouth. A variety of conceptual models have been proposed to explain the structure and function of fluvial systems of which one of the earliest and most influential is the River Continuum Concept (RCC). The RCC provides a simple, linear explanation of ecosystem structure and function for pristine, forested river systems whereby sources and processing of organic matter including large wood and the structure of macroinvertebrate communities vary in a systematic, predictable way with distance downstream (Vannote et al., 1980; Statzner and Higler, 1985). However, many factors can disturb this simple downstream continuum (termed the River Discontinuum by Poole, 2002), notably geological structures, slope processes, and tributary confluences can superimpose discrete process-form domains on different segments of the river channel network (Process Domains, Montgomery, 1999), and major anthropogenic interventions such as water impoundments can completely disrupt the river continuum (Serial Discontinuity Concept, Ward and Stanford, 1983). These processes all have fundamental impacts on the energy of the fluvial system, the downstream transfer of materials and thus the character of the river ecosystem.

Fluvial systems are not only characterised by movement of materials from headwaters to downstream reaches. Important hydrological, geomorphological, chemical and biotic exchanges and interactions also occur in two additional spatial dimensions: laterally, relating to interactions between the river channel and the riparian zone / floodplain; and vertically, relating to interactions between surface and subsurface zones. Furthermore, the fluxes and interactions across all three spatial dimensions vary through time, providing the four dimensions of lotic ecosystems recognised by Ward (1989). The proposal of the Flood Pulse Concept (Junk et al.,

1989) was particularly influential because it was the first explicit attempt to link the river's flow regime (annual flood pulse) with lateral exchanges of water, sediment, organic matter, nutrients and organisms between river and floodplain, and with the life cycles of many organisms. Subsequent research has illustrated that temporal variations in river flows, including flood and flow pulses (Tockner et al., 2000), not only determine lateral connectivity between river and floodplain but also moderate alluvial water tables and vertical connectivity between surface and groundwaters through the hyporheic zone, affecting the four-dimensional dynamics of habitats and the organisms they support (Hyporheic Corridor Concept, Stanford and Ward, 1988; Patch Dynamics, Townsend, 1989).

Four dimensional fluxes drive crucial ecosystem processes by creating alluvial corridors, river channels and associated landforms and habitats, and adjusting their forms as well as dispersing sediments, propagules, seeds, organic matter, nutrients and organisms. For example, Leopold and Maddock recognised the link between channel form and river discharge as early as 1953, and the four-dimensional character and dynamics of fluvial systems were explored across different time and space scales by Leopold et al. (1964), Gregory and Walling (1973) and Schumm (1977). Whilst research on the dynamics of fluvial systems across these spatio-temporal dimensions has progressed over the years, most studies have been carried out within the bounds of specific disciplines, namely river hydrology, fluvial geomorphology or aquatic and riparian ecology. Studies linking research observations across more than one of these disciplines are relatively rare and usually explore only one-way relationships. The fluxes and processes that drive the functioning of fluvial ecosystem cannot be well understood without considering the mutual relationships and feedbacks between biological organisms (most notably vegetation), flow dynamics and geomorphology (Corenblit et al., 2007). Therefore, in order to increase our understanding and fully identify the processes linked to fluvial ecosystem dynamics, conceptual multidisciplinary progress is clearly needed (Corenblit et al., 2007).

Although the influence of vegetation on channel form and aquatic ecosystems had been recognised earlier (Zimmerman et al., 1967; Meehan et al., 1977), however, the role of vegetation in driving hydrogeomorphic processes, the evolution of riparian plant communities and the physical characteristics of fluvial systems have only been recognised relatively recently (e.g. Hickin, 1984; Gurnell, 1995; Gurnell and Petts, 2002; Gurnell et al., 2005; Corenblit et al., 2007; Francis et al., 2008a; Corenblit et al., 2009). Vegetation, either dead (large wood), dormant (propagule bank) and living (standing vegetation), has a fundamental influence on the character of riparian ecosystems across a range of spatio-temporal scales, through its interactions with hydrogeomorphological processes to build landforms and habitats (Gurnell and Petts, 2006; Gurnell et al., 2008a). It might appear that large wood, standing vegetation and propagule bank have little in common, however, these vegetative types share an unusual combination of life-history traits that have important evolutionary consequences on riparian vegetation. The transport and redistribution of sediments, propagules and large wood along the river corridor and their longitudinal and lateral interactions with standing vegetation and particularly large wood structures, which represents an important roughness element within the river corridor, is one aspect of riparian ecosystem function that is little studied, quantified or understood, particularly in association with sedimentary and geomorphological processes and vegetation establishment (Andersson et al., 2000; Naiman et al., 2005).

Accordingly, the assessment of the ecological status of riparian zones, '*can be easily evaluated by taking into consideration some features of the structure and functioning of riverine systems* ………. which are ………. *characterised by the longitudinal continuity of vegetation, the lateral dimensions (width) of the channel containing natural riparian vegetation and the composition and structure of riparian vegetation communities. These attributes basically define the morphology of riparian areas*' (del Tánago and de Jalón, 2006). Therefore, for a better understanding of the functioning of fluvial ecosystems and for the effective restoration and systematic management of the riparian zone, a multidisciplinary understanding of the above elements and their interactions in many river settings (different river styles and sizes) is important. This provides the context for the research in this thesis, which focuses on interactions between large wood, vegetation (particularly propagule banks) and fluvial forms and processes within rivers of different type and environmental setting and their potential influence on river character.

1.2 THESIS STRUCTURE

Following this brief introductory chapter (Chapter 1), this thesis includes seven further chapters. Chapters 2 and 3 present, respectively, a review of relevant published literature leading to the research questions investigated in the thesis and the investigative design that underpins the research. These scene setting chapters are followed by four research chapters which seek to answer specific research questions in the context of four distinct field sites representing rivers of different size and style influenced by different types of wood and standing vegetation (Chapters 4 to 7). A final chapter summarises the research results, draws conclusions and makes suggestions for further research (Chapter 8).

Chapter 2 reviews the published literature that emphasises breadth rather than depth, and puts together knowledge on fluvial geomorphology and riparian ecology and their relations to large wood dynamics within fluvial systems. Detailed literature relevant to the four research sites is reviewed within the relevant research chapter (Chapters 4 to 7).

Chapter 3 provides a context for Chapters 4 to 7 by giving an overview of the factors that influenced the research design, introducing and justifying the selection of the four field sites, detailing the broad sampling design employed across these field sites, and the field and laboratory procedures that are common across the individual site investigations. Fuller details of the site-specific research design and any site-specific field and laboratory procedures are detailed within the four individual research chapters (Chapters 4 to 7).

Chapters 4 to 7 investigate the nature and quantity of large wood, large wood-associated landforms and habitats, and the associated viable propagule bank and sediments found at each of the four research sites. The four field sites represent river reaches of different size and style in different climatic settings, including downstream (Chapter 4) and headwater (Chapter 5) reaches of the braided Tagliamento River, North Italy, and two single-thread low-energy rivers in the UK, one with a natural wood load (Highland Water, Hampshire) and one with reintroduced wood (River Bure, Norfolk). Riparian tree species vary widely between the four sites and, while the downstream reach of the Tagliamento is characterised by large wood capable of resprouting, the other three study sites are characterised by predominantly dead wood.

Finally, Chapter 8 summarises and synthesises the main findings from the four research chapters in relation to the research questions presented in Chapter 2. From these findings, a simple conceptual model is presented to address the research aims and some suggestions for further research are proposed.

CHAPTER 2

THESIS CONTEXT AND AIMS: THE ROLE OF LARGE WOOD IN RIPARIAN ZONE STRUCTURE AND PROCESSES

2.1 INTRODUCTION

This thesis is concerned with interactions between large wood, fluvial geomorphology and plant ecology within the riparian zone of rivers of different size and style.

This chapter provides a context for the research presented in this thesis by reviewing current knowledge of fluvial geomorphology and riparian ecology and its relations to large wood dynamics. It explores the geomorphological and ecological importance of large wood within the river channel and riparian zone and identifies some knowledge gaps. Some definitions relating to the zonation of river corridors are presented in section 2.2. Section 2.3 describes why large wood is the central topic for this research and also provides a geographical context for large wood research. Section 2.4 reviews current and past research on large wood, highlighting its dynamics along river systems. Section 2.5 reviews the geomorphological and ecological significance of large wood within river corridors. Section 2.6 briefly reviews the role of large wood in river restoration. The review concludes (section 2.7) by listing some research questions that require investigation and setting out the broad proposed research design and methodologies of this doctoral research.

2.2 ZONATION OF THE RIVER CORRIDOR

In order to structure understanding of the presence and dynamics of large wood within fluvial systems, it is useful to define the main zones that exist within such systems. A continuum of geomorphic zones exists, which extend laterally from aquatic through riparian environments to the edges of the river corridor, and vary in character and extent from headwater to downstream river reaches. The role of large wood structures in modifying hydrological, geomorphological and ecological processes is likely to vary according to the lateral zone in which the wood is deposited and also the position along the river continuum.

The ‘river corridor’ encompasses the area across which the river interacts with the surrounding landscape. It extends from the low flow channel to the foot of surrounding hills or river terraces and so it widens from river source to mouth (Figure 2.1). Smith et al. (2008) refer to the river corridor as the ‘active river area’ that connects aquatic and riparian habitats and contains dynamic disturbance-driven processes that interact to form and maintain the active channel, riparian zones and their associated habitats. Figure 2.2 shows how Smith et al. (2008) conceptualised changes in the geomorphological structure and width of the river corridor from source to mouth, and illustrates the functional definition of a river corridor that is used in this thesis. Despite changes in width and form along the river continuum, river corridors contain three basic zones: the low flow channel, the active channel and the floodplain.

2.2.1 The Low Flow Channel and Active Channel

The ‘active channel’, as used in this thesis, contains the primary and any secondary channels which support river flows at low flow stages (i.e. the ‘low flow channel’) and the surrounding area of mainly bare sediment that is regularly disturbed by changing river flows (the active floodplain or bankfull) and so does not support established terrestrial vegetation (Riley, 1972; Castro and Jackson, 2001; Radecki-Pawlik, 2002). Active channels can be single- or multi-thread and their morphology is constantly shifting in response to the river’s flow and sediment dynamics. Within the active channel, landforms such as ponds, backwaters, islands, bends, meanders and sand and gravel bars change in position and morphology with cycles of inundation, erosion and deposition (Corenblit et al., 2007; Tracy-Smith et al., 2012). The margins of the active channel also shift in response to erosion and construction of the river’s floodplain and is indicated by deposits of sand or silt at the active scour mark, break in stream bank slope, perennial vegetation limit, rock discoloration, and root hair exposure (SUNY ESF, 2011). The dynamic floodplain edge defines the limit of the active channel and also usually corresponds to the lower limit of perennial terrestrial vegetation (Gurnell et al., 2000a).

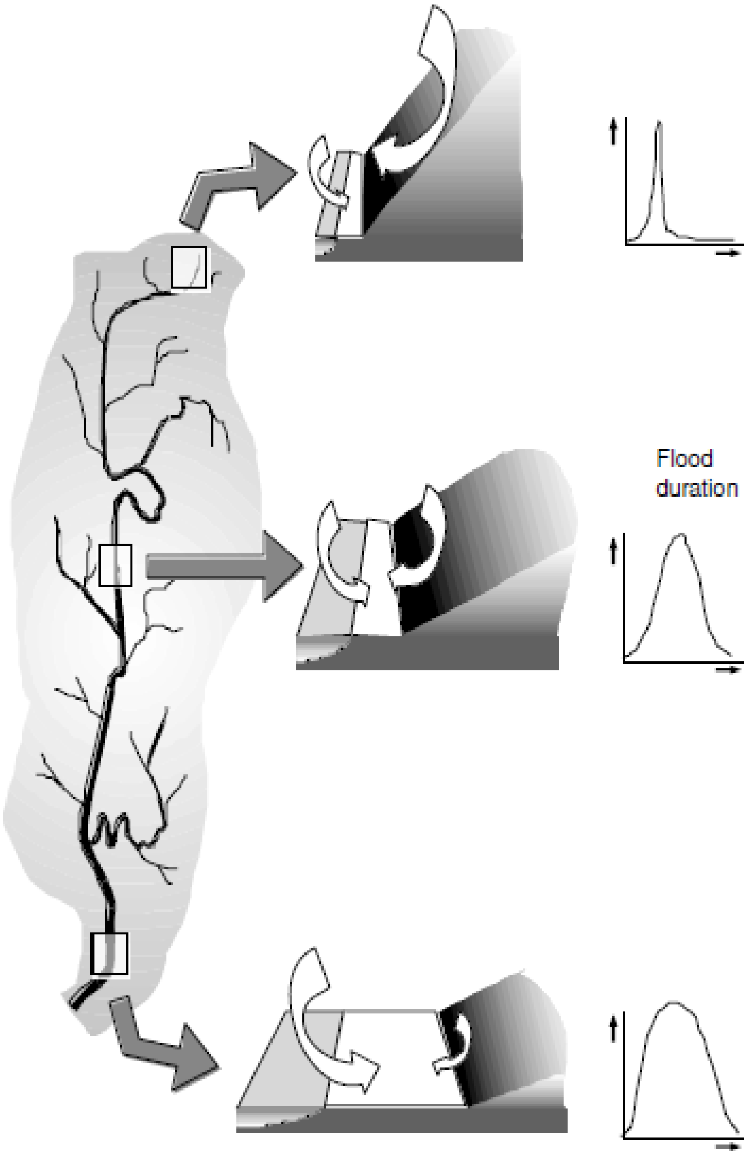


Figure 2.1. Variations in the extent and importance of cross-sectional fluxes of matter as a function of their location within a catchment. Arrows symbolize the transfer of matter between hillslopes and river channel through the riparian zone. Hillslopes bordering the river corridor are shown in dark grey, riparian zones are shown in white and the active river channel in light grey (Source: Adapted from Pinay et al., 2006).

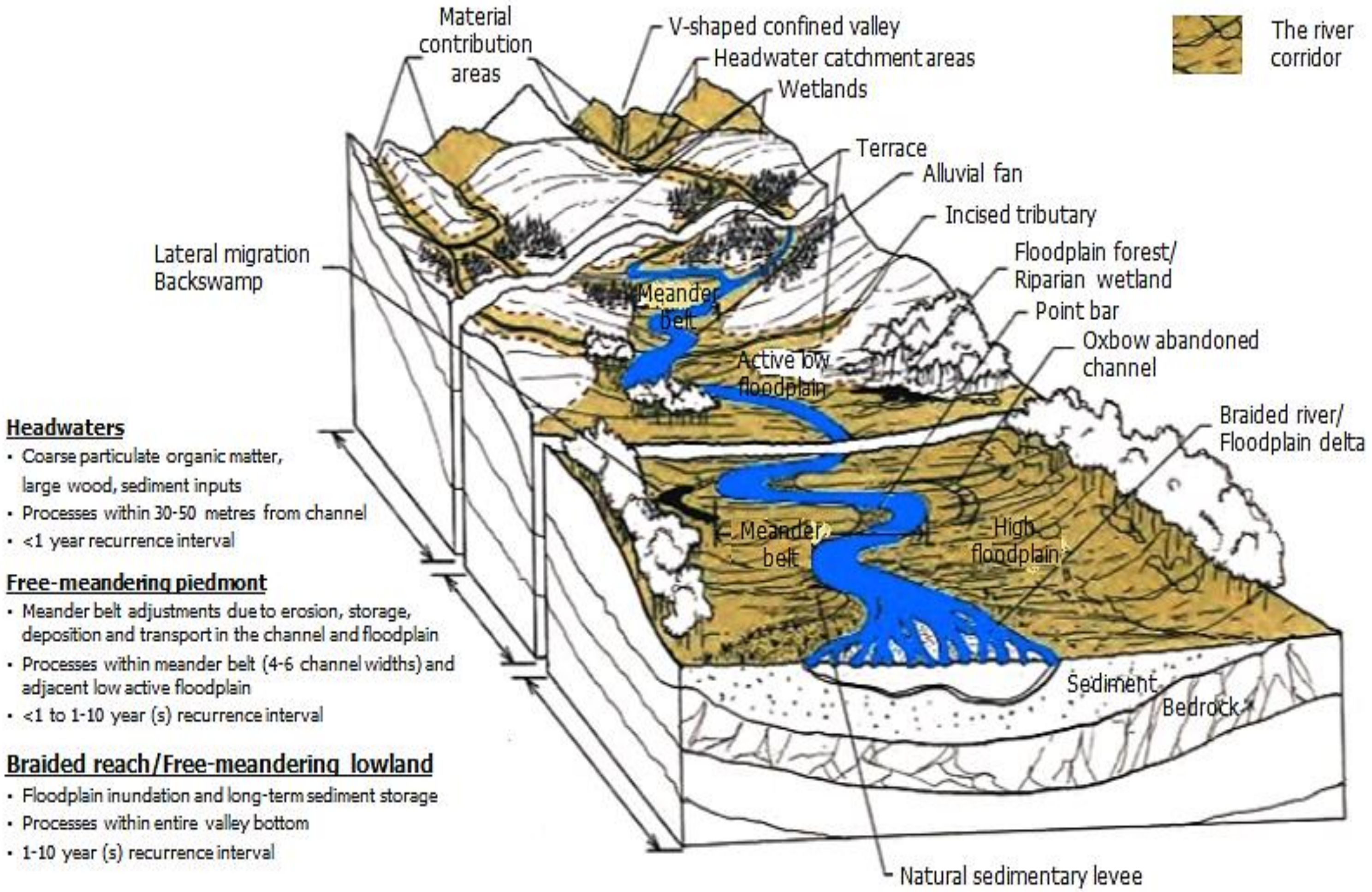


Figure 2.2. The fluvial features and dominant dynamic disturbance processes of the river corridor (Source: Smith et al., 2008).

2.2.2 The Floodplain and Riparian Zone

Rivers construct floodplains. The extent and form of the floodplain is strongly controlled by the magnitude and frequency of fluvial processes. This genetic relationship underpins the classification of floodplains proposed by Nanson and Croke (1992) and explains why floodplains support complex mosaics of landforms, including wetlands, abandoned channels, ridges and swales and levees, which in turn support a wide variety of vegetation units.

Riparian zones are more difficult to define than floodplains because they are ecotonal areas between aquatic (permanently inundated) and terrestrial (rarely inundated) zones of the river corridor. While Tansley (1911) suggested that riparian zones were confined to the bed and banks of the river channel (i.e. the immediate river channel margins), more recently the definition of riparian zone has been broadened (e.g. Figure 2.1). For example, Gregory et al. (1991) defined riparian zones rather loosely as ‘three-dimensional zones of direct interaction between terrestrial and aquatic ecosystems’, while Naiman et al. (2005) stated that ‘riparian zones are transitional semi-terrestrial areas regularly influenced by freshwater, normally extending from the edges of water bodies to the edges of upland communities’. An amalgamation of the definitions of Gregory et al. (1991) and Naiman et al. (2005) is adapted for use in this thesis.

Even with the more extensive recent definitions of the riparian zone, the limits of this zone vary greatly along the river continuum. Schumm (1977) categorised the river network into three zones: (i) uplands or headwaters encompassing first to third order streams and comprising the largest part of the drainage system where sediment production dominates and the riparian zone is topographically constrained and closely connected to hillslopes; (ii) middle or transfer zone covers fourth to sixth order streams, where sediment transfer dominates, floodplains of increasing width are present and the riparian zone is subject to two-way lateral transfers of water and sediment between hillslopes and river channel; and (iii) storage zone includes the lower floodplain reaches of the river network, where sediment deposition dominates and there is negligible connectivity with hillslopes across the wide floodplain-dominated riparian zone (Figure 2.1).

The characteristics of riparian zones also vary widely with the geomorphological style of a river and position along the river continuum. Their character is particularly variable in wide floodplain reaches where rivers of different styles (e.g. single- and multi-thread) and energy generate widely varying suites of landforms (Nanson and Croke, 1992; Knighton and Nanson, 1993; Nanson and Knighton, 1996; Beechie et al., 2006), which support a dynamic mosaic of visually distinct hydromorphological habitats both within the active channel and across the floodplain (i.e. mesohabitats). For example, the riparian zone of island braided rivers (Figure 2.3) are made up of islands, scour pools, sand bars, gravel bars, and patches of pioneer vegetation of varying age that continuously change in position and size as river flows, sediment transport, wood transport, and vegetation growth interact (Gurnell and Petts, 2002; Zanoni et al., 2008). This dynamism and complexity of form, sedimentary structure and hydrological condition influences the structure and heterogeneity of riparian zones (which are differentiated into biophysically distinct mesohabitats) and ensures that natural riparian zones are among the most biologically productive and diverse ecosystems on earth (Tockner and Stanford, 2002; Naiman et al., 2005), and large wood is thought to play a very important role in structuring the mesohabitats in these ecosystems in time and space (Viles et al., 2008).

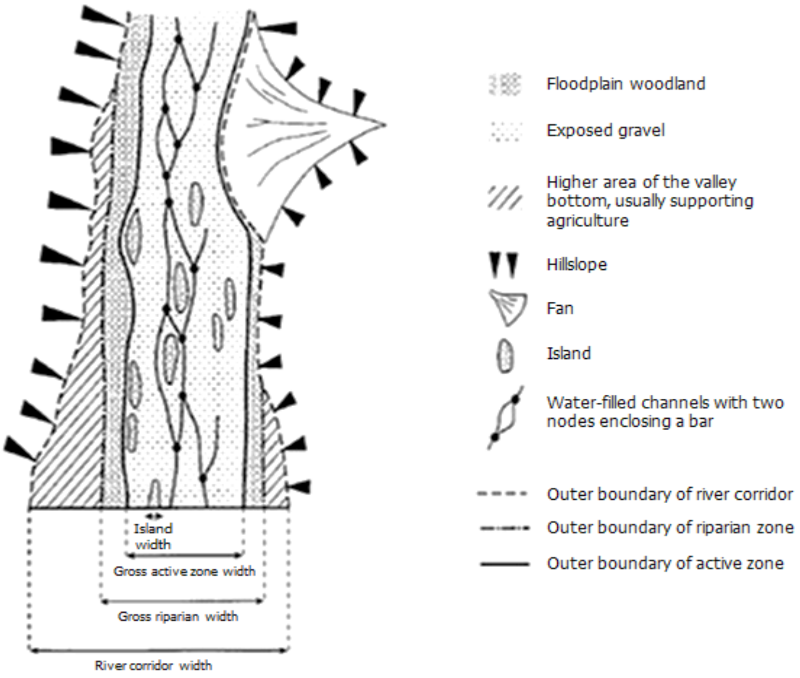


Figure 2.3. Schematic zonation of features within the river corridor of a braided river (Source: Gurnell et al., 2000a).

2.3 LARGE WOOD IN FLUVIAL SYSTEMS

Vegetation, both living and dead, represents a set of important roughness elements that interact longitudinally and laterally with water, sediments, propagules, organic matter and nutrients within fluvial systems. In-channel vegetation significantly influences the downstream hydraulic geometry of fluvial systems by increasing channel bed resistance, decreasing the depth-averaged stream velocity (Rominger et al., 2010) and deflecting flow laterally (Pietsch and Nanson, 2011). Vegetation has the potential to decrease channel erosion and sediment transfer by trapping particulate matter and stabilising it within root systems and other elements of underground biomass. Over time this can lead to the development and modification of floodplains, river banks and river channels (Gurnell et al., 2008b; Crosato and Saleh, 2010; Tanaka and Yagisawa, 2010; Sandercock and Hooke, 2011).

Besides, organic matter entrained and stored in fluvial system is an important product of living and dead vegetation that varies in size and encompasses dissolved, fine and coarse particulate forms. The largest proportion (> 90%) of the standing stock of organic matter in naturally-functioning river channels is large wood (Naiman et al., 2002), including its contribution to the coarse particulate component (CPOM, larger than 1 mm in size) of the organic load (Lamberti and Gregory, 2007). The sub-sections below define the term ‘large wood’ as used in this thesis and generally seek to provide a geographical context for large wood research over the past four decades.

2.3.1 What is Large Wood?

The central focus of this thesis is large wood in fluvial systems. The term ‘large wood’, also known as ‘large woody debris (LWD)’, refers to the largest fraction of the organic material transported by rivers (Lamberti and Gregory, 2007). Many different threshold dimensions have been proposed for large wood, with the aim of defining wood pieces that are large enough to provide a significant physical structure and habitat as well as a source of organic material within fluvial systems. For example, Ralph et al. (1994) indicated that minimum diameters of 5 to 20 cm and minimum lengths of 1 to 3 m have been used in large wood surveys. It has also been suggested that the structural importance of large wood and the threshold size at which it can perform specific geomorphological functions varies with the size of river investigated (Gurnell, 2003). However, several researchers have argued that it is important to have a standard size at which wood pieces are defined as ‘large’ in order to allow comparison between different study sites and time periods (Gregory et al., 2003; Young et al., 2006; Wohl et al., 2010). The most commonly applied threshold size that has been proposed for large wood is wood pieces exceeding 1 m in length and 10 cm in diameter (Hassan et al., 2005) and this is the definition that is adopted in the present research. Large wood aggregates into accumulations called ‘jams’, a term which is used throughout this thesis to represent the accumulations of wood and sediment that form around a nucleus of one or more wood pieces.

2.3.2 The Geographical Context of Large Wood Research

The dynamics of the riparian forest, from which large wood is recruited, varies longitudinally and laterally throughout a catchment as a function of physical processes, valley morphology, vegetative legacies, and life history strategies (Gregory et al., 1991; Naiman et al., 2005; del Tánago and de Jalón, 2006). Over the past four decades, researchers have studied the presence and role of large wood in fluvial systems in an increasing variety of environmental settings. Early work, summarised by Harmon et al. (1986), was undertaken mainly in the Pacific Northwest of the United States. However, a substantial body of research on large wood now exists for many regions of Europe, North America and Australasia (reviewed in Gurnell, 2013). Nevertheless, there remain large geographical areas where research on large wood is very limited, including most of Africa (but see Stewart and Davies, 1990; Pettit and Naiman, 2005; Pettit et al., 2006; Pettit and Naiman, 2006), South and Central America (but see Comiti et al., 2008; Iroumé et al., 2010) and Asia (but see Gomi et al., 2006).

As the geographical extent of studies has expanded, the focus has also extended from near-natural forested catchments in upland areas where wood management is negligible to more human-impacted catchments where riparian zones have been managed over hundreds of years for agriculture, transport, housing and industry (Sear et al., 2000). Intense human occupation has not only been accompanied by forest clearance but also by particularly heavy management of trees along river channel edges and the routine clearance of large wood from river channels to maintain channel capacity for flood conveyance and navigation (Diez et al., 2000;

Hering et al., 2000; Piégay et al., 2000; Gurnell and Petts, 2002; Opperman, 2005). These human activities have had a profound effect on the quantity of wood retained in river systems and, as a consequence, on the character of river channels and floodplains (e.g. Brooks et al., 2003; Zanoni et al., 2008).

2.4 THE DYNAMICS OF LARGE WOOD STORAGE

2.4.1 Large Wood Inventories

Most research on large wood has involved the construction of inventories at the reach-scale, which elucidate spatial and temporal variations in the quantity of large wood stored in river channels. These inventories often include assessment of the locations and structures within which large wood is stored and the nature of the woodland along the channel margins that forms the source of the large wood (e.g. Richmond and Fausch, 1995; Guby and Dobbertin, 1996; Abbe and Montgomery, 2003; Kraft and Warren, 2003; Gomi et al., 2005; Warren et al., 2007; Comiti et al., 2008; Wohl and Jaeger, 2009; Wohl et al., 2009; Angradi et al., 2009).

Most of these inventories have been undertaken on small and medium sized streams (e.g. Gregory and Davis, 1992; Comiti et al., 2008; Wohl and Jaeger, 2009), although there have been a few notable studies on large rivers (e.g. Sedell and Froggatt, 1984; McKenney et al., 1995; Gurnell et al., 2000b; Marcus et al., 2002; Abbe and Montgomery, 2003; Latterell et al., 2006; Lassettre et al., 2008). In this context, stream size is best scaled to the typical wood piece size present, where 'small channels have a narrower width than most of the wood pieces present (e.g., width smaller than the median wood-piece length), medium channels are narrower than the larger wood pieces (e.g., width less than the upper quartile wood-piece length), and large channels are wider than the length of most or all of the wood pieces' (Gurnell, 2013). In small and medium sized streams, many wood pieces span the channel and so can form key pieces supporting distinct wood accumulations. Therefore, many inventories have evaluated the size, spacing and mobility of wood accumulation structures as well as isolated large wood pieces (e.g. Gregory et al., 1985; Gurnell and Sweet, 1998; Abbe and Montgomery, 2003; Kaczka, 2003; Comiti et al., 2008; Gurnell, 2013) and their relationship with wood input quantities and mechanisms (Bilby, 1981; Smock et al., 1989; Lasettre et al., 2008). There have also been attempts to relate wood inventories to catchment, floodplain and river management practices (e.g. Hogan, 1986; Gregory et al., 1993; Piégay and Gurnell, 1997; Collier and Bowman, 2003; Nowakowski and Wohl, 2008). However, a comprehensive evaluation of large wood accumulation typologies especially on large rivers and the factors influencing input and depletion rates of large wood to rivers from riparian zones at contrasting points in the catchment remains lacking (Naiman et al., 2002).

2.4.2 Large Wood Budgets

The quantity and distribution of large wood within river reaches depends on the balance of wood supplied to and removed from the reach over specific periods of time. Wood movements along the channel and between hillslopes, floodplains and the active channel can be very high during large discharge events, particularly when there is extensive bank erosion, and also during other types of large disturbances such as wind storms, snow storms, fires and landslides. Once wood is stored within a river reach, its removal occurs as a result of mechanical disintegration and decomposition as well as physical transfer downstream by fluvial processes. In total, these processes drive the wood budget of river reaches (Keller and Swanson, 1979). As knowledge of the dynamics of wood in fluvial systems has developed through field observations (e.g. Lienkaemper and Swanson, 1987; Crowl and Covich, 1990; Ehrman and Lamberti, 1992; Elosegi et al., 1999; Dahlstrom et al., 2005; Daniels, 2006; Millington and Sear, 2007; Warren and Kraft, 2008; Wohl and Goode, 2008) and, to a lesser extent, flume experiments (e.g. Braudrick et al., 1997; Braudrick and Grant, 2001), the concept of the wood budget has been developed and quantified in increasing detail (e.g. Benda and Sias, 2003; Benda et al., 2003). For example, in the last two decades, modelling of wood recruitment has evolved from relatively simple representations of marginal tree fall (e.g. van Sickle and Gregory, 1990) to more sophisticated simulations incorporating the dynamics of the riparian forest, such as the mix and distribution of tree species and the successional stages of riparian tree stands (e.g. Welty et al., 2002; Meleason et al., 2003, 2007).

However, knowledge remains limited about several aspects of wood budgets, notably the relative importance of upstream inputs in comparison with local supply, the relative importance of wood depletion through decomposition, particularly in larger rivers (Hassan et al., 2005), and the impact of transitional wood storage in the riparian zone.

2.5 THE BIO-GEOMORPHOLOGICAL ROLE OF LARGE WOOD

Large wood can significantly influence flow hydraulics, the retention and sorting of finer organic and inorganic fluvial sediments and thus the morphological characteristics of river channels (Keller and Swanson, 1979; Kochel et al., 1987; Gurnell et al., 1995; Abbe and Montgomery, 2003). Large wood structures also perform important ecological functions as they are habitats in their own right; induce the development of other habitats, such as pools, vegetated and unvegetated bars, and side channels; provide shelter for organisms from predators as well as hydraulic refugia, and are a source of food. As a result, large wood structures support life history stages of many organisms (e.g. Narver, 1971; Shearer, 1972; Anderson et al., 1984; Cranston and McKie, 2006; Francis et al., 2008a). The sub-sections below broadly review literature on the influence of large wood on fluvial geomorphology and ecology.

2.5.1 Large Wood and Fluvial Geomorphology

At an early stage, researchers noted the important effect of in-channel wood on sediment erosion, entrapment and storage (e.g. Megahan, 1982), the overall enhancement of sediment retention through the presence of large wood within river reaches (e.g. Bilby, 1984; Heede, 1985; Adenlof and Wohl, 1994), and the development of particular wood-related landforms or habitats such as pools, bars, riffles and benches (e.g. Bisson et al., 1982; Nakamura and Swanson, 1993). For example, several researchers have shown a strong impact of wood jams on pool spacing and the formation of pools, bars, riffles and benches (e.g. Gurnell and Sweet, 1998; Montgomery et al., 2003a), while others have observed the growth in wood-induced depositional sites (composed of wood and sediment) which are colonized by pioneer vegetation that contributes to their stabilization and further material accumulation (Fetherston et al., 1995; Abbe and Montgomery, 1996; Gurnell et al., 2005; Francis et al., 2008a, 2008b). Thus, a more general appreciation of the relationship between wood and river channel geomorphology has evolved gradually

(Montgomery et al., 2003b), which links bank reinforcement, bar stabilisation, meander cut-offs, side-channel and island development at least in part to the influence of wood. Geomorphological research has also attributed the presence of suites of minor landforms to their immediate proximity to wood (e.g. Gurnell et al., 2001, 2002; Abbe and Montgomery, 2003; Angradi et al., 2004; Gurnell et al., 2005, Andreoli et al., 2007; Acker et al., 2008).

Much of this research has been concerned with in-channel wood along small, single-thread rivers. Nevertheless, the last two decades have seen an increasing research interest in both large and multi-thread rivers and in the differences in the quantity and types of retention of wood within rivers of different style. Piégay and Gurnell (1997) made an early comparison of rivers of different size and style. This underpinned the review by Gurnell et al. (2002) in which contrasts in the type of wood storage between large braided and meandering styles was proposed (Figure 2.4). However, Francis et al. (2008a) further suggested that there is the need to determine the kinds of mesohabitats associated with large wood structures, especially in large rivers, and how these mesohabitats and their characteristics vary at differing spatial and temporal scales and with differing wood management regimes.

In association with geomorphological assessments, several researchers have attempted to quantify the amounts of wood stored in the different zones of large rivers of contrasting style and in association with particular landforms. For example, Piégay (1993) found that the mass of wood deposited along the large, meandering River Ain, France, varied from 0.001 t ha^{-1} to over 200 t ha^{-1}, but that the largest quantities were deposited at the margin between the floodplain and the meandering channel, where the large wood formed a narrow line on the bank top, or sometimes braced against the bank face. Table 2.1 shows estimates of wood stored in some large jams along the mainly single-thread Ariège River, France (Tabacchi and Planty-Tabacchi, 2003). Here occasional islands form hotspots of wood accumulation. On the island braided Tagliamento River, Italy, Gurnell et al. (2000b), found that pioneer islands on gravel bars retained the largest amount of wood per unit area of the active channel (Table 2.2) and that the type of wood storage changed downstream, with dead wood and individual logs dominating in headwater reaches, living wood in the form of single uprooted trees and pioneer islands dominating in the middle reaches, and living wood in the form of wood jams and pioneer islands in the lower reaches (Figure 2.5). On the same river, van der Nat et al. (2003) found that the amount of wood stored in bar braided stretches was much smaller than in island braided stretches of the middle reaches of the river.

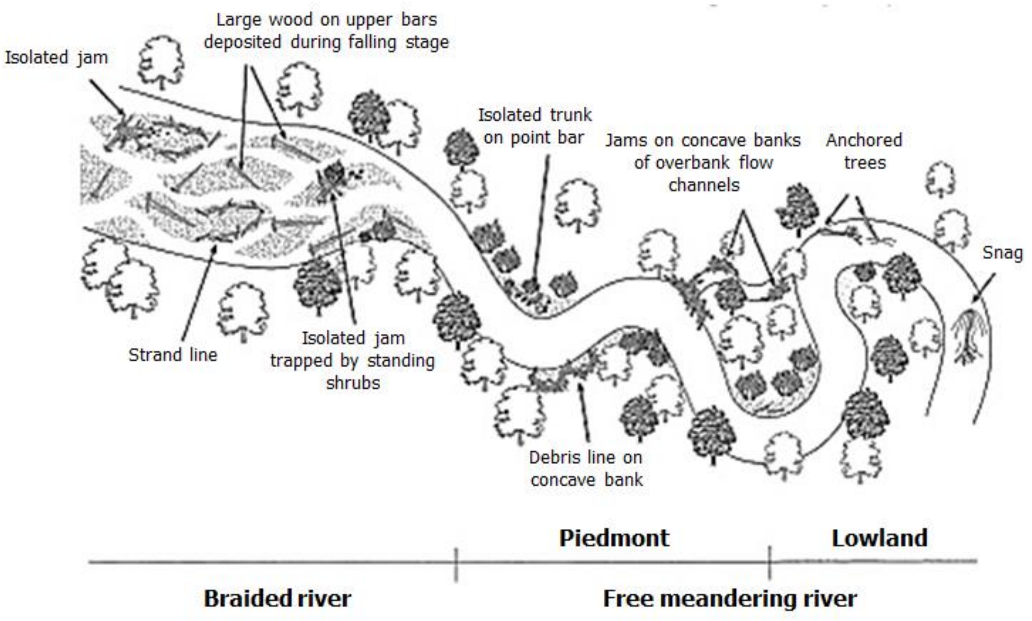


Figure 2.4. Typology of large wood accumulations observed in large rivers from upland braided systems to meandering lowland ones (Source: Gurnell et al., 2002).

Table 2.1. Characteristics of large wood jams located on the Ariège River (Source: Tabacchi and Planty-Tabacchi, 2003).

Site	**A**	**B**	**C**	**D**
Location	Riverside	Inner Island	Bank	Riparian Forest
Distance from channel (m)	10	75	150	350
Jam area (ha)	0.01	0.8	0.25	0.05
Average jam thickness (m)	1.5	3.5	1.5	1.8
Pieces of large wood	230	2856	556	317

The jams were located: along the main channel (A), in the inner part of an island (B), on the bank (C) and within the riparian forest (D). Survey was conducted along a 300 m-long transect of this large lowland river in south-western France.

Table 2.2. Quantities of wood stored (t ha^{-1}) on open gravel and low flow channels, in pioneer islands and associated with established islands in 8 reaches distributed along the River Tagliamento, Italy from headwaters to lower reaches (Source: Gurnell et al., 2000b).

Site	Gravel and Water	Pioneer Islands	Established Islands
A	1	-	24
B	21	-	57
C	6	444	25
D	4	787	-
E	7	911	148
F	7	293	44
G	7	334	186
H	1	1664	-

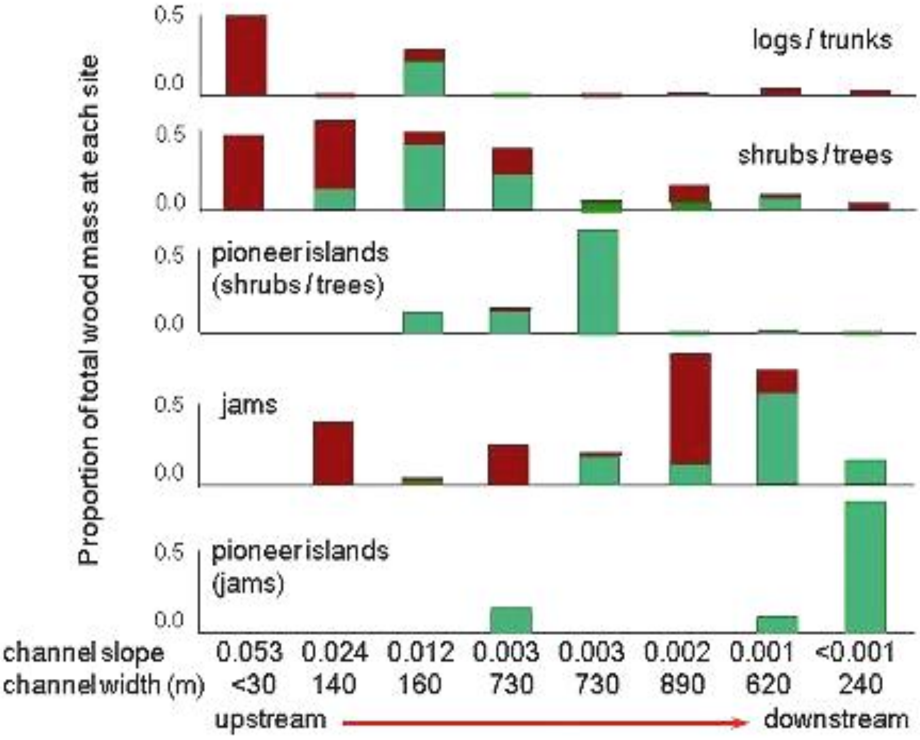


Figure 2.5. A downstream change from dead (red) to living wood (green) associated with a change in tree species as well as adjustments in wood piece and accumulation types along the Tagliamento River, Italy (after Gurnell et al., 2000b, 2013).

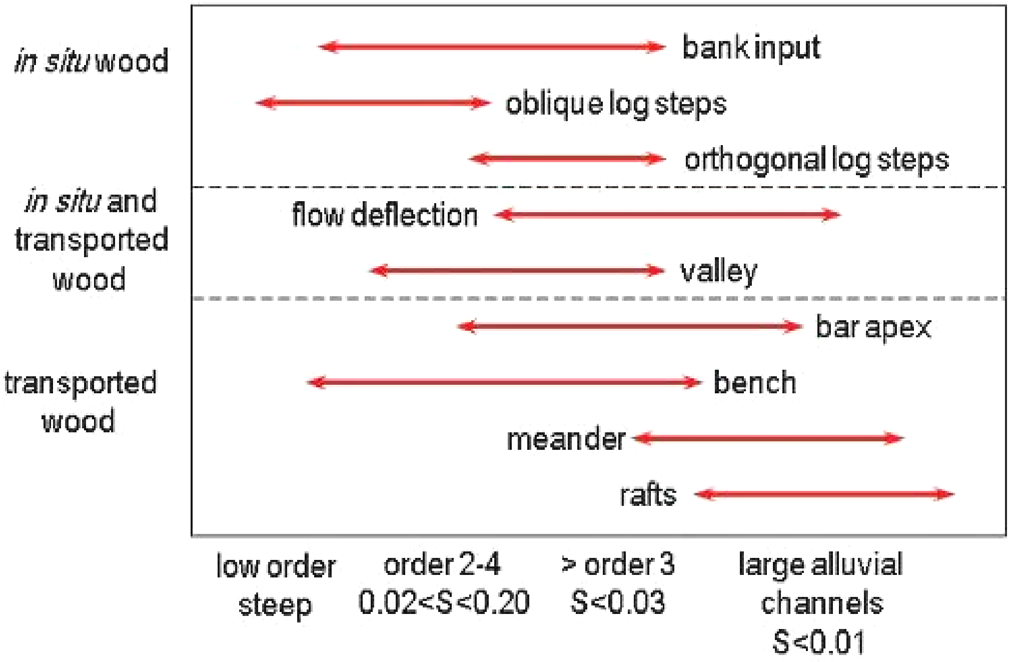


Figure 2.6. A downstream shift from predominantly channel-spanning to predominantly partial jam types along the Queets River, USA. Here the large wood is mainly dead and the downstream changes involve a shift from relatively static obstructions composed of one or a small number of large wood pieces (e.g. log steps) to very large jams of wood pieces that have been transported from upstream sites (e.g. wood rafts) (after Abbe and Montgomery, 2003).

The most comprehensive and integrated assessment of types of wood storage along a large river was by Abbe and Montgomery (2003). This was based on observations along the Queets River, USA (Figure 2.6, Table 2.3). Here the large jams have very significant impacts on fluvial geomorphology by protecting river banks from erosion and forming ‘hard spots’ in the floodplain that support the most mature forested patches (Montgomery and Abbe, 2006). In addition, recent research has been undertaken in the disturbed river corridor of the Sabie River, South Africa following an extremely large flood that stripped soil and vegetation cover exposing the bedrock underlying the river corridor (Pettit et al., 2006). In this highly disturbed large river corridor, large wood deposited in isolated mounds and braced against bedrock outcrops and standing trees, was the focus for fine sediment retention, seedling germination, the resprouting of deposited trees and thus the general recovery of the floodplain morphology, soils and vegetation cover.

In summary, research has explored the quantities and locations of wood stored in river corridors and the importance of large wood in influencing landform development at a range of space and time scales. However, the majority of the work has been concerned with in-channel wood and also with relatively small, single-thread rivers. Despite major advances in flume research and modelling, the capacity to predict geomorphological feedbacks in wooded channels remains limited because of the extreme difficulty of linking complex vegetation dynamics and non-homogenous hydrogeomorphic processes, especially in large rivers. Hence, there remains a large research gap concerning wood and the comprehensive characterisation and / or development of landforms in the riparian zone across all styles and sizes of river corridor, but information on large, multi-thread rivers is particularly sparse.

2.5.2 Large Wood and Ecology

Because wood structures induce hydraulic complexity in river channels, moderate the movement of organic and mineral sediment, and induce sediment sorting and landform development, they have an important impact on the presence and diversity of physical habitats available to aquatic organisms, and the hydrochemical properties of those habitats, particularly in relation to carbon, nitrogen and phosphorus. Indeed, the river continuum concept (Vannote et al., 1980) explicitly linked these factors and hypothesised clear shifts in the structure of macroinvertebrate communities downstream as wood and organic matter recruitment and processing changed.

With respect to hydrochemistry, Collier and Bowman (2003) observed long term impacts of wood on dissolved oxygen concentrations and short-term effects on water temperature, dissolved organic carbon, nitrite-nitrogen and dissolved reactive phosphorus concentrations, in streams affected by different levels of wood management. Large wood, therefore, creates an enabling environment for the colonisation of aquatic biota (Anderson and Sedell, 1979; Gende et al., 2002; Bilby, 2003).

Table 2.3. Typology of large wood accumulations observed in small-, middle- and large-sized rivers.

Channel Spanning Accumulations Types			
Accumulation Categories and Types	**Description**	**Function**	
In-situ (autochthonous)	Key wood piece has not moved down channel.		**Increasing river size with decreasing relative wood piece size**
High dam[2] Underflow dams[4]	Large wood pieces, commonly entire toppled trees, that span the channel from bank top to bank top	Only have a hydraulic effect during bankfull flows but commonly accompanies or directly support partial dams within the channel.	
Bank input[1]	Some or all of key wood pieces tumbled into the channel from their growth locations as a result of bank erosion, wind throw or mass movement.	Form a partial obstruction to flow and have local effects on channel morphology. Forms small pools and bars immediately adjacent the debris.	
Log steps (Oblique / Orthogonal)[1^] Active dam[2*] Dam jam[4*]	Key wood piece completely spanned the channel forming step (scour pools) in channel bed	Form a step in the water surface profile even at low flows.	
Complete dam[2*]		Key wood piece span the channel but are sufficiently leaky to have a negligible effect on the low flow water surface profile	
Partial Dams[3,4]			
Accumulation Categories and Types	**Description**	**Functions**	
Combination	In-situ key wood pieces with additional racked wood debris		
Valley jam[1]	Jam width exceeds channel width and influences valley bottom. Often consist of fallen trees or key wood piece recruited due to massive debris deposits associated with landslides or winds throw.	Obstruct a large portion of the bankfull cross-sectional area, deflecting a substantial portion of flow that results in local bed scour, sediment storage, bank erosion, channel widening, as well as recruitment of additional key wood pieces that can bury much of the jam-initiating WD.	
Flow deflection[1] Deflector jam[4]	Key wood pieces may be rotated. Jam deflects channel course.	Wood pieces partially blocks the channel, inducing erosion of the opposite bank and channel planform adjustment and / or development	

Table 2.3. (Continued)

Accumulation Categories and Types	Description	Function	
Transport (allochthonous)	Key wood pieces moved some distance downstream.		**Increasing river size with decreasing relative wood piece size**
Debris flow / flood[1]	Chaotic wood debris accumulation resulting from the episodic deposition of wood debris entrained in debris flows initiated by shallow landslides. Key wood pieces uncommon or absent.	Dispersed by floodwaters over the floodplain and supply adjacent forests with debris where they are deposited against standing trees.	
Bench[1]	Key wood pieces along channel edge forming bench-like surface.	Wood pieces induces the construction and protection of in-channel benches	
Bar apex[1] Bar head jam[4]	One or more distinct key wood pieces downstream of jam.	Wood pieces snags on the head of bars to induce a sequence of scour, aggradation and sediment sorting. Often associated with development of bar and island.	
Meander[1] Flow parallel jam[4]	Several key wood pieces buttressing large accumulation of racked wood debris upstream. Typically found along outside of meanders	Snags on the downstream bank top and face of meanders during overbank flows. Protects the banks from erosion and forms pools along the upstream and lateral margins of jams.	
Raft[1]	Large stable accumulation of wood debris spanning the channel	Capable of plugging even large channels and causing significant backwater.	
Unstable[1]	Unstable accumulations composed of racked wood debris upon bar tops, channel margins or pre-existing banks.	Limited fluvial geomorphological impact but can act as future wood sources for the fluvial system.	

Names of wood accumulations according to 1. Abbe and Montgomery (2003), 2. Gregory et al. (1993), 3. Gregory et al. (1985), 4. Wallerstein and Thorne (2004)
^ steep high energy (headwater) fluvial systems * lower energy and lower gradient fluvial systems

In relation to aquatic biota, numerous studies have explored the relevance of in-stream wood for microorganisms, macroinvertebrates, fish, amphibians and beavers (e.g. Anderson et al., 1978; Anderson, 1982; Fisher and Petrini, 1983; Fisher and Anson, 1983; Angermeier and Karr, 1984; Bilby, 1984; Benke et al., 1985; Beschta and Platts, 1986; Dolloff, 1986; Albrecht, 1991; Armantrout, 1991; Golladay and Sinsabaugh, 1991; Cederholm et al., 1997; Goh and Hyde, 1998; Hyde, 1999; Kane et al., 2002; Lockaby et al., 2002; Johnson et al., 2003; Steel et al., 2003; Fryar et al., 2004; Entrekin et al., 2009; Wyzga et al., 2009), although to date, most of this ecological research has been concerned with fish and macroinvertebrates and there has been little work on plant ecological implications of in-stream wood.

Over the last ten years, wood research has widened to incorporate ‘living’ as well as dead wood dynamics. An increasing body of research has explored the link between wood dynamics and geomorphological processes (erosion, sediment depositional processes and storage) associated with the development of fluvial features such as meander cut-offs, islands, pools, and bars (Abbe and Montgomery, 1996; Gurnell et al., 2002; Abbe and Montgomery, 2003; Angradi et al., 2004; Andreoli et al., 2007; Acker et al., 2008). These depositional areas such as mid-channel bars, as observed in some of the earlier studies on single-thread rivers linking large wood and geomorphological processes, have been shown to be colonised by pioneer vegetation that contributes to bar stabilization and additional material accumulation (Fetherston et al., 1995; Abbe and Montgomery, 1996). These observations and studies have allowed research on the physical impacts of wood to increasingly interface with aspects of plant ecology.

The importance of living wood, particularly, for river geomorphology and ecology has been mainly noted in Europe (e.g. Gurnell et al., 2000a, 2000b, 2001, 2005; Corenblit et al., 2007, 2009) where the ability of pioneer tree species to reproduce vegetatively is very high, and the importance of living wood may well be enhanced by human pressures on terrestrial tree species. Kollmann et al. (1999) demonstrated strong links between both living and dead wood structures and plant cover and diversity on the Tagliamento River, whilst Francis et al. (2008a) documented the diversity and cover of colonising vegetation associated with specific mesohabitats around pioneer islands during their first few years of development on the same river.

Gurnell et al. (2001) observed seedlings growing in the lee of dead wood jams and suggested this process as a strategy for vegetation establishment that could lead to the development of islands on the Tagliamento River. Nakamura et al. (2012) identified a high number of indicator species and an increase in species diversity in and around jams composed of dead wood deposited on gravel bars along a large bar-braided river. These observations of the standing vegetation can be coupled with seed bank investigations undertaken within wood piles along the Sabie River, South Africa by Petit and Naiman (2006), which illustrate the potential importance of wood for the retention of viable seeds.

Accordingly, these observations suggest that the role of large wood in rivers and streams, both as habitat and as habitat generator for vegetation colonisation may potentially vary with different river styles. Since different river styles and locations along the river continuum exhibit varying fluvial processes that affect the deposition of large wood, the amount of wood-related habitat area (due to differential sediment and viable seed trapping) may change along and across the river continuum. The establishment of seedlings, such as those of white spruce on the Tanana River floodplain in Alaska, has been found to be episodic and related to seed production and dispersal onto freshly deposited silt (Walker et al., 1986). Whilst a large body of research has demonstrated the importance of hydrochory (river dispersal of propagules) for delivering viable plant propagules of many species to riparian zones and structuring riparian plant communities between seasons and years (e.g. Thebauld and Debussche, 1991; Nilsson et al., 1991; Johansson et al., 1996; Cellot et al., 1998; Andersson et al., 2000; Goodson et al., 2002; Merritt and Wohl, 2002; Boedeltje et al., 2003; Vogt et al., 2004, 2007; Truscott et al., 2006; Gurnell et al., 2007, 2008b), there has been no in-depth analysis of the significance of dead and living wood to plant ecology within fluvial systems; thus the links between wood, standing vegetation and propagule bank in different locations and along rivers of different geomorphological style.

Additionally, the fine particulate organic matter observed in wood accumulations jams may be disproportionately distributed among wood-related habitats and may provide the substrate and nutrients necessary for vegetation establishment (Abbe and Montgomery, 1996). The flood pulses of rivers are less predictable and further complicated by the seasonal light / temperature pulse (summer / winter regime) (Adis and Junk, 2002) may cause vegetation to respond differentially in terms of propagule dispersal, flowering, fruiting (Andersson et al., 2000). However, information on these phenomena (seasonal sediment and propagule dynamics) and its association with wood remains fragmented or not available.

Furthermore, large wood increases riparian diversity by increasing the variety of landforms and microclimates in the riparian zone, adding to its structural heterogeneity (Braudrick et al., 1997; Naiman et al., 2002; Abbe and Montgomery, 2003). The structural heterogeneity created by large wood within the riparian zone has been shown to increase faunal diversity and also research has revealed that not only does wood volume strongly influence the diversity of aquatic fauna, but also the species composition of large wood exploited as substrate and its spatial orientation, wood management regimes and the stream's order are important to the diversity of aquatic fauna. Analogous research on the influence of large wood structure and volume, its spatial orientation, and large wood species types on plant and propagule diversity across diverse mesohabitats and along different river sizes and styles is therefore needed to complement studies undertaken on large wood's associations with faunal ecology.

In summary, the broad emphasis of research on wood and ecology has emphasised dead wood, single-thread river systems and aquatic organisms, particularly macroinvertebrates and fish, with very little plant ecological research in relation to large wood in the riparian zones of single- and multi-thread river systems.

2.6 RIVER RESTORATION AND THE ROLE OF LARGE WOOD

The inferred importance of wood for fluvial geomorphology and aquatic organisms (e.g. Gregory and Davis, 1992; Gregory et al., 1993; Abbe et al., 2003) has also led to experimental and field research on impacted and restored rivers, in an attempt to quantify the benefits of wood introduction and the disadvantages of wood removal for fluvial geomorphology and aquatic biotic communities (e.g. Riley and Fausch, 1995; Sundbaum and Naesland, 1998; Kail et al., 2007; Lester and Boulton, 2008). The value of large wood as a resource for river restoration and recovery has been demonstrated by research relating habitat complexity to fish and macroinvertebrate community indices (e.g. Crispin et al., 1993; Sotir, 1998; MacNally et al., 2001; Lester and Boulton, 2008; Nagayama et al., 2008). Furthermore, when Gerhard and Reich (2000) compared regulated and straightened reaches of two third-order streams in Central Germany, they established that variations in channel width and depth, the extent of the riparian zone, and the number and patchiness of microhabitats on the stream bed were considerably larger in the unregulated reaches. They suggested that the quantity of large wood contributed to these differences. Therefore, the conservation of fauna demands optimizing the quantity and sustaining the quality of large wood biomass in fluvial systems.

Despite this, post-project appraisal of the associations between restored large wood, habitat complexity and stream ecology as a result of river restoration is extremely rare and thus scientific knowledge is limited. Research aimed at developing an understanding of the links between large wood and ecology has principally been concerned with small streams (e.g. Schneider and Winemiller, 2008; Angradi et al., 2009; Lester et al., 2009) and has focused largely on macroinvertebrates and fish. There has been little work on plant ecological implications of restored wood.

2.7 RESEARCH GAPS AND RESEARCH QUESTIONS

At any given point along a river system, the role of large wood on riparian zone structure and processes represents the combined influence of many environmental factors acting at different scales (Gurnell, 2013). So far, this chapter has reviewed literature on four main themes: the development and geographical coverage of large wood research (section 2.3); large wood inventories, mobility and budgets (section 2.4); the eco-geomorphological role of large wood (section 2.5); and large wood as a river restoration tool (section 2.6). These reviews have uncovered a series of research gaps, which are summarised below (with underlined, italicised text highlighting those that are incorporated into the aims and research questions outlined below):

(i) **In relation to wood inventories and budgets:** knowledge remains limited about *the relative importance of upstream inputs of wood in comparison* *with local supply and the relative importance of wood depletion through decomposition, particularly in larger rivers*.

(ii) **In relation to wood and fluvial geomorphology:** the majority of previous research has been concerned with in-channel wood and also with relatively small, single-thread rivers. There remains a large research gap concerning *wood, sediment retention and / or landform development in the riparian zone across all styles and sizes of river corridor, but information on large, multi-thread rivers is particularly sparse.* Knowledge also remains limited on *the impact of landforms on transitional wood storage in the riparian zone, particularly in larger rivers.*

(iii) **In relation to wood and ecology:** research has emphasised dead wood, single-thread river systems and aquatic organisms, particularly macroinvertebrates and fish, with *very little plant ecological research in relation to large wood in the riparian zones of single- and multi-thread river systems.*

(iv) **In relation to the relevance of these above processes (ii and iii) to river restoration and recovery,** *post-project appraisals remain limited and there has been very little work on the plant ecological implications of restored wood.*

Following from the above research gaps, three overarching research questions can be defined that will be addressed in this thesis:

1. What are the types and characteristics of large wood accumulations present within the riparian corridor of different styles of river systems?

2. Does deposited large wood within riparian corridors influence sediment structure, landform and physical habitat development and thus the geomorphology of different river systems?

3. Do large wood-related habitats retain plant propagules within the riparian corridor of different river systems and does propagule retention vary in space (within- mesohabitats / river reaches) and through time (age / seasonally / in relation to restoration)?

To address these questions, an experimental approach was designed to:

i. Undertake research on four river reaches of different size and style.

ii. Undertake inventories and construct typologies of wood accumulation types impinging on or present within the riparian zone of these reaches.

iii. Explore the dependence of the plant community on large wood within riparian zones through investigations of the viable propagule bank and / or colonising vegetation assembly associated with wood structures.

iv. Explore the relevance of the above for river restoration and recovery.

CHAPTER 3

RESEARCH DESIGN, RESEARCH SITES AND METHODOLOGIES

3.1 INTRODUCTION

To answer the questions listed in Chapter 2 (restated in section 3.2 of this chapter), the research in this thesis is arranged around a series of distinct field sites, where the specific design of the research is adapted to the size and style of the river and the nature of the wood and standing vegetation. The research conducted at each field site is presented in a set of semi-independent chapters that present the site, methods, results and interpretation in a way that is appropriate to the particular site. This chapter provides a context for these subsequent chapters by giving an overview of the factors that influenced the research design (section 3.2); introducing the nature of the field sites and justifying their selection (section 3.3); detailing the broad sampling design across these field sites (section 3.4), and those field (section 3.5) and laboratory (section 3.6) procedures that are common across the individual site investigations. Site specific methods and modifications to the broader methods are introduced in detail, as appropriate, in Chapters 4, 5, 6 and 7.

3.2 FRAMING THE RESEARCH DESIGN

The research in this thesis focuses on large wood accumulations in rivers of different style, the characteristics of these wood accumulations, and their relevance for landform and vegetation development. Retention of large wood within rivers and their margins influences local hydrogeomorphological processes and may be important for vegetation colonisation and development. This chapter identifies suitable field sites and describes the methods used to explore the wood accumulations that are present and their geomorphological and plant ecological role, particularly their influence on the soil propagule bank of river active channels and margins.

Gurnell et al. (2000a) distinguished four groups of controls on wood retention within river systems:

i. vegetation (forest) character (tree species, sizes and density);
ii. hydrological processes (sediment transport regimes and river discharge);
iii. geomorphology (river channel size, pattern and dynamics; river corridor width, slope and form; river channel bank and bed sediment calibre); and
iv. management as it affects the other three groups of factors.

This thesis is concerned with wood in less-managed, morphologically intact river systems, where the last group of controls has limited significance. In such rivers, the relative significance of the first three groups of controls (vegetation character, hydrological processes and geomorphology) changes in a downstream direction. As rivers increase in size from headwaters to river mouth, physical (hydrological) processes become increasingly important and are increasingly reflected in the size and geomorphological style of the river channel (Gurnell et al., 2000a; Tockner and Stanford, 2002). River style (e.g. single-thread meandering, bar-braided, island-braided, anastomosing), provides the suite of retention structures and locations within which wood may accumulate, and so influences the locations and characteristics of large wood accumulations (Piégay and Gurnell, 1997). As a result, the selected field sites need to provide opportunities to consider wood retention in rivers of different size as well as geomorphological style.

Furthermore, sampling needs to reflect different types of wood accumulation within different field sites. Attempts to define typologies for large wood stored within river corridors have reflected position along the river continuum and river channel geomorphological style. Of the many attempts to classify large wood accumulations that are reviewed in Chapter 2, the most comprehensive in terms of both position along the river continuum and also river channel style, is that proposed by Abbe and Montgomery (2003).

Abbe and Montgomery (2003) characterised large wood accumulations on the Queets River, Washington (USA), into nine physically distinct types (see Table 2.3 in Chapter 2) spanning those found in steep, narrow headwater (small to medium sized) channels and those present in larger channels in downstream floodplain reaches of the river. Therefore, Abbe and Montgomery's (2003) classification produces a useful starting point for designing sampling strategies for the different field sites investigated in this thesis. This classification can be modified for particular field sites in the light of research conducted on large wood on rivers of the specific size and style of each site.

Importantly, the classification proposed by Abbe and Montgomery (2003) is concerned with large wood that comes from mainly coniferous trees and so is morphologically simple and does not sprout once it has been uprooted or broken from the parent tree. In the present research, it is important to consider those properties of large wood that reflect the tree species from which the wood is drawn. Gurnell (2013) reviewed the literature that has classified large wood, exploring the different accumulation types that have been observed in rivers of different size and style in different environments. Building on the classification of Abbe and Montgomery (2003), she introduced the additional complexities associated with wood that is able to sprout following deposition (Gurnell et al., 2001) as well as wood piece morphology, which affects the structure and stability of wood accumulations. By doing this, she introduced some aspects of the impact of vegetation character on wood retention across rivers of different size and style. This provides a further context for identifying field sites and methods for the present research, ensuring that rivers of different size and style are considered and also rivers bordered by vegetation that delivers both dead and 'living' (i.e. capable of sprouting) wood.

Of particular relevance to the present research, is that large wood accumulations can potentially receive and store plant propagules as well as sediment, and so may be able to influence regeneration of riparian vegetation as well as the landforms on which that regeneration may occur. The extent to which large wood may influence vegetation (propagule bank and standing vegetation) within fluvial systems has not been addressed in previous research. This study investigates this topic within rivers of different size and style subject to both dead and living wood dynamics, and so the investigative design adopted at each study site (summarised in Table 3.1) emphasises indicators of wood, morphology, standing vegetation, propagule bank and the interactions between them to reveal aspects of the geomorphological and plant ecological roles of riverine large wood. Therefore, the investigative design adopted at each study site in this present research is aimed at addressing the following research questions;

1. What are the types and characteristics of large wood accumulations present within the riparian corridor of different styles of river systems?

2. Does deposited large wood within riparian corridors influence sediment structure, landform and physical habitat development and thus the geomorphology of different river systems?

3. Do large wood-related habitats retain plant propagules within the riparian corridor of different river systems and does propagule retention vary in space (within- mesohabitats / river reaches) and through time (age / seasonally / in relation to restoration)?

3.3 FIELD SITES: SELECTION AND RATIONALE

Three gravel-bed river reaches subject to near-natural inputs of large wood but with different hydrogeomorphological settings (hillslope-confined, unconfined island-braided and floodplain reaches), river styles (single- and multi-thread) and riparian tree species (e.g. *Betula pubescens*, *Alnus incana*, *Populus nigra*, *Salix spp.*) were selected for study. In addition one restored site was investigated where wood had been reintroduced to emulate, as far as was possible, natural wood supply and retention properties. Therefore, a total of four study sites were investigated:

i. Multi-thread, island-braided reach: Tagliamento River, Italy, at Flagogna (Figure 3.1 and 3.2).

ii. Multi-thread, hillslope-confined, braided reach: Tagliamento River, Italy, at Forni di Sotto (Figure 3.1 and 3.3).

iii. Single-thread, floodplain reach: Highland Water, New Forest, UK (Figure 3.4 and 3.5).

iv. Single-thread floodplain reach that had been restored using large wood was also included in the study: River Bure, Norfolk, UK (Figure 3.6 and 3.7).

3.3.1 The Tagliamento River, Italy

The Tagliamento River, Italy, flows from its headwaters in the Italian Alps to the Adriatic Sea. It has been proposed as a reference river for the European Alps (Ward et al., 1999) as it is morphologically intact, bordered by riparian woodland along most of its ca. 170 km length, and it retains near-natural geomorphological and ecological dynamics in many reaches (Gurnell et al., 2000b; Tockner et al., 2003). For most of its length, the river displays a multi-thread braided planform which is island-braided in its middle reaches at Flagogna (Figure 3.1 and 3.2), and confined by mountain- and hill-slopes in its headwater reaches at Forni di Sotto (Figure 3.1 and 3.3). Variations in valley gradient, sediment calibre and supply, and the species composition of the riparian woodland result in contrasts in the nature of large wood delivered to the river and its interactions with fluvial processes in different reaches (Gurnell et al., 2000b).

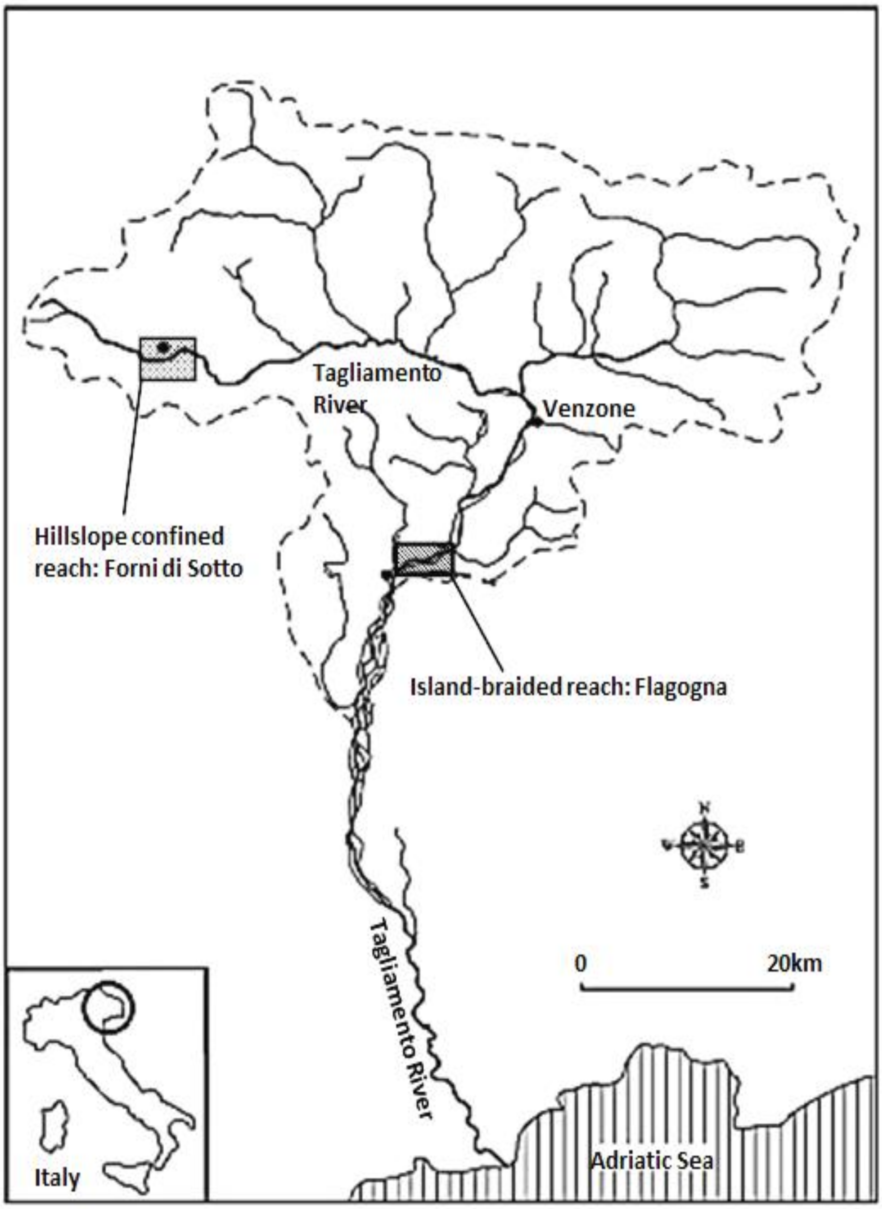


Figure 3.1. Locations of the two study reaches along the Tagliamento River.

(i) Multi-Thread, Island-Braided Reach: Flagogna, Tagliamento River, Italy

A multi-thread, island-braided, 2 km long, study reach was investigated in the middle-reaches at Flagogna, located 74 to 76 km from the river's source (Gurnell et al., 2000a and 2000b; Gurnell and Petts, 2006) (Figure 3.2). Although confined on one side by hillslopes, it has developed a floodplain on its right bank, where the riparian woodland is dominated by *Populus nigra* and several *Salix* species (Gurnell and Petts, 2006). The same species cover established islands in the reach and provide large amounts of wood that is capable of resprouting to the river (Gurnell et al., 2005). In this reach, the braidplain extends to an average width of approximately 600 m, and has an average slope of 0.0029 $m.m^{-1}$ (Gurnell and Petts, 2006). Bed material is cobble-sized on the coarsest riffles (D_{50} ~ -6 phi) and there is a plentiful supply of finer gravel-pebble sheets (D_{50} ~ -4 phi), sand and silt to the reach that accumulates around vegetation to build pioneer and then larger islands (Gurnell et al., 2001, 2005; Gurnell and Petts, 2006).

Figure 3.2. Pioneer and established islands and resprouting wood in the Flagogna reach of the Tagliamento River. (Photograph by N.A. Osei.)

(ii) Multi-Thread, Hillslope-Confined Reach: Forni di Sotto, Tagliamento River, Italy

A multi-thread, 2 km long, hillslope-confined study reach was investigated in the Tagliamento River headwaters at Forni di Sotto, 11.2 to 13.5 km from the river's source (Gurnell et al., 2000a and 2000b; Gurnell and Petts, 2006) (Figure 3.1). This bar and island-braided reach has an average braidplain width of 160 m, valley gradient of 0.0188 $m.m^{-1}$ and the riparian woodland is dominated by *Alnus incana, Salix eleagnos*, and a variety of coniferous tree species (Gurnell and Petts, 2006).

The coarse bed material reaches small boulder size in the coarsest riffles (D_{50} ~ -8 phi) and fines to coarse sand (D_{50} -2 phi) on some bar surfaces (Petts et al., 1999). Because of the relatively high elevation (approximately 700 m), coarse free-draining substrate, and importance of conifers to the wood supply, the large quantity of wood delivered to the braidplain is predominantly dead wood (Figure 3.3) (Gurnell et al., 2000b; Gurnell and Petts, 2006).

Figure 3.3. Dead wood on a gravel bar in the hillslope-confined, headwater reach of the Tagliamento River at Forni di Sotto. (Photograph by N.A. Osei.)

3.3.2 Single-Thread, Floodplain Reach: Highland Water, New Forest, UK

This lowland river drains a catchment underlain by a broad and shallow syncline known as the Hampshire Basin and is located in the New Forest National Park (Figure 3.4). In the study reach, the river is bordered by unmanaged, mixed deciduous woodland, dominated by sessile oak (*Quercus petraea*), birch (*Betula pubescens*), ash (*Fraxinus excelsior*), alder (*Alnus glutinosa*) and *Salix spp.* that supplies a steady supply of large wood to the river channel (Figure 3.5). Wood dynamics, storage, accumulation types and their geomorphological impacts have

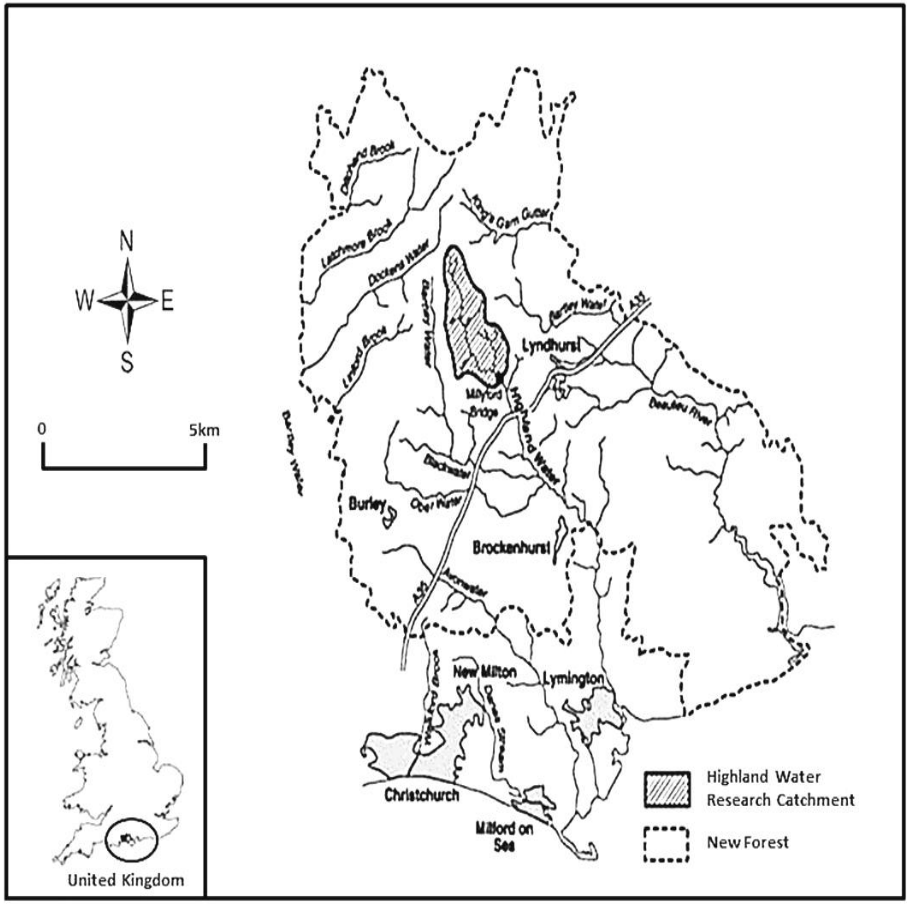


Figure 3.4. The Highland Water study site in Southern England located in the New Forest catchment: the site is located immediately upstream of the A35 (Modified from Jeffries et al., 2003).

Figure 3.5. Riparian vegetation along the margins of the Highland Water. (Photograph by N.A. Osei)

been the focus of much previous research (e.g. Gregory et al., 1985; Gregory et al., 1993; Piégay and Gurnell, 1997; Gurnell and Sweet, 1998, Gurnell et al., 2002; Jeffries et al., 2003; Millington and Sear, 2007), leading to the designation of the river network as a Site of Special Scientific Interest (SSSI) on geomorphological grounds. The study reach is 2 km in length with an average channel width of 3 m and slope of 0.0057 $m.m^{-1}$ (Jeffries et al., 2003) and the bed material in open sections between wood jams is typically pebble sized (D_{50} ~ -2.5 phi; coarse gravel). Although located in the headwaters of the Highland Water, the river has developed a small floodplain across which shallow side channels support surface water flow during high discharge events.

3.3.3 Restored, Single-Thread, Floodplain Reach: The River Bure, Norfolk, UK

The River Bure, United Kingdom, is a lowland river that flows south-easterly from its headwaters near Melton Constable to the sea at Great Yarmouth. The River Bure has historically been heavily managed as large sections of its 80 km length have been affected by over-widening and vegetation removal due to dredging, which is aimed at enhancing navigation (Moss et al., 1984; Whitehead, 2006). Since the River Bure drains a fertile agricultural catchment, it has been subject to diffuse nutrient pollution from cultivated land, stock wastes, sediments and agricultural drainage systems (Timms and Moss, 1984; Moss et al., 1988; Phillips et al., 1994). These factors among others influence its morphology and ecological dynamics in many reaches. As a result, the 240 m study reach, which is bordered by a floodplain (particularly farmland), has become heavily silted.

As part of a river restoration project implemented by the National Trust in 2008 and 2010, large wood has been reintroduced into the study reach (Figure 3.6 and 3.7). Entire trees have been introduced into the channel in an attempt to narrow it and to achieve an increase in hydraulic diversity that may lead to greater morphological and habitat complexity. The large size of the wood pieces, their orientation and the fact that artificial anchoring has been minimised gives them a semi-natural appearance and potential function, providing an opportunity to observe early sediment and propagule retention and compare them with observations from the semi-natural, single-thread study reach on the Highland Water.

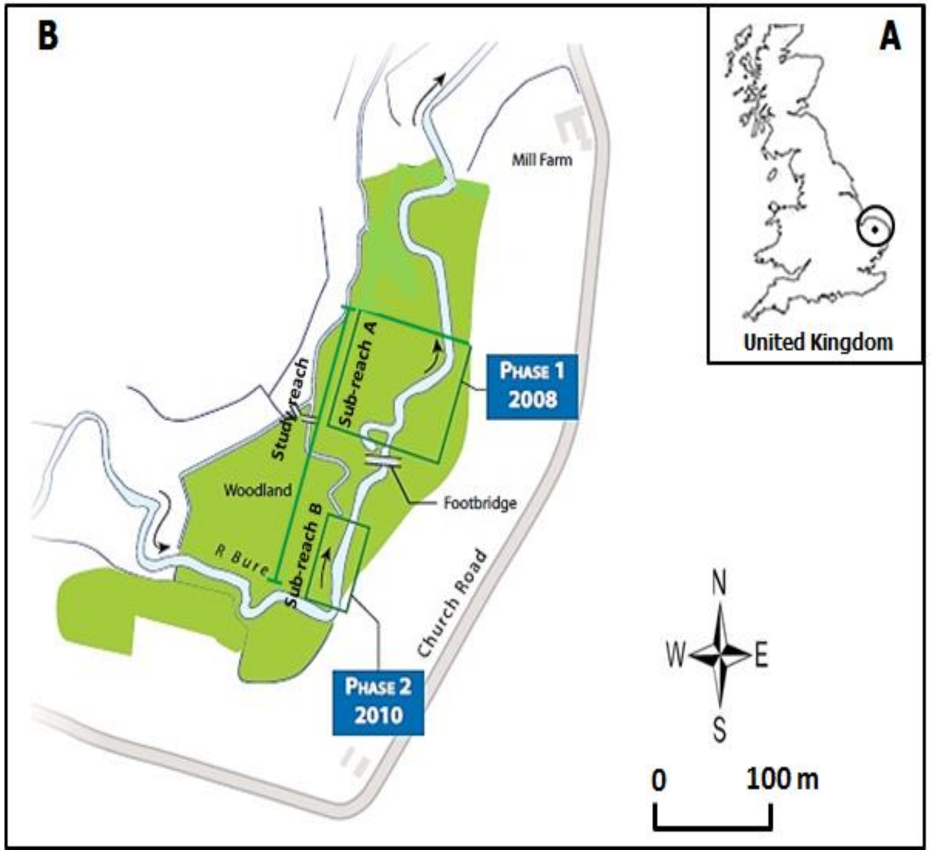


Figure 3.6. The River Bure study site in (A) Norfolk, East England; and (B) the Blickling Hall estate near Aylsham (Source: Modified from RRC, 2013). (Note that wood was reintroduced in two phases: in autumn 2008 and 2010).

Figure 3.7. Newly introduced trees in the River Bure. (Photograph by N.A. Osei.)

3.4 RESEARCH DESIGN

The research design is summarised in Table 3.1 and includes methods that address the project research aims outlined in Chapter 2, specifically:

Research Aim 1: Undertake inventories and construct typologies of wood accumulation types impinging on or present within the riparian zone of all three rivers of different size and style.

Research Aim 2: Investigate wood and landform development in the riparian zone across all styles and sizes of rivers especially that of large, multi-thread rivers as information on this process is particularly sparse.

Research Aim 3: Explore the relevance of large wood to plant ecology within the riparian zones in all rivers through investigations of the viable propagule bank and / or colonising vegetation assembly associated with wood structures.

Research Aim 4: Explore the relevance of these processes to river restoration and recovery based on a study of the River Bure, where deliberate reintroduction of wood is being used as the main restoration tool.

Addressing these research aims will result in a model illustrating key controls and process interactions relating to the role of large wood in riparian systems.

A similar research design was applied to the two single-thread reaches investigated (Highland Water and River Bure). However, the research design was modified for application to the two multi-thread reaches investigated at Forni di Sotto and Flagogna because of their large channel width and the fact that only one summer field campaign was possible at each of these sites whereas it was possible to revisit the single-thread sites, permitting research visits during both spring and summer. Descriptions of the field methods and laboratory methods applied to more than one field study site are presented in sections 3.5 and 3.6, respectively, to avoid detailed repetition in the following chapters.

Table 3.1. Overview of research design at the four field sites outlined according to the project research aims.

Aims	**Method / Technique**	**Scale**	**Single-thread reaches**		**Multi-thread channel**	
			Floodplain (Highland Water)	**Restored (River Bure)***	**Hillslope-confined (Forni di Sotto)**	**Island-braided (Flagogna)**
Research Aim 1	Wood survey	Reach	Wood accumulations surveyed along the entire study reach.		Wood accumulation surveys within eight 60 m wide transects across the entire braidplain.	Dimensions of wood (living / resprouting) within pioneer islands of different age (1 year (yr.), 7 years (yrs.), 11yrs.).
Research Aim 2	Geomorphological characterisation	Reach and Patch	Field mapping of physical features of the channel and margins along the entire study reach.		Mapping and delimitation of detailed survey areas from remotely-sensed imagery (e.g. satellite, airborne, oblique ground photographs).	
					Topographic surveys of eight transects across the braidplain.	Dimensions of pioneer islands of different age (1yr., 7yrs., 11yrs.) and their associated mesohabitats.
Research Aim 3	Species present in the standing vegetation	Reach and Patch	Dominant tree species in reach.		Dominant tree species in reach.	Species list for all woody, herbaceous and grass species within each surveyed pioneer island.
	Species present in the soil propagule bank^	Reach and Patch	Replicate samples collected from different mesohabitats in and around wood accumulations along the study reaches.		Replicate samples collected from in and around wood accumulations, and on pioneer island and open gravel bar surfaces.	Replicate samples taken from different mesohabitats in and around pioneer islands of different age (1yr., 7yrs., and 11yrs).

* Used in the investigation of **Research Aim 4;**

^ Involves germination trials, sediment particle size analyses and organic matter analyses.

3.5 FIELD METHODS

3.5.1 Reach Geomorphological Characterisation

The broad geomorphology of each study reach was mapped to provide a context for interpreting the other data sets that were collected and place them in the context of the study reach as a whole. At each field site, surveys were conducted to describe the position, distribution and structure of wood accumulations and associated mesohabitats that might be relevant for interpreting wood / morphological complexity and their relevance to propagule retention. Due to the differences in channel size and also the way in which wood was retained and influenced channel morphology at the different study sites, the survey methods varied.

For single-thread reaches, the survey focused on the active channel and recorded the location and extent of key channel bed (pool, riffle, bar, silt or organic accumulations), channel bank (undercutting, erosion), tree (exposed roots) and wood (accumulations and wood pieces) locations. The mapping of each reach was conducted within a period of two days and under low flow conditions.

For multi-thread reaches, remotely sensed imagery was used to delimit the 60 m wide transects (Forni di Sotto) and the areas of pioneer islands of different age (Flagogna) that were investigated in detail in the field. For the multi-thread hillslope-confined, headwater reach, eight cross profiles were surveyed by total station at the mid-points of the 60 m wood survey transects. These cross profiles were used to investigate the elevation of the surveyed wood accumulations, river channels and island surfaces within each transect as well as the overall channel dimensions of the braidplain. At the multi-thread island-braided reach, survey was confined to the sampled pioneer islands, since this is the geomorphic feature influenced by the type of wood accumulation that dominates this reach. The dimensions (length, width, height / depth) of ten pioneer islands belonging to each of the different age classes that were present (1yr., 7yrs. and 11yrs.) and their associated mesohabitat features such as scour pools and fine sediment accumulations were measured using a 30 m tapes and metre rule.

3.5.2 Wood Surveys

The objective of the large wood surveys was to quantify key properties of the wood that would characterise its size, structure and distribution and would underpin investigations of its interaction with the soil propagule bank and, where appropriate, standing vegetation. Due to the large differences in channel size and also the way in which wood was retained and influenced channel morphology at the different study sites, the design of the wood survey varied between single-thread and multi-thread reaches.

For single-thread reaches, a wood accumulation survey based on that of Gurnell and Sweet (1998) was used (Appendix I). The survey provides a standardised, repeatable method for recording wood accumulation characteristics and dimensions, channel dimensions in the vicinity of wood accumulations, and the accumulation-associated geomorphic features / mesohabitat. Recordings were based either on visual assessment (e.g. classification of accumulation types, identification of geomorphic features / mesohabitats) or on measurements of dimensions (channel, accumulation, wood pieces) using a 30 m measuring tape and metre ruler. Characteristics of all wood accumulations present in the entire study reach were recorded, including length, diameter / width, height of the accumulation and its key pieces.

For the multi-thread reaches, the size of the river corridor prevented the recording of all wood accumulations. Furthermore, the considerable difference in corridor width and the predominance of resprouting wood at Flagogna and dead wood at Forni di Sotto meant that each site required a different sampling strategy. At the multi-thread hillslope-confined reach (Forni di Sotto), all wood pieces / accumulations were recorded within eight 60 m wide transects spanning the active corridor. The survey recorded the position, dimensions, and type of each large wood accumulation, using a hand-held GPS, 30 m tape and metre rule.

At the multi-thread, island-braided reach (Flagogna), wood (commonly entire trees) is deposited mainly as discrete large pieces which either sprout, trap fine sediment and evolve into pioneer islands (Gurnell et al., 2001, 2005), or decay rapidly. Since wood tends to be deposited in discrete areas of the braidplain by different large floods, the survey focussed on three such areas where the pioneer islands were of known age (time since flood deposition): 1, 7, 11 yrs.; reflecting floods in 2010, 2004 and 2000, respectively. At each sampled pioneer island, the diameter and length of each deposited tree (1yr. pioneer islands) or height of the tallest sprout / tree (1, 7 and 11 yrs. pioneer islands) were recorded using a 30 m tape and clinometer.

3.5.3 Sediment and Propagule Bank Sampling

At each study site, sediment samples were collected to characterise both sediment and propagule bank properties. At each site a systematic, random design was adopted to provide a set of replicate (random) samples of different (systematic) mesohabitats. In this way, the samples could answer the question in relation to contrasts in sediment and propagule bank properties between sampling locations that were or were not impacted by wood accumulations. The locations from which samples were obtained at each of the study sites is summarised in Table 3.2.

Table 3.2. Characteristics of the four field sites and locations at which sediment and propagule bank were sampled (For definitions of sampling locations see Tables 3.3 and 3.4).

Characteristics	**Highland Water**	**River Bure**	**Tagliamento River (Forni di Sotto)**	**Tagliamento River (Flagogna)***
River Size, Style and Large Wood Type				
Average channel width (m)	~ 3.0	7.6	160	600
River style	Single-thread, sinuous with floodplain	Single-thread, restored	Multi-thread, hillslope-confined	Multi-thread, island-braided
Dead / living wood	Dead	Dead	Predominantly Dead	Predominantly Living
Sediment / Propagule Bank Mesohabitats Sampled				
Bare gravel bar / channel bed	●	●	●	●
Within wood jam (Jam)	●	●	●	○
Bank	●	●	○	○
Jam bank	●	●	○	○
Floodplain	●	●	○	○
* Pioneer island surface	○	○	○	●
Established island surface	○	○	●	○

* Islands of three different ages (1, 7, 11 yrs.) were sampled. For the youngest island, additional mesohabitats were sampled including root bole and scour pool; ● Mesohabitats sampled; ○ Mesohabitats not sampled.

For the single-thread study sites, the studied reaches were divided into sub-reaches within which sediment samples were collected from five different mesohabitat types (Table 3.3). Sediment sampling was undertaken twice, once during spring and once during mid-summer. These sampling times were selected, following Gurnell et al. (2008a) to capture the changes in propagule bank from predominantly persistent propagule species and those few species that set seed late in the year and are present in spring to those additional more transient species that set seed through the summer. Since the sediment propagule bank can be highly spatially variable (Benoit et al., 1989; Fenner and Thompson, 2005), within each sub-reach of the single-thread field sites, three randomly located sediment cores (four for bare gravel bars / channel bed) were taken from each of the five mesohabitats within the river corridor and were bulked prior to laboratory analysis. The number of bulked samples obtained from each mesohabitat within each single-thread reach is shown in Table 3.5.

For the multi-thread study sites, sediment samples were collected from characteristic mesohabitats within each site (Table 3.4). In the multi-thread, hillslope-confined reach, samples were collected from the three main mesohabitats present, namely bare gravel bars, established islands and large dead wood jams, within 5 of the 8 surveyed transects. For the multi-thread, island-braided reach, samples were collected from mesohabitats present on five pioneer islands within each of the island age classes (1, 7, and 11 yrs.). In both reaches, three (four for open gravel bars) randomly located sediment core samples were collected from each of the mesohabitats and were then bulked for laboratory analysis to give the sample numbers listed in Table 3.6. The number of samples obtained and the single mid-summer (July) sampling period were constrained by the single field campaign and restrictions on the weight of samples that could be returned by air to the UK. Thus the sampled propagule species are constrained by the time of year and persistence of their propagule bank, but species abundance provides a relative measure of propagule retention in the sampled mesohabitats.

In all cases, sediment cores were obtained to a depth of 5 cm using a 6 cm diameter corer, supported where necessary by a trowel to prevent loss of sediment from the corer. Propagule bank samples are typically collected to depths of 5 cm because this region of the soil typically contains the highest density of viable propagules

(Galatowitsch and van der Valk, 1996; Harwell and Havens, 2003). The replicate samples for each sub-reach / cross section / pioneer island were aggregated in a sealed plastic bag to yield bulked samples for germination trials and sediment analysis.

Table 3.3. Mesohabitats from which sediment and propagule bank samples were obtained along single-thread river reaches.

Mesohabitat	**Definition**
Bare gravel bars / channel bed	Surface sediment of exposed, unvegetated mid-channel bars or of the submerged unvegetated river bed
Jam	Sediment accumulated within a large wood jam
Bank	Surface of an actively eroding river bank face midway between the bank top and the bank toe
Jam bank	The face / toe of banks immediately adjacent or downstream of jams
Floodplain	Floodplain surface close to the river channel (i.e. bank top)

Table 3.4. Mesohabitats from which sediment and propagule bank samples were obtained along multi-thread river reaches.

Mesohabitat	**Multi-thread reach**	**Definition**
Bare gravel bars	Island-braided and Hillslope-confined	Open (unvegetated) bar surface
Root bole	Island-braided	Sediment accumulated in and under the root bole of a recently (1yr.) deposited tree
Scour pool	Island-braided	Surface within scoured areas or scour pools adjacent to the root bole and trunk of a recently (1yr.) deposited tree
Pioneer island	Island-braided	Sediment from the (vegetated) surface of a pioneer island
Jam	Hillslope-confined	Sediment accumulated within large wood jam formed on bar surface
Established island	Hillslope-confined	Sediment from the (vegetated) surface of an established island

Table 3.5. Bulked sediment samples obtained from mesohabitats at single-thread river sites.

Mesohabitat	**Number of bulked samples per study site**	
	Floodplain reach (Highland Water)*	**Restored reach (River Bure)[n]**
Bare gravel bars / channel bed	9	12
Jam	9	12
Bank	9	12
Jam bank	9	12
Floodplain	9	12
Total number of samples per study site	45	60

* Nine sub-reaches along the study reach; [n] Twelve wood accumulations along the study reach.

Table 3.6. Bulked sediment samples obtained from mesohabitats at multi-thread Tagliamento river reaches.

Mesohabitat	**Number of Samples (Reaches)**				
	Cores per sample	**Multi thread, hillslope-confined reach (Forni di Sotto)[n]**	**Multi-thread, island-braided reach (Flagogna)**		
			Pioneer island age*		
			1	**7**	**11**
Bare gravel bars	4[m]	5	5	5	5
Root bole	3	-	5	-	-
Scour pool	3	-	5	-	-
Pioneer island	3	-	5	5	5
Jam	3	5	-	-	-
Established island	3	5	-	-	-
Total number of samples for reach		15	20	10	10

[m] Randomly collected sediment samples to increase the volume of fine sediments required for propagule bank germination trials and sediment analyses; [n] Five randomly selected cross-sections from upstream to downstream; * Five randomly selected pioneer islands from each age class.

3.5.4 Vegetation Survey

Since all of the sediment samples obtained for germination trials were from within or adjacent to the river channel, it is likely that the propagule bank was heavily affected by hydrochorous dispersal and so is likely to reflect the species pool present in the riparian zone of the upstream catchment. Therefore, detailed surveys of the standing vegetation were not undertaken, although the dominant tree species were recorded at all study sites, to aid interpretation of wood and propagule bank characteristics. However, at the multi-thread, island-braided reach, the standing vegetation was surveyed at all of the pioneer islands from which propagule bank samples were obtained. These surveys were undertaken to aid interpretation of the propagule bank data according to pioneer island age, since it was hypothesised that a second key control after hydrochory (and anemochory) on propagule bank composition at these sites would be the degree of development of the vegetation community on islands of different age and thus differences in the species composition of local seed fall.

3.6 LABORATORY METHODS

3.6.1 Sediment Storage and Preparation

The sediment samples were transported to the laboratory, weighed and cold stored (over -18°C) for approximately six to eight weeks (Maas, 1989; Matlack and Good, 1990; Looney and Gibson, 1995; Lévesque et al., 1996; Walters et al., 2005; Bidlack and Jansky, 2011) to prevent propagules germinating prematurely (Baskin and Baskin, 1998; Miao et al., 2001), and to prevent microbial activities and the decay of viable propagules until processed. Although the storage of propagules at low temperatures usually allows preservation for long periods of time (Cromarty et al., 1982; Pritchard, 1995), cold storage may lead to loss of viability depending on species (Roberts and Ellis, 1984; Baskin and Baskin, 1998). However, given constraints on the present research imposed by the wide geographical distribution of the study sites and thus issues of access timing; the necessity for completing field surveys, often at the expense of laboratory work; and time limitations on the availability of space and facilities for germination trials; it was decided that low temperature storage was the best solution for ensuring comparability in the data generated from germination trials, even if this reduced the number of viable propagules and range of species germinated. On removal from cold storage, the bulk samples for each study reach were thoroughly mixed and two sub-samples were extracted for germination trials and for sediment analysis.

All bulk samples were concentrated by sieving through a 4 mm sieve (Goodson et al., 2001). The < 4 mm fraction includes the entire propagule bank (Thompson et al., 1997) and so concentrates the propagules within the sample extracted for germination trials. For the Tagliamento River samples, this sieving was undertaken in the field to reduce the weight of samples returned to the laboratory. The volume and weight of the > 4 mm and < 4 mm fractions were measured for inclusion in the particle size analysis of the sediments.

3.6.2 Sediment Analyses

Sediment sub-samples obtained from the bulk samples from each mesohabitat were analysed to establish their particle size distribution and organic matter content. 100 ml sub-samples obtained from the bulked sediment samples (< 4 mm) were analysed to establish their particle size distribution and organic matter content. The sub-samples were weighed (initial weight, W_1) into precombusted aluminium crucibles, dried in an oven for 48 hours at 55°C, desiccated (24 hrs.) to a constant weight, weighed (dry weight, W_2), combusted in a furnace (for 5 hrs. at 550°C), desiccated (24 hrs.), and reweighed (ash weight, W_3) to determine percentage loss-on-ignition of organic matter (Formulae 3.1; see Bott, 2006). The % organic matter content of the 100 ml sample (< 4 mm fraction) was then calculated.

$$\% \text{OM} = \frac{[(W_2) - (W_3)]}{(W_2)} \times 100 \qquad \text{[Formulae 3.1]}$$

The final mineral sediment sample was then sieved through 2 mm and 1 mm meshes and a 5g sub-sample of the < 1 mm fraction was analysed using a Beckman Coulter Counter laser sizer to obtain a particle size distribution for the < 1 mm fraction. The resultant data were combined with information on the coarser fractions obtained in the laboratory and field to provide a complete particle size distribution for the original field sample and thus the gravel, sand, silt and clay proportions (%).

3.6.3 Germination Trials

A 250 ml sub-sample of the bulked sediment sample (< 4 mm) was subjected to germination trials to estimate the species abundance of viable propagules (Goodson et al., 2002). Germination trials were undertaken for 12 weeks to permit the growth of most viable propagules as it takes some time for certain species to break dormancy (Baskin and Baskin, 2003; Finch-Savage and Leubner-Metzger, 2006). To reveal significant difference between sites, seasons and mesohabitats, a free draining soil treatment (Gurnell et al., 2007) was applied in the germination trials. A free-draining soil treatment mimics field capacity conditions to support germination and growth of propagules and seedlings respectively.

The 250 ml sub-samples were spread on top of 500 ml sterilised compost (FertileFibre®) in bottom-draining 20.5 x 15 x 5 cm plastic seed trays and 50 ml of vermiculite was sprinkled on top to help prevent desiccation. Seed trays were arranged randomly in the germination room, watered daily and then illuminated using 600-W Growmaster model Metal-Halide lamps for a period of 16 hrs. per day as propagules germinate best in alternating light and darkness at the stipulated photoperiod (Gurnell et al., 2008a). Seed trays were periodically rotated in position to avoid differences in light exposure and the soil surface was periodically disturbed to break up any surface barriers created by mould or algae (Amrein et al., 2005; Adams and Steigerwalt, 2011). The seedling emergence method was used to determine the number of viable propagules in the sediment sample (Thompson et al., 1997; see Boedeltje et al., 2002 for aquatic plants). As propagules germinated they were identified to species level using various printed references (e.g. Rose, 2006) and on-line sources and then removed from the seed tray. Where seedlings proved difficult to identify, they were transplanted into pots and grown-on until it was possible to identify their species.

Seedling species were assigned to four main groups (herbs, rushes, grasses and woody species). In addition to the number of species recorded in each sample (propagule species richness), the number of viable propagules per unit volume (propagules per litre) and surface area (propagules per square metre) of the original bulk sample were estimated (Formulae 3.2 and 3.3) to allow comparison with other published data (Butler and Chazdon, 1998; Gurnell et al., 2007).

Number of viable
propagules per litre = A*(B/C)*(1000/D) [Formulae 3.2]

Number of viable
propagules per m^2 = $[A*(B/C)] / (n*\pi* r^2)$ [Formulae 3.3]

where A is the abundance of viable propagule species per mesohabitat; B is the total volume of < 4 mm sediment fraction (ml); C is the volume of < 4 mm sediment fraction (ml) used for germination trials; D is the total volume of the bulk sediment sample (ml); n is the number of sediment core replicates; π is pi equal to 3.1416; r is the radius of the corer cutting edge.

The above, standardised approach to seed storage and germination aimed to provide comparable (relative) germination trial results based on a manageable laboratory effort. However, it is important to note that more complex and time-consuming treatments are needed if the germination requirements of all species are to be met and a more comprehensive evaluation of the viable seed bank is to be achieved (e.g. Boedjelte et al., 2002, 2003).

CHAPTER 4

RESPROUTING WOOD AND ISLAND DEVELOPMENT ALONG AN ISLAND-BRAIDED RIVER: THE FLAGOGNA REACH, TAGLIAMENTO RIVER, ITALY

4.1 INTRODUCTION

In naturally-functioning river reaches, aquatic and riparian systems are usually tightly coupled through the longitudinal and lateral transfer of energy, water, mineral and organic sediment and plant material (Tockner et al., 1999; Ward et al., 2002). Where the riparian zone is dominated by woodland, large wood is an important component of the material that is mobilised, transported and deposited by the river, and it has a fundamental influence on the retention and stabilisation of transported material and the consequent development of landforms and habitats within the river channel and its margins (Fetherston et al., 1995; Abbe and Montgommery, 1996; Edwards et al., 1999a, 1999b; Gurnell et al., 2005; Gurnell, 2013).

As outlined in Chapter 2, the dynamics, morphology and geomorphological role of large wood varies with the river type (e.g. Gurnell et al., 2002) and tree species (Gurnell, 2013). This chapter focuses on a large island-braided river influenced by tree species that are capable of sprouting once deposited on exposed river sediment. Previous geomorphological research on large wood in this type of river environment has proposed a model of island development that depends upon interactions between fluvial processes and large wood to create pioneer islands which enlarge, aggrade and coalesce to form building islands and eventually established islands (Gurnell et al., 2001, 2005). In parallel, plant ecological research has identified an increase in species diversity and a change in species composition of island vegetation as the islands follow the trajectory from pioneer (typically 1 to 5 years in age) to established islands that have persisted for 10-20 years (Kollmann et al., 1999), and has also found a positive association between the morphology and size of the geomorphic features (e.g. depth of scour hole induced by flow divergence at the upstream face and depth of fine sediment retained at the core of the island) associated with pioneer islands of a fixed age and the species richness of island vegetation (Francis et al., 2008a). In these studies, differences in island vegetation composition were inferred to relate to (i) the species abundance of plant propagules retained along with fine sediments during island development, (ii) the morphological and sedimentary structure of islands as they enlarge and aggrade, offering different habitats for vegetation colonisation, and (iii) competition between species as island vegetation cover develops. However, to date no study has explicitly investigated any of these possible relationships.

Therefore, this chapter investigates the physical properties and vegetation characteristics of pioneer and building islands of three different ages within the same island-braided reach of the Tagliamento River, Italy, which is characterised by tree species that are capable of sprouting following uprooting and deposition by the river. The reported research explores relationships between the standing vegetation, mid-summer propagule bank and the morphology and sediment characteristics within and between islands of different age, focusing on the following research questions:

i. Do the physical characteristics (morphology, sediments, and wood) of pioneer islands that build around deposited wood change with increasing pioneer island age?

ii. Does the species composition of the standing vegetation on pioneer islands change with increasing pioneer island age?

iii. Does the species abundance of the sediment / soil propagule bank found on pioneer islands and their associated habitats change with pioneer island age?

iv. Are there any significant associations between the physical characteristics of pioneer islands of different age and their standing vegetation and propagule banks?

4.2 STUDY SITE

An overview of the research design and research sites included in this thesis was provided in Chapter 3. The research for this chapter was conducted along the gravel-bed, island-braided Tagliamento River reach at Flagogna (Figure 4.1A), which is located between 74 to 76 km from the river's source (Gurnell et al., 2000a and 2000b; Gurnell and Petts, 2006).

The 2 km study reach (Figure 4.1B) has an average slope of 0.0029 $m.m^{-1}$ and the active, braided corridor extends to an average width of approximately 600 m (Gurnell and Petts, 2006). The size of the bed material within the active corridor is highly variable, ranging from the coarsest channel lag deposits (D_{50} ~ -6 phi; cobbles) to the coarsest bar top deposits (D_{50} ~ -4 phi; pebbles) to sands and silts on some bars and within the islands (Gurnell and Petts, 2006). These sediments form an alluvial aquifer with a water table that fluctuates widely through the year, maintaining varying water levels within scour pools around pioneer islands (Francis et al., 2008a). The unconstrained braided corridor is characterised by a continually changing mosaic of water bodies (active river channels, scour ponds), bare sediment (dry channels, bars), and vegetation (from areas of young sparse seedlings and saplings on bar and dry channel surfaces to mature closed tree cover on established islands) that is driven by the flashy flow regime of the river (Figure 4.2), and a plentiful supply of sediment and large wood (Tockner et al., 1999; Gurnell et al., 2000a; Arscott et al., 2002; van der Nat et al., 2003). The strongly varying water levels associated with the river's flashy flow regime disturb sediments and vegetation within the active corridor leading to widespread erosion of bars and islands and also deposition of sediment and large wood (Bertoldi et al., 2009, 2013)

Although confined on one side by steep hillslopes, the river in the study reach has developed a floodplain on its right bank, where many plant species coexist in the riparian woodland. The dominant pioneer riparian tree species is *Populus nigra*, but *Alnus incana*, and several willow species (*Salix elaeagnos*, *S. daphnoides*, *S. alba*, *S. purpurea*, *S. triandra*) are also abundant (Karrenberg et al., 2003). Although *Alnus incana* is less prone to regenerate from wood fragments and entire uprooted trees, *Populus nigra* and the several willow species regenerate freely vegetatively (Gurnell et al., 2000a, 2000b). These pioneer species cover established islands in the reach and provide large amounts of wood to the river (Gurnell et al., 2005).

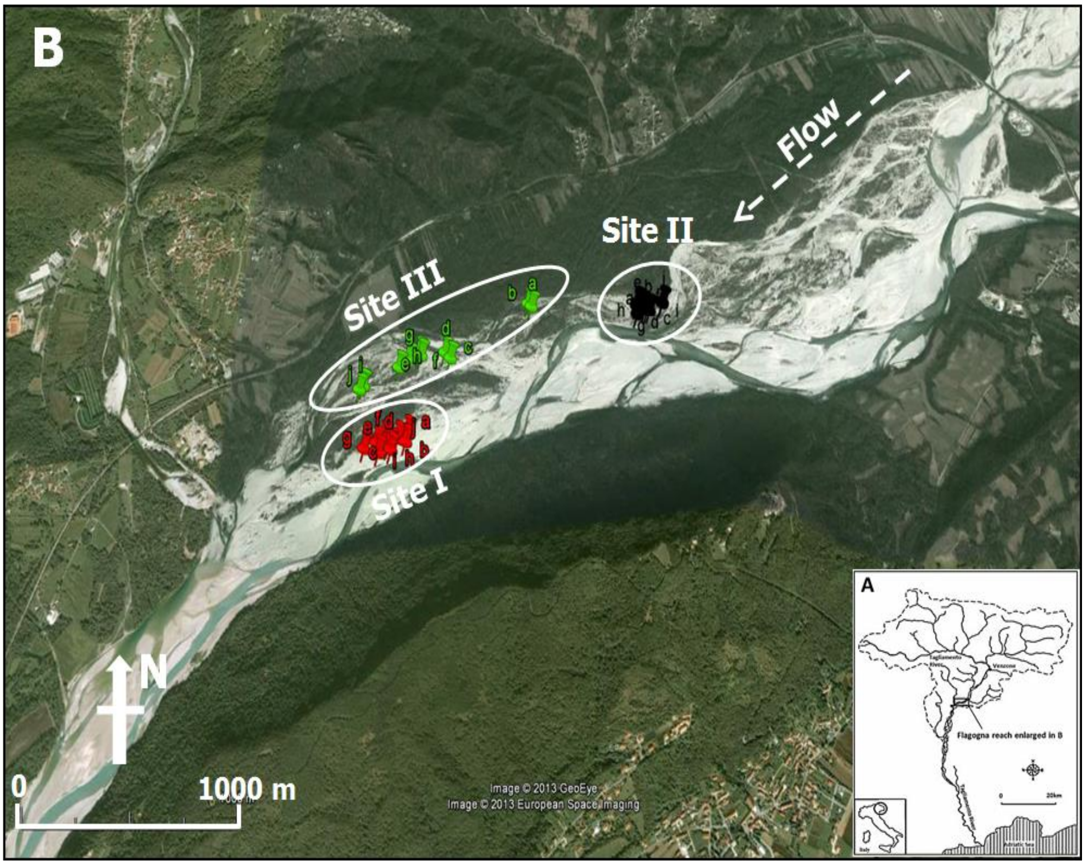


Figure 4.1. (A) The catchment of the Tagliamento River, showing the location of the Flagogna study reach; (B) Aerial image of the Flagogna study reach, showing the location of sampling Sites I, II and III and the pioneer islands that were investigated (Source: Google earth accessed on 22/01/2013, 06:04).

Three sampling sites were identified in the study reach where islands of different age were abundant (Figure 4.1B). These were areas where uprooted trees were deposited during floods in the winters of 2000-2001, 2004-2005 and 2009-2010 (Figure 4.2), giving pioneer islands of known ages (i.e. time since initial deposition of wood by a flood event): 1 year (Site I), 7 years (Site II) and 11 years (Site III) at the time of field sampling. The floods in the winter of 2000-2001 were the largest, mobilising a large quantity of wood over a wide area, hence Site III covers a larger area than Sites I and II. In contrast, the floods in the winters of 2004-2005 and 2009-2010 were less intensive resulting in more localised deposition of wood and thus more confined sampling areas at Site I and Site II.

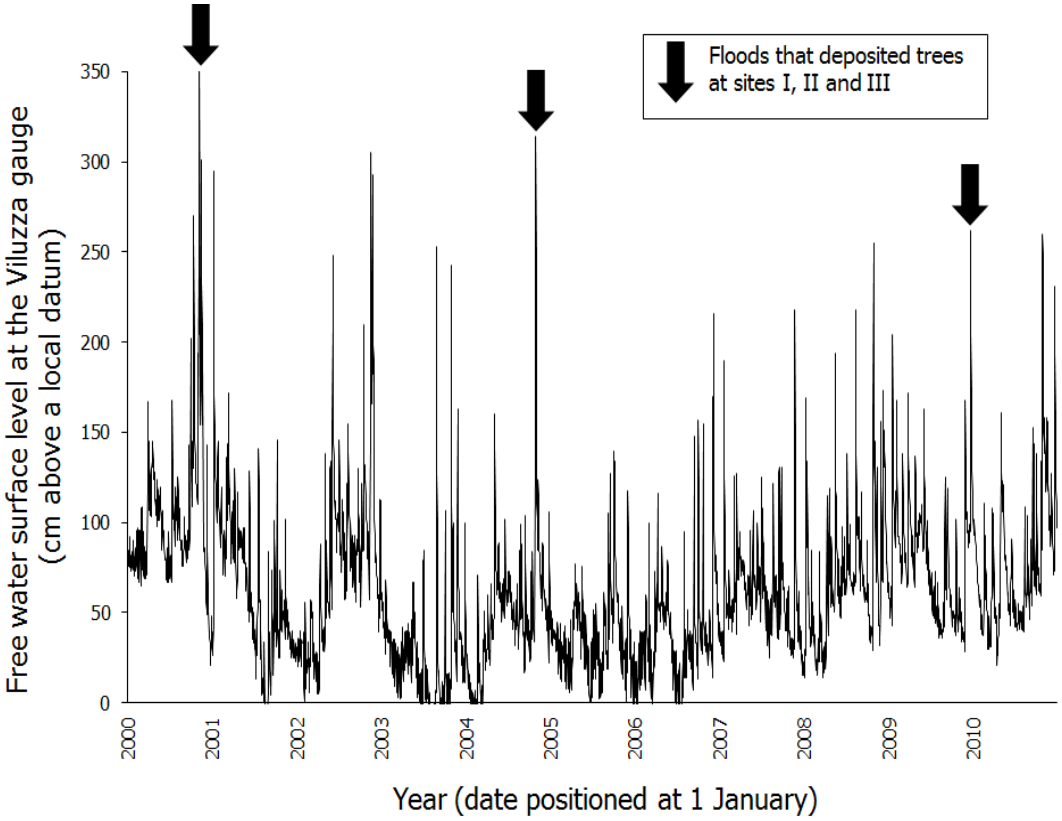


Figure 4.2. River stage recorded at the Villuzza gauge (1 January 2000 to 31 December 2010), showing the 2000, 2004 and 2009 wood-mobilizing flood events that deposited the sampled trees at Sites I, II and III.

4.3 METHODS

4.3.1 Research Design

Figure 4.3 illustrates the stages of development of pioneer islands suggested by Gurnell et al. (2001, 2005). In order to investigate the characteristics of pioneer islands of different age, ten islands were selected from each of three sites (I, II and III, Figure 4.1). The ten islands were selected at random within each site, although only discrete pioneer islands were selected that were centred on a single deposited tree (Site I) or showed a discrete elongated morphology (Sites II and III). The typical character of pioneer islands graded between Figure 4.3A and B at Site I and was similar to C at Sites II and III. All field measurements and sampling were conducted between 22 and 30 July 2011 when river levels were low and most plant species were in flower.

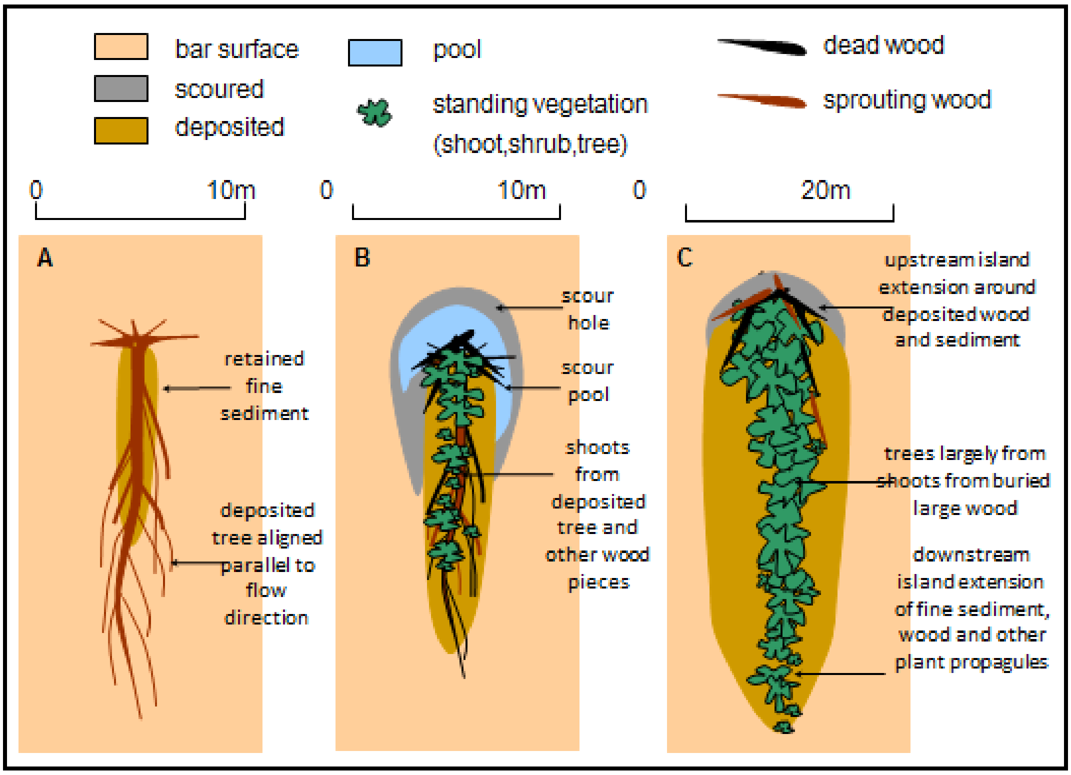


Figure 4.3. Phases of development of a pioneer island: A. early retention of sediment by a deposited tree / main large wood piece; B. sprouting of roots and shoots to create a flow obstruction that results in significant fine sediment accumulation around the deposited tree and, frequently in scour of the bar surface and trapping of wood at the upstream end and; C. complete burial of the original tree and extension of the island upstream, downstream and laterally, leaving a line of new trees that have sprouted from buried wood and trapped propagules and extension of the island upstream, downstream and laterally (modified from Gurnell, 2013).

4.3.2 Field Methods

Three types of measurements and / or samples were collected from the three field sites (Figure 4.1); (i) at all ten islands within each site, measurements were made of the dimensions of each island and the deposited tree (Site I only) and the longest shoot (Site I) or growing tree (Sites II and III); (ii) at five islands within each site, sediment samples were collected to provide data on sediment calibre, organic content and the plant propagule bank; (iii) at the same five islands within each site, a detailed survey of the standing vegetation was conducted, recording species presence and the percentage vegetation cover of the island surface.

(i) Island and wood dimensions

The dimensions of pioneer islands and their deposited tree (Site I) or the longest shoot / tree (Sites I, II and III) were obtained for all ten pioneer islands at each of the three sites. Dimensions were measured using a 30 m tape, 1 m rule and clinometer (to estimate tree heights).

Three island dimensions were measured at all three sites (Figure 4.4B and C): the maximum elevation of the island surface above the surrounding bar surface (PIH); the maximum length of the island defined by the length of the area of finer retained sediment (PIL); and the maximum width defined by the width of the area of retained finer sediment (PIW). At Site I, the depth of scour pool (DSP) around the apex (upstream) of the deposited tree and the dimensions of the deposited tree and its root bole were also measured as these may influence the subsequent dimensions of the pioneer island (Figure 4.4A). The depth of scour pool was not measured at Sites II and III because few scour pools were readily identifiable on the sampled islands. Measurement of deposited tree dimensions at Site I focused on the total length of the deposited tree (LT), the diameter of the tree 1 m above the root bole (DT), the height (HST) and diameter (DST) of the tallest new shoot (i.e. shoot that had sprouted following tree deposition), and the width (WTC), length (LTC) and height (HTC) of the tree canopy. For the root bole, its maximum width (WRB), length (LRB) and height (HRB) were measured. At Sites II and III, the original deposited trees could no longer be identified because they were buried within the pioneer island. However, the species, height (HST) and trunk diameter at 1 m above the ground surface (DST) were recorded for the largest tree on the island. In addition, a core was taken from the trunk of the largest tree on the island, at 1m above the ground surface, in order to estimate the tree age from its growth rings. The largest tree was selected since it was assumed to be the oldest regenerated shoot from the original deposited tree, thus could be used to estimate and confirm the age of the island.

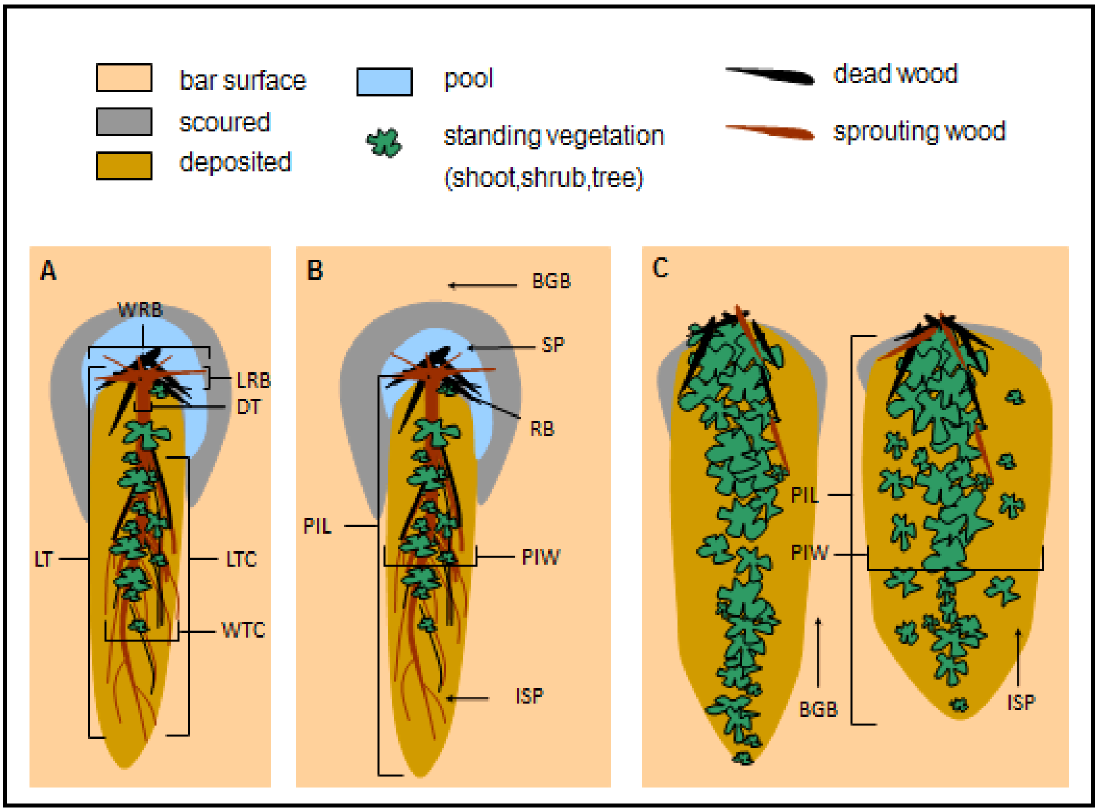


Figure 4.4. Typical patterning of landforms (mesohabitats) around islands and measured island and tree dimensions at: Site I (A and B) and Sites II and III (C). Mesohabitats readily identified at Site I are scour pool (SP), root bole (RB), bare gravel bar (BGB) and island sediment plume (ISP), while BGB and ISP are also identifiable at Sites II and III. Additional measured island and tree dimensions at Site I are length of deposited tree (LT), diameter of deposited tree trunk (DT), length of deposited tree root bole (LRB), width of deposited tree root bole (WRB), height of deposited tree root bole (HRB, not illustrated), length of deposited tree canopy (LTC), width of deposited tree canopy (WTC), and height of deposited tree canopy (HTC, not illustrated). Additional dimensional measurements at Sites I, II and III are pioneer island length (PIL), pioneer island width (PIW) and pioneer island height (PIH, not illustrated), and the height (HST, not illustrated) and diameter (DST, not illustrated) of the largest shoot / tree.

(ii) Sediment and propagule bank sampling

The number of pioneer islands selected for sampling, number of samples obtained and the single mid-summer (July) sampling period were constrained by the single field campaign and restrictions on the weight of samples that could be returned by air to the UK. Therefore, sediment samples were collected at only five out of the ten pioneer islands investigated at each site.

Bulked sediment samples were collected from up to four specific mesohabitats associated with each sampled pioneer island in order to characterise mesohabitat sediment and propagule bank properties. The surfaces of pioneer islands (fine sediment plume retained within each island) and the nearby open gravel bars were two mesohabitats sampled at all three sites, and at Site I additional bulked samples were obtained from two further mesohabitats: the root bole of the deposited tree and the bed of the scour hole associated with each sampled pioneer island (Figure 4.4, Table 4.1). At Sites II and III, scour holes were not a prominent feature of the pioneer islands, probably because of lack of recent inundation of the sites which would have prevented wind-blown and rain-washed sediments from completely filling these depressions. Additionally, the root boles of the deposited trees were not present, either as a result of burial or decomposition.

Table 4.1. The number of bulked samples obtained to characterise mesohabitats associated with pioneer islands at Sites I, II and III. Each bulked sample was assembled from 3 replicate samples, apart from open bar surfaces where 4 replicate samples* were bulked to ensure sufficient finer sediment for laboratory analysis from these relatively coarse sediments.

Mesohabitats	**Abbreviations**	**Definitions**	**Number of mesohabitats per site**		
			Site I	**Site II**	**Site III**
Bare gravel bar	BGB	Open (unvegetated) bar surface	5*	5	5
Root bole	RB	Sediment accumulated in and under the root bole of a recently deposited tree	5	-	-
Scour pool	SP	Surface within scoured areas or scour pools adjacent to the root bole and trunk of a recently deposited tree	5	-	-
Island sediment plume	ISP	Sediment from the (vegetated) surface of a pioneer island	5	5	5

Samples were bulked mainly to provide a more representative composite sample of the propagule species present, because propagule banks tend to be highly spatially heterogeneous (Fenner and Thompson, 2005), and also to obtain a representation of the sediment calibre across the mesohabitat. Each bulked sample was a composite of three samples extracted from random locations within the sampled mesohabitat apart from the bulked samples from open bar surfaces where four samples were combined to ensure sufficient fine sediment for analysis in these predominantly gravel deposits. The individual samples were obtained using a 6 cm diameter cylindrical corer to a depth of 5 cm. Propagule bank samples are typically collected to depths of 5 cm because this region of the soil usually contains the highest density of viable propagules and is most likely to include propagules that form part of the transient as well as the persistent propagule bank (Thompson et al., 1997; Fenner and Thompson, 2005). It is important to note that propagule banks are not only highly variable in space but also through time (Fenner and Thompson, 2005), and so the sampling undertaken is only representative of one point in the year (mid-summer). As a result, the samples that were obtained should be representative of the persistent propagule bank and of short-lived propagule species released close to the time of sampling. The samples are unlikely to reflect the extremely short-lived propagules of the poplar and willow species present at the sites, which are released early in the summer with a half-life of only a few weeks (Karrenberg and Suter, 2003).

(iii) Vegetation survey

Standing vegetation was surveyed at the same five islands from which propagule bank samples were obtained at each of the three sites. These surveys included an estimate of the overall percentage cover of vegetation on the island (% VC), plus a presence / absence list of all vascular plant species present (Appendix II). From the presence / absence list, species richness of each island (SR) was calculated.

Recorded plant species were also categorised according to their life form (herb, graminoid (hereafter called grass species) and woody species) and life-history (annual, biennial and perennial species). Plant life form and life history were presented in proportions (%) and counts.

4.3.3 Laboratory Methods

Common laboratory methods used in this thesis are described in Chapter 3. The laboratory methods of (i) sediment storage and preparation, (ii) sediment analysis and (iii) germination trials used in this study are described in Chapter 3 (Section 3.6).

4.3.4 Data Analysis

Table 4.2 lists the variables investigated in this study and defines how these were derived from the raw field and laboratory measurements. The variables fall into three broad groups: (i) those that reflect the physical characteristics of the islands (deposited trees and living shoot or tree dimensions; island dimensions and sediment characteristics); (ii) those that reflect the diversity, life forms and life-history of standing riparian vegetation; and (iii) those that describe characteristics of the propagule bank.

The data set was characterised using descriptive statistics and box and whisker plots. These techniques revealed that most of the variables were not normally distributed and the variables frequently showed differences in variance between sites or mesohabitats, so non-parametric statistical methods were used for data analysis.

The primary means of assessing the research questions 1, 2 and 3 was through comparison of medians of the measured variables, via non-parametric analysis of variance (Kruskal-Wallis (KW) tests). KW tests were used to explore whether there were statistically significant differences in island morphology, sediment, wood, propagule bank and standing vegetation variables between the three sites and between the different mesohabitats. Where KW tests indicated a significant difference ($p < 0.05$) in a particular variable between the three sites or between the different mesohabitats, multiple pairwise comparisons were then performed using Dunn’s procedure (Bonferroni corrected significance level) to identify those sites or mesohabitats that exhibited significant contrasts in the variable.

The nature, strength and significance of associations between pairs of variables were explored using the non-parametric Spearman’s rank-order correlation coefficient to identify bivariate physical and biotic associations among early-stage pioneer islands (at Site I) and across islands of different age (Sites I, II and III).

Multivariate associations were then explored using a combination of ordination (Principal Components Analysis – PCA, Detrended Correspondence Analysis – DCA and Direct Gradient Analysis – DGA (Redundancy Analysis (RDA) or Canonical Correspondence Analysis (CCA) as appropriate) and classification (Agglomerative Hierarchical Clustering – AHC) methods. These analyses together with Spearman's rank-order correlation address research question 4.

PCA was applied to the rank correlation matrix among physical variables measured for island and mesohabitats at Sites I, II and III to identify the principal gradients in the measured physical (island morphology, tree and sediment) variables and to explore how these gradients are related to the pioneer island age and mesohabitat types at the sites. Associations between the gradients defined by the principal components (PCs) and study sites or mesohabitats were then investigated by (i) producing scatterplots showing PC scores coded by study site and by mesohabitat types; (ii) applying KW tests to PC scores for island age groups and mesohabitat groups to assess the statistical significance of any apparent differences observed in scatterplots.

AHC (Dissimilarity index: Bray and Curtis distance; clustering algorithm: Ward's method) was applied to the standing vegetation species lists (i.e. presence / absence data) to identify whether there were any clear groupings in species composition reflecting pioneer island age (e.g. Hewson and Fuhrman, 2004; Tabacchi et al., 2005).

DCA was then applied separately to the standing vegetation and propagule data sets (presence / absence list) in order to investigate whether there were any gradients in standing vegetation or propagule species composition that reflected island age or mesohabitat types.

Lastly, a direct gradient analysis (DGA) technique was applied to the standing vegetation data sets (presence / absence list) in order to investigate the extent to which species presence or absence reflected changes in physical variables associated with different island age, thus building upon the DCA results. DGA techniques investigate each species' abundance using measured environmental variables (ter

Braak and Prentice, 1988; ter Braak and Verdonschot, 1995). The type of DGA technique used is usually predetermined by the gradient lengths obtained by performing DCA on the specific dataset of interest. If the resulting gradient lengths are > 4 then a non-linear (or unimodal) response model is appropriate (i.e. Canonical Correspondence Analysis (CCA)), whereas if the gradient lengths are < 4 a linear method is appropriate (ReDundancy Analysis (RDA)) (ter Braak and Prentice, 1988; ter Braak, 1996).

KW tests, Spearman's rank-order correlation, PCA and AHC were performed using XLSTAT-Pro software (version 9.1.3, 2009), while DCA and DGA were performed using CANOCO v4.5 (ter Braak and Smilauer, 2002).

Table 4.2. Variables resulting from field measurements and laboratory measurements of samples collected from study sites.

Variables and Abbreviations	**Full name**	**Site of measured variable**	**Description**
Wood variables			
(i) Deposited tree			
LT	Length of deposited tree	Site I	The total length of the core deposited trees on each pioneer islands (m).
DT	Diameter of deposited tree	Site I	The diameter of the deposited tree at 1m above the root bole (m).
LRB	Length of deposited tree root bole	Site I	Longitudinal distance from the base of the tree trunk to the base of the root bole (m).
WRB	Width of deposited tree root bole	Site I	Horizontal width of the root bole perpendicular to the trunk (m).
HRB	Height of deposited tree root bole	Site I	Vertical height of the root bole measured from the ground surface (m).
LTC	Length of deposited tree canopy	Site I	The maximum horizontal length of the deposited tree canopy parallel to the trunk (m).
WTC	Width of deposited tree canopy	Site I	The maximum horizontal diameter of the deposited tree canopy perpendicular to the trunk (m).
HTC	Height of deposited tree canopy	Site I	The maximum vertical height of the deposited tree canopy from the ground surface (m).
(ii) Longest shoot / largest tree			
HST	Height of longest shoot / largest tree	Sites I, II and III	The height of the tallest shoot (Site I) or the largest tree (Sites II and III) on each pioneer islands (m).
DST	Diameter of longest shoot / largest tree	Sites I, II and III	The diameter of the longest shoot at its base (Site I) or the diameter of the largest tree at 1m above the ground surface (Sites II and III) (m).
Island morphology variables			
PIL	Pioneer island length	Sites I, II and III	The maximum length of the island defined by the length of the retained sediment plume (m).
PIW	Pioneer island width	Sites I, II and III	The maximum width defined by the width of the retained sediment plume (m).
PIH	Pioneer island height	Sites I, II and III	The maximum elevation of the island's sediment surface above the surrounding bar surface (m).
DSP	Scour pool depth	Site I	The difference in elevation between the lowest point in the scour hole and the highest point on the pioneer island sediment surface (m).

Table 4.2. (Continued)

Variables and Abbreviations	**Full name**	**Sites of measured variable**	**Description**
Standing vegetation variables (see Appendix II)			
SR	Species richness	Sites I, II and III	The number of vascular plant species present on a pioneer island.
% VC	Vegetation cover	Sites I, II and III	The percentage cover (nearest 5 %) of vegetation on pioneer island.
HB	Number of herb species	Sites I, II and III	The number of herb species present on a pioneer island.
GM	Number of grass species	Sites I, II and III	The number of grass species present on a pioneer island.
WS	Number of woody species	Sites I, II and III	The number of woody species present on a pioneer island.
% HB	Percentage of herb species	Sites I, II and III	The percentage of the total plant species present that are herb species ((Number of herb species on island ÷ Species richness of island) x 100).
% GM	Percentage of grass species	Sites I, II and III	The percentage of the total plant species present that are grass species ((Number of grass species on island ÷ Species richness of island) x 100).
% WS	Percentage of woody species	Sites I, II and III	The percentage of the total plant species present that are woody species ((Number of woody species on island ÷ Species richness of island) x 100).
Ann	Number of annual species	Sites I, II and III	The number of annual species present on a pioneer island.
Bien	Number of biennial species	Sites I, II and III	The number of biennial species present on a pioneer island.
Per	Number of perennial species	Sites I, II and III	The number of perennial species present on a pioneer island.
% Ann	Percentage of annual species	Sites I, II and III	The percentage of the total plant species present that are annual species ((Number of annual species on island ÷ Species richness of island) x 100).
% Bien	Percentage of biennial species	Sites I, II and III	The percentage of the total plant species present that are biennial species ((Number of biennial species on island ÷ Species richness of island) x 100).
% Per	Percentage of perennial species	Sites I, II and III	The percentage of the total plant species present that are perennial species ((Number of perennial species on island ÷ Species richness of island) x 100).

Table 4.2. (Continued)

Variables and Abbreviations	Full name	Sites of measured variable	Description
Propagule bank variables			
T PropSR	Propagule species richness	Sites I, II and III	The total number of propagule species identified in germination trials.
T Prop/l	Propagules per litre	Sites I, II and III	The number of viable propagules per unit volume of sampled mesohabitat sediment; Prop/l = Number of viable propagule species in sediment sample x (Total volume of < 4 mm sediment fraction ÷ volume of < 4 mm sediment fraction used in germination trials) x (1000 / Total volume of sediment sample).
T Prop/m^2	Propagules per square metre	Sites I, II and III	The number of viable propagules per unit surface area of sampled mesohabitat; Prop/l = Number of samples collected with the corer x pi (3.1416) x (Radius of the corer)^2.
	Number of herb propagules	Sites I, II and III	The number of herb propagules present at the sampled mesohabitat.
	Number of grass propagules	Sites I, II and III	The number of propagules present at the sampled mesohabitat.
	Number of rush propagules	Sites I, II and III	The number of rush propagules present at the sampled mesohabitat.
	Number of woody propagules	Sites I, II and III	The number of woody propagules present at the sampled mesohabitat.
Sediment characteristics variables			
% OM	% Organic Matter	Sites I, II and III	Percentage organic matter content of bulk mesohabitat sediment sample.
D_{50}	Median D_{50} (phi) value	Sites I, II and III	Median particle size of bulk mesohabitat sediment sample expressed in phi units.
% G	% Gravel	Sites I, II and III	Percentage of gravel in bulk mesohabitat sediment sample.
% S	% Sand	Sites I, II and III	Percentage of sand in bulk mesohabitat sediment sample.
% ST	% Silt	Sites I, II and III	Percentage of silt in bulk mesohabitat sediment sample.
% C	% Clay	Sites I, II and III	Percentage of clay in bulk mesohabitat sediment sample.

4.4 RESULTS

4.4.1 Physical and Biotic Characteristics of Pioneer Islands

Summary statistics describing the magnitude and variability of the investigated variables across the sampled mesohabitats and / or sites are provided in Table 4.3 and through box and whisker plots (Figures 4.5 to 4.11). The results of KW tests (followed by multiple pairwise comparisons) investigating differences in the magnitude of some of the investigated variables in relation to pioneer island age and / or mesohabitats are presented in Table 4.4.

(i) Wood (deposited trees and largest shoots / trees) characteristics

At Site I, pioneer islands consisted of single uprooted trees deposited by floods during the winter of 2009-2010 floods. Eight of the sampled islands at Site I were developed around *Populus nigra* or *Salix spp*. and the remaining two islands were associated with *Alnus incana*. The uprooted trees show median length and diameter of 17.10 m and 0.19 m and its root bole and canopy show median length, diameter / width and height of 1.80 m, 3.75 m and 0.95 m, and 11.13 m, 4.70 m and 1.13 m, respectively (Table 4.3). These relatively large uprooted trees had produced new shoots (sprouting trees), averaging 0.85 m (median 0.81 m) in height, following deposition. At Sites II and III the largest trees on the sampled islands were *Populus nigra* or *Alnus incana* with no *Salix spp*. recorded as the largest tree.

The median and interquartile range of both the diameter and length / height of the largest shoot (Site I) or tree (Sites II and III) varied greatly across the three sites (Table 4.3) and there was a statistically significant increase in shoot / tree size with increasing island age (Table 4.4, Figure 4.5).

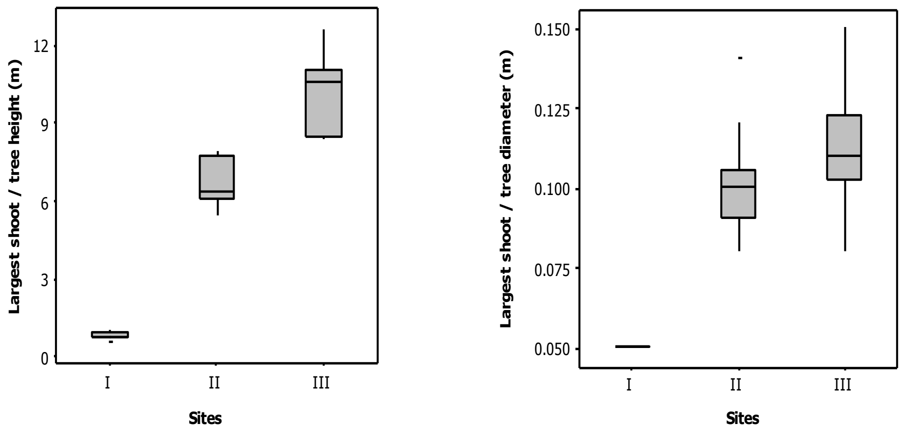


Figure 4.5. Box-whisker plots illustrating the length / height and diameter of the longest shoot / largest trees on pioneer islands surveyed at Sites I, II and III.

(ii) Island morphology characteristics

Scour holes associated with pioneer islands at Site I had a median depth of 0.55 m and showed little variability (Q1 = 0.38 m, Q3 = 0.68 m; Table 4.3). Pioneer islands varied greatly in size within and between Sites I to III (Figure 4.6) but showed no significant difference in size (length - PIL, width - PIW) between sites. In contrast, multiple pairwise comparisons showed Site I to have statistically significantly lower island surface elevation relative to the adjacent bar surface than Sites II and III (PIH, Table 4.4). This suggests that island surface elevation increases with increasing age of islands although islands at Site II (7 yrs.) and Site III (11 yrs.) did not show statistically significant differences in their elevation above surrounding bar surfaces.

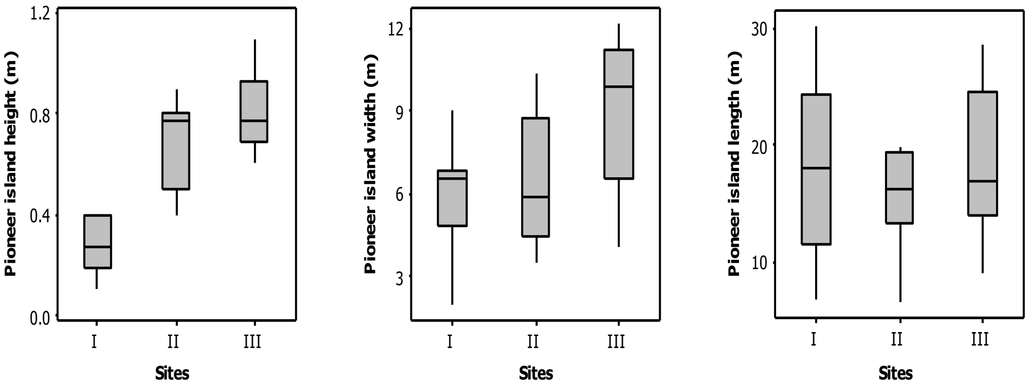


Figure 4.6. Box-whisker plots illustrating the height, width and length of islands surveyed at Sites I, II and III.

Table 4.3. Summary of physical (longest shoot / largest tree, island morphology and sediment) and biotic (standing vegetation and propagule bank) characteristics of islands and / or mesohabitats across Sites I, II and III.

	Site I				**Site II**				**Site III**			
	Mean	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**
Longest shoot / largest tree [a]												
HST	0.85	0.81	0.80	0.88	6.75	6.44	6.23	7.59	10.20	10.69	8.73	10.89
DST	0.05	0.05	0.05	0.05	0.10	0.10	0.09	0.10	0.11	0.11	0.11	0.12
LT	16.83	17.10	12.00	23.50								
DT	0.20	0.19	0.14	0.25								
LRB	2.06	1.80	1.25	2.70								
DRB	3.23	3.75	1.85	4.20								
HRB	1.07	0.95	0.70	1.36								
LTC	10.93	11.13	5.28	16.10								
WTC	4.32	4.70	3.33	5.20								
HTC	1.28	1.13	0.80	1.65								
Island morphology [a]												
PIL	18.28	18.00	13.35	22.93	15.69	16.25	13.78	19.33	18.69	16.75	14.28	23.40
PIW	5.98	6.50	5.03	6.70	6.47	5.90	4.73	8.15	8.96	9.85	6.68	10.85
PIH	0.28	0.28	0.20	0.39	0.69	0.78	0.53	0.80	0.80	0.78	0.70	0.88
DSP	0.58	0.55	0.38	0.68	0.69	0.78	0.53	0.80	0.80	0.78	0.70	0.88
Standing vegetation [b]												
SR	19.20	22.00	12.00	23.00	27.80	26.00	26.00	33.00	31.00	30.00	25.00	33.00
% VC	8.00	10.00	5.00	10.00	88.00	90.00	80.00	95.00	99.00	100.00	100.00	100.00
HB	10.40	11.00	6.00	14.00	16.20	18.00	12.00	20.00	19.60	19.00	15.00	21.00
GM	3.20	4.00	2.00	5.00	4.40	5.00	4.00	5.00	3.40	3.00	2.00	5.00

Table 4.3. (Continued)

	Site I				Site II				Site III			
	Mean	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**
WS	5.60	6.00	4.00	7.00	7.20	8.00	7.00	9.00	8.00	8.00	8.00	9.00
% HB	53.29	50.00	50.00	55.56	56.76	60.61	46.15	65.71	62.18	63.33	60.00	63.64
% GM	15.02	18.18	16.67	18.52	15.72	18.18	11.43	19.23	11.24	9.09	8.00	11.63
% WS	31.69	31.82	25.93	33.33	27.52	22.86	21.21	34.62	26.58	27.27	25.00	30.00
Ann	1.40	1.00	1.00	2.00	1.80	2.00	1.00	2.00	1.80	1.00	1.00	2.00
Bien	1.00	1.00	0.00	2.00	0.80	1.00	1.00	1.00	2.00	2.00	1.00	2.00
Per	16.80	19.00	11.00	21.00	25.20	25.00	23.00	28.00	27.20	27.00	23.00	29.00
% Ann	6.54	8.33	4.55	8.70	5.87	5.71	3.85	7.69	5.37	4.17	4.00	6.06
% Bien	4.89	7.41	0.00	8.33	3.00	3.03	2.86	3.85	6.04	6.06	4.17	6.67
% Per	88.58	91.67	82.61	91.67	91.13	91.43	88.46	94.74	88.59	90.00	87.88	91.67

		Site I				Site II				Site III			
	Mesohabitats	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**
Sediment characteristics [b]													
% OM	BGB	1.42	1.38	1.31	1.43	2.65	2.57	2.30	3.38	2.38	2.68	1.99	2.71
	ISP	1.71	1.93	1.91	2.11	2.81	2.70	2.59	2.81	3.50	3.10	2.88	3.16
	SP	2.23	2.29	2.02	2.46								
	RB	2.46	2.44	2.43	2.46								
D_{50}	BGB	-1.70	-2.06	-2.09	-2.05	2.34	3.23	3.06	3.67	2.93	3.08	2.65	3.71
	ISP	3.39	3.31	2.98	3.70	3.69	3.92	3.50	3.99	3.80	3.70	3.11	4.33
	SP	1.45	0.88	0.82	2.14								
	RB	4.21	4.55	3.51	4.77								

Table 4.3. (Continued)

		Site I				**Site II**				**Site III**			
	Mesohabitats	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**
% G	BGB	65.30	66.91	62.71	68.98	22.93	11.22	6.43	28.57	17.97	10.34	0.02	34.67
	ISP	2.35	3.19	0.00	3.25	0.01	0.00	0.00	0.00	1.25	0.00	0.00	2.75
	SP	23.07	31.53	13.31	31.73								
	RB	1.27	0.34	0.00	2.70								
% S	BGB	30.99	31.86	28.71	32.62	43.82	46.13	31.84	56.02	49.37	45.07	40.06	59.97
	ISP	60.18	64.48	53.34	64.54	58.24	52.54	50.39	64.74	54.33	59.60	37.34	72.81
	SP	56.54	56.39	52.14	59.45								
	RB	44.74	37.20	34.05	57.13								
% ST	BGB	3.17	1.93	1.77	3.97	28.94	34.02	27.92	37.34	29.31	31.10	16.93	36.23
	ISP	32.92	28.59	26.42	38.60	37.17	42.83	31.17	44.79	39.37	36.77	23.97	53.06
	SP	17.40	20.84	10.11	23.82								
	RB	46.01	51.86	33.22	55.17								
% C	BGB	0.53	0.38	0.31	0.70	4.32	4.75	4.09	5.57	3.34	2.89	2.32	3.79
	ISP	4.55	3.82	3.62	4.87	4.57	4.63	4.09	4.82	5.05	3.63	3.22	6.85
	SP	2.99	2.45	1.97	3.85								
	RB	7.99	8.25	6.46	9.80								

Table 4.3. (Continued)

		Site I				Site II				Site III			
	Mesohabitats	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**	**Mean**	**Median**	**Q1**	**Q3**
Propagule bank variables [b]													
T PropSR	BGB	1.2	1	1	1	2	1	1	2	0.6	0	0	1
	ISP	1.4	1	1	2	2	2	2	2	1.4	1	1	2
	SP	1.2	1	1	1								
	RB	3	3	2	4								
T Prop/l	BGB	5.17	2.83	2.08	3.96	11.02	8.89	4.60	16.15	3.88	0.00	0.00	4.00
	ISP	6.98	5.17	4.00	11.86	14.20	15.81	11.86	16.00	7.53	7.62	3.95	8.44
	SP	6.73	5.21	4.34	8.32								
	RB	16.82	15.52	11.67	15.77								
T Prop/m^2	BGB	222.66	132.63	128.61	176.84	1583.96	1222.59	813.05	2268.17	115.65	0.00	0.00	136.17
	ISP	305.00	214.57	179.95	522.11	675.78	669.65	580.05	792.27	317.09	338.31	179.20	381.99
	SP	249.23	196.49	171.49	338.31								
	RB	610.99	539.84	495.17	660.22								

The number of samples used in the analyses at the different sites and mesohabitats are represented with different superscripts (a = 10 and b = 5).

Table 4.4. Kruskal-Wallis tests exploring the statistical significance of difference in the values of physical and biotic variables between islands and / or mesohabitats at Sites I, II and III.

Variables	**Kruskal-Wallis *p* value**	**Degrees of freedom**	**Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)**
Longest shoot / largest tree [a]			
HST	< 0.0001	2	Site III > Site II > Site I
DST	< 0.0001	2	Site III, Site II > Site I
Island morphology variables [a]			
PIL	0.598	2	n.s.
PIW	0.038	2	n.s.
PIH	< 0.0001	2	Site III, Site II > Site I
Standing vegetation variables [b]			
SR	0.082	2	n.s.
% VC	0.002	2	Site III > Site I
HB	0.080	2	n.s.
GM	0.514	2	n.s.
WS	0.108	2	n.s.
% HB	0.262	2	n.s.
% GM	0.470	2	n.s.
% WS	0.763	2	n.s.
Ann	0.875	2	n.s.
Bien	0.168	2	n.s.
Per	0.028	2	Site III > Site I
% Ann	0.784	2	n.s.
% Bien	0.194	2	n.s.
% Per	0.732	2	n.s.

Table 4.4. (Continued)

	Mesohabitats at Site I			**Mesohabitats at Sites I, II and III**					
	RB, BGB, ISP and SP mesohabitats			**BGB mesohabitats**			**ISP mesohabitats**		
Variables	**Kruskal-Wallis *p* value**	**Degrees of freedom**	**Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)**	**Kruskal-Wallis *p* value**	**Degrees of freedom**	**Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)**	**Kruskal-Wallis *p* value**	**Degrees of freedom**	**Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)**
Sediment characteristics ^{b}									
% OM	0.009	3	RB > BGB	0.067	2	n.s.	0.005	2	Site III > Site I
D_{50}	0.001	3	RB, ISP > BGB	0.034	2	Site III > Site I	0.691	2	n.s.
% G	0.002	3	BGB > ISP, RB	0.017	2	Site I > Site III	0.280	2	n.s.
% S	0.015	3	ISP > BGB	0.196	2	n.s.	0.932	2	n.s.
% ST	0.002	3	RB, ISP > BGB	0.013	2	Site III, Site II > Site I	0.878	2	n.s.
% C	0.002	3	RB > BGB	0.017	2	Site II > Site I	0.990	2	n.s.
Propagule bank ^{b}									
T PropSR	0.156	3	n.s.	0.220	2	n.s.	0.749	2	n.s.
T Prop/l	0.157	3	n.s.	0.100	2	n.s.	0.400	2	n.s.
T Prop/m^2	0.125	3	n.s.	0.010	2	Site II > Site III	0.278	2	n.s.

Kruskal-Wallis tests were separately performed on the values of each of the variables within the sites and mesohabitats associated to islands at the sites to assess the degree to which the sites and mesohabitats represented statistically significantly different ($p < 0.05$) values of the variables. Multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those sites and mesohabitats that were significantly different from one another ($p < 0.05$). The number of samples used in the analyses at the different sites and mesohabitats are represented with different superscripts (a = 10 and b = 5).

(iii) Sediment characteristics

Four mesohabitats were investigated at Site I and their sediment characteristics are summarised in Figure 4.7 and Table 4.3. The median of D_{50} grain sizes in samples obtained from bare gravel bar (BGB), scour pool (SP), island sediment plume (ISP) and root bole (RB) mesohabitats was -2.1, 0.9, 3.3 and 4.6 phi, respectively. The D_{50} particle size of the sediment deposits associated with young pioneer islands (around the root bole and island sediment plume) was finer than the bare gravel bar sediment deposits and was characterised by significantly higher % silt and lower % gravel than the deposits on adjacent bare gravel bar surfaces (Table 4.4). Root bole mesohabitats were characterised by significantly higher % clay and % organic matter than bare gravel bar mesohabitats, whereas island sediment plume mesohabitats were characterised by significantly higher % sand (median 64.5 %) than bare gravel bar mesohabitats (median 31.9 %) (Table 4.4). This suggests that the finer sediment deposits at root bole mesohabitats contain more clay, silt and organic matter than the other mesohabitats associated with young pioneer islands at Site I.

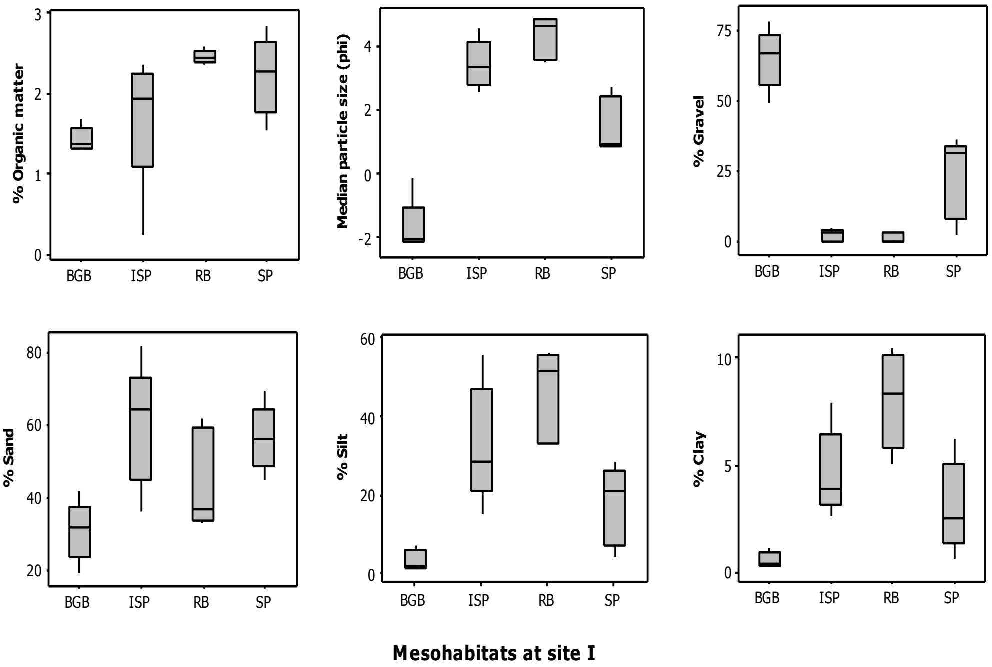


Figure 4.7. Box-whisker plots illustrating organic matter content and particle size characteristics of sediment samples from BGB, ISP, RB and SP mesohabitats associated with the islands at Site I.

Figure 4.8 illustrates the variability in sediment characteristics across bare gravel bar (BGB) and island sediment plume (ISP) mesohabitats at Sites I, II and III. For the island sediment plume samples, only % organic matter differed significantly between Sites with % organic matter increasing with island age. Sediment plumes on islands at Sites I and III were highly variable in % organic matter and median particle size particularly for the islands at Site III. For the bare gravel bar samples, samples at Site I were significantly coarser and characterised by significantly lower % silt and higher % gravel than at Site III, suggesting that bare gravel bar sediment deposits become finer as nearby islands increase in age.

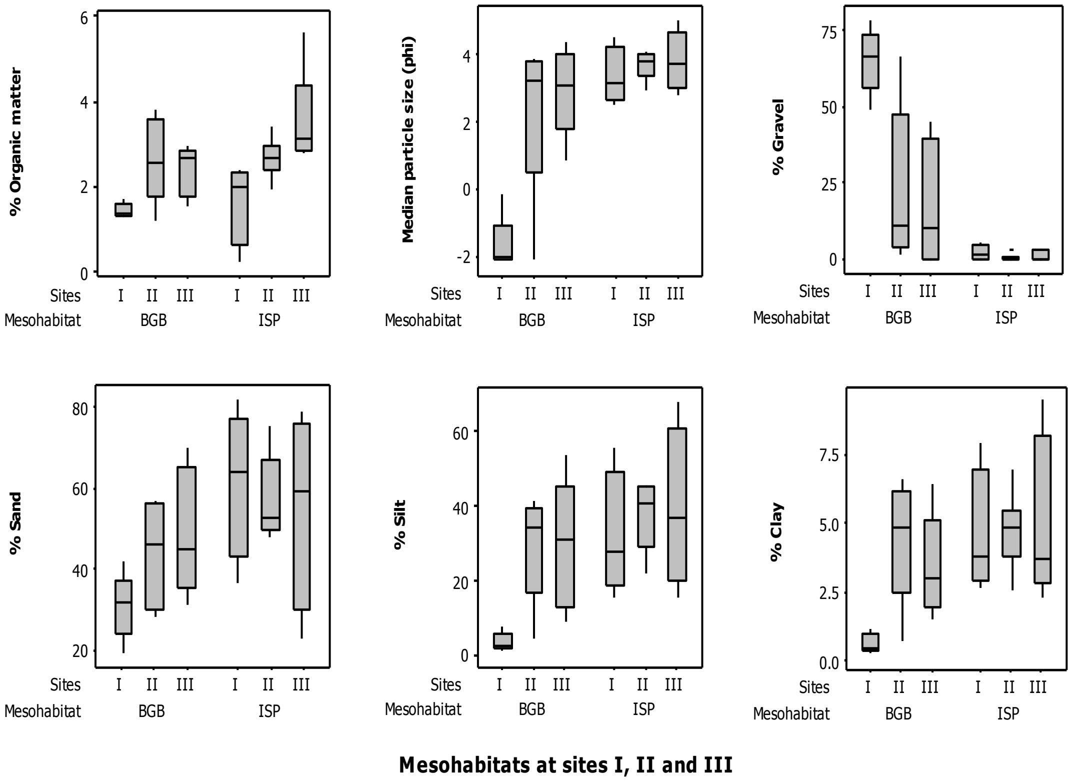


Figure 4.8. Box-whisker plots illustrating organic matter content and particle size characteristics of sediment samples from BGB and ISP mesohabitats associated with the islands at Sites I, II and III.

(iv) Standing vegetation characteristics

Overall, 103 plant taxa were identified on the surveyed islands (see Appendix II). The plant species present consisted of 14 grass, 69 herb and 20 woody species, and 10 annual, 7 biennial and 86 perennial species. The composition of the standing vegetation varied widely, even among islands of the same age (see Appendix II). As a result, although there was an increase in species richness with island age (Figure 4.9), this was not statistically significant (Table 4.4).

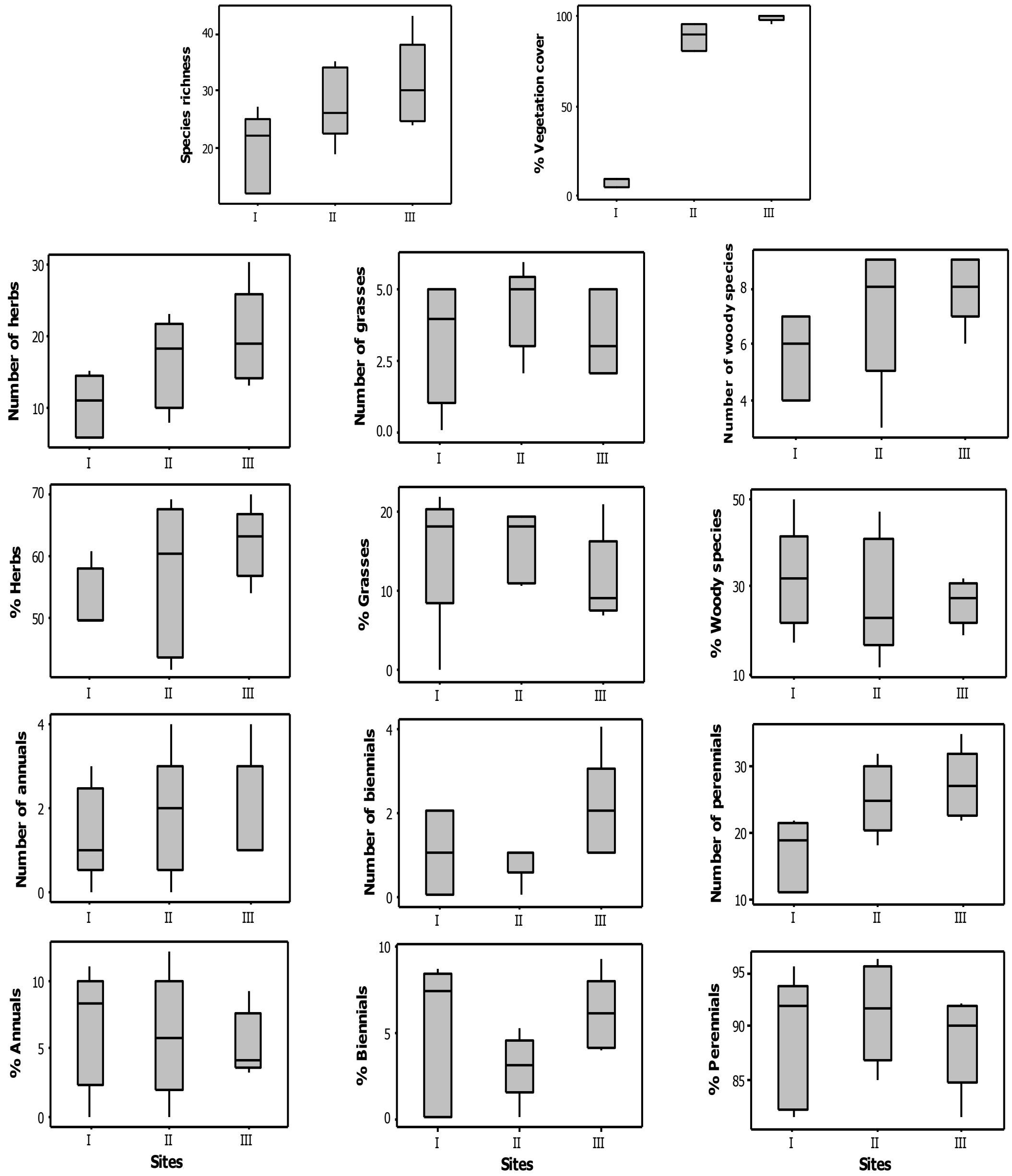


Figure 4.9. Species richness, % vegetation cover, life form (number of and % grass, herb and woody species), and life-history (number of and % annual, biennial and perennial species) of standing vegetation on islands at Sites I, II and III.

At Site I, the vegetation cover associated with the sediment plume around deposited trees was lower (median 5 % cover) and poorer in plant species (median 22 plant species) compared to the older sites (Sites II and III). Vegetation at Site I was observed to be concentrated around the root bole and scour pool. Compared to the older sites (Site II and III) , the vegetation covering on sampled islands at Site I were high in woody (median 31.82 %) and grass (median 18.18 %) species, and annual (median 8.33 %) and biennial (median 7.41 %) species. However, vegetation covering islands at Site I were largely perennials (median 91.67 %) which mostly comprised of herb (median 50 %) and woody (median 31.82 %) species.

Vegetation cover significantly increased with island age (Table 4.4). The number of perennial species also significantly increased with island age (Table 4.4). Although not statistically significant, there was also a trend towards increasing species richness with increasing island age particularly in the number of herb and woody species, and the number of biennial species (Figure 4.9) but there was no apparent trend in the number of annual and grass species across the island age groups.

When the relative proportions of the vegetation groups were considered, there was a trend towards an increasing proportion (%) of herb species and a decreasing proportion of annual, perennial and grass species with increasing island age (Figure 4.9), but there was no apparent trend in the proportion of woody and biennial species with island age.

Across islands at Sites I, II and III, the most frequently present perennial woody species were *Amorpha fruticosa*, *Populus nigra*, *Salix elaeagnos* and *Salix purpurea* and herb species were *Convolvulus arvensis, Melilotus alba, Rubus caesius, Solidago canadensis* and *Tripleurospermum maritimum*.

(v) Viable propagule bank characteristics

Table 4.5 lists the propagule species and the median number of viable propagules germinated. A total of 25 species emerged from the sediment samples during the germination trials. The most frequently found species were *Agrostis stolonifera* and *Conyza sumatrensis* (particularly present on the bare gravel bar mesohabitats).

Figure 4.10 illustrates the species richness and abundance of the propagule banks of mesohabitats found at Site I. The species richness of the viable propagule bank varied considerably between mesohabitats at Site I (Figure 4.10). Root bole mesohabitats showed the greatest variability and had a higher propagule species richness and number of viable propagules per unit volume (propagules per litre (per litre)) and surface area (propagules per square metre (m^2)) than bare gravel bar, island sediment plume and scour pool mesohabitats although this difference was not statistically significant.

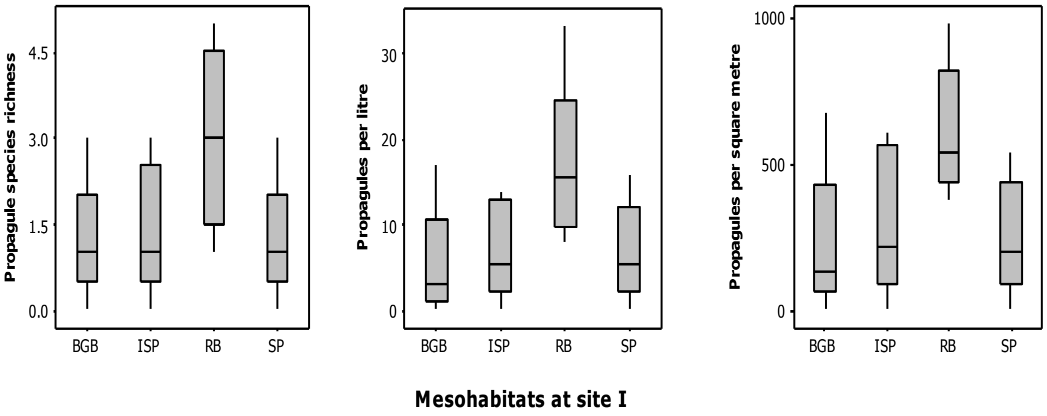


Figure 4.10. Propagule species richness, viable propagules per square metre and viable propagules per litre of BGB, ISP, RB and SP mesohabitats associated with islands at Site I.

Figure 4.11 illustrates the species richness and abundance of the propagule banks of mesohabitats found at Site I, II and III. Propagule species richness and abundance (per litre and per m^2) within bare gravel bar and island sediment plume mesohabitats varied greatly within and between Sites I, II and III (Figure 4.11) and there was no clear trend in the number of propagule species or propagule abundance across the island age groups. Kruskal-Wallis analyses revealed that the propagule species richness and the median number of propagules deposited (per litre) across bare gravel bars and island plume mesohabitat were not significantly different between the three study sites. The highest propagule species richness and abundance for island sediment plume and bare gravel bar mesohabitats were found at Site II, with propagule abundance (per m^2) at BGB mesohabitats being significantly higher at Site II than at Site III.

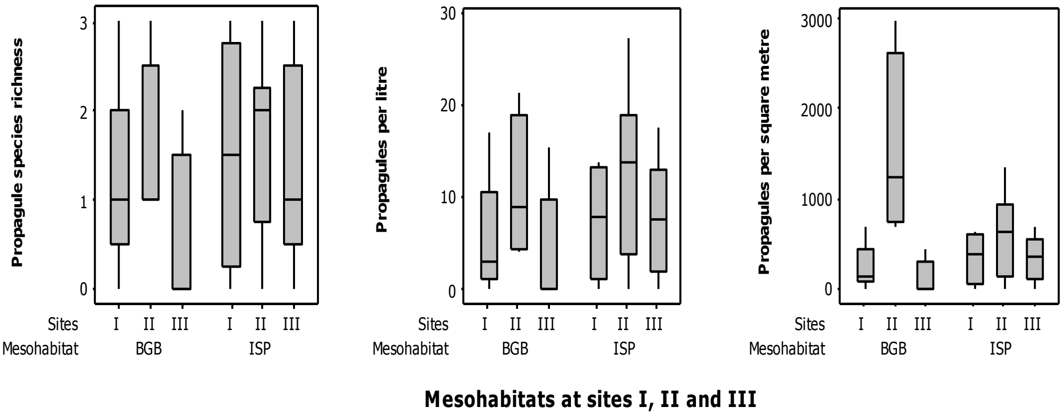


Figure 4.11. Propagule species richness, viable propagules per square metre and viable propagules per litre of bare gravel bar (BGB) and island sediment plume (ISP) samples at Sites I, II and III.

The vegetation group proportions within bare gravel bar, island sediment plume, scour pool and root bole mesohabitat samples at Site I all varied slightly (Table 4.5). Kruskal-Wallis analyses for mesohabitats associated with islands at Site I revealed no significant difference in the number of herb, rush, grass and woody propagules. However, root bole mesohabitats samples were found to contain a relatively large number of herb propagules (particularly *Rorippa nasturtium-aquaticum* and *Urtica dioica*). In comparing bare gravel bar and island sediment plume mesohabitat samples from Sites I, II and III, mesohabitats associated with islands at Site II contained a larger number of herb, grass and rush propagules. Rush propagules were present in relatively large quantities in all samples from Site II. Grass propagules increased in quantity markedly from bare gravel bars to island sediment plume mesohabitats across the three study sites, whereas woody propagules (all *Buddleja davidii*) decreased in quantity from bare gravel bars to island sediment plume mesohabitats across Sites II and III.

Table 4.5. Propagule species list and median number of propagules per litre and square metre found within the sampled sediment from mesohabitats at Sites I, II and III.

		Propagules per litre (prop/l)								**Propagules per square metre (prop/m^2)**							
		Site I				**Site II**		**Site III**		**Site I**				**Site II**		**Site III**	
Species	**Abbr.**	**BGB**	**ISP**	**SP**	**RB**	**BGB**	**ISP**	**BGB**	**ISP**	**BGB**	**ISP**	**SP**	**RB**	**BGB**	**ISP**	**BGB**	**ISP**
Agrostis stolonifera	Agros s	0	2	0	0	2	9	0	3	0	71	0	0	295	409	0	145
Aster x salignus	Aster x	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	34
Barbarea vulgaris	Barb v	0	0	0	2	0	0	0	0	0	0	0	74	0	0	0	0
Borago officinalis	Borag o	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	36
Buddleja davidii	Budl d	0	0	0	0	3	1	3	0	0	0	0	0	396	40	86	0
Capsicum annuum	Caps a	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	34
Centaurium erythraea	Cent e	1	0	0	0	0	0	0	0	34	0	0	0	0	0	0	0
Chenopodium album	Chen a	0	0	0	1	0	0	0	0	0	0	0	39	0	0	0	0
Chenopodium sp.	Chen sp	0	0	0	1	0	0	0	0	0	0	0	39	0	0	0	0
Conopodium majus	Cono m	0	0	0	1	0	0	0	0	0	0	0	39	0	0	0	0
Conyza canadensis	Cony c	0	0	0	0	2	0	0	0	0	0	0	0	295	0	0	0
Conyza sumatrensis	Cony s	2	3	4	4	2	2	1	0	94	110	141	173	314	77	30	0
Daucus carota	Dau c	0	0	0	1	0	0	0	0	0	0	0	39	0	0	0	0
Epilobium sp.	Epi sp	2	2	1	0	0	0	0	1	69	84	36	0	0	0	0	34
Euphorbia cyparissias	Eupho cy	0	0	1	0	0	0	0	0	0	0	36	0	0	0	0	0
Galium mollugo	Galli m	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypericum humifusum	Hydro h	0	0	1	0	0	0	0	0	0	0	36	0	0	0	0	0
Juncus effusus	Jun ef	0	0	0	1	0	1	0	0	0	0	0	39	0	40	0	0
Juncus sp.	Jun sp	0	0	0	0	1	1	0	0	0	0	0	0	133	34	0	0
Lycopersicon lycopersicum	Lycop l	1	0	0	0	0	0	0	0	26	0	0	0	0	0	0	0
Persicaria lapathifolia	Pers la	0	0	0	1	0	0	0	0	0	0	0	33	0	0	0	0
Rorippa nasturtium-aquaticum	Rorip n	0	0	0	1	0	0	0	0	0	0	0	33	0	0	0	0
Urtica dioica	Urti d	0	0	0	2	0	0	0	0	0	0	0	69	0	0	0	0
Veronica sp.	Vero sp	0	0	0	1	0	0	0	1	0	0	0	33	0	0	0	34
Veronica beccabunga	Vero b	0	1	0	0	1	2	0	0	0	41	0	0	151	77	0	0
Total number of propagules		6	8	7	16	11	16	4	8	223	306	249	610	1584	677	116	317
Number of herb propagules		6	6	7	15	5	4	1	4	223	235	249	571	760	154	30	138
Number of grass propagules		0	2	0	0	2	9	0	3	0	71	0	0	295	409	0	145
Number of rush propagules		0	0	0	1	1	2	0	0	0	0	0	39	133	74	0	0
Number of woody propagules		0	0	0	0	3	1	3	1	0	0	0	0	396	40	86	34

4.4.2 Relationship between Physical Characteristics of Islands and Their Standing Vegetation and Propagule Banks

(i) Spearman's rank correlation analyses

Table 4.6 presents Spearman rank correlations between wood, island morphology, sediment, standing vegetation and propagule bank variables of the early-stage pioneer islands at Site I. Correlations between wood and island morphology variables were estimated using data from all ten sampled pioneer islands. Other correlations were conducted with data from five pioneer islands. In the case of the sediment, standing vegetation and propagule bank data, these refer to the island sediment plume samples only. Due to the small number of samples used in the correlations, very high values of the correlation coefficient were needed to achieve a statistically significant result.

Considering the inter-correlations among tree and island dimensions at Site I (n = 10), the diameters and lengths of the deposited trees are significantly positively correlated with island length, and the width of the deposited tree canopies are significantly positively correlated with the depth of scour holes, suggesting that larger deposited trees are associated with longer islands and deeper scour holes.

Correlations between island and tree dimensions, sediment and propagule bank variables (n = 5), illustrate a positive association between tree size (diameter) and the % clay of island plume sediment and a negative association with the % sand of island plume sediment. In addition the width of pioneer islands is negatively associated with the % gravel, propagule species richness and propagule abundance in island plume sediments. Thus, overall there is a trend towards finer sediments and relatively low propagule abundance and species richness in the plumes associated with larger young pioneer islands.

Correlations between the dimensions of deposited trees and vegetation variables (n = 5), illustrate a decrease in the proportion of herb and biennial species and an increase in the proportion of perennial species with increasing tree size (length and diameter); an increase in the number of woody species with increasing root bole length and tree canopy height; and an increase in vegetation species richness, vegetation cover, and the number of herb, grass, annual and perennial species with tree canopy width.

Correlations between island dimensions and vegetation variables (n = 5), illustrate an increase in vegetation species richness, vegetation cover, number of herb and perennial species with scour pool depth; and an increase in the number of perennial species and the proportion of biennial species with sediment plume height and length, respectively.

Overall, despite the small sample size and the restriction to early-stage pioneer islands, these correlations illustrate the importance of tree dimensions for island dimensions and the importance of both of these sets of properties for the characteristics of the retained sediment and standing vegetation.

Table 4.7 presents Spearman's rank correlations among core tree, island morphology, sediment, standing vegetation and propagule bank variables of pioneer islands of different age across Sites I, II and III. Correlations between the core tree dimensions and island dimensions were estimated using data from all ten pioneer islands at each site (30 samples). However, correlations between tree and island dimensions and variables describing sediment, standing vegetation and propagule bank characteristics were conducted with data from five islands at each site (15 samples). In the case of the sediment, standing vegetation and propagule bank data, these refer to the island sediment plume.

Considering inter-correlations between tree and island dimensions, pioneer islands show a significant positive correlation between both the height and diameter of longest shoots / largest trees and the height or relative elevation of the island surfaces above the surrounding bar surfaces, suggesting that aggradation of the surface of pioneer islands increases significantly with island age.

Table 4.6. Spearman rank correlations among physical and biotic variables measured on islands at Site I (emboldened correlations are statistically significant, $p < 0.05$; emboldened underlined correlations are for small samples of 5 observations, where the correlation is very high but not quite statistically significant.

Variables	Abbr.	HST	LT	DT	LRB	WRB	HRB	LTC	WTC	HTC	DSP	PIL	PIW	PIH
Tree and deposited wood	HST	**1.0**												
	LT	-0.4	**1.0**											
	DT	-0.4	**0.9**	**1.0**										
	LRB	-0.1	**0.7**	0.5	**1.0**									
	WRB	-0.6	0.2	0.5	0.2	**1.0**								
	HRB	-0.5	0.6	0.4	0.4	0.3	**1.0**							
	LTC	0.2	0.4	0.1	0.4	-0.3	-0.1	**1.0**						
	WTC	-0.1	0.1	-0.1	0.5	-0.1	0.3	0.2	**1.0**					
	HTC	0.0	0.5	0.3	**0.7**	0.0	0.6	0.0	**0.7**	**1.0**				
Island morphology	DSP	0.3	-0.1	0.0	0.5	0.1	-0.1	0.1	**0.7**	0.5	**1.0**			
	PIL	-0.4	**1.0**	**0.9**	**0.7**	0.3	0.6	0.4	0.0	0.4	-0.1	**1.0**		
	PIW	-0.4	0.0	0.1	0.1	0.6	0.1	0.1	0.4	0.0	0.5	0.0	**1.0**	
	PIH	0.6	-0.3	-0.3	0.1	-0.5	-0.2	0.2	0.4	0.3	**0.6**	-0.4	0.1	**1.0**
Sediment	% OM	0.4	0.4	0.6	0.6	-0.4	-0.2	-0.3	0.1	0.7	0.6	0.4	-0.2	0.7
	D_{50}	0.3	0.3	0.7	0.2	-0.3	-0.2	-0.6	-0.3	0.4	0.3	0.3	-0.1	0.5
	% G	0.7	0.6	0.1	0.2	-0.7	0.1	0.7	-0.2	-0.1	-0.4	0.6	**-0.9**	-0.3
	% S	-0.1	-0.5	**-0.9**	0.0	0.1	-0.2	0.7	0.6	-0.3	0.1	-0.5	0.2	-0.1
	% ST	0.3	0.3	0.7	0.2	-0.3	-0.2	-0.6	-0.3	0.4	0.3	0.3	-0.1	0.5
	% C	0.1	0.5	**0.9**	0.0	-0.1	0.2	-0.7	-0.6	0.3	-0.1	0.5	-0.2	0.1
Standing vegetation	SR	0.1	-0.4	-0.6	0.6	-0.1	-0.4	0.4	**1.0**	0.4	**0.9**	-0.4	0.2	0.8
	% VC	-0.3	-0.3	-0.3	0.6	0.3	-0.1	0.0	**0.9**	0.6	**0.9**	-0.3	0.4	0.7
	HB	0.1	-0.4	-0.6	0.6	-0.1	-0.4	0.4	**1.0**	0.4	**0.9**	-0.4	0.2	0.8
	%HB	-0.2	-0.7	**-0.9**	0.1	0.2	-0.3	0.4	0.8	-0.1	0.4	-0.7	0.5	0.3
	GM	-0.1	-0.6	-0.7	0.4	0.1	-0.5	0.2	**0.9**	0.2	0.8	-0.6	0.5	0.7
	% GM	-0.3	-0.7	-0.7	0.2	0.3	-0.4	0.1	0.8	0.1	0.7	-0.7	0.7	0.6
	WS	0.3	0.6	0.5	**0.9**	-0.3	0.2	0.2	0.5	**0.9**	0.6	0.6	-0.5	0.6
	% WS	0.3	0.7	0.7	-0.2	-0.3	0.4	-0.1	-0.8	-0.1	-0.7	0.7	-0.7	-0.6
	Ann	0.1	-0.2	-0.6	0.7	-0.1	-0.2	0.7	**1.0**	0.4	0.7	-0.2	0.0	0.5
	% Ann	0.1	-0.1	-0.6	0.6	-0.1	-0.1	0.8	**0.9**	0.3	0.5	-0.1	-0.2	0.4
	Bien	0.2	-0.8	**-0.9**	0.0	-0.2	-0.7	0.5	0.6	-0.3	0.5	-0.8	0.4	0.4
	% Bien	-0.2	**-1.0**	**-0.9**	-0.6	0.2	-0.6	0.1	0.2	-0.7	0.1	**-1.0**	0.7	0.0
	Per	0.2	-0.1	-0.2	0.8	-0.2	-0.3	0.2	**0.9**	0.7	**1.0**	-0.1	0.1	**0.9**
	% Per	-0.4	0.5	**0.9**	-0.2	0.4	0.6	-0.8	-0.7	0.2	-0.4	0.5	0.0	-0.3
Propagule bank	T PropSR	0.8	0.6	0.2	0.7	-0.8	-0.1	0.7	0.2	0.4	0.2	0.6	**-0.9**	0.3
	T Prop/l	0.7	0.7	0.3	0.3	-0.7	0.2	0.6	-0.2	0.1	-0.3	0.7	**-1.0**	-0.2
	T Prop/m^2	0.7	0.7	0.3	0.8	-0.7	0.1	0.6	0.3	0.6	0.3	0.7	**-0.9**	0.4

Abbr., Abbreviations of variables; HST, Height of new shoot / sprouting tree (m); LT, Deposited tree length (m); DT , Deposited tree diameter (m); LRB, Root bole length (m); DRB, Root bole diameter (m); HRB, Root bole height (m); LTC, Tree canopy length (m); WTC, Tree canopy width (m); HTC, Tree canopy height (m); DSP, Depth of scour pool (m); PIL, Pioneer island length (m); PIW, Pioneer island width (m); PIH, Pioneer island height (m); % OM, Organic matter; D_{50}, Median sediment particle size (phi); % G, % gravel; % S, % sand; % ST, % silt; % C, % clay; SR, Species richness; % VC, % vegetation cover; HB, the number of herb species; % HB, % herb species; GM, the number of grass species; % GM, % grass species; WS, the number of woody species; % WS, % woody species; Ann, the number of annual species; % Ann, % Annual species; Bien, the number of biennial species; % Bien, % biennial species; Per, the number of perennial species; % Per, % Perennial species; T PropSR, Propagule species richness; T Prop/l, Propagules per litre; T Prop/m^2, Propagules per metre square.

Table 4.7. Spearman rank correlations among physical and biotic variables measured on islands at Sites I, II and III (emboldened correlation coefficients (r_s) are statistically significant, $p < 0.05$).

Variables	Abbr.	HST	DST	PIL	PIW	PIH
Tree	HST	**1**				
	DST	**0.8**	**1**			
Island morphology	PIL	-0.1	-0.14	**1**		
	PIW	0.38	0.23	0.32	**1**	
	PIH	**0.71**	**0.74**	-0.02	0.31	**1**
Sediment	% OM	**0.79**	**0.71**	0.04	0.31	**0.72**
	D_{50}	0.26	0.3	0.36	0.1	0.07
	% G	-0.07	-0.49	0.12	-0.3	-0.28
	% S	-0.18	-0.2	-0.39	0.01	0.09
	% ST	0.16	0.21	0.35	0.06	-0.04
	% C	0.04	0.07	0.35	0.03	-0.13
Standing vegetation	SR	0.52	**0.67**	0.08	0.29	**0.63**
	% VC	**0.88**	**0.69**	-0.02	0.41	**0.65**
	HB	0.5	0.57	0.11	0.26	**0.59**
	% HB	0.31	0.35	0.16	0.11	0.39
	GM	-0.02	0.2	-0.35	0.09	0.54
	% GM	-0.26	-0.08	-0.52	-0.12	0.19
	WS	**0.59**	**0.63**	-0.06	0.41	0.24
	% WS	-0.04	-0.14	0.13	0.01	-0.43
	Ann	0.1	0.29	-0.08	0.3	0.37
	% Ann	-0.18	-0.03	-0.02	0.18	0.11
	Bien	0.35	0.27	-0.29	0.53	0.16
	% Bien	0.15	-0.03	-0.42	0.46	-0.03
	Per	**0.61**	**0.74**	0.11	0.31	**0.7**
	% Per	-0.09	-0.2	0.21	-0.43	-0.13
Propagule bank	T PropSR	0.11	0.18	0.33	-0.03	0.08
	T Prop/l	0.1	0.26	0.27	-0.28	0.13
	T Prop/m^2	0.08	0.29	0.22	-0.2	0.23

Abbr., Abbreviations of variables; HST, Height of new shoot / sprouting tree (m); DST , Diameter of new shoot / sprouting tree (m); PIL, Pioneer island length (m); PIW, Pioneer island width (m); PIH, Pioneer island height (m); % OM, Organic matter; D_{50}, Median sediment particle size (phi); % G, % gravel; % S, % sand; % ST, % silt; % C, % clay; SR, Species richness; % VC, % vegetation cover; HB, the number of herb species; % HB, % herb species; GM, the number of grass species; % GM, % grass species; WS, the number of woody species; % WS, % woody species; Ann, the number of annual species; % Ann, % Annual species; Bien, the number of biennial species; % Bien, % biennial species; Per, the number of perennial species; % Per, % Perennial species; T PropSR, Propagule species richness; T Prop/l, Propagules per litre; T Prop/m^2, Propagules per metre square

The height and diameter of the largest shoot or tree also show significant positive correlations with % organic matter in the retained sediment, % vegetation cover of the island, number of woody species and number of perennial species in the standing vegetation. The height of the island surface above the surrounding bar surface also shows a significant positive correlation with % vegetation cover, vegetation species richness, the number of herb and perennial species. These results suggests that island and core tree growth are associated with changes in the diversity and structure of the standing vegetation and also soil development.

(ii) Multivariate analysis and classification of island characteristics

Island physical characteristics were explored using Principal Components Analysis. This was followed by an analysis of the composition of the standing vegetation using a combination of Hierarchical Cluster Analysis and Detrended Correspondence Analysis. The associations between the composition of the standing vegetation and the physical and biotic characteristics of sampled islands were then investigated using a direct gradient analysis (DGA) technique.

Principal Components Analysis (PCA) was performed on variables measured for islands at Sites I, II and III to identify the principal gradients in the measured physical variables and to explore how these gradients are related to pioneer island age and mesohabitat type. PCA was performed on a rank correlation matrix. The sediment variables included in the PCA were derived from island sediment plume samples. A reduced set of sediment variables (D_{50}, % OM, % G, % ST + % C) was used to minimise the number of variables included in the analysis, avoid including sets of variables that summed to 100 %, and also avoid duplication (e.g. % ST and % C were both highly correlated and so a combined fine sediment variable (% ST + % C) was used).

Principal Components Analysis performed on variables measured for islands across Sites I, II and III (n = 15), identified three PCs with eigenvalues greater than 1 (Table 4.8). However, only the first two PCs showed high loadings on more than two variables and these two PCs explained 66 % of the variance in the data set. The loadings on PC1, which explains 43 % of the variance in the data set, indicate that it describes a gradient of sediment fining and increasing organic matter content (high positive loadings on % OM, D_{50}, % ST + % C and negative loadings on % G), associated with increasing sediment aggradation (high positive loading on PIH) as islands increase in age (high positive loading on HST and DST). PC2, which explains a further 23 % of the variance, describes a gradient of sediment fining (high positive loadings on D_{50} and % ST + % C) associated with longer islands (positive loading on PIL).

Table 4.8. Eigenvalues, percentage variation explained and variable loadings on the first four components of a PCA performed on pioneer island physical (wood and sediment) variables (loadings greater than 0.5 are emboldened and those greater than 0.6 are also underlined). Results of KW tests applied to the scores of islands at Sites I, II and III on the first two PCs.

	PC1	**PC2**	**PC3**	**PC4**
Eigenvalue	3.88	2.09	1.04	0.92
% variance explained	43.13	23.20	11.54	10.17
Cumulative variance (%)	43.13	66.33	77.87	88.04
Loadings				
HST	**0.797**	*-0.362*	*0.329*	*-0.163*
DST	**0.836**	*-0.278*	*-0.109*	*-0.212*
PIL	*0.032*	**0.600**	**0.626**	*0.255*
PIW	*0.437*	*-0.164*	*0.016*	**0.838**
PIH	**0.718**	*-0.483*	*0.184*	*0.026*
% OM	**0.919**	*-0.079*	*0.125*	*-0.095*
D_{50}	**0.621**	**0.753**	*-0.022*	*-0.103*
% G	**-0.579**	*-0.171*	**0.687**	*-0.211*
% ST + % C	**0.526**	**0.811**	*-0.063*	*-0.108*

	KW *p* **value**	**Degrees of freedom**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Island at Sites I, II and III ^{n}			
PC1	0.007	2	Site III > Site I
PC2	0.512	2	n.s.

All loadings less than 0.5 are shown in italics; n = 15 samples (5 for each site).

Figure 4.12 plots the 15 islands in relation to their scores on PC1 and PC2, and codes them according to Sites I, II and III. In Figure 4.12, islands at Site I are clearly separated and distributed to the left of islands at Sites II and III (which overlap). KW tests confirm statistically significant differences between islands at Site III and Site I according to their scores on PC1 (Table 4.8), indicating that the older islands are characterised by a combination of larger trees, and more elevated island aggraded surfaces comprised of finer sediments with higher organic content. Scores on PC2 show no statistically significant discrimination between islands of different age, but the relatively high score of some Site I and III islands on PC2 (Figure 4.12) may reflect the fact that longer islands retain finer sediment relative to other islands at Site I and III.

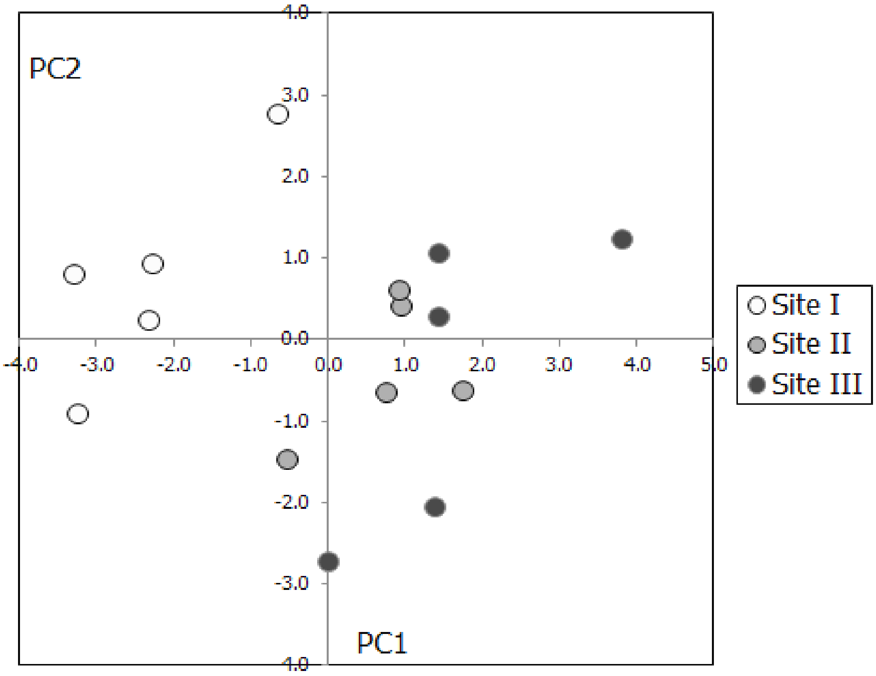


Figure 4.12. Distribution of pioneer islands of different ages at Sites I, II and III in relation to their scores on PCs 1–2.

Hierarchical Agglomerative Cluster analysis was applied to the presence / absence data set describing the standing vegetation on islands at Sites I, II and III. The analysis was performed using the Bray and Curtis index as a distance measure and Ward's method to perform the clustering. The resulting agglomeration plot (Figure 4.13) reveals three distinct clusters that largely reflect island age. Heterogeneity (within-cluster group variance) of standing vegetation composition within sites increases with increasing island age (Table 4.9), and the standing vegetation communities on older islands (Sites II and III) show greater similarity with one another than with islands at Site I (Figure 4.13).

Table 4.9. The number of observations and the variability within the three clusters identified using species present in the standing vegetation on the 15 surveyed islands.

Clusters	**1**	**2**	**3**
Number of observations	6	5	4
Within-cluster group variance	9.033	13.500	16.917

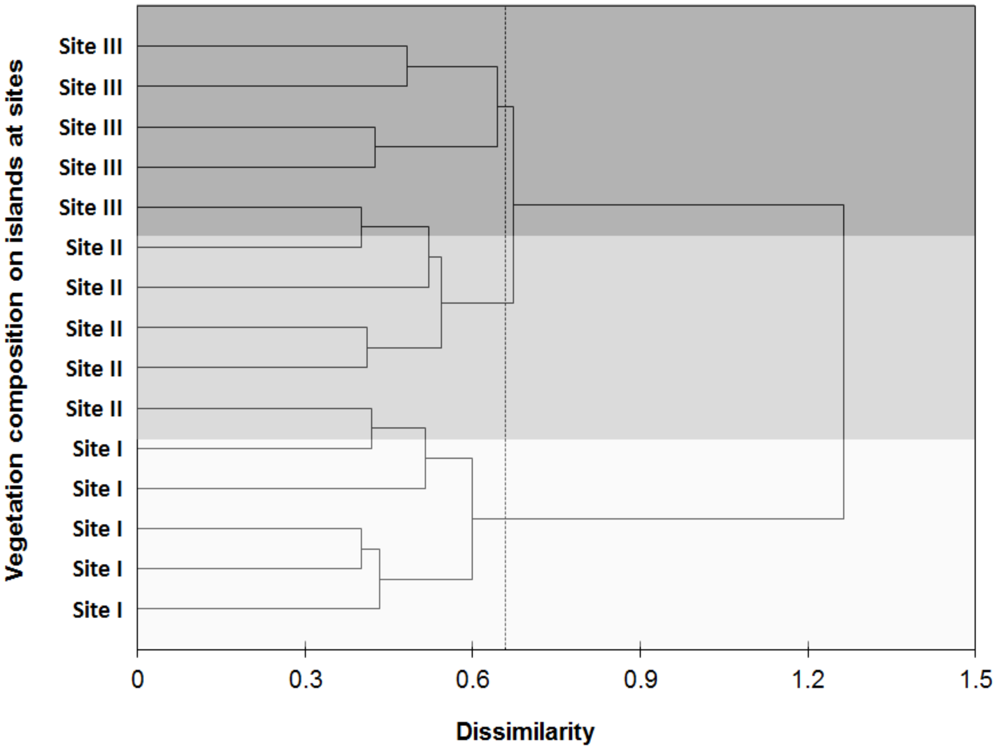


Figure 4.13. Cluster groupings of standing vegetation communities based upon all plant species observed at Sites I, II and III. The shaded areas (from bottom to top) indicate the sites from which the islands are drawn.

Having established the level of similarity in the species composition between islands of different age, species assemblages were further investigated using Detrended Correspondence Analysis. Figure 4.14 shows the DCA biplot for (a) species and (b) sampled islands. All species were used in the analysis with no downweighting of rare species. Eigenvalues for the first two axes were 0.348 and 0.266 and the lengths of gradient (beta diversity) were 2.435 and 2.127. The cumulative % variance within the species data explained by the axes scores were 13.0 and 22.9 %, respectively.

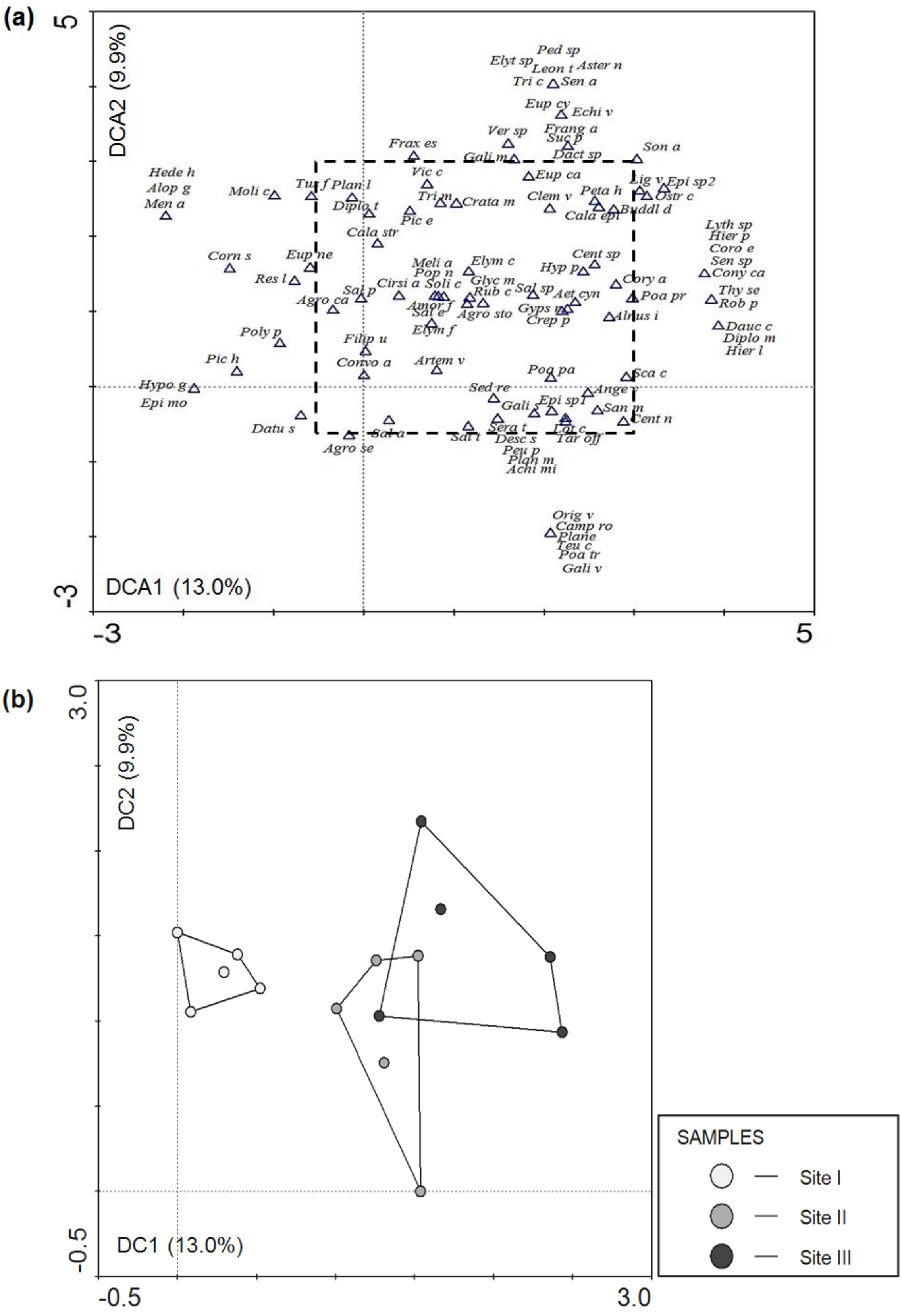


Figure 4.14. DCA ordination plot of (a) plant species and the limits of the plot shown in (b); and (b) sampled islands grouped within polygons reflecting island age (for full species names associated with abbreviations see Appendix II).

The plot in Figure 4.14 (a) shows the distribution of plant species and indicates the limits of the expanded plot shown in Figure 4.14 (b). Figure 4.14 (b) shows the distribution of sampled islands enclosed by polygons of island age. Although no significant trend is observed along DCA axis 2 (p = 0.174), islands are best discriminated by axis 1 (which represents a temporal gradient), with a clear significant distinction of the polygon containing Site I islands from those containing Site III islands (Site III > Site I; p = 0.006), indicating a notable difference in vegetation composition. Furthermore, the increasing trend in the length of gradients (along axis 1) and the size of the polygons from Site I to II to III indicates increasing degree of divergence and heterogeneity in the composition of standing vegetation communities with increasing island age. These observations are similar to conclusions drawn from the cluster analysis. In addition, species observed within and close to the extremes (left for Site I and right for Site III) of the polygons indicate species that are associated with those polygons, whereas species located towards the ends of axis 1 and beyond the limits of the polygons are (often relatively rare) species that are causing the polygons to separate along axis 1. For example, islands at Site I were distinguished from islands at Sites II and III by species occurring towards the left end of axis 1, including *Agrostis canina* (*Agro ca*), *Agrostis setacea* (*Agro se*), *Cornus sanguinea* (*Corn s*), *Datura stramonium* (*Datu s*), *Diplotaxis tenuifolia* (*Diplo t*), *Molinia caerulea* (*Moli c*), *Picris hieracioides* (*Pic h*), *Reseda lutea* (*Res l*) and *Tussilago farfara* (*Tus f*) (Figure 4.14). Plant species that are more strongly associated with islands at Sites II and III (both sites share similar plant species) than at Site I are *Aethusa cynapium* (*Aet cyn*), *Alnus incana* (*Alnus i*), *Angelica vulgaris* (*Ange v*), *Calamagrostis epigejos* (*Cala epi*), *Centaurea nigra* (*Cent n*), *Gypsophila repens* (*Gyps r*), *Hypericum perforatum* (*Hyp p*), *Petasites hybridus* (*Pets h*), *Sanguisorba minor* (*San m*) and *Scabiosa columbaria* (*Sca c*).

After evaluating the variations in standing vegetation species composition across the island age groups using DCA, the associations between the composition of standing vegetation species and the physical and biotic characteristics of sampled islands were investigated using Redundancy Analyses (RDA), a direct gradient analysis (DGA) technique, since the DCA gradient lengths for the standing vegetation dataset for all sites was less than 4. The analysis included the sediment and propagule characteristics of the island sediment plume as well as the core shoot / tree dimensions and island dimensions.

Figure 4.15 shows the RDA biplot locating the sampled sites (based on their vegetation species composition) in relation to the physical and biotic (propagule bank) characteristics (arrows points) of each island. Eigenvalues for the first two axes were 0.156 and 0.109, which are low but this is not unusual for ecological data. The species-environment correlations for the first two axes were 0.995 and 0.963, and the cumulative percentage variance of species data were 15.6 and 26.5 %, which is the variance between sampled sites explained by the standing vegetation species alone. The cumulative percentage variance for the species-environment relationships (i.e. the combination of the physical-biotic characteristics of the islands) as explained by the first two axes was 19.2 and 32.6 %. The environmental variables explained 81.3 % of the variability in the standing vegetation composition. Overall, the standing vegetation data exhibit a strong significant association with island age (HST: $p = 0.002$; F-ratio = 2.04; number of permutations = 499) and elevation in island aggraded surfaces (PIH: $p = 0.028$; F-ratio = 1.52; number of permutations = 499) after a Monte Carlo permutation test of significance for all the physical and biotic variables. Therefore, the relationships between the standing vegetation data and the physical and biotic variables provided a good indication of the principal controls on vegetation structure as the islands develop.

Figure 4.15 illustrates notable groupings and associations between the sampled islands and their physical and biotic characteristics. The relative position of the physical and biotic variables (arrows points) on the RDA biplot reflects their interactions with sampled sites (i.e. the direction of maximum change) and the arrow length is proportional to this maximum rate of change. In Figure 4.15, islands at Site I are clearly separated and distributed to the right of islands at Sites II and III (which overlap) and they plot close to the % gravel vector. Most Site II islands and some Site III islands plot close to variable vectors indicating fine sediments with a relatively high number and richness of propagules in the island sediment plume. The relative position of islands at Sites II and III towards the left on axis 1 reflects their relatively larger core trees, higher island surfaces and greater organic matter content.

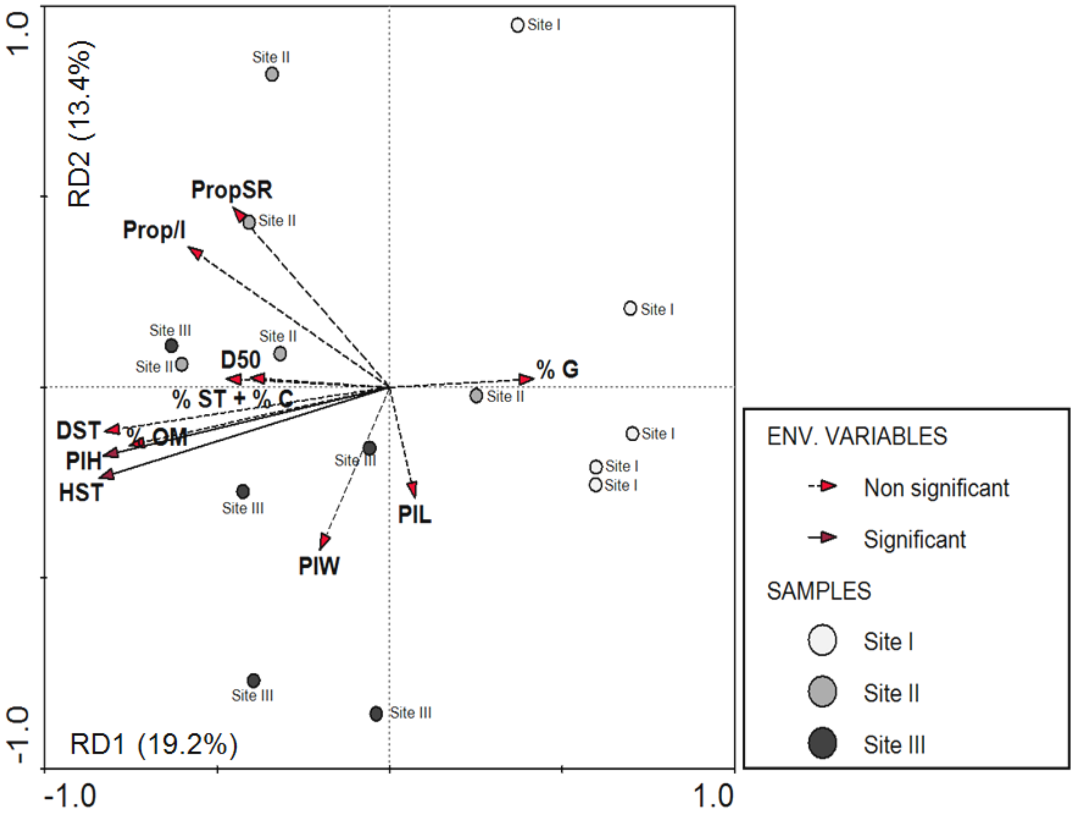


Figure 4.15. RDA ordination plot of sampled sites and their physical and biotic characteristics (arrow points).

(iii) Multivariate analysis and classification of the characteristics of mesohabitats associated with islands

The mesohabitat characteristics of the sampled Sites (I, II and III) were also explored using Principal Components Analysis, followed by an analysis of the composition of the propagule bank using Detrended Correspondence Analysis.

Principal Components Analysis was performed on a rank correlation matrix of mesohabitat sediment variables. The analysis, which was applied to all mesohabitats sampled at Sites I, II and III, identified two PCs which together explained over 91 % of the variability in the data set (Table 4.10).

PC1, which explains over 78 % of the variance in the data set, describes a gradient of increasingly fine sediment (high positive loadings on D_{50}, % ST + % C and negative loading on % G) associated with increasing % organic matter (positive loading on %

OM). PC2, which explains a further 13 % of the variance, describes a gradient of increasing % organic matter (positive loading on % OM) that is independent of the other variables.

Table 4.10. Eigenvalues, percentage variation explained and variable loadings on the first two components of a Principal Components Analysis performed on all Sites I, II and III mesohabitat sediment variables. Kruskal-Wallis tests compare the scores of mesohabitats of different type on the first two PCs.

	PC1	**PC2**
Eigenvalue	3.15	0.52
% variance explained	78.77	13.00
Cumulative variance (%)	78.77	91.78
Loadings		
% OM	**0.770**	**0.620**
D_{50}	**0.958**	*-0.233*
% G	**-0.818**	*-0.013*
% ST + % C	**0.932**	*-0.285*

	KW *p* value	**Degrees of freedom**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Study sites (all mesohabitats associated with islands at Sites I, II and III) [n]			
PC1	0.102	2	n.s.
PC2	0.125	2	n.s.
Mesohabitats shared by all islands at Sites I, II and III (BGB & ISP) [a]			
PC1	0.024	2	n.s
PC2	0.137	2	n.s.
Distinct mesohabitats sampled at Sites I, II and III [b]			
PC1	0.002	7	Site I RB, Site III ISP, Site II ISP > Site I BGB
PC2	0.005	7	Site III ISP > Site I ISP

All loadings > 0.6 are in boldface with all other loadings are shown in italics; n = 40 samples (20 and 10 for mesohabitats sampled at each Site I and Sites II and III respectively); a = 30 samples (10 for mesohabitats sampled at each site); b = 40 samples (5 for each mesohabitat sampled at each site).

Figure 4.16 locates the samples in relation to their scores on PC1-PC2, coded according to (a) study sites, i.e. all mesohabitats associated with islands at each site; (b) those mesohabitats only shared by all islands at Sites I, II and III (ISP and BGB); and (c) distinct mesohabitats sampled at Sites I, II and III. Figure 4.16 (a) shows no clear separation between sites and this is confirmed by the KW tests of scores on PCs 1-2 which showed no statistically significant distinctions between the sites. However, bare gravel bar (BGB) and island sediment plume (ISP) samples at Sites II and III separate marginally along PC1 from BGB and ISP samples at Sites I (Figure 4.16 (b)), suggesting that mesohabitats associated with older islands (Sites II and III) retain relatively finer and more organic sediments (although not statistically significant different from BGB and ISP at Site I). Figure 4.16 (c) shows that bare gravel bar (Site I BGB) and scour pool samples (Site I SP) at Site I separate from root bole samples (Site I RB), Sites II and III island sediment plume samples (Site II ISP and Site III ISP) and bare gravel bar samples at Sites II (Site II BGB). This suggests that bare gravel bar (Site I BGB) and scour pool samples (Site I SP) at Site I are associated with coarser deposits, whereas root bole mesohabitat samples (Site I), bare gravel bar samples at Sites II and island sediment plume samples at Sites II and III are associated with finer and more organic sediment. These distinctions between the mesohabitats associated with islands at the sites were confirmed by KW tests of scores on PCs 1-2, where PC1 successfully discriminated root bole (Site I RB) and island sediment plume samples at Sites II and III (Site II ISP and Site III ISP) from bare gravel bar samples at Site I (Site I BGB) (Table 4.10). The scattering of bare gravel bar samples at Sites II (Site II BGB) mostly among island sediment plume samples at Sites I, II and III (Site I ISP, Site II ISP and Site III ISP) in Figure 4.16 (c), illustrates their transitional position between island sediment plume mesohabitats at Sites II.

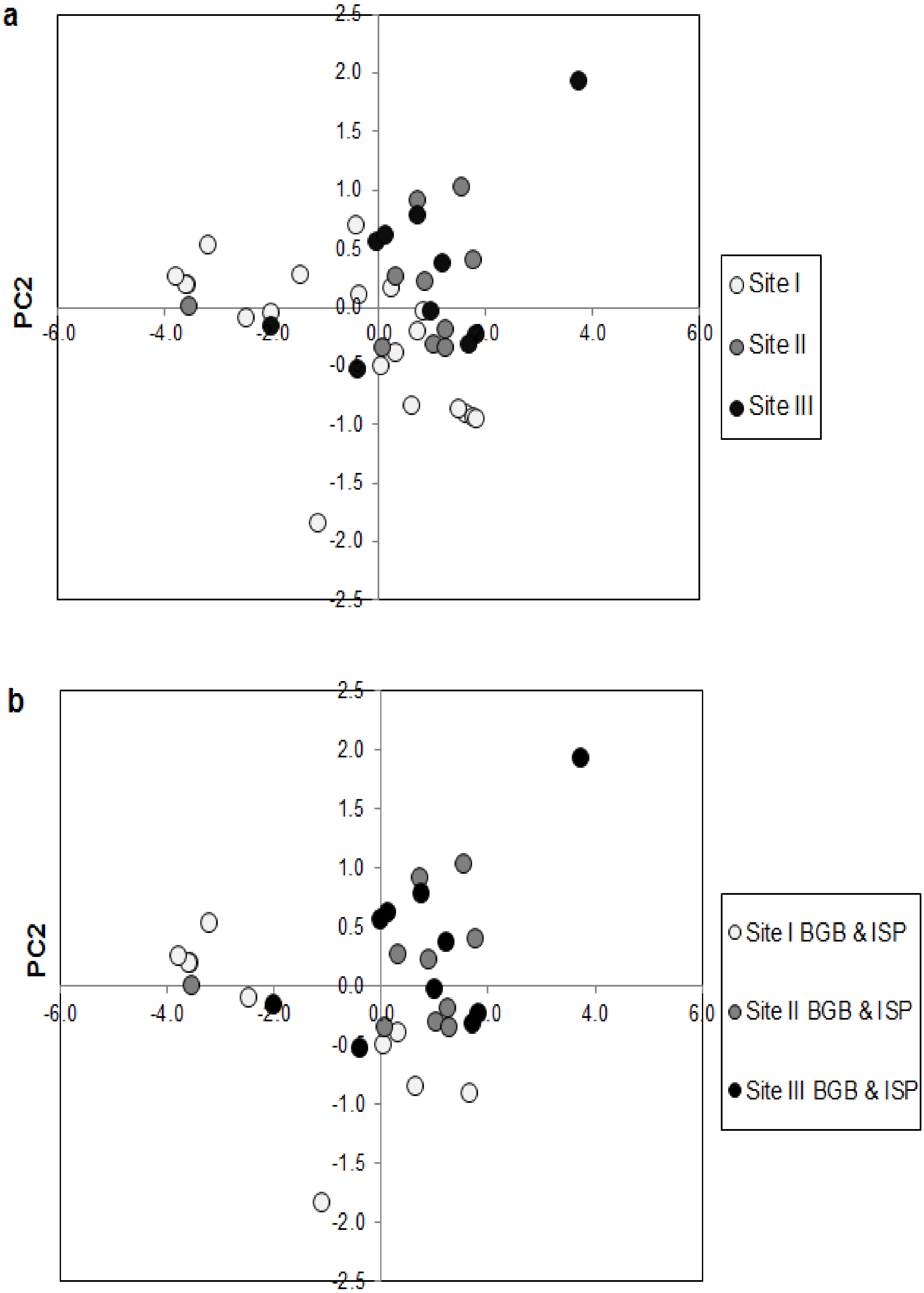


Figure 4.16. Distribution of (a) all mesohabitats associated with islands at Sites I to III; (b) mesohabitats shared by all islands at Sites I, II and III (ISP and BGB only); in relation to their scores on PCs 1-2 (for meaning of abbreviations see Table 4.2).

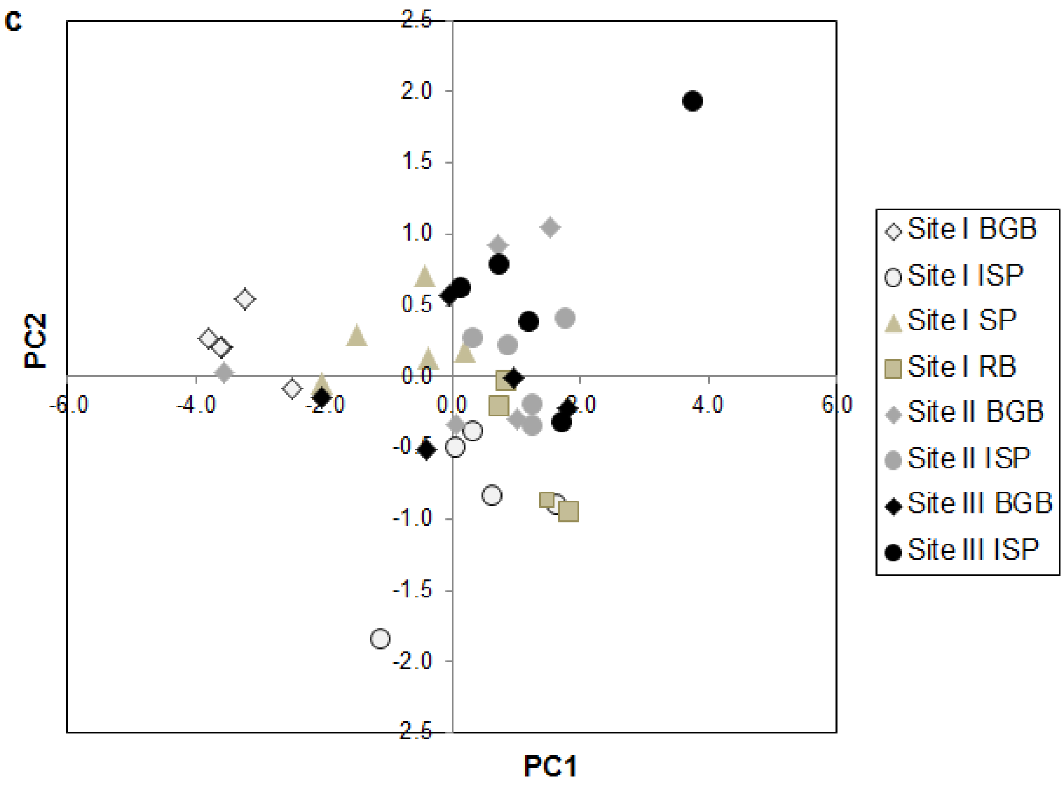


Figure 4.16 (c). Distribution of distinct mesohabitats sampled at study sites in relation to their scores on PCs 1-2 (for meaning of abbreviations see Table 4.2).

Having established the contrasts in mesohabitat sediment characteristics using PCA and KW tests, the propagule species dataset for mesohabitats associated with the island age groups was then analysed using DCA to evaluate variations in propagule species composition across the island age groups and mesohabitat types. Eigenvalues for the first two axes were 1.000 and 0.933 and the cumulative % variance within the species data explained by the axes scores were 10.6 and 20.5 %, respectively.

Figure 4.17 shows the DCA biplot for (a) the distribution of propagule species (b) distribution of all sampled mesohabitats associated with islands at each site; and (c) all distinct sampled mesohabitats at the study sites of different ages (Sites I, II and III). All species were included in the analysis and there was no downweighting of rare species. Although no significant trend is observed along DCA axis 1 and 2 (p = 0.355 and 0.292 for axis 1 and 2 respectively), the sampled mesohabitats associated with island age groups are best discriminated by axis 1, with a clear separation of the mesohabitats at Site I from Sites II and III indicating a notable difference in propagule species composition (Figure 4.17 (b)). Root bole mesohabitats (associated with islands at Site I (1RB)) and island sediment plume mesohabitats at Site II and III separate from the other mesohabitats (Figure 4.17 (c)). Additionally, species observed within the central area of the ordination plot (Figure 4.17 (a)) are associated with all mesohabitats, whereas species located towards the ends of axis 1 (left for Site I and right for Sites II and III) show distinctions between the sites. Bare gravel bar mesohabitats at Site I (1BGB) are associated with *Epilobium sp.*, (*Epi sp.*), and *Lycopersicon esculentum* (*Lycop l*). *Chenopodium album* (*Chen a*), *Daucus carota* (*Dau c*), *Juncus effusus* (*Junc ef*), *Rorippa nasturtium-aquaticum* (*Rorip n*), *Urtica dioica* (*Urti d*) and *Veronica sp.* (*Vero sp*) are associated with root bole samples at Site I (1RB). The propagules of *Agrostis stolonifera* (*Agros s*) and *Conyza sumatrensis* (*Cony s*) are most frequently found in association with island sediment plume samples at Site II (7ISP), while propagules of *Aster x salignus* (*Aster x*) and *Borago officinalis* (*Bora o*) are associated with island sediment plume samples at Site III (11ISP). Island sediment plume mesohabitats at Sites II are associated with *Conyza sumatrensis*, *Buddleja davidii*, *Juncus sp*.and *Veronica beccabunga*.

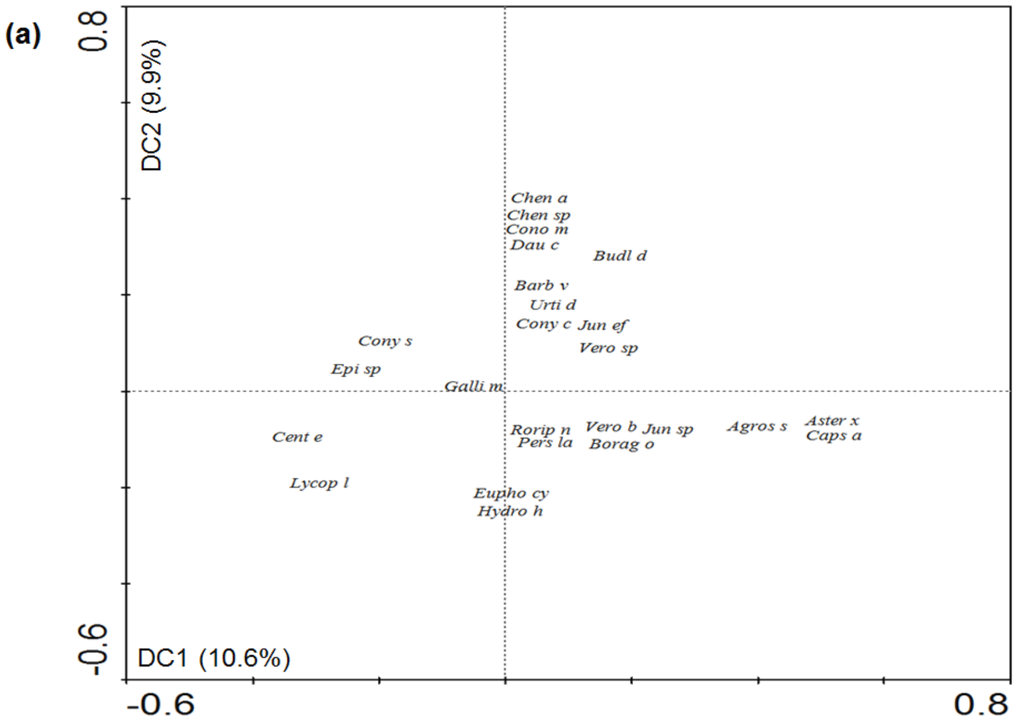


Figure 4.17 (a). DCA ordination plot of the distribution of propagule species (for full species names associated with abbreviations see Table 4.5).

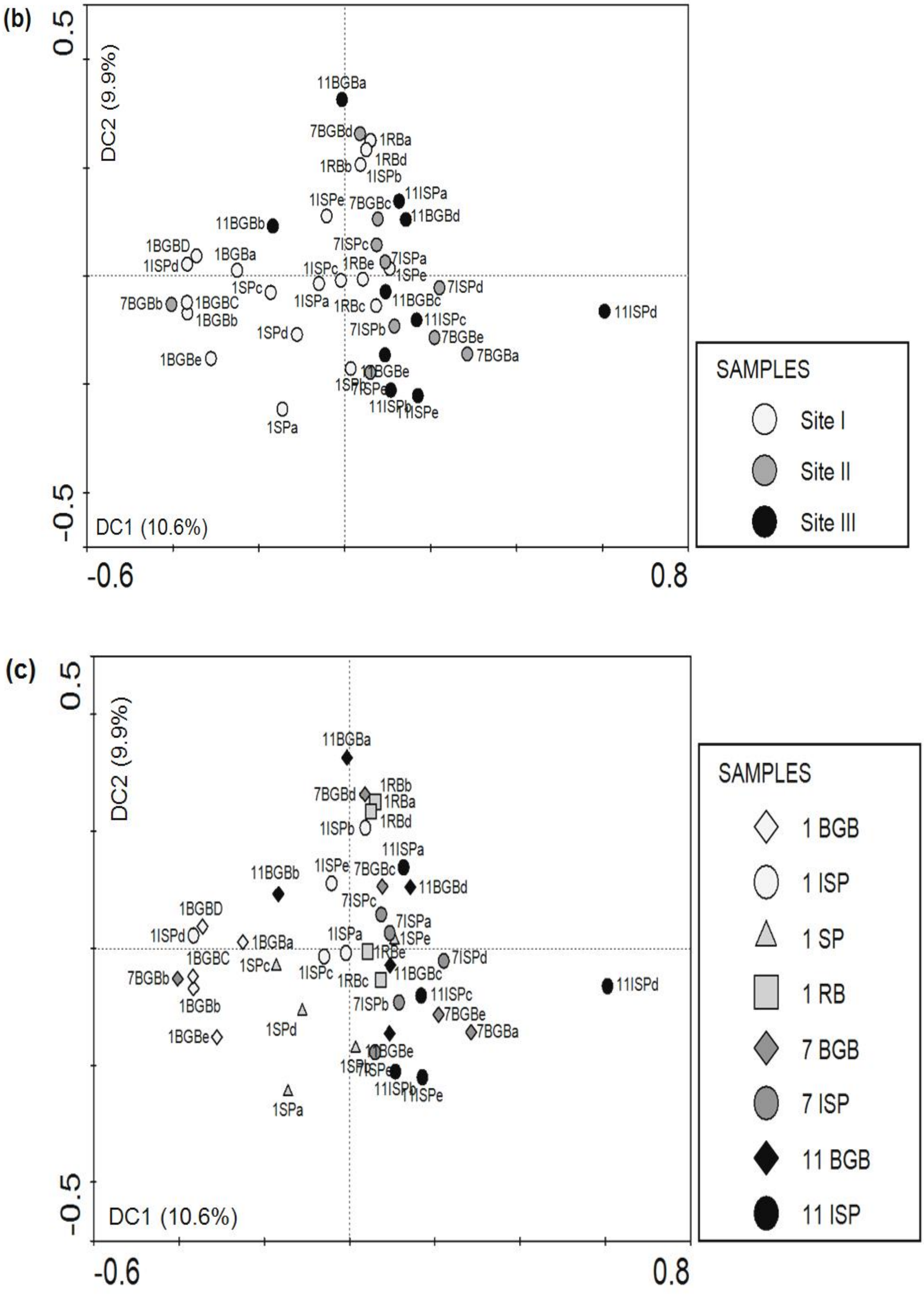


Figure 4.17 (Continued). DCA ordination plot of (b) study sites, i.e. all mesohabitats associated with islands at each site; (c) all distinct sampled mesohabitats at study sites of different ages.

4.5 DISCUSSION

The discussion is subdivided into four subsections to address the four research questions that were introduced in section 4.1.

4.5.1 Do the Physical Characteristics (Morphology, Sediments, and Wood) of Pioneer Islands that Build around Deposited Wood Change with Increasing Pioneer Island Age?

(i) Wood (deposited trees and largest shoots / trees) characteristics

The results show that early-stage pioneer islands (at Site I) developed around single uprooted *Populus nigra*, *Alnus incana* and *Salix sp*. deposited by floods during the winter of 2009-2010 floods. These relatively large uprooted tree species with a high rate of survival following deposition on exposed gravel bars (Francis, 2007), regenerate by producing fast-growing new shoots (Karrenberg et al., 2002), thus forming an even-aged pioneer stand of tree shoots averaging 0.85 m (i.e. mean) in height. Similar new shoots averaging < 1.0 m (i.e. mean) were observed by Kollmann et al. (1999) on early-stage pioneer islands within the braided active corridor of the Tagliamento River.

As expected, the tallest shoot / tree on pioneer islands increased significantly in size (diameter and height) as the pioneer island increased in age. *Populus nigra* or *Alnus incana* were the largest tree species on the intermediate- and later-stage pioneer islands (at Sites II and III). The occurrence of *Populus nigra* as the largest tree species on the intermediate-stage and later-stage pioneer islands was anticipated as this species has been identified by Karrenberg et al. (2003) and Gurnell et al. (2002, 2005) as the dominant riparian tree species on mature islands within the active corridor of the middle and lower Tagliamento River. However, the occurrence of *Alnus incana* on older islands was contrary to the findings of Kollmann et al. (1999) who asserted that this species was less capable of regeneration and dominance within the braided active corridor of the Tagliamento River. The height of the largest tree observed on the intermediate- and later-stage pioneer islands in the present study are different from the observations made by Kollmann et al. (1999) on 2-5 years pioneer islands (mean 3.4 m) and 13.5 years islands (mean 15.8 m), reflecting the different island ages in this latter study.

(ii) Pioneer island morphology characteristics

The variability in the erosion, sorting and deposition of sediment by flash floods and flow determines the morphological evolution and the geomorphological features associated with pioneer islands (Salo et al., 1986; Robertson and Augspurger, 1999; Bendix and Hupp, 2000; Hupp, 2000). Early-stage pioneer islands are highly variable in lengths and width, but show significantly lower surface elevation relative to the adjacent gravel bar surface compared to the older islands. Crescent-shaped scour pools of varying depths were associated with early-stage pioneer islands. Buffington et al. (2002) demonstrated that the majority of scour holes or pools are formed by flow obstructions and that size of the scour hole or pool largely depends on the obstruction characteristics (e.g. size and type). Deep scour holes (about 0.6 m) were observed around the apex (root boles of deposited tree) of early-stage pioneer islands as a result of the obstruction and deflection of flood flow by the root bole leading to high turbulence, vigorous scouring and deposition (Mutz, 2000) of a long tail of sediments downstream of the root bole. Francis et al. (2008a) and Kollmann et al. (1999) observed scour holes 0.4 m and 2 m deep, respectively, around the margins of the deposited trees on the Tagliamento River.

Intermediate- and later-stage pioneer islands are larger (length and width) and significantly higher in surface elevation relative to the adjacent bar surface than early-stage pioneer islands apparently as a result of repeated sediment deposition during floods. The variability in height, width and length of intermediate-stage pioneer islands shows the dynamic nature of these islands. The variability in pioneer island morphology at this intermediate-stage of development is possibly induced by flash floods producing spatial variations in erosion of islands and in sediment accretion, resulting in the variable island size (length and width) and relative elevation of later-stage pioneer islands.

(iii) Pioneer island sediment characteristics

The analyses of sediment characteristics of mesohabitats associated with the deposited whole trees that form the nucleus of early-stage pioneer islands revealed that root bole sediment deposits and sediment plume deposits on the island were finer and contained more organic matter than the adjacent gravel bar sediment deposits. These results suggest that the obstruction of flood flow by deposited trees, results in the deposition of finer sediments (clay and silt) around the root bole and the deposition of predominantly sand downstream (of the root bole) around the deposited tree trunk and canopy, thus forming an area of sediment plume. However, the particularly fine, organic sediment associated with root boles may also reflect the presence of soil retained within the root bole when the tree was transported to its deposition site.

As pioneer islands increased in age, the proportion of organic matter retained within the sediment plume on islands and the proportion of fine sediment retained within and between open bars associated with islands was observed to increase significantly. Rivers transport sediment and organic material downstream (Robertson et al., 1999), and roughness elements within the active channel and riparian zone, such as pioneer islands, provide sites whose flow resistance allows retention of organic material and sediment. Flow resistance increases with island age and size, thus the increase in organic material and sediment retention. In addition, the increase in vegetation cover and vegetation development with increasing island age is a significant source of organic matter to the sediment plume.

4.5.2 Does the Species Composition of the Standing Vegetation on Pioneer Islands Change with Increasing Pioneer Island Age?

Vegetation species richness increased (although not statistically significantly) as islands increased in age. This trend was expected since previous research indicated that vegetation communities on islands increase in species richness as islands increase in size and habitat heterogeneity and suitability (Kohn and Walsh, 1994; Kollmann et al., 1999; Cook et al., 2002) with age. Also, increased seed fall as standing vegetation matures and the trapping and deposition of seeds from other sources (e.g. floods) may have contributed to an increase in species richness as islands increased in age. The level of plant species richness recorded on early-stage pioneer islands in this study (mean 19.2) are comparable to that identified by Francis et al. (2008a) on young (~ 3 years) pioneer islands (mean 19.7) and higher than that recorded by Kollmann et al. (1999) for 1st year wood accumulations (mean 17.3) at the same site on the Tagliamento River. Furthermore, species richness on intermediate-stage pioneer islands in this study (mean 27.8) is comparable to 2-5 years pioneer islands (mean 26.2) surveyed by Kollmann et al. (1999).

Standing vegetation cover significantly increased across the study sites with increasing island age. Early-stage pioneer islands were generally open with a low vegetation cover (median 5 %) which was observed to be concentrated mainly around the deposited tree canopy and root bole. The open vegetation on early-stage pioneer islands was mostly composed of woody and grass species with a comparatively weakly developed herb layer, similar to observations by Kollmann et al. (1999). As pioneer islands increased in age, the number of perennial woody species (e.g. *Amorpha fruticosa*, *Populus nigra*, *Salix elaeagnos* and *Salix purpurea*), and the number of perennial herb species (e.g. *Convolvulus arvensis*, *Melilotus alba*, *Rubus caesius*, *Solidago canadensis* and *Tripleurospermum maritimum*) increased. The increase in the number of perennial herb and woody species may indicate improving habitat suitability with increasing island age, deposition of propagules by wind or floods, and possibly the impact of floods through physical heterogeneities created by the erosion and deposition of organic matter and silt (Kohn and Walsh, 1994; Naiman and Décamps, 1997; Cook et al., 2002).

4.5.3 Does the Species Abundance of the Sediment / Soil Propagule Bank Found on Pioneer Islands and their Associated Habitats Change with Pioneer Island Age?

Although not statistically significant, the species richness and abundance (per litre and per m^2) of propagules differed among the four mesohabitats associated with early-stage pioneer islands. In particular, root bole mesohabitats showed a higher propagule abundance and species richness than island sediment plume, scour pool and bare gravel bar mesohabitats. This may reflect the hydraulic roughness induced by root boles, confirming Bilby's (2003) suggestion that large wood potentially affects propagule distribution along rivers, but it may also result from the retention of soil and propagules within the root bole during uprooting, transport and deposition of the tree from the reach's adjoining floodplain or established islands. Root bole and sediment plume mesohabitats were observed to be successfully colonised by short-lived and perennial herbaceous plant species, many of which produce numerous small, light seeds that are dispersed widely via different vectors including wind (Soons et al., 2004) and water (Nilsson et al., 2002; Boedeltje et al., 2004). Root bole mesohabitats were also found to contain a relatively large quantity of herb propagules particularly of *Rorippa nasturtium-aquaticum* and *Urtica dioica*. *Rorippa nasturtium-aquaticum* and *Urtica dioica* both have long-lived, persistent seeds, capable of retaining their viability within the soil propagule bank for more than 5 years (Thompson et al., 1997), supporting the possibility that part of the root bole propagule bank in these early-stage pioneer islands may have survived through uprooting, transport and deposition of the parent tree or because root boles may have been the primary obstruction to propagules. *Conyza sumatrensis* and *Epilobium sp*. were the most frequent propagule species found in the sediment plume of early-stage pioneer islands. The propagules of *Conyza sumatrensis* and *Epilobium sp*. are small and light, allowing them to be dispersed widely by wind and water and tend to accumulate within the hydraulically sheltered sediment plume. With the exception of the root bole, the propagule banks of mesohabitats associated with early-stage pioneer islands showed low propagule abundance and species richness. This probably reflects frequent disturbances by wind and water at a stage when the hydraulic resistance of the pioneer island is relatively low, leading to weak propagule retention. Overall, it appears that the propagule bank of mesohabitats associated with pioneer islands at their early-stage of development may be linked to a combination of propagule traits (size, weight and mode of propagule dispersal), hydraulic characteristics of the mesohabitats in which they are found, and in some cases, the dispersal history of the parent tree.

Sediment plumes on islands and gravel bar sediment associated with intermediate-stage islands contained comparatively more propagules than the same mesohabitats associated with early- and later-stage pioneer islands, but these were highly variable in richness and abundance (per litre and per m^2). The bar sediment of the intermediate-stage pioneer islands that were investigated, was also finer than that of the early- and later-stage pioneer islands. This suggests that islands at Site II were generally more retentive of fine sediments than islands at Sites I and III. The islands at Site II were quite closely spaced in comparison with those at Sites I and III, which may explain the higher retention of finer sediments and propagules on the islands and also on the intervening bar surfaces. Furthermore, the propagules of *Veronica beccabunga* (herbs), *Agrostis stolonifera* (grass) and *Juncus effusus* (rush) were highly abundant in the sediment deposits of mesohabitats associated with intermediate-stage pioneer islands, further indicating the existence of finer calibre sediments associated with these islands that are capable of higher water retention and thus the storage of propagules that are frequently found in wet soils. Overall, the high variability and abundance of propagules in the island sediment plume and the open bar sediment within and between Sites may be due to the proximity of islands to adjacent riparian seed sources, differences in the dispersal and retention of propagules between islands of different spacing and different hydraulic resistance, and / or may also reflect different levels of flood disturbance between the sites.

Across the islands of different age, propagules of grass species such as *Agrostis stolonifera* were observed to have a lower abundance on open bar surfaces in comparison with sediment plumes, suggesting that the relatively fine sediment plumes on pioneer islands store relatively large quantities of small-seeded grasses compared to open bar surfaces. This confirms Alvarez-Buylla and García-Barrios's (1991) observation that propagule concentrations progressively decrease in proportion to the distance from propagule sources (i.e. the pioneer island forests). The only woody propagule that emerged from the propagule bank of the mesohabitats associated with the pioneer islands was *Buddleja davidii*. Although seedlings of *Populus nigra*, *Alnus incana* and several *Salix sp*. were observed within the standing vegetation, the seeds of these species are viable for only a short period, at most a few weeks (Peterken and Hughes, 1995; Karrenberg et al., 2002; Schulze et al., 2005), and so their absence from the seed bank was expected. In contrast, the seeds of *Buddleja davidii* have a much longer viability than those of the Salicaceae. In the laboratory, viability has been found to be very high (at least 2.5 years), although it is likely to be lower in field conditions, and the relatively small, light seeds (< 0.5 mm in length and < 0.06 mg in weight) allow wide dispersal by both wind and water (Tallent-Halsell and Watt, 2009). The seeds were found to decrease in abundance from open bar surfaces to sediment plume mesohabitats associated with intermediate-stage and later-stage pioneer islands, suggesting *Buddleja davidii* propagules are readily retained and maintain their viability within the relatively coarse bar substrate.

4.5.4 Are There Any Significant Associations Between the Physical Characteristics of Pioneer Islands of Different Age and their Standing Vegetation and Propagule Banks?

(i) Importance of large wood in early-stage pioneer island development

The differential sorting of sediment by deposited trees on gravel bars, the colonisation of sediment by patchy vegetation consisting of resprouting uprooted *Populus* and *Salix* trees and a large pioneer set of woody, herb and grass species, which is supported by an essential latent plant community within the propagule bank suggests that large wood is certainly an important nucleus for the development of pioneer islands in the island-braided reach of the Tagliamento River.

Sediment dynamics in terms of both scouring and deposition that is induced by obstructions is a key factor affecting the morphology of pioneer islands and the dispersal and storage of propagules and organic matter (Metzler and Smock, 1990). The study indicates that larger deposited trees produce longer early-stage pioneer islands and deeper scour holes around the root bole of the deposited tree. According to Hilderbrand et al. (1997) and Francis et al. (2008a), channel scouring typically occurs around the apex of large wood pieces oriented perpendicular to stream flow; while aggradation occurs downstream along the axis of the large wood (Abbe and Montgomery, 1996), consequently forming a sediment plume around the length of the large wood piece. Sediment plumes on larger (height and length) early-stage pioneer islands were observed to be relatively fine (mostly containing sand and silt) and supported a propagule bank relatively low in abundance and richness, possibly indicating feedbacks between the local standing vegetation and the propagule bank.

Generally, larger early-stage pioneer islands retained a relatively large number of woody species in addition to the core deposited tree, and these wood pieces were mainly *Populus nigra* and *Salix sp*. capable of resprouting. Most of the standing vegetation surrounded the root bole (upstream end) and canopy (downstream end) of the deposited tree. Standing vegetation around the large canopy of the deposited tree was particularly rich in woody species, ruderal short-lived (annuals and biennials) and perennial grass (e.g. *Agrostis canina*, *Agrostis setacea* and *Molinia caerulea*) and herb species, while the large root bole of the deposited trees and its associated deep scour holes were colonised by standing vegetation rich in woody species and ruderal perennial herbs. Francis et al. (2008a) observed significantly higher species richness and vegetation cover at the scour holes around the root boles of deposited trees in their investigations at the same study site, but their early-stage pioneer islands were slightly older (~3 years) than the newly deposited trees (~1 year) investigated in the present study. The relatively high cover and number of standing vegetation species around the root bole and canopy of large deposited trees may be attributed to the 'filtering' of fine sediment, propagules and organic matter from floods by the tree foliage and root bole and the subsequent good substrate and microclimate for the growth of propagules. Further, the different combinations of the naturally stiff and flexible deposited tree foliage and the relative high cover of grass species in the standing vegetation may have contributed to the trapping of sediment around the deposited tree, as these have been found to influence the uniformity of runoff by transforming channelized flows into expanded shallow flows, which in some instances have been found to reduce the critical shear stress for sediment transport by 10-50 % (Dillaha et al., 1989; Prosser et al., 1995; Järvelä, 2002). Wallace et al. (1995) similarly observed fine sediment and particulate organic matter deposition over coarse substrate after the addition of logs to a stream, while Gurnell et al. (2002) and Pettit et al. (2005) noticed the growth of propagules deposited on the fine sediment within wood piles. Therefore, large wood-induced sedimentary characteristics, and propagule dispersal patterns and growth are key processes determining the spatial structure of plant populations and presumably influence plant colonization success of new habitats that have implications for the initial trajectory of vegetation succession (Wang and Smith, 2002; Levine and Murrell, 2003; Pettit et al., 2005; Francis et al., 2008b).

(ii) Propagule bank dynamics during pioneer island morphogenesis

Temporal variation and spatial pattern of propagule banks originate from differences in the relative propagule output of plant species, mode of propagule dispersal and the structure of substrates available for propagule deposition or retention (Nathan and Muller-Landau, 2000). The composition of propagule banks associated with pioneer islands (and their mesohabitats) during their development, as identified in this study, primarily reflects sediment characteristics. Propagule bank composition on the sediment plume of pioneer islands was positively associated with fine sediments with relatively high organic matter content. Sediment plumes on the early-stage pioneer islands retained a less diverse propagule bank than later-stage pioneer islands, and the latter showed sediment plumes that were significantly finer (silt and clay) and higher in organic matter than the early-stage pioneer islands. The mesohabitats associated with pioneer islands also contained propagule banks of higher diversity compared to gravel bars adjacent to early-stage pioneer islands. These observations support the assertion that the substrate available for propagule deposition or retention might lead to differential propagule retention patterns (Nathan and Muller-Landau, 2000; Gurnell et al., 2007) where elevated concentrations of organic matter even in quite small quantities may increase soil elasticity and porosity and thus support retention of more propagules (Soane, 1990).

Propagules identified in the sediment deposits of mesohabitats associated with early-stage pioneer islands were mostly from pioneer species that disperse large quantities of long-lived seeds. Propagules of pioneer species are generally characterized by high dormancy and longevity (Fleming and Williams, 1990; Vázquez-Yanes and Orozco-Segovia, 1996). Gravel bars adjacent to early-stage pioneer islands predominantly contained propagules of *Epilobium sp.* and *Lycopersicon esculentum*, while *Conyza sumatrensis* and *Epilobium sp.* were frequent propagule species within the sediment plume of early-stage pioneer islands. The propagules frequently identified on gravel bars and sediment plume associated with early-stage pioneer islands were of ruderal plant species which thrive in relatively coarse sediments containing relatively low quantities of organic matter. However, propagules of *Chenopodium album*, *Daucus carota*, *Juncus effusus*, *Rorippa nasturtium-aquaticum*, *Urtica dioica* and *Veronica sp.* were frequently associated with the root bole area of the deposited tree that forms the nucleus of early-stage pioneer islands, representing plant species that prefer humus-rich, fertile and finer sediment habitats.

Most wetland propagules are distributed by floodwaters, a phenomenon known as hydrochory, with propagules floating on the water surface and subsequently depositing in habitats located at the water's edge (e.g. Haukos and Smith, 1993, 1994). This process may explain the deposition of large quantities of propagules across the open bar and sediment plume surfaces of the intermediate-stage pioneer islands as a consequence of the relatively closer spacing and potential coalescence of islands at that site. As a result, bar surfaces between the intermediate-stage pioneer islands at Site II were ‘transitional’ mesohabitats which were covered with finer, propagule- and organic-rich sediments, probably transported from adjacent plant communities on adjoining islands. These bar surfaces showed propagule banks containing relatively large, diverse and persistent propagule banks of species such as *Conyza sumatrensis, Buddleja davidii, Juncus sp.* and *Veronica beccabunga*, while the propagules of *Agrostis stolonifera* and *Conyza sumatrensis* were frequently found in the island sediment plumes.

Furthermore, the propagules of *Aster x salignus* and *Borago officinalis* associated with sediment plume of later-stage pioneer have been found to thrive both in ruderal and riparian areas of high productivity, especially on humus-rich and moist to humid soils (Walters, 1989; Cascorbi, 2007) that are typical of these islands.

(iii) Vegetation successional processes during pioneer island morphogenesis

The dynamic characteristics of the standing vegetation plays a critical role in shaping vegetation communities of landscapes such as islands as they fluctuate through different stages of a developmental cycle (vegetation succession) (McPherson and DeStefano, 2003). Huston’s (1994) dynamic-equilibrium model predicts that temporal asynchrony of disturbances across a landscape creates spatial heterogeneity; therefore increasing vegetation diversity by creating patches of different seral stages containing different suites of species (Pollock et al., 1998). The progressive change in pioneer island structure (notably surface elevation and sediment characteristics) and associated vegetation development (indicated by the age of the oldest tree) over time, observed in this study, accounted for approximately 81 % of the variation in the vegetation community composition and structure (i.e. seral stages) on pioneer islands as they develop over time. The distinctions in vegetation community composition and structure were especially noticeable for early-stage and later-stage pioneer islands where later-stage pioneer islands were inhabited by standing vegetation containing a larger number of woody species and perennial herb species. These results indicate that hydrological, geomorphic and ecological processes promote spatially complex but anticipated patterns of vegetation succession as pioneer islands increase in age at the study sites, with primary succession occurring on early-stage islands while secondary succession influences intermediate- and, particularly, later-stage pioneer islands.

Cluster analysis and DCA of the species composition of the standing vegetation data revealed that the vegetation composition on pioneer islands gradually increased in heterogeneity with island age, suggesting that the plant community responded to island-specific processes as well as to the increasing age of the islands. Early-stage and later-stage pioneer islands were characterised by a higher proportion of rarer species indicating that these islands were highly suitable for certain plant species, whereas the composition of the standing vegetation on intermediate- and later-stage pioneer islands showed greater similarity with one another than with early-stage pioneer islands. The dominant woody species on early-stage pioneer islands were *Cornus sanguinea* and resprouting pioneering *Populus nigra*, *Salix elaeagnos* and *Salix purpurea*. Ruderal herb species such as *Datura stramonium*, *Diplotaxis tenuifolia*, *Picris hieracioides* and *Reseda lutea*, and ruderal grass species such as *Agrostis canina*, *Agrostis setacea* and *Molinia caerulea* were co-dominant with woody species on early-stage pioneer islands. Edwards et al. (1999a) and Francis et al. (2008a) similarly observed a large cover of *Agrostis sp.*, *Diplotaxis tenuifolia*, *Populus nigra*, *Salix elaeagnos* and *Reseda lutea* on young (1-3 years) wood accumulations and pioneer islands. These plant species characteristically survive well on surfaces that are of low nutrient content and are exposed to frequent disturbances (Walters, 1989), reflecting the characteristics of sediment on early-stage pioneer islands. However, the resemblance in vegetation composition on intermediate- and later-stage pioneer islands reflects a comparable trend in surface aggradation, sediment calibre and organic content of the sediments comprising the islands' sediment plume. Mid-successional phase plants species such as *Aethusa cynapium*, *Alnus incana* (recognised by Kollmann et al. (1999) as characteristic of 7-13 years old pioneer islands), *Angelica vulgaris*, *Calamagrostis epigejos*, *Centaurea nigra*, *Gypsophila repens*, *Hypericum perforatum*, *Petasites hybridus*, *Sanguisorba minor* and *Scabiosa columbaria* were more strongly associated with intermediate- and later-stage pioneer islands. These plant species favour relatively deep, well-drained, moist and moderately humus-rich soils characteristic of intermediate- and later-stage pioneer islands (Walters, 1989). Overall, the large presence of early and mid-successional phase plant species on the studied islands confirms the earlier observations by Hupp and Osterkamp (1996) and Schnitzler (1997) that vegetation succession in the active zone of Alpine Floodplain Rivers never reaches the stage of mature softwood or hardwood forests that are typical for less frequently disturbed or higher elevation sites on floodplains.

4.6 SYNOPSIS

Four different components of structural and biotic diversity within the study sites on the Tagliamento River were explored; geomorphic, substrate (sediment and organic matter), propagule and vegetation heterogeneity. Based on the results of the study presented in this chapter, the following conclusions can be drawn:

1. Large uprooted trees deposited on bars were found to be important for engineering their environment and driving sedimentary, propagule and vegetation diversity. Large deposited trees interact with flowing water to create mesohabitats such as extensive scour features and fine sediment plumes that differ in sediment calibre and organic matter content, and propagule and standing vegetation composition from open bar surfaces. This has implications for the initial trajectory of vegetation succession on pioneer islands.

2. The sediment calibre and organic matter content of deposited soils was also found to be correlated with the abundance and species composition (i.e. richness) of the propagule bank, and may have implications for the successful germination, growth and (re) colonization of vegetation in the broader island-braided riverine landscape. The surface elevation of pioneer islands, and the quantity of fine sediments (silt and clay) and organic matter retained within mesohabitats associated with pioneer islands increased with its age.

3. The progressive change in pioneer island surface elevation particularly, and sediment (increase in organic matter) and propagule characteristics paralleled changes in the vegetation community composition and structure of the standing vegetation (increase in vegetation cover and the number of perennial species) on pioneer islands as they developed over time (i.e. different seral stages).

4. The studied pioneer islands supported distinct vegetation composition and structure at each stage of development. Vegetation cover, species composition, particularly the number of woody species and perennial herb species, and species heterogeneity gradually increased from initial succession (around deposited tree on early-stage pioneer islands) to mid-succession (on intermediate- and later-stage pioneer islands) as pioneer islands increased in age.

5. Early vegetation establishment was not limited to the germination and growth of grass and herb propagules that had been retained in association with fine sediment around the root bole and tree canopy of large deposited trees. An important component of initial vegetation establishment was the growth of woody plants as a result of regeneration (sprouting) of wood pieces of particularly *Populus and Salix* species that had been retained around the core tree, particularly around the root bole. A similar process may also affect the coverage and species composition of vegetation on intermediate- and later-stage islands. However, the evidence for this process is disguised by retained sediment, which accumulates around wood pieces preventing any easy distinction between plants that have developed from seeds or sprouting wood pieces.

In summary, deposited large wood and pioneer islands play pivotal roles, directly and indirectly, in maintaining both mesohabitat and floral (propagule and vegetation) diversity across the study sites in the island-braided reach of the Tagliamento River. The natural influences of flood disturbance, deposited large trees, vegetation growth, and island development that characterises braided rivers of this type, allows island-dominated reaches to undergo highly dynamic sequences of island growth and degeneration that are related to cycles of mesohabitat development, modification and stabilization. The next chapter investigates the physical properties and propagule bank characteristics of key morphological features within a headwater reach of the Tagliamento River, Italy, which is characterised by deposition of dead large wood rather than wood capable of regeneration.

CHAPTER 5

DEAD WOOD AND PROPAGULE BANK STRUCTURE ALONG A HILLSLOPE-CONFINED HEADWATER OF A LARGE MULTI-THREADED RIVER: THE FORNI DI SOTTO REACH, TAGLIAMENTO RIVER, ITALY

5.1 INTRODUCTION

The headwater reaches of naturally-functioning large braided rivers, typically reflect intense and erratic hillslope and channel processes that are diverse and distinctive in nature and scope from the other reaches of large rivers (Sedell et al., 1989; Tockner et al., 1999). Fluvial processes in the headwaters of large rivers produce a mix of characteristic morphological assemblages of wood, course particulate organic matter (leaves, fruits and propagules, twigs and debris), boulders, stretches of exposed bedrock, and thin patches of poorly sorted alluvium and residual sediment deposits that support patches of species-poor vegetation communities (Benda et al., 2004; Bigelow et al., 2007) and consequently the development of landforms and habitats within the river (Gurnell et al., 2001; Gurnell, 2013).

As outlined in Chapter 2, the dynamics, morphology and geomorphological role of large wood varies with the river type (e.g. Gurnell et al., 2002) and the nature of wood (living or dead) (Gurnell et al., 2001; Gurnell, 2013). This chapter focuses on the headwater reach of a large braided river influenced by predominantly dead wood accumulations deposited on exposed river sediment and islands. Previous research on the dynamics of large wood and vegetation along the Tagliamento River identified dead logs, whole shrubs / trees and jams as the predominant forms of wood accumulation and *Alnus incana* as the most important riparian tree species within the headwater reaches (Gurnell et al. 2000a, 2000b, 2001). In investigating the ecological and geomorphological role of dead wood accumulations in the headwater reach of the same river, Gurnell et al. (2001) observed seedlings growing in the lee of dead wood jams and suggested this process as a strategy for vegetation establishment that could lead to the development of islands. In contrast, *Populus* *nigra* was identified as the most important riparian tree species influencing island development within the lower island-braided reaches of the Tagliamento River (see Chapter 4). Plant ecological research in the headwaters of similar large river environments has identified a high number of indicator species and an increase in species diversity in and around large wood jams deposited on gravel bars (Nakamura et al., 2012). In these studies, vegetation establishment on bar and island surfaces were inferred to relate to (i) the growth of diffusely deposited propagules retained along with fine sediments within the shelter of vegetation and related debris, particularly in the shelter of patches of riparian forest and accumulations of dead wood, and (ii) the sedimentary structure of a dynamic active corridor, which offers different habitats for vegetation colonisation. Nevertheless, to date no study has explicitly investigated any of these possible relationships.

This chapter investigates the physical properties and propagule bank characteristics of wood accumulations and associated mesohabitats within the active corridor of the headwaters of the Tagliamento River, Italy. The research explores relationships between the type and spatial organisation of deposited dead wood accumulations, and relationships between the sediment characteristics and the mid-summer propagule bank of key mesohabitats, by addressing the following research questions:

i. What are the types and characteristics of large wood accumulations?

ii. Are there any associations between large wood accumulations and geomorphological features?

iii. Are there any differences in the sediment characteristics of different mesohabitats?

iv. Are there any differences in the propagule bank of different mesohabitats?

v. Are there any significant associations between the physical (large wood jams and / or sediment) and biotic (propagule banks) characteristics of mesohabitats?

5.2 STUDY SITE

An overview of the research design and research sites included in this thesis was provided in Chapter 3. The research for this chapter was conducted along the gravel-bed, hillslope-confined multi-thread headwater reach of the Tagliamento River at Forni di Sotto in Italy (Figure 5.1A), which is located between 11.2 to 13.5 km from the river's source.

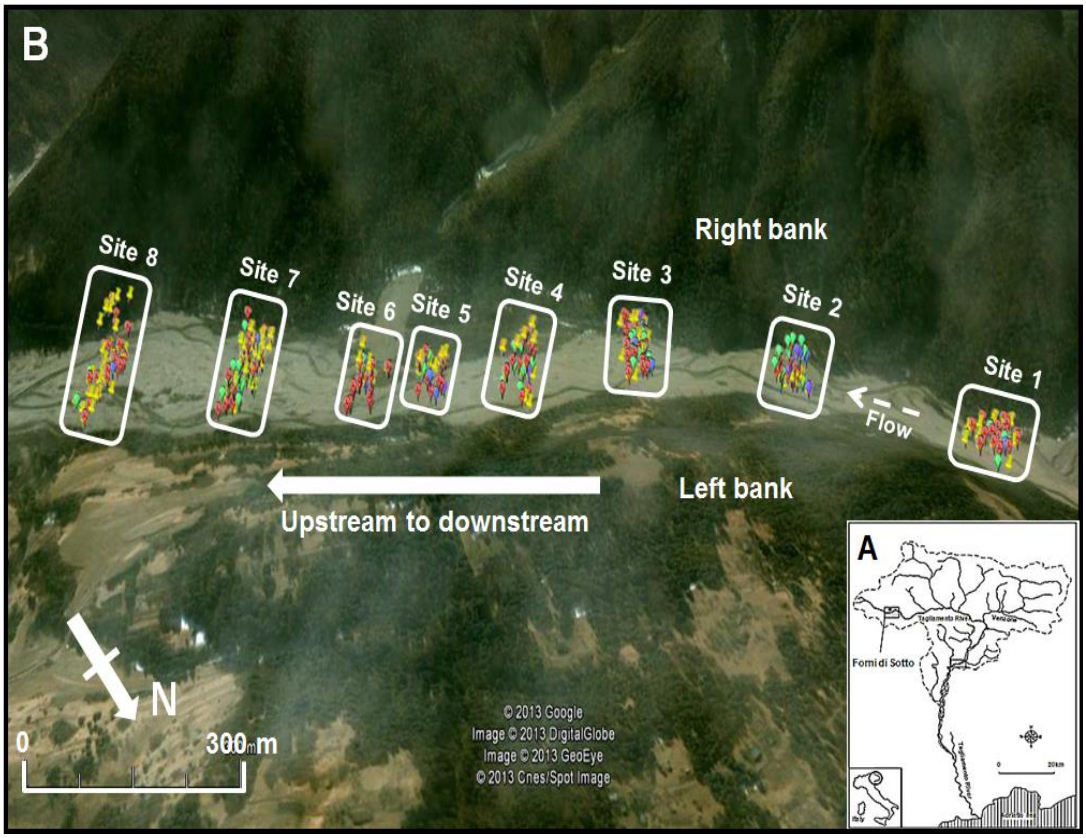


Figure 5.1. (A) The catchment of the Tagliamento River, showing the location of the Forni di Sotto study reach; (B) Aerial image of the Forni di Sotto study reach, showing the location of the sampling sites from upstream to downstream (Source: Google earth accessed on 26/02/2013, 21:30).

The 2 km study reach (Figure 5.1B) has an average slope of 0.0188 $m.m^{-1}$ and the average width of the active multi-threaded corridor (braided with occasional islands) is approximately 160 m (Gurnell et al., 2000a and 2000b; Gurnell and Petts, 2006). The size of the bed material within the active corridor is highly variable, ranging from coarse lag and riffle deposits (D_{50} ~ -8 phi; boulders) to extensive coarse bar top deposits (D_{50} ~ -6 phi; cobbles) to finer gravel-pebble sheets (D_{50} ~ -4 phi; coarse gravel) to sands and silts within the islands (Petts et al., 1999; Gurnell and Petts, 2006). The active multi-threaded corridor is characterised by a continually changing mosaic of active channels, bare sediment (dry channels, bars), and vegetation (from areas of young sparse seedlings and saplings on bar and dry surfaces to mature closed tree cover on established islands) that is driven by a strong hydrological connectivity with the hillslopes, the flashy flow regime of the river, and a plentiful supply of sediment and large wood from hillslopes and alluvial fans (Tockner et al., 1999; Gurnell et al., 2000a and 2000b). The varying water levels associated with the river's flashy flow regime disturb sediments and vegetation within the active corridor leading to widespread erosion of bars and established islands and also deposition of sediment and large wood (Bertoldi et al., 2009, 2013).

The Tagliamento River within the study reach is hillslope-confined on both sides and has developed multiple river channels, gravel bars and established islands that are covered by dead wood and colonised by a few plant species which coexist in the riparian woodland (Gurnell et al., 2000a). The most important riparian tree species in the headwaters is *Alnus incana* (which is less capable of regenerating when uprooted than *Populus nigra* which is abundant in the middle and lower reaches of the Tagliamento; see Chapter 4), which coexists with several willow species, most notably *Salix elaeagnos*, that are capable of regenerating freely when damaged or uprooted. A variety of coniferous tree species are abundant on the surrounding hillslopes and on more established islands (Gurnell and Petts, 2006). The interactions between valley gradient, frequent lateral movement of active channels, sediment calibre and supply, and the dead wood supplied from the riparian woodland result in contrasts in the nature, quantity and types of large wood accumulations within the headwater reach (Gurnell et al., 2000b; Gurnell et al., 2001; Gurnell and Petts, 2006).

5.3 METHODS

5.3.1 Research Design

Data were collected in July 2011 at eight sampling sites along the study reach. The sampling sites were established from upstream to downstream within the headwater reach in order to capture any variability along the reach and in its cross profile in relation to its sedimentary structure, propagule banks, and the character of large wood accumulations and their association with specific geomorphological features of the river's active braided corridor (Figure 5.1B). The sampling sites encompassed cross profiles 2 (site 1 in the present research), 4 (site 2), 6 (site 3), 7 (site 4), 9 (site 5), 10 (site 6), 11 (site 7) and 13 (site 8) investigated by Gurnell and Petts (2006). Site 7 also corresponds with the single cross section investigated in detail by Gurnell et al. (2000a, 2001).

5.3.2 Field Methods

Three types of measurements and / or samples were collected from the study reach; (i) at all eight sampling sites, the locations, types and dimensions of all large wood accumulations within the active corridor were recorded; at five sampling sites (1, 2, 5, 6 and 7), (ii) a central topographic cross profile was surveyed and (iii) sediment samples were collected to provide data on sediment calibre, organic content and the plant propagule bank within a prescribed set of mesohabitat patches.

(i) Large wood and topographic survey

Due to the wide active corridor of the Tagliamento River within the sampling sites, each of the eight sampling sites was restricted to a 60 m wide belt transect spanning the entire active corridor (left bank to right bank). A detailed cross-sectional topographic survey was recorded along a central transect within five of the sampling sites in order that surveys of large wood accumulations within the 60m wide belt transect could be associated with particular topographic levels and geomorphological features. The locations of all wood accumulations including large, discrete jams of wood on bars and island surfaces, and wood stored around the margins of islands were recorded as were the type and dimensions of the wood. Since the large wood data relate to a single survey undertaken between the 22 and 29 July 2011, they only reflect a snapshot of a very dynamic wood storage regime, which is governed by the magnitude and timing of the most recent major flood event. Each accumulation was assigned to one of five accumulation types observed in the study reach: uprooted trees (entire, uprooted trees usually with their roots and canopy virtually intact (UT)); large wood jams (condensed accumulations of logs, shrubs, trees, root masses and other wood pieces (LWJ)); individual logs (individual, unbranched trunks or major pieces of wood (IL)); uprooted shrubs (entire, uprooted shrubs usually with their roots and canopy virtually intact (US)); and root boles (root mass of a tree plus a portion of the trunk (RB)) (Figure 5.2 and 5.3). The status of the wood in terms of whether it was alive or dead was also recorded, but since the overwhelming majority of the wood was dead, no further analysis of this aspect is presented. The position of each large wood accumulation was determined using a hand-held GPS and the dimensions of large wood accumulations were measured (length, width / diameter and / or height) using a 30 m tape (Figure 5.2).

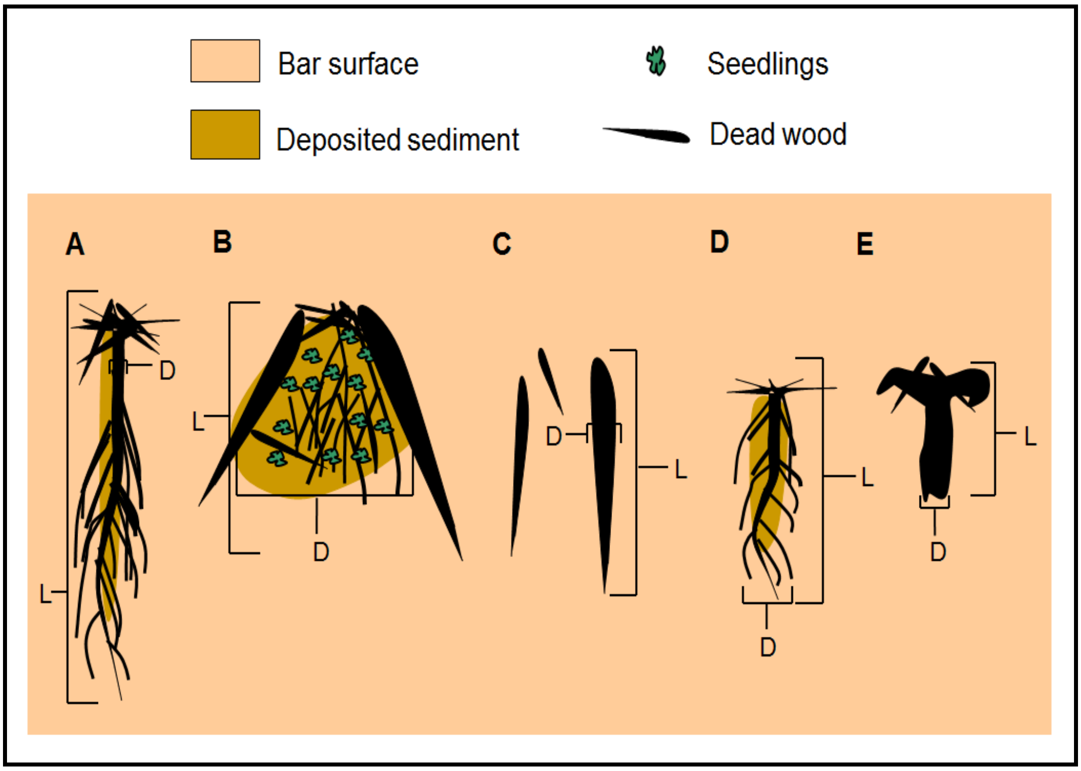


Figure 5.2. The different types of large wood accumulations observed within the active corridor of the headwater reach of the Tagliamento River: A. Uprooted trees (UT); B. Large wood jams (LWJ); C. Individual logs (IL); D. Uprooted shrubs (US) and; E. Root boles (RB). Dimensional measurements of the five types of large wood accumulations are length of accumulation (L) and diameter of accumulation (D). Additional dimensional measurement for uprooted shrubs (US), root boles (RB) and large wood jams (LWJ) that is not illustrated was their height above the sediment surface (H).

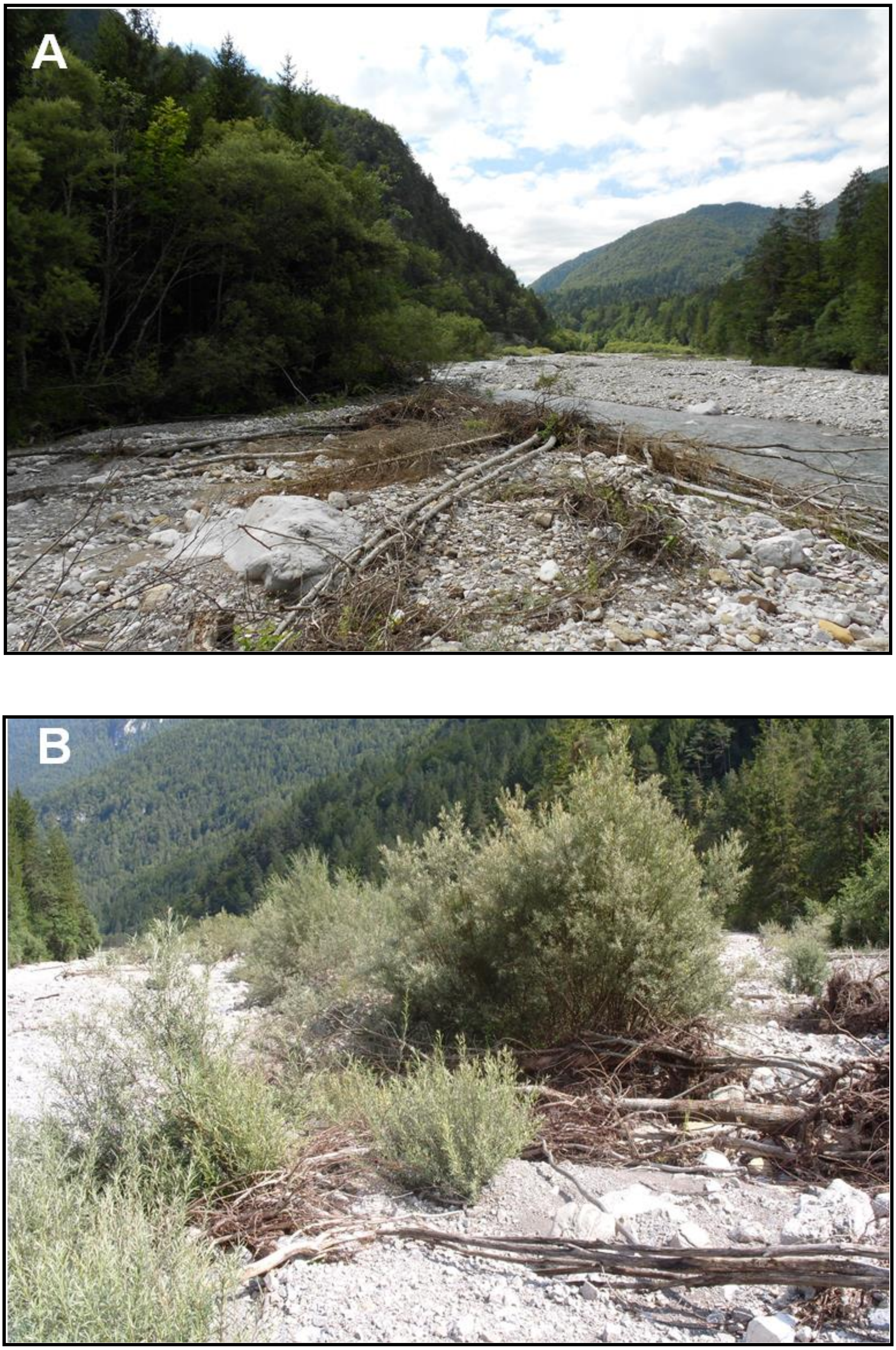


Figure 5.3. Types of large wood accumulation within the active corridor of the headwater of the Tagliamento River: A. Uprooted trees; B. Individual logs; C (i). Crescent-shaped large wood jams (LWJ) on bars and, C (ii) LWJ at the apex of established islands; D. Uprooted shrubs and; E. Root boles.

Figure 5.3 (b). C (i) and C (ii)

Figure 5.3 (b). D and E

(ii) Sediment and propagule bank sampling

The number of sites selected for sampling, the number of sampling times and the number of samples obtained were constrained by the single mid-summer field campaign and restrictions on the weight of samples that could be returned by air to the UK. Therefore, sediment samples were collected at only five out of the eight sampling sites (Sites 1, 2, 5, 6 and 7) investigated within the study reach. At each of the five sites, sediment samples were collected from three mesohabitats characteristic of this headwater reach: the surfaces of established islands (EI), bare gravel bar surfaces (BGB) and fine sediment plumes retained within large wood jams (LWJ) (Figure 5.4, Table 5.1).

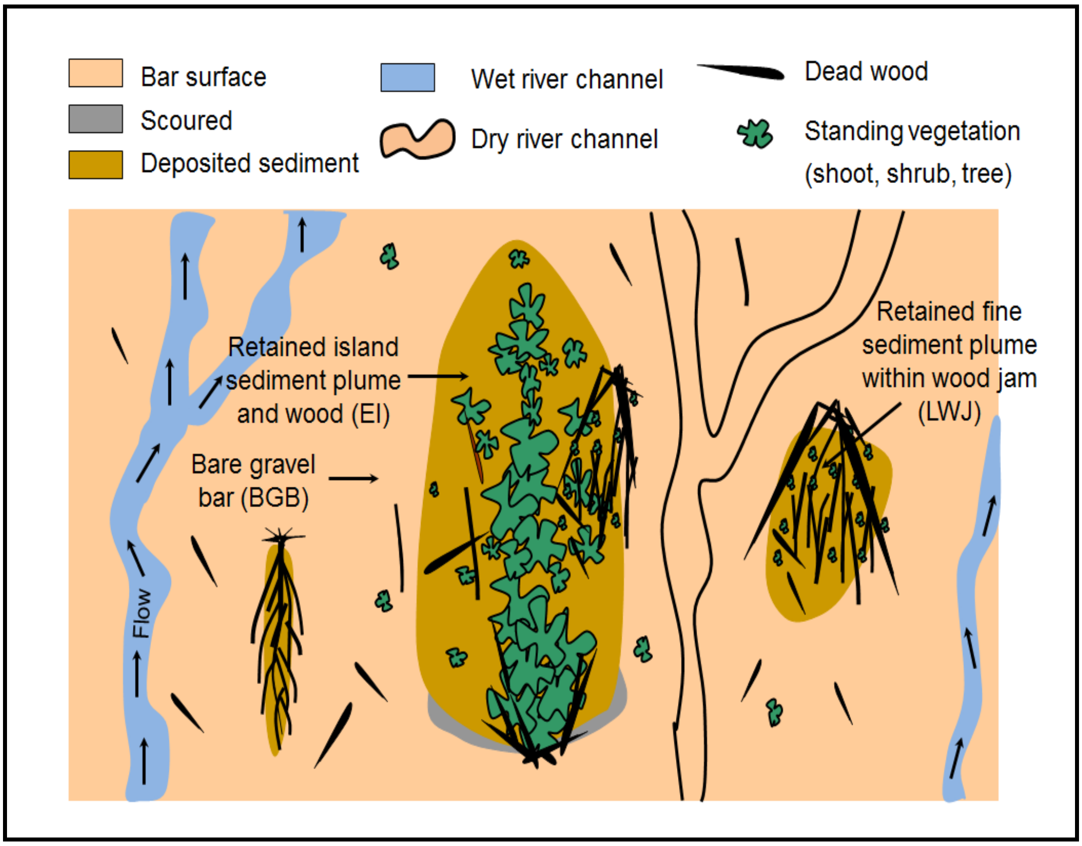


Figure 5.4. Typical patterning of riparian habitat patches (mesohabitats) representative of the headwater geomorphological landscapes. Mesohabitats readily identified within the active corridor of the headwater are bare gravel bar (BGB), large wood jam (LWJ) and established island (EI).

Table 5.1. The number of bulked sediment samples obtained to characterise mesohabitats associated with the headwater reach. Each bulked sample was assembled from 3 replicate samples, apart from open bar surfaces where 4 replicate samples* were bulked to ensure sufficient finer sediment for laboratory analysis from these relatively coarse sediments.

Mesohabitats	Abbreviations	Definitions	Number of sampled sites
Bare gravel bar	BGB	Open (unvegetated) bar surface	5*
Large wood jam	LWJ	Sediment accumulated within large wood jam formed on bar surface	5
Established island	ISP	Sediment from the (vegetated) surface of an established island	5

Each sample was a composite of three samples extracted from random locations within the sampled mesohabitat apart from the bulked samples from open bar surfaces where four samples were combined to ensure sufficient fine sediment for analysis in these predominantly gravel deposits. The individual samples were obtained using a 6 cm diameter cylindrical corer to a depth of 5 cm. It is important to note that propagule banks are not only highly variable in space but also through time (Fenner and Thompson, 2005), and so the sampling undertaken is only representative of one point in the year (mid-summer). As a result, the samples that were obtained should be representative of the persistent propagule bank and of short-lived propagule species released close to the time of sampling. The samples are unlikely to reflect the extremely short-lived propagules of the willow species present at the sites, which are released early in the summer and have a half-life of only a few weeks (Karrenberg and Suter, 2003), or the alder (*Alnus incana*) propagules that are released during late winter.

5.3.3 Laboratory Methods

Common laboratory methods used in this thesis are described in Chapter 3. The laboratory methods of (i) sediment storage and preparation, (ii) sediment analysis and (iii) germination trials used in this study are described in Chapter 3 (Section 3.6).

5.3.4 Data Analysis

Table 5.2 lists the variables investigated in this study and defines how these were derived from the raw field and laboratory measurements. These data plus the information of propagule species obtained in germination trials were analysed using a number of descriptive, bivariate and multivariate statistical analysis techniques. For the large wood accumulation, propagules and sediment results, descriptive statistics were used to identify trends in the raw data. Descriptive statistical techniques revealed that most of the variables were not normally distributed and the variables frequently showed differences in variance between sites or mesohabitats, so non-parametric statistical methods were used for data analysis.

Table 5.2. Variables resulting from field measurements and laboratory measurements of samples collected from study sites.

Variables and Abbreviations	Description
Large wood accumulation variables	
Length of large wood accumulation (L)	The total length of the uprooted trees, individual logs, uprooted shrub, root boles, or large wood jam (the longitudinal distance from the base to the top of the large wood jam parallel to the river flow) (m).
Diameter of large wood accumulation (D)	The diameter of the uprooted trees (1 m above the root bole), individual logs (mid-stem of each piece), uprooted shrub (mid-way of canopy perpendicular to the trunk), root boles (perpendicular to the trunk), or the large wood jam (horizontal width of the large wood jam perpendicular to the river flow) (m).
Height of large wood accumulation (H)	The maximum vertical height of the large wood jam, root bole and uprooted shrub above the sediment surface (m).
Frequency of large wood accumulation/ha	The total number of each large wood accumulation type per hectare of sampled river sub-reach (sampling site).
Area of large wood accumulation (m^2 or m^2/ha)	The smallest rectangular area of the ground surface into which the wood accumulation would fit (m^2) or the total area of these per hectare (m^2/ha).
Volume of large wood accumulation (m^3 or m^3/ha)	The total volume of the smallest rectangular box (of air) into which each large wood accumulation type would fit (m^3) or the total volume of these per hectare of sampled river sub-reach (m^3/ha for the sampling site).
Wood volume of large wood accumulation (m^3 or m^3/ha)	Following Gurnell et al. (2000b), the above wood+air volumes were adjusted to produce estimates of wood volumes by multiplying the volumes of uprooted shrubs by 0.1, jams by 0.2, and logs, uprooted trees and root boles by 1.0.
Wood mass of large wood accumulation (t/ha)	Following Gurnell et al. (2000b), the above wood+air volumes were adjusted to produce estimates of wood volumes by multiplying the total volumes of uprooted shrubs by 50 kg/m^3, jams by 100 kg/m^3, and logs, uprooted trees and root boles 500 kg/m^3.

Table 5.2. (Continued)

Variables and Abbreviations	Full name	Description
Propagule bank variables		
PropSR	Propagule species richness	The total number of propagule species identified in germination trials.
Prop/l	Propagules per litre	The number of viable propagules per unit volume of sampled mesohabitat sediment; Prop/l = Number of viable propagule species in sediment sample x (Total volume of < 4 mm sediment fraction ÷ volume of < 4 mm sediment fraction used in germination trials) x (1000 / Total volume of sediment sample).
Prop/m^2	Propagules per square metre	The number of viable propagules per unit surface area of sampled mesohabitat; Prop/l = Number of samples collected with the corer x pi (3.1416) x (Radius of the corer) ^{2}.
Number of herb propagules		The total number of viable herb propagules (prop/m^2 or prop/l) present at the mesohabitat.
Number of grass propagules		The number of viable grass propagules (prop/m^2 or prop/l) present at the mesohabitat.
Number of rush propagules		The number of viable rush propagules (prop/m^2 or prop/l) present at the mesohabitat.
Number of woody propagules		The number of viable woody propagules (prop/m^2 or prop/l) present at the mesohabitat.
Sediment characteristics variables		
% OM	% Organic Matter	Percentage organic matter content of bulk mesohabitat sediment sample.
D_{50}	Median particle size (phi units)	Median particle size of bulk mesohabitat sediment sample expressed in phi units.
% G	% Gravel	Percentage of gravel in bulk mesohabitat sediment sample.
% S	% Sand	Percentage of sand in bulk mesohabitat sediment sample.
% ST	% Silt	Percentage of silt in bulk mesohabitat sediment sample.
% C	% Clay	Percentage of clay in bulk mesohabitat sediment sample.

The primary means of addressing the research questions 1, 3 and 4 was through comparison of medians of the measured variables, via non-parametric analysis of variance (Kruskal-Wallis (KW) tests). KW tests were used to explore the differences in types of large wood accumulation within the whole reach, and differences in sediment and propagule bank variables between the different mesohabitats. Where KW tests indicated a significant difference ($p < 0.05$) in a particular variable, multiple pairwise comparisons were then performed using Dunn's procedure (Bonferroni corrected significance level) to identify those types of wood accumulation or mesohabitats that exhibited significant contrasts in the variable.

The nature, strength and significance of associations between pairs of variables were explored using the non-parametric Spearman's rank-order correlation coefficient to identify (i) bivariate associations among sediment and propagule bank characteristics of mesohabitats across the active corridor of the headwater; and (ii) bivariate associations among the physical (wood and sediment) and biotic (propagule) variables associated with large wood jams in the active corridor of the headwater.

Multivariate associations were then explored using a combination of ordination methods (Principal Components Analysis – PCA, and Direct Gradient Analysis – DGA (Redundancy Analysis (RDA) or Canonical Correspondence Analysis (CCA) as appropriate). These analyses together with Spearman's rank-order correlation analyses address research question 5.

PCA was applied to the rank correlation matrix among physical (sediment) variables measured for mesohabitats within the active corridor to identify the principal gradients in the measured physical variables and to explore how these gradients are related to the mesohabitat types. Associations between the gradients defined by the principal components (PCs) and mesohabitats were then explored by (i) producing scatterplots showing PC scores coded by mesohabitat types; and (ii) applying KW tests to PC scores for mesohabitat groups to assess the statistical significance of any apparent differences observed in scatterplots.

Lastly, DGA was applied to the propagule data sets (presence / absence list) in order to firstly assess floristic trends in the propagule bank samples and secondly to investigate the extent to which species presence or absence reflected changes in physical (sediment) variables associated with different mesohabitats.

KW tests, Spearman's rank-order correlation and PCA was performed using XLSTAT-Pro software (version 9.1.3, 2009), whiles DGA was performed using CANOCO v4.5 (ter Braak and Smilauer, 2002).

5.4 RESULTS

Summary statistics describing the magnitude and variability of the investigated variables across the whole reach, sampled sites or mesohabitats are provided in Tables (5.3, 5.5, 5.6, 5.7 and 5.9), through box and whisker plots (Figures 5.5, 5.12 and 5.13) and bar graphs (Figures 5.6, 5.7, 5.8, 5.9 and 5.11). The results of KW tests (followed by multiple pairwise comparisons) investigating differences in the magnitude of the investigated variables in relation to the whole reach, sites or mesohabitats are presented in Table 5.4, 5.8 and 5.12.

5.4.1 Characteristics of Large Wood Accumulations within the Headwater Reach

This section first presents the data collected on large wood accumulations across all eight study sites and then considers the relationship between wood accumulations and topography within the five sites where cross profiles were surveyed.

(i) Frequency and volume (or mass) of large wood accumulations

Wood accumulations were measured in the field according to their length, width and height dimensions, apart from logs and uprooted trees, whose length and diameter were measured. A volume was then calculated from these measurements, which, with the exception of logs and uprooted trees, represented the smallest rectangular box that could include the wood accumulation and was therefore a wood plus air volume. In addition, an estimate of the wood volume and wood mass in each accumulation was estimated based on conversion factors proposed by Gurnell et al. (2000b) for the Tagliamento River, using the method of Thevenet et al. (1998). Conversions to estimates of wood volume used multipliers of 0.1 for uprooted shrubs, 0.2 for wood jams and 1.0 for logs, root boles and uprooted trees (since these volumes were already estimates of the cylindrical volume of the log or main trunk of the tree / root bole), while conversions to estimates of wood mass used multipliers of 50, 100 and 500 kg m^{-3} for uprooted shrubs, wood jams, and logs, root boles and uprooted trees respectively. Both volumes (volume and wood volume (or mass)) are reported below because the former is directly based on field measurements, whereas the latter, although attempting to quantify true wood volume, is likely to be subject to some level of error because of the simplicity of the conversion factors.

A total of 832 large wood accumulations were recorded, amounting to a total volume of 1730 m^3 (wood volume of 426.81 m^3) along the eight sampled belt transects that covered an area of 7.71 ha within the study reach. The frequency of large wood accumulations across the total area of the eight sites averaged 112 per hectare, while the volume of large wood accumulations averaged 223.08 m^3/ha (wood volume and mass averaged 55.64 m^3/ha and 27.82 t/ha respectively).

Figure 5.5 presents the total frequency, volume and wood volume (or mass) of different accumulation types that differed significantly (KW $p < 0.001$, Table 5.3 and 5.4) for the whole study reach. The most frequently occurring type of wood accumulation was individual logs (median 44/ha), followed by large wood jams (median 32/ha) and uprooted shrubs (median 25/ha), although all three showed considerable variability between the eight sites. Frequencies of entire uprooted trees and root boles were considerably lower (median 2/ha and 5/ha respectively) and their frequency was less variable between sites. Large wood jams accounted for the largest median volume in the study reach (median volume 166.59 m^3/ha; median wood volume and mass 33.32 m^3/ha, 16.66 t/ha respectively) although there was high variability between the eight sites (18.73 m^3/ha to 304.73 m^3/ha for volume, 3.75 m^3/ha to 60.95 m^3/ha for wood volume and 1.87 t/ha to 30.47 t/ha for wood mass). Root boles and uprooted trees were characterised by lower volumes that showed relatively lower variability among the eight sites (volume and wood volume (or mass) medians 0.53 m^3/ha (0.27 t/ha) and 1.16 m^3/ha (0.58 t/ha) respectively).

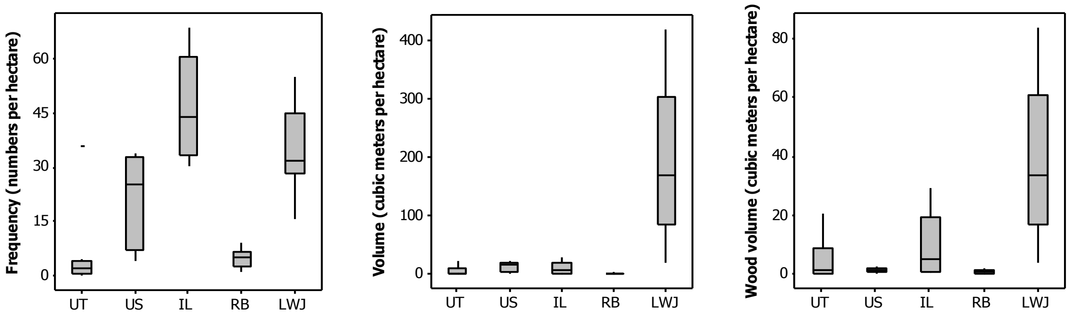


Figure 5.5. The frequency, volume and wood volume (m^3/ha) of the different types of large wood accumulation across the 8 sites within the active corridor of the headwater reach of the Tagliamento River. The ordering of large wood accumulations on the x-axis follows a natural continuum from 'whole simple' (uprooted trees (UT) and uprooted shrubs (US)) to 'derivative and complex' (individual logs (IL), root boles (RB) and large wood jams (LWJ)) types of accumulation.

Table 5.3. Summary statistics relating to large wood accumulations within the active corridor of the eight sites in the headwater reach of the Tagliamento River.

Variables	**Types of large wood accumulation**	**Mean**	**Median**	**Q1**	**Q3**
Frequency of large wood accumulation/ha					
	Large wood jams (LWJ)	34.28	31.61	28.47	39.58
	Individual logs (IL)	46.13	43.99	34.37	54.42
	Uprooted trees (UT)	5.95	1.87	1.17	2.89
	Root boles (RB)	4.72	4.74	3.02	6.37
	Uprooted shrubs (US)	21.06	25.10	9.29	31.86
Volume of large wood accumulation (m^3/ha)					
	Large wood jams (LWJ)	195.55	166.59	111.29	297.17
	Individual logs (IL)	9.78	4.68	1.15	17.82
	Uprooted trees (UT)	4.77	1.16	0.01	6.59
	Root boles (RB)	0.75	0.53	0.25	1.11
	Uprooted shrubs (UT)	12.22	14.01	7.33	18.12
Wood volume of large wood accumulation (m^3/ha)					
	Large wood jams (LWJ)	39.11	33.32	22.26	59.43
	Individual logs (IL)	9.78	4.68	1.15	17.82
	Uprooted trees (UT)	4.77	1.16	0.01	6.59
	Root boles (RB)	0.75	0.53	0.25	1.11
	Uprooted shrubs (UT)	1.22	1.40	0.73	1.82
Wood mass of large wood accumulation (t/ha)					
	Large wood jams (LWJ)	19.55	16.66	11.13	29.72
	Individual logs (IL)	4.89	2.34	0.57	8.91
	Uprooted trees (UT)	2.39	0.58	0.01	3.29
	Root boles (RB)	0.38	0.27	0.12	0.55
	Uprooted shrubs (UT)	0.61	0.70	0.37	0.91

Table 5.4. Kruskal-Wallis (KW) tests exploring the statistical significance of differences in the frequency and volume of large wood accumulations between eight study sites and five wood accumulation types in the headwater reach of the Tagliamento River.

Variables	**KW** *p* **value**	**Degrees of freedom**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Upstream to downstream trends			
Frequency of wood accumulation/ha	0.483	7	n.s.
Volume of wood accumulation (m^3/ha)	0.457	7	n.s.
Wood volume of wood accumulation (m^3/ha)*	0.245	7	n.s.
Types of large wood accumulation			
Frequency of wood accumulation/ha	< 0.0001	4	IL, LWJ > RB, UT
Volume of wood accumulation (m^3/ha)	< 0.0001	4	LWJ > UT, RB
Wood volume of wood accumulation (m^3/ha)*	0.001	4	LWJ > UT, US, RB

Kruskal-Wallis tests were performed on the values of each of the variables (a) grouped according to the eight headwater sites and (b) grouped according to the five types of wood accumulation to assess the degree to which they represented statistically significantly different ($p < 0.05$) values of the variables. Multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those sites and large wood accumulation types that were significantly different from one another ($p < 0.05$).*There are exactly similar results for wood volume of large wood accumulation and wood mass of large wood accumulation.

(ii) Large wood accumulation dimensions

The large wood accumulations identified within the eight sampling sites were characteristically diverse in type, dimensions and size (Table 5.5). Figure 5.6 shows the relative frequency of the lengths (Figure 5.6a), diameters (b) and heights (c) for each of the types of large wood accumulation across the eight sites.

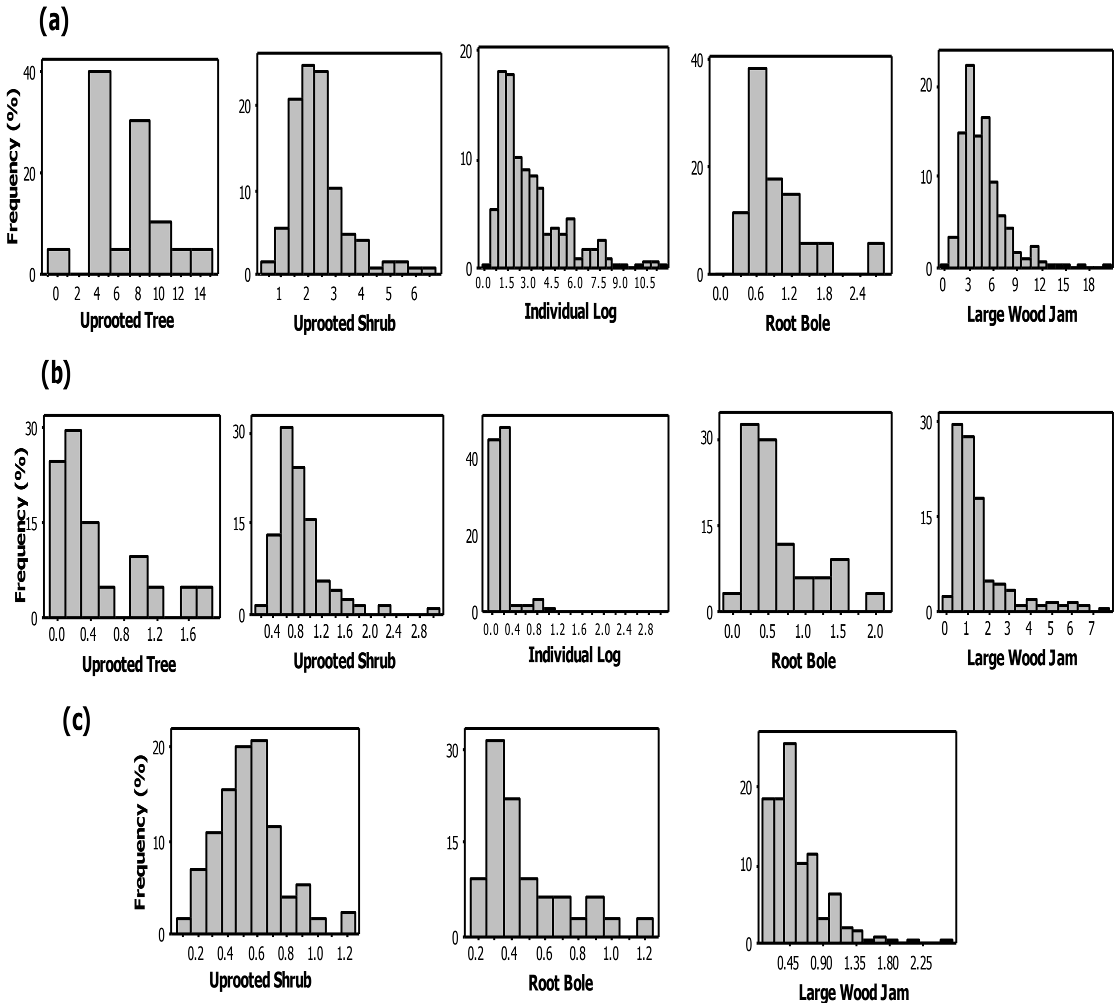


Figure 5.6. Frequency distributions of the dimensions of large wood accumulation types along the headwater reach of the Tagliamento River: (a) length (m), (b) diameter (m) and, (c) height (m).

Large wood jams, the largest type of wood accumulation by volume and wood volume, had median length, diameter and height of 3.9 m, 1.0 m and 0.40 m, respectively, and their volume, wood volume and area varied widely, ranging from 0.01 m^3 to 272.11 m^3 (median volume 1.32 m^3), 0.003 m^3 to 54.42 m^3 (median 0.26 m^3) and 0.06 m^2 to 110 m^2 (median 4.15 m^2) respectively (Table 5.5). Overall, the vast majority of the large wood jams belonged to length, diameter and height classes between 1.5-5.5 m, 0.25-1.75 m and 0.1-0.53 m, respectively, which accounted for 15-22 % (length), 18-30 % (diameter) and 19-26 % (height) of the total number of large wood jams (Figure 5.6 a, b and c). There are peaks in the length, diameter and height frequency distribution of large wood jams at the 2.5-3.5 m, 0.25-0.75 and 0.38-0.53 m classes respectively (Figure 5.6 a, b and c), accounting for 22 % (length), 30 % (diameter) and 26 % (height) of the total number of large wood jams.

Table 5.5. Summary statistics describing the dimensions (mean, median and percentiles) of the different types of large wood accumulations within the active corridor of the headwater reach of the Tagliamento River.

Types of large wood accumulation	Dimensions	Mean	Median	Q1	Q3
Large wood jams (LWJ)	Length (m)	4.59	3.90	2.73	5.60
	Diameter (m)	1.46	1.00	0.66	1.70
	Height (m)	0.53	0.40	0.30	0.70
	Area (m^2)	8.40	4.15	2.04	8.16
	Volume (m^3)	6.00	1.32	0.54	3.62
	Wood volume (m^3)	1.20	0.26	0.11	0.72
Individual logs (IL)	Length (m)	2.86	2.20	1.30	3.70
	Diameter (m)	0.16	0.10	0.07	0.14
	Volume (m^3)	0.24	0.02	0.01	0.05
	Wood volume (m^3)	0.24	0.02	0.01	0.05
Uprooted trees (UT)	Length (m)	6.72	6.65	4.38	8.58
	Diameter (m)	0.46	0.20	0.10	0.60
	Volume (m^3)	1.57	0.23	0.09	0.53
	Wood volume (m^3)	1.57	0.23	0.09	0.53
Root boles (RB)	Length (m)	0.92	0.73	0.51	1.10
	Diameter (m)	0.63	0.48	0.30	0.80
	Height (m)	0.45	0.35	0.26	0.58
	Volume (m^3)	0.16	0.06	0.03	0.24
	Wood volume (m^3)	0.16	0.06	0.03	0.24
Uprooted shrubs (US)	Length (m)	2.37	2.18	1.70	2.70
	Diameter (m)	0.78	0.70	0.50	0.90
	Height (m)	0.53	0.50	0.40	0.60
	Volume (m^3)	0.72	0.40	0.24	0.82
	Wood volume (m^3)	0.07	0.04	0.02	0.08

Even though 2.5-3.5 m long, 0.25-0.75 wide and 0.38-0.53 m high large wood jams were the most common in the study reach, it is important to evaluate which diameter, length and height classes comprise most of the large wood jams in volumetric terms, because less frequent long / wide / high large wood jams may contribute importantly to the large wood jam volume. This is confirmed by the graphs in Figure 5.7, where relative volumes (a) and relative wood volumes (b) of large wood jams (i.e. class volume / total volume) associated with each length, diameter and height class is shown. The contribution of each length, diameter and height class to the overall large wood jam volume (and large wood jam wood volume) was estimated by comparing the respective length, diameter and height classes to the large wood jam volume (or large wood jam wood volume).

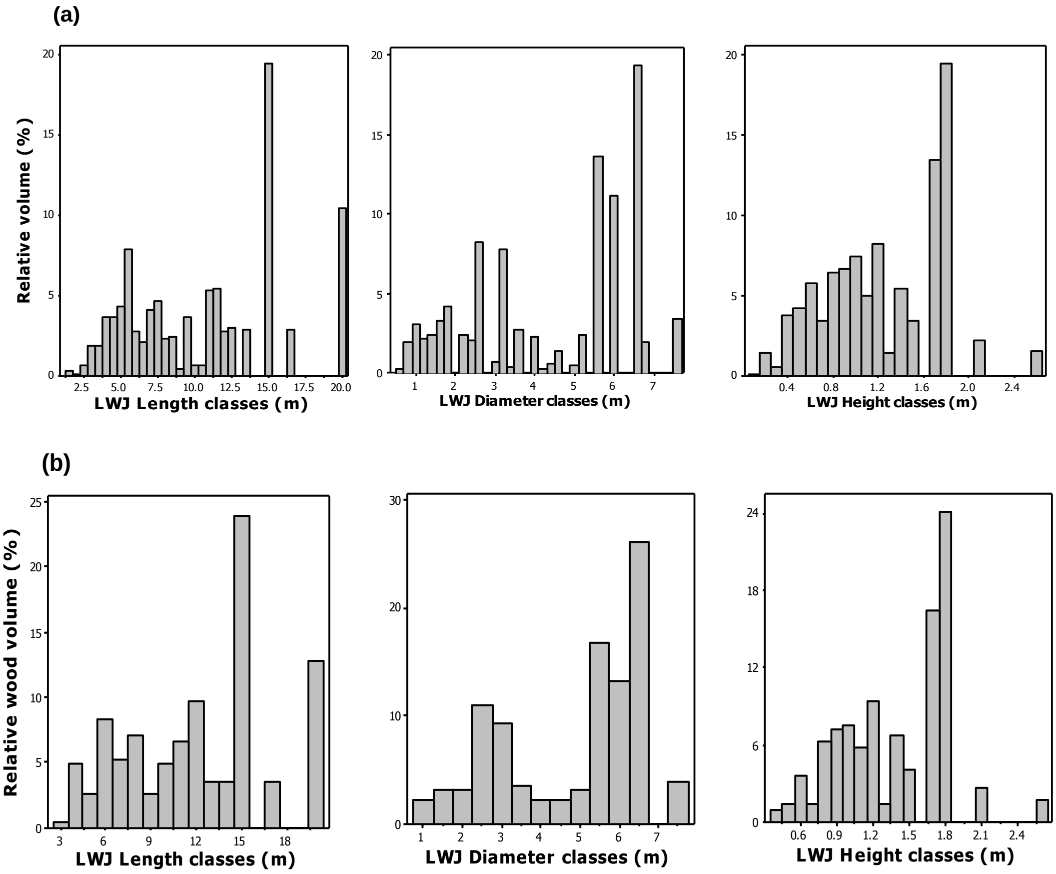


Figure 5.7. Relative volume (a) and wood volume (b) of the length, diameter and height classes of large wood jams (LWJ) within the headwater reach of the Tagliamento River.

The 2.5-3.5 m length, 0.25-0.75 diameter and 0.38-0.53 m height classes that were the most common in the study reach for large wood jams contributed to the 2.5 % (0.4 %), 0.3 % (< 0.1 %), and 7.9 % (2.2 %) respectively of the overall large wood jam volume (large wood jam wood volume). However, very irregular frequency distributions are apparent, where few wood jams of larger length, diameter and height classes dominate the volume distribution of the total number of large wood jams. The 5.25-5.75 m, 14.75-15.25 m and 19.75 -20.25 m length classes represented 7.9 % (8.4 %), 19.3 % (23.9 %) and 10.4 % (12.8 %) respectively of the overall large wood jam volume (large wood jam wood volume), 5.5-5.7 m, 5.9-6.1 m and 6.5-6.7 m diameter classes represented 13.7 % (16.8 %), 11.3 % (13.3 %) and 19.4 % (26.1 %) respectively of the large wood jam volume (large wood jam wood volume), whiles 1.15-1.25 m, 1.65-1.75 m and 1.75-1.85 m height classes represented 8.3 % (9.3 %), 13.4 % (16.4 %) and 19.4 % (24 %) respectively of the large wood jam volume (large wood jam wood volume).

Individual logs, uprooted shrubs, root boles and uprooted trees that represent relatively small accumulations in volumetric terms, show median length, diameter and / or height dimensions of 2.2 m and 0.1 m; 2.18 m, 0.7 m and 0.5 m; 0.73 m, 0.48 m and 0.35 m; and 6.65 m and 0.2 m, respectively (Table 5.5). The majority of the individual logs belong to diameter and length classes between 0.1-0.3 m and 0.75-1.75 m, respectively, accounting for approx. 18 % (length) and 45-48 % (diameter) of the total number of individual logs, whereas most uprooted shrubs belong to length, diameter and height classes between 1.25-2.75 m, 0.5-0.7 m and 0.45-0.65 m, respectively, accounting for 21-25 % (length), 31 % (diameter) and 20-21 % (height) of the total number of uprooted shrubs (Figure 5.6 a, b and c). Unlike uprooted shrubs, the length of root boles peaked at the 0.45-0.75 m class, accounting for 38 % of the total number of root boles. The majority of the root boles belonged to diameter and height classes between 0.13-0.63 m and 0.25-0.45 m, respectively, accounting for 29-32 % (diameter) and 22-31 % (height) of the total number of root boles (Figure 5.6 a, b and c). The length of uprooted trees peaked at the 3-5 m class and secondly at 7-9 m, accounting for 40 % and 30 %, respectively, of the total number of uprooted trees. The smallest diameter class (0.1-0.3 m) of the uprooted trees is the most common, with frequencies ranging between 25 and 30 % of the total number of uprooted trees (Figure 5.6 a, b and c).

(iii) Upstream to downstream trends in large wood accumulation frequency and volume

Figure 5.8 depicts the upstream to downstream trends in the frequency of the total and different types of large wood accumulations per hectare, respectively, across the eight sampling sites. The data suggest a general trend of decreasing frequency of large wood accumulations per unit area with distance downstream, although there are anomalies and the relationship is not statistically significant (KW p = *0.483,* Table 5.4). When individual types of accumulation are considered separately, the downstream trend is most apparent for large wood jams and individual logs that contributed hugely to the total number of large wood accumulations while the other types of accumulation (uprooted trees, root boles and uprooted shrubs) do not show a downstream trend in frequency. Sites 1, 3 and 7 recorded high frequencies of large wood jams (medians 47/ha, 37/ha and 55/ha, respectively) and individual logs (medians 68/ha, 64/ha and 51/ha, respectively), while no uprooted trees were recorded at sites 7 and 8 (Table 5.6). Comparatively, site 2 contained consistently large frequencies of the different types of large accumulations, especially root boles and uprooted trees (Table 5.6).

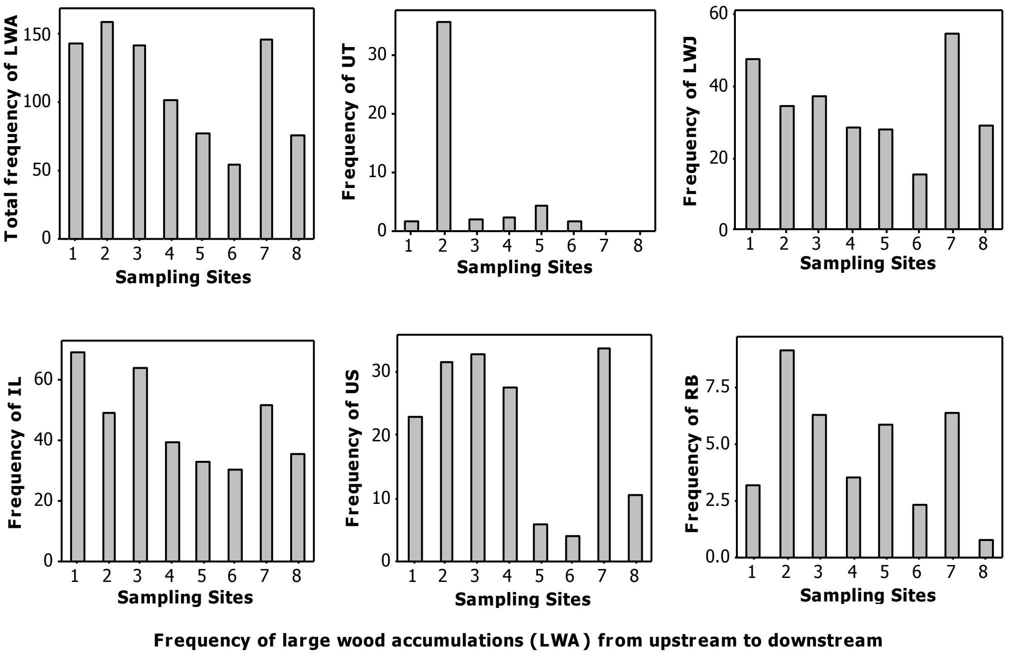


Figure 5.8. The frequency of the different types of large wood accumulation (uprooted trees (UT), large wood jams (LWJ), individual logs (IL), uprooted shrubs (US) and root boles (RB)) per hectare across the 8 sampled sites within the active corridor of the headwater reach of the Tagliamento River.

Table 5.6. Summary information on active corridor features and wood storage at eight sites along the headwater reach of the Tagliamento River.

Sampling sites from upstream to downstream	Active corridor features		Number of large wood accumulation per hectare (ha)						Volume of large wood accumulation per hectare (m^3/ha)						Wood volume of large wood accumulation per hectare (m^3/ha)					
	Wood survey area (ha)	Active channel width (m)	Total	LWJ	IL	UT	RB	US	Total	LWJ	IL	UT	RB	US	Total	LWJ	IL	UT	RB	US
1	0.61	102.39	143	47	68	2	3	23	201.69	187.83	2.65	0.02	0.27	10.93	41.60	37.57	2.65	0.02	0.27	1.09
2	0.76	126.78	159	34	49	35	9	32	486.95	417.23	29.11	20.64	1.94	18.04	136.94	83.45	29.11	20.64	1.94	1.80
3	0.95	157.52	142	37	64	2	6	33	175.46	145.36	1.32	9.65	0.76	18.37	42.64	29.07	1.32	9.65	0.76	1.84
4	0.84	139.82	101	29	39	2	4	27	165.73	124.65	17.03	5.56	1.39	17.10	50.62	24.93	17.03	5.56	1.39	1.71
5	0.68	112.89	77	28	33	4	6	6	75.10	71.22	0.63	1.90	0.31	1.05	17.18	14.24	0.63	1.90	0.31	0.11
6	1.29	214.55	54	16	30	2	2	4	21.41	18.73	0.59	0.42	0.17	1.49	5.08	3.75	0.59	0.42	0.17	0.15
7	1.25	207.55	146	55	51	0	6	34	323.89	294.64	6.70	0.00	1.01	21.53	68.80	58.93	6.70	0.00	1.01	2.15
8	1.34	223.82	75	29	35	0	1	10	334.39	304.73	20.21	0.00	0.18	9.27	82.26	60.95	20.21	0.00	0.18	0.93

LWJ, large wood jams; IL, individual logs; UT, uprooted trees; RB, root boles; US, uprooted shrubs

Table 5.6. (Continued)

Sampling sites from upstream to downstream	Wood mass of large wood accumulation per hectare (t/ha)					
	Total	LWJ	IL	UT	RB	US
1	20.80	18.78	1.33	0.01	0.13	0.55
2	68.47	41.72	14.56	10.32	0.97	0.90
3	21.32	14.54	0.66	4.84	0.38	0.92
4	25.31	12.46	8.51	2.78	0.71	0.85
5	8.59	7.12	0.32	0.95	0.15	0.05
6	2.54	1.87	0.31	0.21	0.08	0.07
7	34.40	29.46	3.35	0.00	0.51	1.08
8	41.13	30.47	10.11	0.00	0.09	0.46

LWJ, large wood jams; IL, individual logs; UT, uprooted trees; RB, root boles; US, uprooted shrubs

Figure 5.9 depicts the upstream to downstream trends in the volume of the total and different types of large wood accumulation per hectare respectively across the sampling sites within the headwater reach of the Tagliamento River. The total volume and wood volume of large wood accumulations shows no statistically significant upstream to downstream trends across the sampling sites (KW p = *0*.457 and *0.245* for volume and wood volume (or mass) respectively, Table 5.4). However, large variations in the volume of large wood accumulation types occur even between adjacent sub-reaches. With the exception of site 1, the volume of uprooted trees decreases from upstream to downstream but this trend is not statistically significant and there are no clear downstream trends for the other types of large wood accumulations (large wood jams, uprooted shrubs, root boles and individual logs). With the exception of uprooted shrubs that were largest in volume at site 7 (median volume 21.53 m^3/ha, median wood volume 2.15 m^3/ha (or median wood mass 1.08 t/ha)), the other large wood accumulations showed the largest volumes at site 2 (large wood jams: volume 417.23 m^3/ha, wood volume 83.45 m^3/ha (or wood mass 41.72 t/ha); individual logs: volume and wood volume 29.11 m^3/ha (or wood mass 14.56 t/ha); uprooted trees: volume and wood volume 20.64 m^3/ha (or wood mass 10.32 t/ha); root boles: volume and wood volume 1.94 m^3/ha (or wood mass 0.97 t/ha)) (Table 5.6).

(iv) Distribution of large wood accumulation types relative to the topography of the active corridor of the headwater reach

In Figures 5.10, the locations of recorded large wood accumulations were mapped with respect to the main topographic features of the surveyed transects at sites 1, 2, 5, 6 and 7. The cross profiles are represented with different horizontal and vertical scales so that the detailed topography, distribution of the different types of large wood accumulation and features such as active channels, bar surfaces and established island surfaces can be clearly seen. The different types of large wood accumulation are displayed using different symbols, and areas of established island with at least a 10 % vegetation cover are indicated by a line close to the topographic profile on the horizontal axis of each graph.

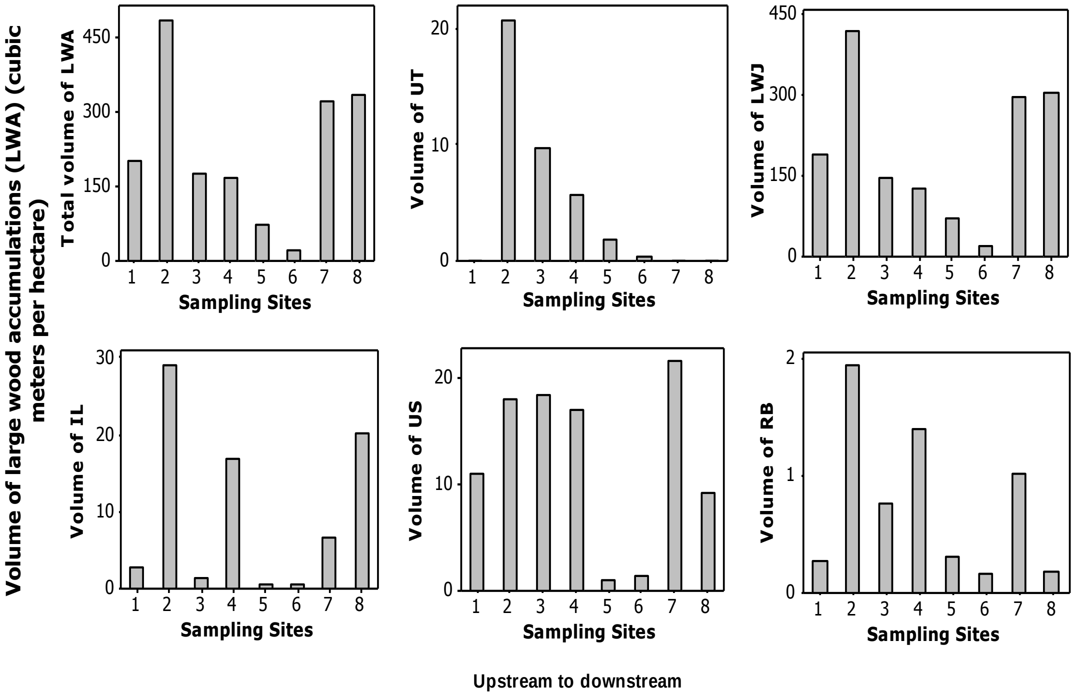


Figure 5.9. The volume of the different types of large wood accumulation (uprooted trees (UT), large wood jams (LWJ), individual logs (IL), uprooted shrubs (US) and root boles (RB)) per hectare across the 8 sampled sites within the active corridor of the headwater reach of the Tagliamento River. (Note that wood volume and wood mass graphs are not presented, since they would show the same pattern for each wood accumulation type as the total volume).

Even though the surveyed sites were relatively contiguous, there were great differences in channel morphology among these sites that may influence the distribution of large wood accumulation types and consequently have diverse geomorphic effects. Site 1 had a large area of boulder covered bars, a large alluvial fan on the right bank and an active channel on the left bank. Site 2 was characterised by a large area of boulder covered bars, an active channel on the left and right banks and an elevated established island divided into two halves by a depression. The cross sections of sites 1 and 2 were comparatively narrow (102.4 m and 126.8 m respectively). The predominant geomorphological features at site 5 were discontinuous open gravel bars and dry channels, and an active channel on the left bank. The relatively wider active corridor (214.6 m) of site 6 had a large alluvial fan on the right bank, discontinuous open gravel bars and dry channels, and an active channel that was eroding an established island near the left bank. Site 7 had an active channel eroding the left bank, and discontinuous open gravel and bouldered bars, dry channels and secondary wet channels. Site 7 was also characterised by an extensive area of established islands within the relatively wider active corridor.

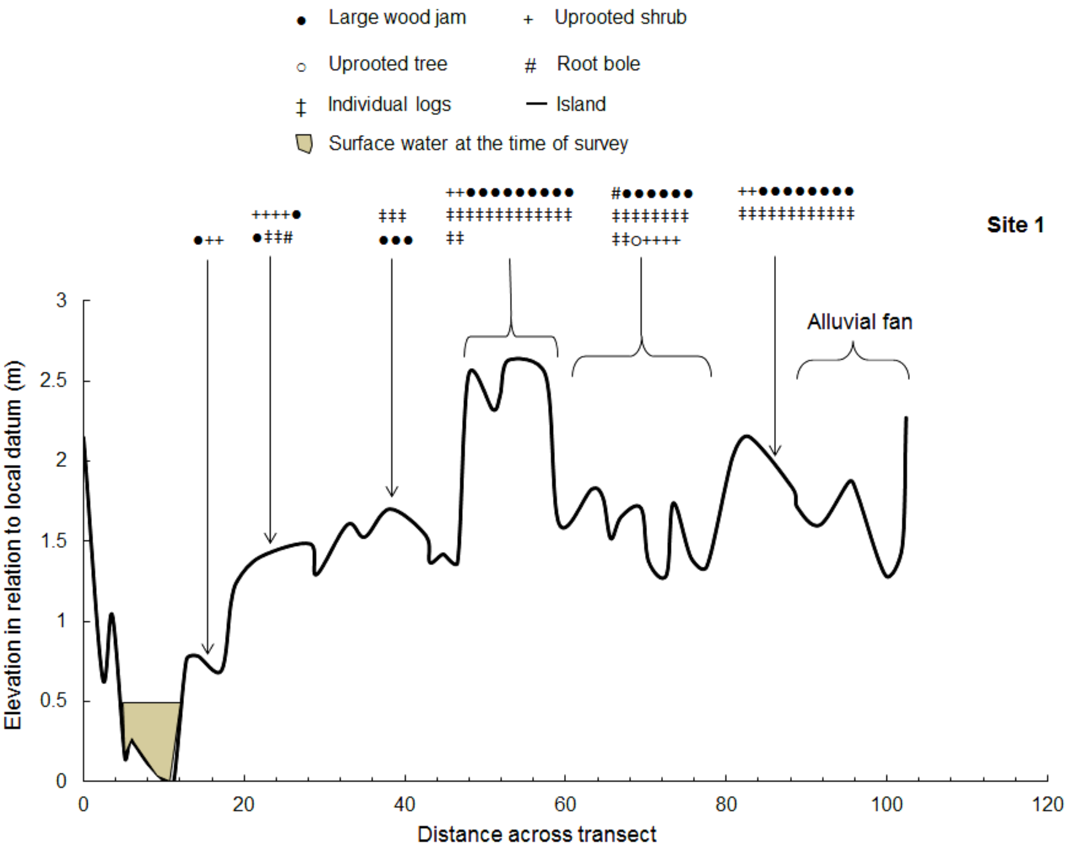
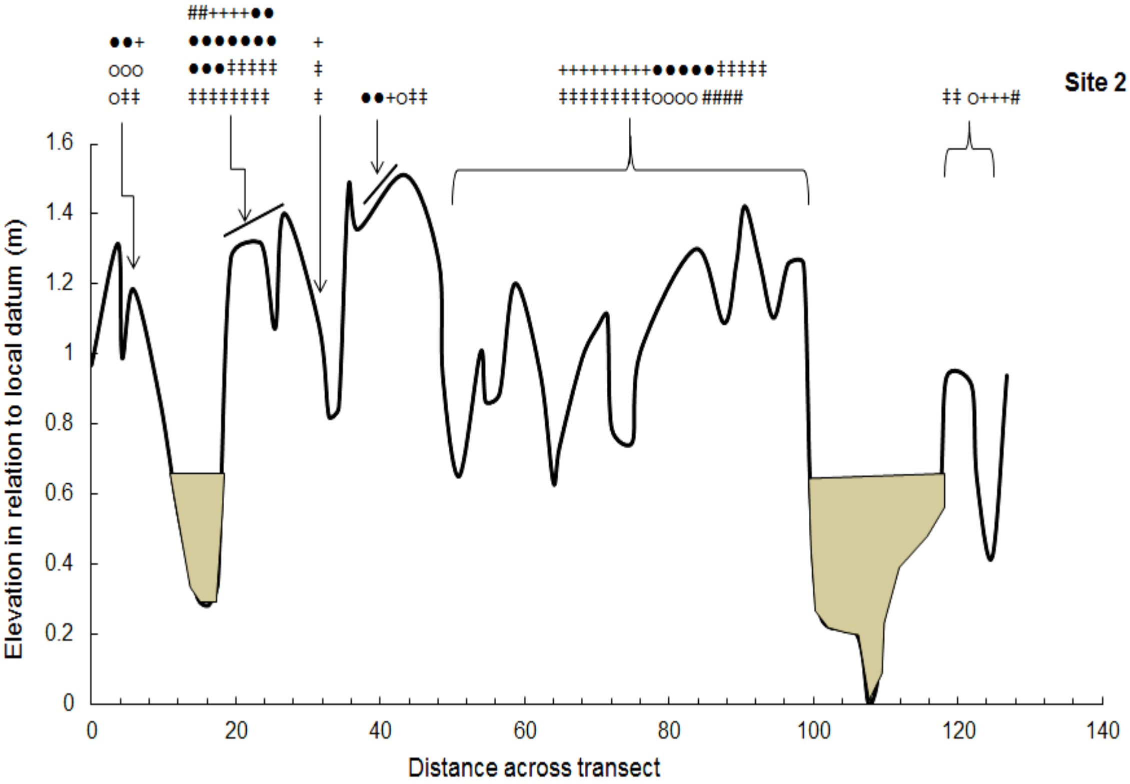


Figure 5.10. Distribution of large wood accumulation types across the active corridor of the headwater reach at sites 1, 2, 5, 6 and 7. All graphs are constructed with the left bank to the left of the horizontal axis. The arrows and lines marked above the surface of the active corridor indicate the lateral extent of the features (bars and dry channels, margins of active (wet) channels, and established island surfaces). The different types of large wood accumulation are differentiated by symbols: uprooted trees (open circle), large wood jams (filled circle), individual logs (double plus), uprooted shrubs (plus) and root boles (hash).



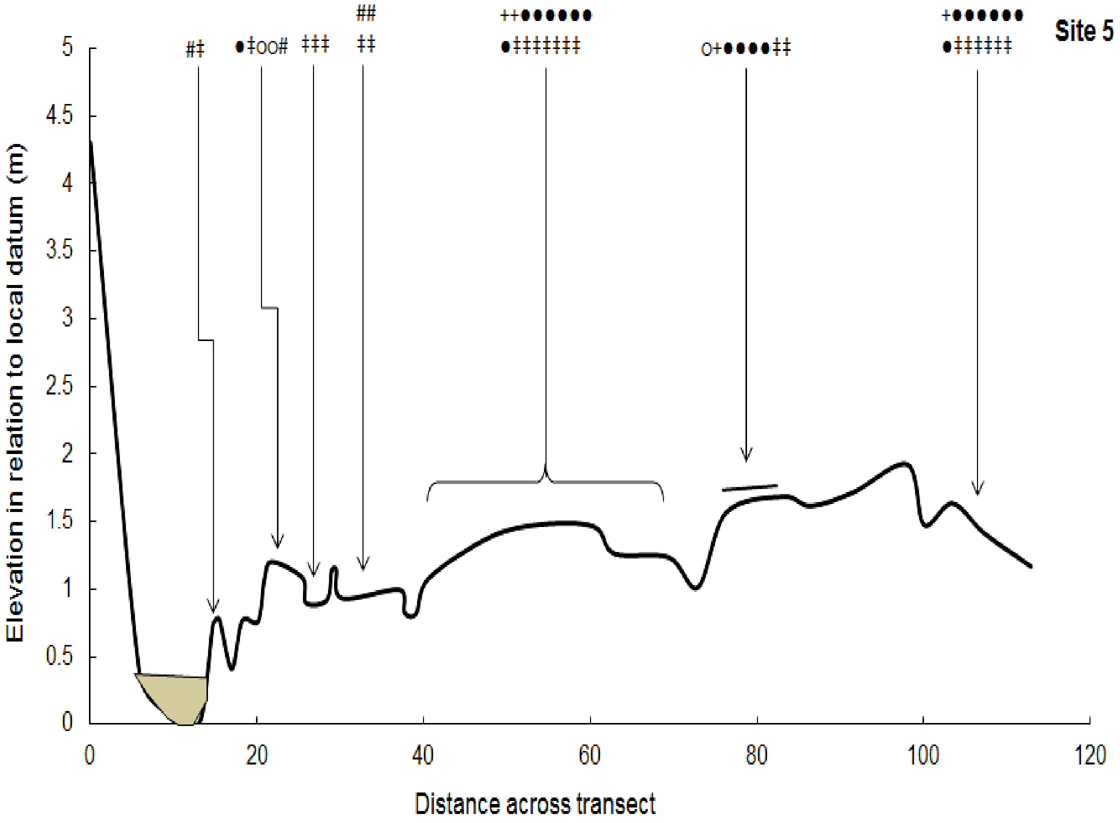


Figure 5.10 (Continued). Sites 2 and 5.

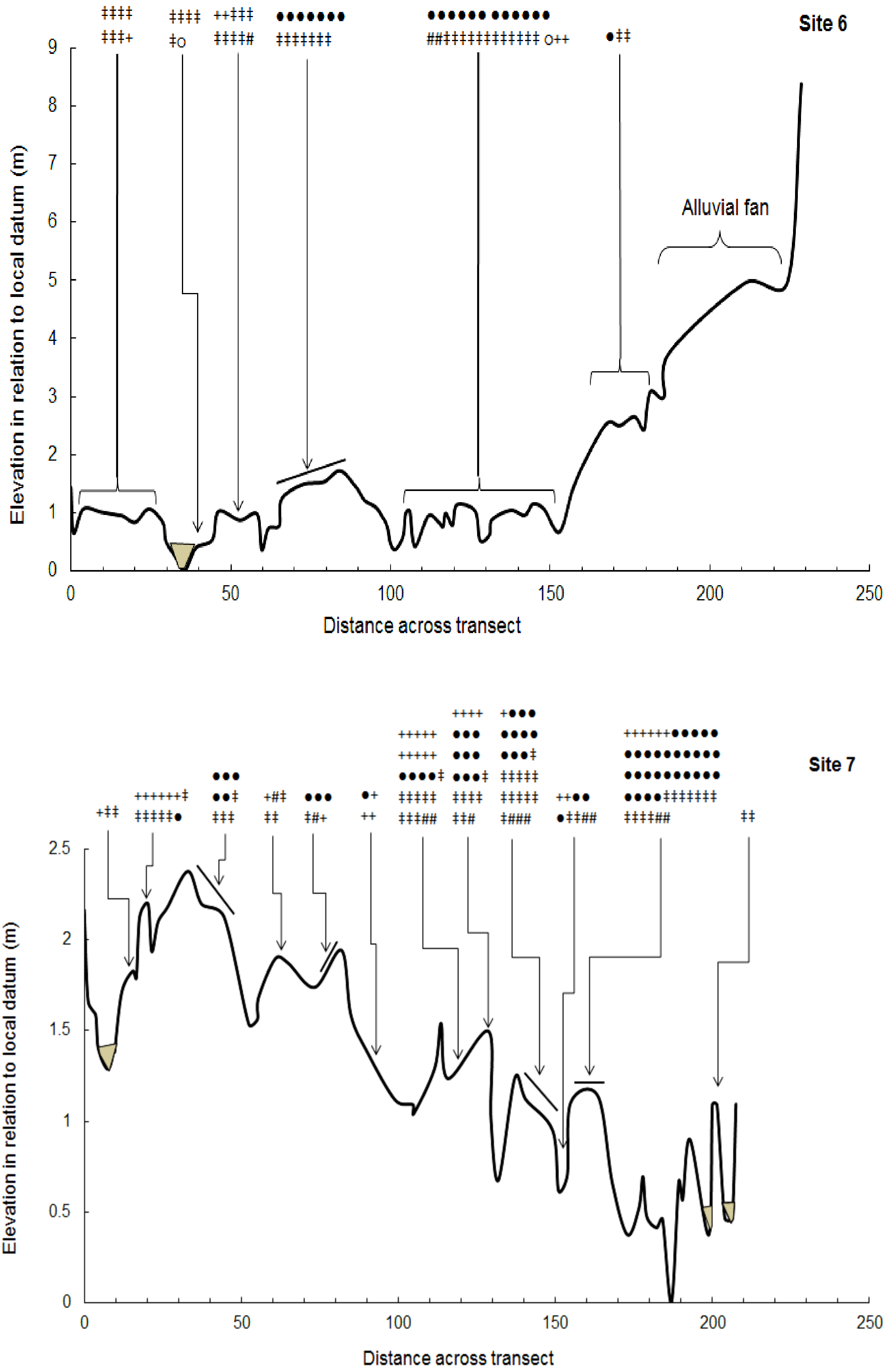


Figure 5.10 (Continued). Site 6 and 7.

From Figure 5.10, it is apparent that large wood accumulations were not uniformly distributed among the geomorphological features within the five sites. Large numbers of wood jams and individual logs were observed across the crests and edges of boulder bars at site 1. At site 2, a mixture of uprooted shrubs and trees, jams, logs, and root boles were preferentially distributed on both the crests and edges of boulder bars, and on the surface and margins of established islands. At site 5, there was a relatively lower density of wood accumulations than at the other four sites, and these generally comprised jams and individual logs distributed across bar surfaces or associated with a small island. The accumulations at site 6 were predominantly individual logs, although jams were found in the central part of the cross section on and around an island and stranded across an area of dry channels and intervening small bars. Site 7 showed large numbers of accumulations associated mainly with the crests of bars and the surfaces and margins of islands. Across the five sites, the main locations for wood retention were the surfaces and margins of islands, the crests of bars and along strand lines at the edges of bars and intervening dry channels (henceforth abbreviated to ‘bare sediment surfaces’). Wood was also frequently present along the margins of active channel(s).

Figure 5.11 illustrates the total wood volumes represented by the different large wood accumulation types with respect to these three classes of geomorphological feature across the five sites. All of these estimates are expressed per hectare of the entire sampled area, because the area covered by each geomorphological feature was difficult to determine accurately. The types and volumes of wood retained by the three surface types differ, with jams comprising most of the volume retained around islands and across bare sediment surfaces but being absent from active channel margins. Along the active channels, there was little wood at sites 1 and 2, but logs were present at sites 5 and 6 and form a notable volume at site 7. Site 6 also shows a notable volume of wood as uprooted trees and also uprooted shrubs adjacent to the active channel.

Although the data in Figure 5.11 are expressed per unit of the entire sampled area, it is apparent that if the relative areas of these geomorphological surface types could have been taken into account, the islands would have been shown to be the most important retention sites in terms of the volume of wood retained. The wood volumes associated with islands (93.71 m^3/ha) are already quite high relative to the other geomorphological surfaces (bare bar surface: 81.62 m^3/ha, active channel: 2.27 m^3/ha) in Figure 5.11, and, as can be seen from their relative extent in the surveyed cross sections in Figure 5.10, the areas of island sampled were very small in comparison with the areas of bare sediment surface.

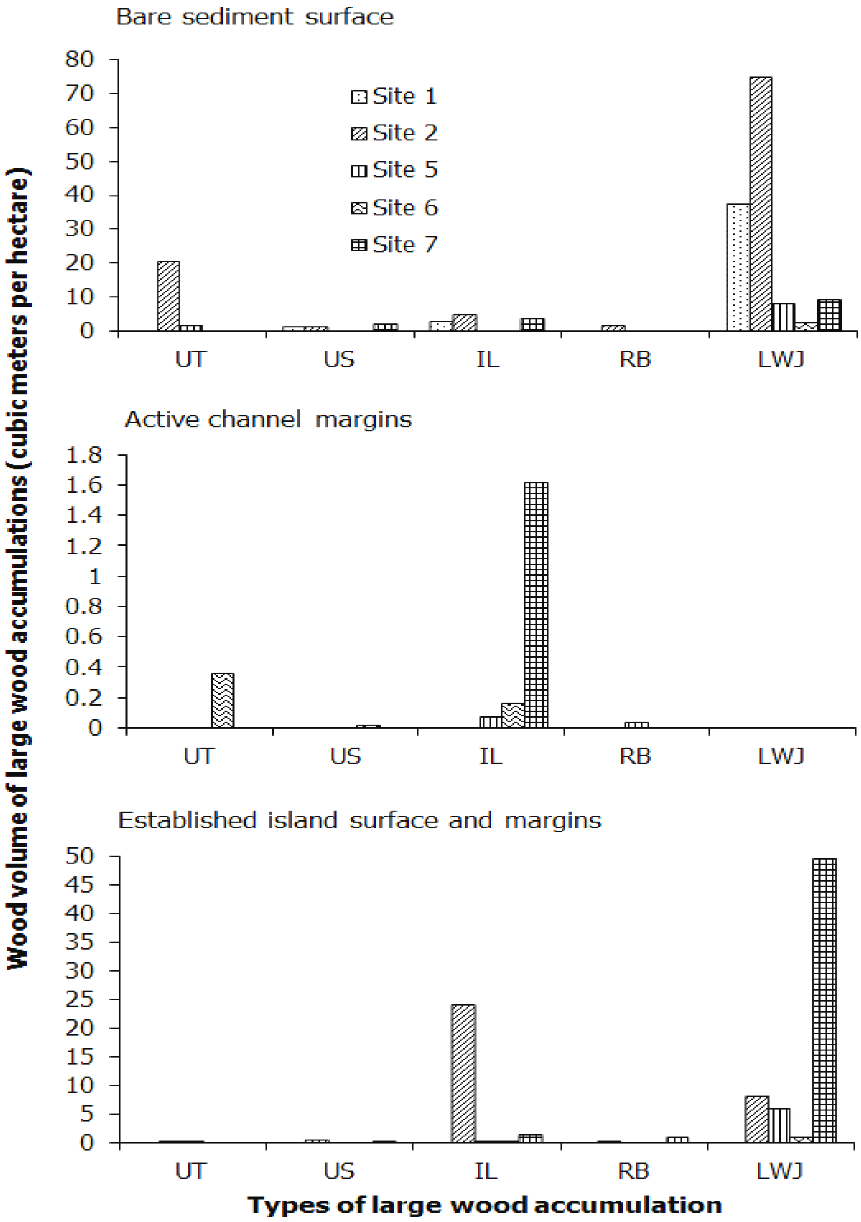


Figure 5.11. The wood volume (m^3/ha across the entire sampled area at each site) of the different types of large wood accumulations (uprooted trees (UT), large wood jams (LWJ), individual logs (IL), uprooted shrubs (US) and root boles (RB)) associated with the different geomorphological features within the active corridor at sites 1, 2, 5, 6 and 7.

5.4.2 Sediment Characteristics of Three Key Mesohabitats

The sediment characteristics of three key mesohabitats (bare gravel bar (BGB, i.e. surface sediment away from any deposited wood), large wood jam (LWJ, i.e. ground surface sediment within the jam area), and established island (EI, i.e. sediment at the island surface)) are presented in Table 5.7 and Figure 5.12. Large wood jams were selected as the wood-related sampling sites because these were the most common type of wood accumulation along the reach and because they were also observed to consistently retain sediment that could be easily sampled in a replicable way. Overall, organic matter content was highest for established islands (median 5.35 %) and lowest for the bare gravel bars (median 0.69 %), although values were highly variable, particularly for the established islands. Sediment (median particle size (D_{50})) was finest for the established island samples (median 4.1 phi) and coarsest for the bare gravel bar samples (median -2.08 phi) but again this was variable across the three mesohabitats. Bare gravel bars were associated with the highest % gravel and lowest median % sand, silt and clay, large wood jams were associated with the highest % sand and established islands were associated with the lowest % gravel and the highest % silt and clay.

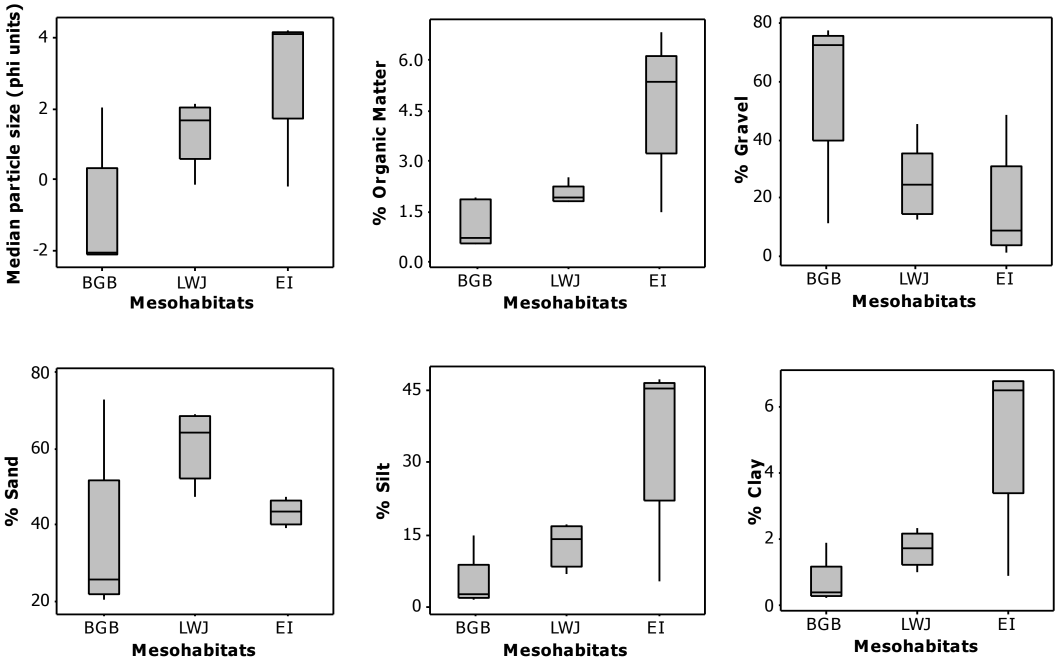


Figure 5.12. Box-whisker plots illustrating organic matter content and particle size characteristics of sediment samples from bare gravel bars (BGB), large wood jams (LWJ) and established islands (EI) mesohabitats across the active corridor of the headwater reach of the Tagliamento River.

Table 5.7. Summary of the sediment and propagule bank characteristics of bare gravel bar (BGB), large wood jam (LWJ) and established island (EI) surface sediments within the active corridor of the headwater reach of the Tagliamento River. Five bulk samples were analysed for each mesohabitat (each bulk sample was comprised of 3 replicate samples for LWJ and EI and 4 replicates for BGB).

Variables	**Mesohabitats**	**Mean**	**Median**	**Q1**	**Q3**
Sediment characteristics					
% OM	BGB	1.11	0.69	0.59	1.83
	LWJ	2	1.89	1.83	2.01
	EI	4.82	5.35	4.97	5.44
D_{50}	BGB	-1.13	-2.08	-2.09	-1.43
	LWJ	1.39	1.67	1.36	1.96
	EI	3.18	4.1	3.59	4.16
% G	BGB	60.84	72.86	68.49	74.26
	LWJ	24.62	24.54	15.94	25.01
	EI	15.4	8.54	6.11	12.27
% S	BGB	34.04	25.13	22.68	30
	LWJ	60.98	64.23	56.44	68.35
	EI	42.91	43.2	40.38	45.11
% ST	BGB	4.49	2.28	1.73	2.64
	LWJ	12.73	13.99	9.83	16.27
	EI	36.4	45.14	38.73	45.89
% C	BGB	0.64	0.37	0.29	0.42
	LWJ	1.67	1.73	1.41	1.94
	EI	5.3	6.41	5.81	6.68
Propagule bank variables					
	Mesohabitats	**Mean**	**Median**	**Q1**	**Q3**
Prop/l	BGB	5.46	3.36	3.11	7.26
	LWJ	12.97	6.36	2.79	16.92
	EI	10.4	10.73	7.55	11.64
Prop/m^2	BGB	268.56	162.1	162.1	275.87
	LWJ	694.18	330.11	183.92	1037.49
	EI	613.06	657.86	516.39	679.09
PropSR	BGB	1	1	1	1
	LWJ	1	1	1	1
	EI	2.2	2	2	3

Kruskal-Wallis (KW) tests (Table 5.8) revealed that sediment on established islands contained significantly more organic matter and a higher proportion of fine sediments (silt and clay) than bare gravel bars (KW p = 0.032, 0018 and 0018, respectively) and bare gravel bars typically contained a significantly higher % gravel than established islands (KW p = 0.046). Large wood jams contained a significantly higher % sand than bare gravel bars (KW p = 0.039).

Table 5.8. Statistically significant differences in the sediment and propagule bank variables between samples obtained from three mesohabitats within the active corridor of the headwater reach of the Tagliamento River, identified using Kruskal-Wallis tests with multiple pairwise comparisons performed using Dunn's procedure with Bonferroni correction.

Variables	**KW *p* value**	**Degrees of freedom**	**Significantly different subgroups (*p* < 0.05, n.s. if no significant differences)**
*Sediment characteristics**			
% OM	0.032	2	EI > BGB
D_{50}	0.022	2	EI > BGB
% G	0.046	2	BGB > EI
% S	0.039	2	LWJ > BGB
% ST	0.018	2	EI > BGB
% C	0.018	2	EI > BGB
*Propagule bank**			
PropSR	0.063	2	n.s.
Prop/l	0.385	2	n.s.
Prop/m^2	0.212	2	n.s.

KW tests were separately performed on the values of each of the variables associated with the mesohabitats within the active corridor to assess the degree to which the mesohabitats represented statistically significantly different (p < 0.05) values of the variables. Multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those mesohabitats that were significantly different from one another (p < 0.05). Five samples* were used in the analyses for each mesohabitat within the headwater reach.

5.4.3 Viable Propagule Content of Deposited Sediments

Figure 5.13 illustrates the poorly-developed and highly variable propagule banks found across bare gravel bar (BGB), large wood jam (LWJ) and established island (EI) mesohabitats. Overall, the number of propagules (median propagules per litre and per square metre) was very low but were found to be highest in the sediment samples from established islands (10.73 propagules per litre and 657.86 propagules per square metre), lowest in the sediment samples from bare gravel bars, and intermediate in the sediment samples from large wood jams, although this was variable and no significant differences between mesohabitats were found (KW p = 0.385 for propagules per litre and KW p = 0.212 for propagules per square metre; Table 5.8). Propagule species richness was very low but was also highest for the established islands (median 2) compared to both gravel bars and large wood jams (median 1 and 1 respectively), although no significant differences between mesohabitats were found (KW p = 0.063).

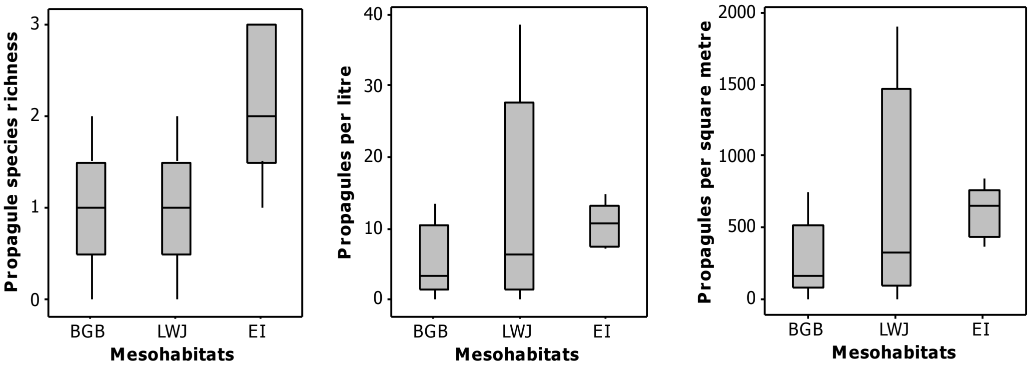


Figure 5.13. Box-whisker plots illustrating propagule species richness, propagules per litre and propagules per square metre of bare gravel bar (BGB), large wood jam (LWJ) and established island (EI) mesohabitats across the active corridor of the headwater reach of the Tagliamento River.

Table 5.9 lists the propagule species, the vegetation groups and the mean number of viable propagules and vegetation groups germinated from sediment samples collected from each of the three mesohabitats. Seedlings of 9 species emerged from the sediments during the germination trials. The assemblage structure was a mixture of ruderal species. The most frequently found species was *Conyza sumatrensis* (particularly present on the large wood jam mesohabitats). Only one species (*Conyza* *sumatrensis*) was common to all mesohabitats and several species appear constrained to a particular mesohabitat: *Urtica dioica* was found only within the large wood jams (median 83 propagules per m^2); *Epilobium sp.* were found only within the bare gravel bar samples (median 25 propagules per m^2); and *Artemisia vulgaris, Atropa belladonna*, and *Poa palustris and Poa trivialis* (the only grass species) were found only within established islands.

Table 5.9. Propagule species list and mean number of propagules per litre and square metre found within the sampled sediment from bare gravel bar (BGB), established island (EI) and large wood jam (LWJ) mesohabitats in the active corridor of the headwater reach of the Tagliamento River.

		Propagules per litre (prop/l)			**Propagules per square metre (prop/m^2)**		
Species / Mesohabitats	**Abbr.**	**BGB**	**LWJ**	**EI**	**BGB**	**LWJ**	**EI**
Artemisia vulgaris	Arte v	0	0	2	0	0	91
Barbarea vulgaris	Barb v	0	1	1	0	37	42
Atropa belladonna	Atop b	0	0	1	0	0	44
Conyza sumatrensis	Cony s	4	11	4	189	574	226
Epilobium sp.	Epilo sp	1	0	0	25	0	0
Galium mollugo	Galli n	2	0	1	55	0	85
Poa palustris	Poa pa	0	0	1	0	0	44
Poa trivialis	Poa tr	0	0	2	0	0	82
Urtica dioica	Urti d	0	1	0	0	83	0
Total number of propagules		7	13	12	269	694	614
Number of herb propagules		7	13	10	269	694	488
Number of grass propagules		0	0	2	0	0	126
Number of rush propagules		0	0	0	0	0	0
Number of woody propagules		0	0	0	0	0	0

5.4.4 Relationship between Physical and Biotic Characteristics of Mesohabitats within the Headwater Reach

(i) Spearman’s rank correlation analyses

Correlations between sediment and propagule bank variables were estimated using data from bare gravel bar, established island and large wood jam mesohabitats (15 samples). Table 5.10 presents Spearman rank correlations among sediment and propagule bank variables of mesohabitats within the active corridor of the headwater reach of the Tagliamento River.

Considering inter-correlations among sediment characteristics, organic matter content displays a significant positive correlation with indicators of sediment fining such as sediment particle size expressed in phi units (r_s = 0.88), % silt (r_s = 0.9) and % clay (r_s = 0.86), and a significant negative correlation with % gravel (r_s = -0.85).

Table 5.10. Spearman rank correlations among sediment and propagule bank variables of mesohabitats (n = 15) within the active corridor of the headwater reach of the Tagliamento River (emboldened correlations are statistically significant, p < 0.05).

Variables	**Abbr.**	**% OM**	**D_{50}**	**% G**	**% S**	**% ST**	**% C**	**Prop/l**	**PropSR**	**Prop/m^2**
Sediment	% OM	**1.00**								
	D_{50}	**0.88**	**1.00**							
	% G	**-0.85**	**-0.97**	**1.00**						
	% S	0.33	0.44	**-0.53**	**1.00**					
	% ST	**0.90**	**0.96**	**-0.91**	0.39	**1.00**				
	% C	**0.86**	**0.94**	**-0.91**	0.40	**0.98**	**1.00**			
Propagule bank	Props/l	0.17	0.35	-0.38	0.21	0.21	0.26	**1.00**		
	PropSR	**0.53**	0.50	-0.47	-0.15	0.42	0.44	**0.70**	**1.00**	
	Props/m^2	0.21	0.39	-0.40	0.21	0.26	0.31	**0.98**	**0.72**	**1.00**

Abbr.., Abbreviations of variables; % OM, Organic matter; D_{50}, Median particle size (phi units); % G, % Gravel; % S, % Sand; %ST, % Silt; % C, % Clay; PropSR, Propagule species richness; Prop/l, Propagules per litre; Prop/m^2, Propagules per metre square.

Considering inter-correlations among sediment and propagule bank characteristics, propagule species richness displays a significant positive correlation with sediment organic matter content (r_s = 0.53). This suggests that sediments rich in organic matter also retain a larger number of propagule species.

Table 5.11 presents Spearman rank correlations among the physical (large wood jam and sediment) and biotic (propagule bank) characteristics related to large wood jams. Correlations between large wood jam variables were conducted with data from all eight sampled sites (n = 8). However, correlations between large wood jam variables and variables describing sediment and propagule bank characteristics (within the large wood jam) were conducted with data from five sites (n = 5). Due to the small number of samples used in the correlations, very high values of the correlation coefficient were needed to achieve a statistically significant result.

Considering inter-correlations between large wood jam and sediment variables, wood jam height shows a positive correlation with % gravel in the retained sediment, suggesting that sediment plumes become coarser as large wood jam size increasingly protrude above the bar surface.

Table 5.11. Spearman rank correlations among the physical (large wood jam (LWJ) and sediment) and biotic (propagule bank) characteristics related to large wood jams in the active corridor of the headwater reach of the Tagliamento River (emboldened correlations are statistically significant, $p < 0.05$; emboldened underlined correlations are for small samples of 5 observations, where the correlation is very high but not quite statistically significant).

Variables	Abbr.	JL	JD	JH	JV	JA	% OM	D_{50}	% G	% S	% ST	% C	PropSR	Prop/l	Prop/m^2
Large wood jam	JL	**1.0**													
	JD	**0.9**	**1.0**												
	JH	0.6	0.5	**1.0**											
	JV	**0.7**	0.6	**0.8**	**1.0**										
	JA	**0.8**	0.7	**0.7**	**1.0**	**1.0**									
Sediment	% OM	-0.3	0.3	0.2	0.0	0.0	**1.0**								
	D_{50}	-0.6	-0.6	**-0.9**	-0.6	-0.6	0.1	**1.0**							
	% G	0.7	0.5	**0.9**	0.8	0.8	-0.3	**-0.9**	**1.0**						
	% S	-0.7	-0.5	**-0.9**	-0.8	-0.8	0.3	**0.9**	**-1.0**	**1.0**					
	% ST	-0.3	-0.3	-0.6	-0.2	-0.2	0.2	**0.9**	-0.7	0.7	**1.0**				
	% C	0.1	-0.1	-0.5	0.1	0.1	-0.1	0.7	-0.4	0.4	**0.9**	**1.0**			
Propagule bank	PropSR	0.7	0.7	0.3	0.2	0.2	-0.2	-0.7	0.4	-0.4	-0.7	-0.4	**1.0**		
	Prop/l	0.3	0.0	-0.4	-0.3	-0.3	-0.7	-0.1	0.0	0.0	-0.3	-0.1	0.7	**1.0**	
	Prop/m^2	0.3	0.0	-0.4	-0.3	-0.3	-0.7	-0.1	0.0	0.0	-0.3	-0.1	0.7	**1.0**	**1.0**

Abbr.., Abbreviations of variables; JL, Median LWJ length (m); JD, Median LWJ diameter (m); JH, Median LWJ height (m); JV, Median LWJ volume (m^3/ha); JA, Median LWJ area (m^2/ha); % OM, Organic matter; D_{50}, Median particle size (phi units); % G, % Gravel; % S, % Sand; % ST, % Silt; % C, % Clay; PropSR, Propagule species richness; Prop/l, Propagules per litre; Prop/m^2, Propagules per metre square.

(ii) Multivariate analysis and classification of mesohabitat characteristics

Mesohabitat physical characteristics were further explored using Principal Components Analysis. The associations between the composition of the propagule bank and the physical and biological characteristics of sampled mesohabitats were then investigated using a direct gradient analysis (DGA) technique.

Principal Components Analysis (PCA) was used to integrate the sediment variables measured at mesohabitats (15 samples, 5 for each mesohabitats) across the active corridor to identify patterns in the measured sediment variables and to explore how these patterns are related to the mesohabitat types. Because the variables were not normally distributed, PCA was performed on a rank correlation matrix. A reduced set of sediment variables (D_{50}, % OM, % G, % Silt + % Clay) was used to minimise the number of variables included in the analysis, to avoid including sets of variables that summed to 100 %, and also to avoid duplication (e.g. % ST and % C were both highly correlated and so a combined fine sediment variable (% Silt + % Clay) was used).

PCA revealed that the first two PCs explained over 95 % of the variance in the data set, therefore the first two PCs are retained and interpreted as they account for a substantial amount of variance (Table 5.12). The loadings on PC1, which explains 79 % of the variance in the sediment data set, indicate that it describes a gradient of sediment fining (indicated by the high negative loadings on % Gravel and positive loadings on D_{50} and % Silt + % Clay) and increasing organic matter content (indicated by the high positive loadings on % OM) associated with the mesohabitats. PC2, which explains a further 16 % of the variance, describes a gradient of increasing sand (indicated by the high positive loadings on % S).

Figure 5.14 plots the 15 mesohabitat samples in relation to their scores on PC1 and PC2, and codes them according to their mesohabitat type. In Figure 5.14, most bare gravel bar samples are clearly separated and distributed to the extreme lower left of most established island samples, with large wood jams occupying the a central position with respect to PC1 between bare gravel bar and established island samples, but with high positive scores on PC2. This indicates that established islands are associated with comparatively high amounts of fine sediment and organic matter while bare gravel bars are associated with high amounts of coarse sediment (gravel) and low quantities of fine sediment and organic matter. KW tests applied to the scores on PC1 confirm that these differences are statistically significant (Table 5.12). Scores on PC2 show statistically significant differences between large wood jams and established islands (Table 5.12), indicating that large wood jams retain more sand than established islands.

Table 5.12. Eigenvalues, percentage variation explained and variable loadings on the first two components of a PCA performed on mesohabitat physical (sediment) variables (loadings greater than 0.8 are emboldened and underlined). Results of KW tests applied to the scores of bare gravel bar, established island and large wood jam mesohabitats on the first two PCs.

	PC1	**PC2**
Eigenvalue	3.98	0.79
% variance explained	79.59	15.73
Cumulative variance (%)	79.59	95.32
Loadings		
% Organic Matter	**0.919**	*-0.224*
Median particle size (D_{50})	**0.980**	*-0.104*
% Gravel	**-0.974**	*-0.013*
% Sand	*0.546*	**0.835**
% Silt + % Clay	**0.964**	*-0.166*

	KW *p* value	Degrees of freedom	Significantly different subgroups (p < 0.05, n.s. if no significant differences)
Mesohabitats within the active corridor of the headwater reach [a]			
PC1	0.022	2	Established island > Bare gravel bar
PC2	0.031	2	Large wood jam > Established island

All loadings > 0.80 are in boldface and underlined with all other loadings shown in italics; a = 15 samples (5 for each mesohabitats) used in the KW analyses.

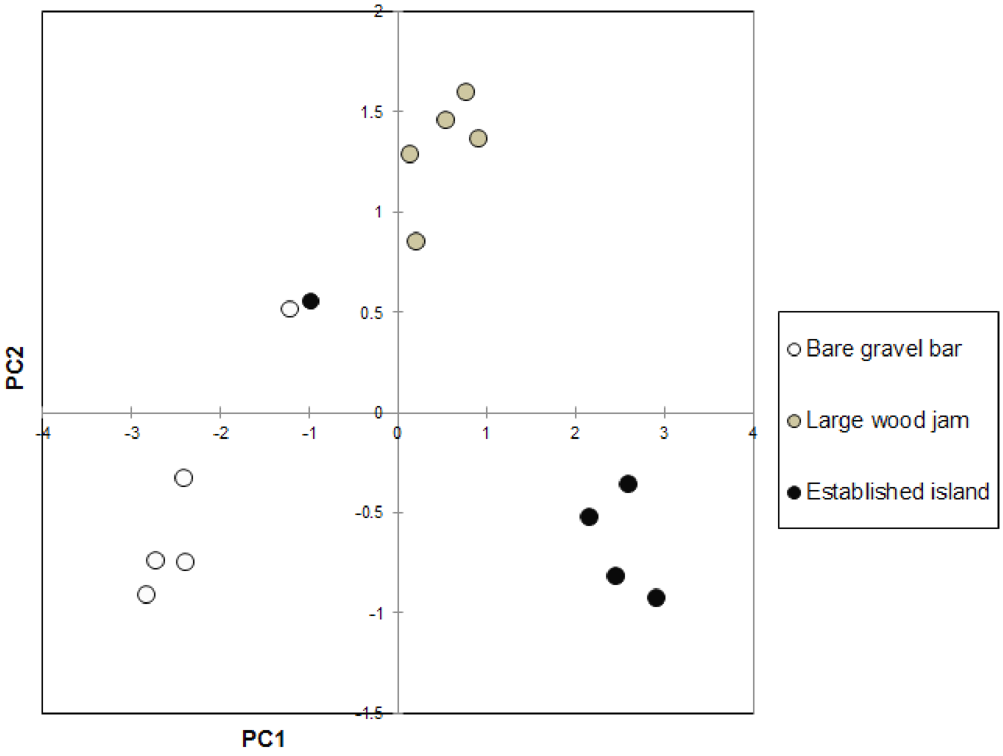


Figure 5.14. Distribution of mesohabitats across the active corridor of the headwater sites in relation to their scores on PCs 1-2.

Having established the contrasts in mesohabitat sediment characteristics using PCA and KW tests, a preliminary Detrended Correspondence Analyses (DCA) showed a similar contrast in mesohabitat propagule bank composition as was identified by the PCA for sediment characteristics. Therefore, the results for the DCA were not presented. Following the PCA and KW tests for mesohabitat sediment characteristics and the preliminary DCA for mesohabitat propagule bank composition, associations between the composition of the propagule bank and the physical (sediment) characteristics of sampled mesohabitats were investigated using a direct gradient analysis (DGA) technique. The DCA gradient lengths for the propagule bank dataset for all the mesohabitats was less than 4 (axis 1 = 3.717 and axis 2 = 2.591), therefore ReDundancy Analysis (RDA) was selected to evaluate relationships between the composition of the propagule bank and the physical (sediment) characteristics of sampled mesohabitats (see Chapter 4, Section 4.3.4).

For the RDA, all physical variables were included. Of the physical variables included in the RDA, median particle size was the only variable found to be significant ($p = 0.004$; F-ratio = 3.09; number of permutations = 499) in explaining the sample variation after a Monte Carlo permutation test of significance for all the physical variables. Despite the eigenvalues for the first two axes (0.228 and 0.110) being low (but not exceptional for ecological data), a Monte Carlo permutation test of significance on the first and all calculated axes was highly significant ($p = 0.038$ and 0.026 respectively). The species-environment correlations were 0.890 and 0.937, showing that despite the limited species abundance of the sampled propagule banks there are stronger relationships between the first two axes and the species and environment data. The cumulative percentage variance explained by the species alone for the first two axes was 22.8 % and 33.7 %, and the cumulative percentage variance explained by the species-environment relationships was 60.1 % and 89.1 %, which shows that a high proportion of the sample data variation was explained by the sediment variables. Overall, the propagule species data appear to have a strong association with mesohabitats and sediment variables, particularly median particle size, are helpful in discriminating between mesohabitats.

Figure 5.15 shows the RDA biplot for associations between (a) the propagule species of sampled mesohabitats and their physical characteristics (arrow points) and (b) sampled mesohabitats and their physical characteristics. The relative position of the physical variables (arrows points) on the RDA biplot reflects their interactions with sampled mesohabitats or species (i.e. the direction of maximum change) and the arrow length is proportional to this maximum rate of change. Figure 5.15 (a) shows that *Poa trivialis* (*Poa tr*) and *Artemisia vulgaris* (*Arte v*) are associated with increasing organic matter and fine sediment, while *Epilobium sp*. (*Epilo sp*) are associated with increasing % gravel. In Figure 5.16 (b), the relative position along axis 2 of established island samples (high scores) and bare gravel bars and large wood jams (low but similar scores) reflects the relatively fine sediments of the former, which contain relatively higher organic content. Large wood jam and bare gravel bar samples plot close to the % gravel vector on axis 2 and % sand vector on axis 1, indicating that these mesohabitats contain relatively higher amounts coarse sediment.

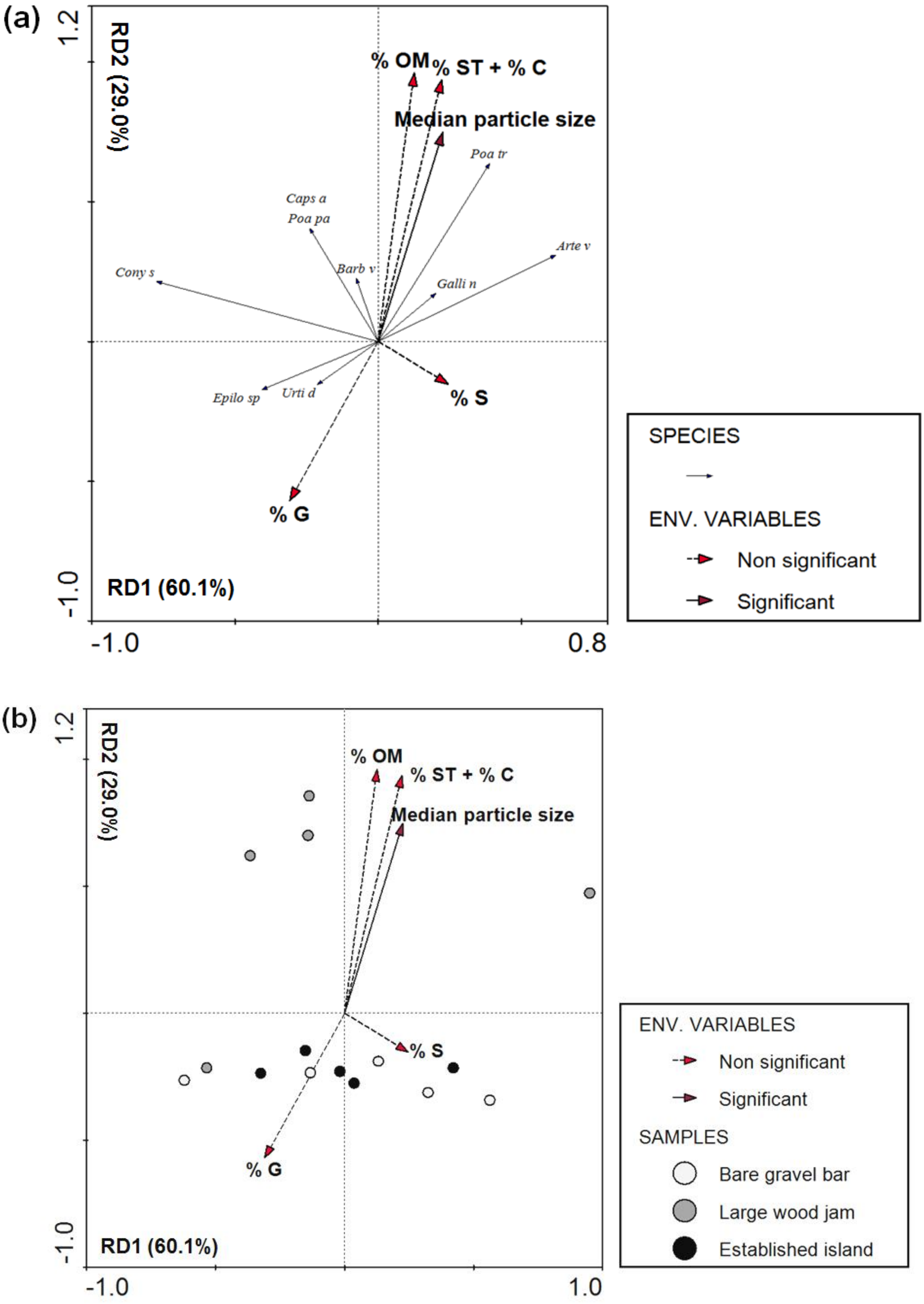


Figure 5.15. RDA ordination plots of (a) propagule species and physical characteristics (arrow points) of sampled mesohabitats; (b) sampled mesohabitats and their environmental variables (for full species names associated with abbreviations see Table 5.9).

5.5 DISCUSSION

The discussion is subdivided into five subsections to address the five research questions that were introduced in section 5.1.

5.5.1 What are the Types and Characteristics of Large Wood Accumulations within the Headwater of the Tagliamento River?

The different types of large wood accumulation identified within the active corridor of the headwater reach of the Tagliamento River were uprooted trees (entire, uprooted trees), large wood jams (condensed accumulations of logs, shrubs, trees, root masses and other wood pieces), individual logs (individual, unbranched trunks or major pieces of wood), uprooted shrubs (entire, uprooted shrubs) and root boles (root mass of a tree plus a portion of the trunk). With the exception of root boles, Gurnell et al. (2000b) and Gurnell and Petts (2006) also identified logs, whole shrubs, whole trees and jams as the main forms of large wood accumulation within the headwater of the Tagliamento River.

The frequency of occurrence of large wood accumulations (832 large wood accumulations) within the headwater of the Tagliamento River in this study is comparatively higher than that recorded by Gurnell and Petts (2006) in the same reach (445 large wood accumulations) despite the fact that the number of 60m wide transects was higher (13 sites) during the study of Gurnell and Petts (2006) in comparison with the present study (8 sites). These marked differences indicate the highly dynamic nature of the wood loading in this reach, probably reflecting relatively higher inputs of wood to the study reach prior to the present survey from processes such as landslides and floods. Although no flow data are available for this study reach, the downstream record at Villuzza (Figure 4.2) shows a pattern of numerous medium-sized flood events in the two years prior to the present survey, while Gurnell and Petts (2006) survey was conducted in 2001, immediately after the largest flood recorded since 1980. Although a large flood might be expected to generate large amounts of deposited wood, in this confined valley the wood may not be retained readily and so intermediate floods may be more important in generating wood that can be retained.

Generally, large wood accumulation was high and variable in quantity (volume and mass), reaching values (~3 to ~68 t/ha, average wood volume and mass 56 m^3/ha and 28 t/ha respectively) relatively similar to that reported previously for the headwater (average wood mass 29 t/ha) and the bar-braided (15 to 70 t/ha) reaches of the Tagliamento River (Gurnell et al. 2000a, 2000b; van der Nat et al., 2003). The average large wood accumulation volume (55.64 m^3/ha) across the eight sites in this study is typical of that reported for Salicaceae-dominated rivers (mean 57 m^3/ha, median 44 m^3/ha) by Gurnell (2013) and similar to that estimated by Comiti et al. (2006) in their study of five mountain rivers of the Dolomites, Italy (73 m^3/ha).

The different large wood accumulation types were plentiful but variable in their relative frequency and quantity in the headwater of the Tagliamento River. Individual logs and large wood jams were considerably more frequent than root boles and uprooted trees, and large wood jams accounted for a greater quantity of wood than uprooted trees and shrubs and root boles. In contrast, Gurnell et al. (2000b) found that for site 7 alone, uprooted trees and shrubs (combined) and wood jams accounted for almost the entire wood mass, with the former accounting for a larger proportion of the wood mass than the latter. However, it is important to stress that many of the large wood jams were composed of a mixture of uprooted shrubs and trees, branches, root boles, twigs, and other pieces of tree or shrub, suggesting that the way in which the wood is distributed across the river corridor may affect the proportions of the different wood types that are recorded. Large wood jams in many forested channel reaches have been found to be stable channel features (O’Connor et al., 2003; Curran, 2010), but this seems unlikely on the Tagliamento River where uprooted trees are relatively small and where wood decomposition rates are high. Where larger tree species and / or with lower decomposition rates dominate the river margins, wood storage tends to be higher. For example, Gurnell (2013) found median wood storage volumes of 1000, 227, 158, 144, 70, 44 m^3/ha for rivers bordered by redwood species, conifers, tropical rain forest, deciduous trees and the Salicaceae respectively. Of course, the highly disturbed active corridor of this study reach tends to support riparian woodland dominated by pioneer species such as the Salicaceae, and so the combination of forest and river type may partly explain these differences in wood storage.

The total frequency of large wood accumulations decreases from upstream to downstream, with some anomalies. Large wood jams and individual logs, which contribute enormously to the total number of large wood accumulations, also appear to decrease from upstream to downstream. The decrease in the total frequency of large wood accumulations and the frequency of large wood jams and individual logs may not only be due to the decrease in wood delivery processes to the active corridor along the Tagliamento River but also the decrease in the frequency of retentive and wood-storage geomorphic structures as the river widens from upstream to downstream. The quantity of uprooted trees decreases from upstream to downstream, suggesting that local bank undercutting and wind throw were probably the principle wood delivery processes to the active corridor (and the bank length varies little as the active width increases), or that as hillslope stability increases (and slope decreases), lateral wood delivery reduces from upstream to downstream.

The dimensions (length, diameter, height) and size (wood volume, area) of the different types of large wood accumulation within the active corridor of headwaters are important factors in determining its stability and possibly its influence on channel morphology (Abbe and Montgomery, 2003; Gurnell, 2003). The types of large wood accumulation identified in the wood survey within the headwater were characteristically diverse in dimensions and size (volume and area), especially large wood jams. Their dimensions are all small in comparison with the dimensions of the river but they may be larger than that in many other environments in Europe where selective-cutting and clearing of large wood pieces is practiced. Nevertheless, the wood is small compared to other environments (e.g. Pacific Northwest) where trees reach much larger dimensions because of climate, species, stand age, and forest management history.

5.5.2 Are There Any Associations Between Large Wood Accumulations and Geomorphological Features within the Headwater of the Tagliamento River?

The source area and quantity of contributing large wood accumulations to river systems varies according to the species, composition and age of riparian forests, local topography, channel characteristics and disturbance history. The relative importance of geomorphic and hydrologic processes that controls input, loadings, redistribution and morphological influence of large wood accumulations vary with position in the river channel and network (Keller and Swanson, 1979; Bilby and Bisson, 1998; Gurnell, 2003; Swanson, 2003; Chen et al., 2006). In the single studied headwater reach, position within the active corridor may influence wood retention.

Across the five sites where the association between retained wood and topography was investigated, the main geomorphic structures associated with wood retention were the surfaces and margins of islands, the crests of bars and strand lines at the edges of channels. These observations support Gurnell et al. (2000a) hypothesis that geomorphological style of river reach is an indicator of wood retention potential. The largest frequency and quantity (volume or mass) of large wood accumulations were associated with sites where island development was extensive. This confirms Gurnell and Petts (2006), van der Nat et al. (2003) and Gurnell et al. (2000b) findings that vegetated islands increase large wood retention within the active corridor of the Tagliamento River. The types and quantity of wood retained by the three geomorphic structures differ. As in the study of Gurnell et al. (2000a, 2000b), jams comprised most of the volume retained around the surfaces and margins of islands and across the crests and edges of bars but were absent from active channel margins. Vegetation on islands efficiently filters and traps even small pieces of wood from floodwaters, consequently leading to the formation of wood jams around the upstream ends of islands and around individual trees on the islands. Similar to observations by Gurnell and Petts (2006), sediment plumes were noticed within jams. Along the active (flowing) channels, there was little wood retained and it was mostly comprised of individual logs. Individual logs, uprooted trees and shrubs, and root boles were distributed fairly widely on open bar surfaces probably during the falling limb of flood events.

It has been suggested that in less-managed river systems, where river channels are morphologically intact and are bordered by riparian forest throughout their length, the relative importance of riparian forest character, hydrological processes and geomorphology to large wood dynamics changes in a downstream direction (Gurnell et al., 1995). In the headwater of the Tagliamento River, point sources of large wood and sporadic processes such as windstorms, landslides resulting from hillslope instability and bank undercutting of riparian forests and established islands, are more important to large wood delivery than more spatially and temporally continuous processes such as mortality / senescence. In particular, large quantities of wood accumulations were present in cross sections bordered by large alluvial fans (e.g. sites 1 and 6) and actively eroding vegetated islands (e.g. site 7). In spite of the high transport capacity in steep, bedrock controlled cross sections (such as sites 1 and 2), large quantities of wood were observed as in other studies (e.g. Montgomery and Buffington, 1997; Gurnell et al., 2001; Lancaster and Grant, 2006) probably due to the cumulative effects of high wood delivery (e.g. from landslides) to a small cross section comprised of a rough, retentive, topography of coarse (boulder) bars. However, the influence of channel width on large wood accumulation retention diminishes in the downstream cross sections of the headwater (e.g. Site 7). Uprooted trees were absent in the downstream cross sections of the headwater probably due to the declining influence of bank undercutting and wind throw from adjacent riparian forests. Also, uprooted trees entrained from upstream cross sections may have been broken up into individual logs and root boles. The broken wood pieces from uprooted trees may have contributed to the increase in the number and volume of large wood jams, individual logs, and root boles in the downstream cross sections of the headwater.

5.5.3 Are There Any Differences in the Sediment Characteristics of Different Mesohabitats within the Headwater of the Tagliamento River?

The substrate in the active corridor of the headwater reach of the Tagliamento River showed high heterogeneity. Established islands were unsurprisingly covered by significantly finer sediments (clay and silt) that contained more organic matter than bare gravel bars which were typically coarser. Large wood jams characteristically accumulated relatively high proportions of sand compared to both islands and gravel bars and were generally found to contain intermediate proportions of organic matter, fine sediments (silt and clay) and gravel. The sediment particle size of bare gravel bars (average D_{50} -1.13 phi), large wood jams (average D_{50} 1.39 phi) and established islands (average D_{50} 3.18 phi) were comparatively finer than the coarsest bar top deposits (average D_{50} -5.6 phi), finer gravel-pebble sheets (average D_{50} -4.0 phi) and floodplain woodland margins (average D_{50} -0.1 phi) respectively reported by Gurnell and Petts (2006) and Gurnell et al. (2000b), but the sampling protocols were different. In either case, these data suggest an increase in the potential water and nutrient retention of sediments from bare gravel bars to large wood jams to established islands that may be highly relevant to the processes governing island development. An increase in water and nutrient retention of sediments from bare gravel bars to large wood jams indicates that deposited propagules can sprout and establish quickly, consequently trapping sediment and organic matter, resources important for the aggradation and development of pioneer islands.

There was considerable variability in % Gravel and % Sand, % Silt and % Clay, and % Sand and % Organic matter exhibited by bare gravel bars, establish islands, and large wood jams, respectively. These data suggest that large wood jams influence the routing of sediment and particulate organic matter through the active corridor. They may alter patterns of scouring and deposition, and create areas of low shear stress where finer materials can be stored (Gomi et al., 2004; Oswald and Wohl, 2008; Gurnell, 2013).

5.5.4 Are There Any Differences in the Propagule Bank of Different Mesohabitats within the Headwater of the Tagliamento River?

The study showed that the propagule bank was generally poor in abundance and species richness across all of the sampled mesohabitats. This pattern may partly reflect the time of sampling as it captures the persistent propagule bank and short-lived propagule species, but other influential factors include the extreme exposure of these mesohabitats to erratic floods, the harsh physical environment such as strongly fluctuating diel and seasonal temperatures, and the low proportion of fine sediments available to contribute to propagule bank development in this steep, high energy, coarse sediment, headwater environment (Richter and Stromberg, 2005). Furthermore, propagules of different species differ in their germination requirements and so the standardised storage and germination conditions in this study may not have been suitable for the germination of some species (Lyaruu and Backéus, 1999), although it ensures that comparisons between samples are controlled. However, the germination conditions used in this study are suitable for most of the species potentially occurring in the soil propagule bank.

Although not statistically significant, the species richness and abundance (per litre and per m^2) of propagules differed among the three mesohabitats investigated. Propagule species richness and abundance were generally found to be highest in the sediment samples from established islands, intermediate in the sediment samples from large wood jams and lowest in the sediment samples from bare gravel bars, suggesting a decline in propagule species richness and abundance with the extent of exposure of these mesohabitats to hydrological processes (e.g. floods). Goodson et al. (2002, 2003) established that the highest density of viable seeds in the riparian seed banks along several rivers in the United Kingdom was found where erosion was least severe, comparable to conditions associated with established islands in the present study. Large wood jams in this study showed very high spatial variation in propagule abundance (median = 0 propagule per m^2 to 1919 propagules per m^2) although efforts were made to counteract the effect of spatial aggregation of propagules in the soil by collecting and pooling several replicate samples in each mesohabitat. The high variation in propagule abundance in large wood jams may be attributed to the variations in large wood jam size and structure and heterogeneity in sediment scouring and deposition within the sampled large wood jams.

The propagule species identified in the headwater of the Tagliamento River were generally pioneering ruderal species (i.e. propagules of plant species usually associated with open environments exposed to disturbances). This observation is similar to many studies which have found riparian zone propagule banks to be dominated by ruderals (e.g. Abernethy and Willby, 1999; Goodson et al., 2001; Tabacchi et al., 2005). These early-successional germinants, particularly *Conyza sumatrensis*, are adapted to nutritionally poor moist or dry soils, reflecting the open, disturbance prone environment of the headwater of the Tagliamento River. Established island sediment samples contained large quantities of propagules probably due to local seed rain from plants on the islands. This may consequently have influenced the occurrence of a relatively large number of herb propagules of different species such as *Artemisia vulgaris* and *Atropa belladonna* on the established islands, and also islands were the only mesohabitats that contained grass propagules (*Poa palustris* and *Poa trivialis*). These species are commonly found in disturbed areas shaded by trees with soils that are relatively fine and well-drained (Cross, 2012) similar to the environment on the established islands. The effects of currents created by successive floods are more important in influencing the presence and abundance of *Urtica dioica* and *Epilobium sp*. (Vogt et al., 2007), which were identified only in the sediments of large wood jams and bare gravel bars, respectively. The long-lived, persistent seeds of the less light-demanding and competitive *Urtica dioica* are capable of retaining their viability within the soil propagule bank for more than 5 years (Thompson et al., 1997) while the propagules of *Epilobium sp*. are small and light, dispersed widely by wind and water (Thompson et al., 1997) and are readily retained and maintain their viability within the relatively coarse bar substrate.

5.5.5 Are There Any Significant Associations between the Physical (Large Wood Jams and / or Sediment) and Biotic (Propagule Banks) Characteristics of Mesohabitats within the Headwater of the Tagliamento River?

(i) Are there relationships between the physical (wood and sediment) and propagule variables associated with large wood jams in the active corridor of the headwater?

The analysis of the relationships between large wood jam, sediment and propagule bank variables revealed that sediment plumes retained in large wood jams become coarser as large wood jam size increasingly protrudes above the bar surface. This suggests that the dimensions of large wood jams, particularly their height, is important for the characteristics of sediment retained in the large wood jam and their consequent influence in altering the bed elevations and channel morphology of gravel-bed reaches (Baillie et al., 2008; Nowakowski and Wohl, 2008; Cadol et al., 2009). However, no defining relationships were identified between the physical characteristics of large wood jams and propagule bank properties, probably due to the small sample size used in estimating the associations.

(ii) Are there relationships between the sediment and propagule variables associated with mesohabitats in the active corridor of the headwater?

The spatial pattern of propagule banks originate from differences in the relative structure of substrates available for propagule deposition or retention (Nathan and Muller-Landau, 2000). The sediment characteristics of the different geomorphological features (mesohabitats) within the active corridor of the headwater of the Tagliamento River, investigated in this study, accounted for approximately 89 % of the variation in the composition of propagule banks. Most of the variation in propagule species richness and propagule bank composition across the mesohabitats, as indicated by the correlation and redundancy analyses respectively, were significantly explained by the amount of organic matter and fine sediment, with propagule species richness increasing with increases in the proportion of fine deposits and organic matter within the sediment. These observations support the assertion that the substrate available for propagule deposition or retention might be related to differential propagule retention patterns (Nathan and Muller-Landau, 2000;

Gurnell et al., 2007) where elevated concentrations of fine sediment and organic matter even in quite small quantities may increase soil elasticity and porosity and thus support retention of more propagules (Soane, 1990; Gurnell et al., 2007).

The relatively species rich propagule banks of established islands were associated with significantly finer sediments (silt and clay) that contained relatively higher organic matter content, while the propagule banks of bare bar surfaces, whose sediments were coarser and retained little organic matter, were extremely species poor. Large wood jams retained significantly more sand (an unstable and mobile substrate), than established islands and generally contained sediment and propagules that were intermediate in fineness and species richness, respectively, between bare gravel bars and established islands. Seedlings were observed to be growing in the shelter of some large wood jams, which may have further led to the accumulation of propagules (Gurnell et al., 2001), confirming Naiman and Décamps (1997), Gurnell et al. (2004) and Gurnell and Petts (2006) assertions and observations that large wood jams create depositional areas suitable for colonization and establishment of riparian vegetation unable to withstand extremely saturated or dry soil conditions. Large wood jams may therefore be termed a 'transitional habitat', providing an important link between open gravel surfaces and the adjacent riparian forest and consequently they have implications for the initial trajectory of vegetation colonisation and the eventual establishment of islands (Gurnell et al., 2001).

Redundancy Analyses (RDA) of the species composition of the propagule bank data revealed that some propagule species within the headwater of the Tagliamento River were strongly associated with sediment characteristics. *Poa trivialis* and *Artemisia vulgaris* were associated with increasing organic matter and fine sediment deposits, while *Conyza sumatrensis* and *Epilobium sp*. were associated, respectively, with increasing propagule abundance and increasing proportion of gravel. This appears to suggest that the propagules of *Poa trivialis* and *Artemisia vulgaris* favour relatively deep, fine, well-drained, moist and moderately humus-rich soils characteristic of established islands, while the propagules of *Conyza sumatrensis* and *Epilobium sp*. generally occur in larger densities across the gravel dominated active corridor of the headwater of the Tagliamento River.

5.6 SYNOPSIS

Based on the results of the study presented in this chapter, the following conclusions can be drawn:

1. The different types of large wood accumulation identified in the study within the active corridor of the headwater reach of the Tagliamento River were uprooted trees (entire, uprooted trees), large wood jams (condensed accumulations of logs, shrubs, trees, root masses and other wood pieces), individual logs (individual, unbranched trunks or major pieces of wood), uprooted shrubs (entire, uprooted shrubs) and root boles (root mass of a tree plus a portion of the trunk). These types of large wood accumulation were virtually entirely comprised of dead wood and were characteristically diverse in dimensions and size (volume and area), especially the large wood jams.

2. The frequency and quantity (mass or volume) of the different types of large wood accumulation identified within the active corridor of the headwater of the Tagliamento River were significantly different. The frequency of individual logs and large wood jams were significantly higher than root boles and uprooted trees, while the quantity (mass or volume) of large wood jams was significantly greater than that of uprooted trees, uprooted shrubs and root boles. This shows the important contribution of large wood jams and individual logs to the overall large wood frequency and quantity (mass or volume) recorded in the active corridor of the headwater of the Tagliamento River.

3. Large wood accumulation distribution and storage vary within and between cross sections of the Tagliamento headwater river system, generally reflecting local geomorphic features, vegetation extent and hillslope stability. Large wood accumulations were identified to be retained on the surfaces and margins of islands, the crests and edges of bars and along strand lines within intervening dry channels, and along the margins of active channel(s). In terms of the quantity of wood accumulations retained relative to geomorphological features within the active corridor of the headwater,

islands were the most important geomorphic retention sites and they retained the largest wood jams (the largest wood accumulation by volume).

4. The substrate in the active corridor of the headwater of the Tagliamento River shows high heterogeneity. Established islands were covered by significantly finer sediments (clay and silt) that contain more organic matter than bare gravel bars, which were typically coarser. Large wood jams accumulated significantly a higher proportion of sand than gravel bars and were generally found to contain intermediate proportions of organic matter, fine sediments (silt and clay) and gravel.

5. The propagule bank of mesohabitats within the headwater of the Tagliamento River showed a very low abundance of viable propagules and they were generally species poor, being largely composed of ruderal species. Propagule species richness and abundance were generally found to be highest in the sediment samples from established islands, intermediate in the sediment samples from large wood jams, which also showed high spatial variation in propagule retention, and lowest in the sediment samples from bare gravel bars, suggesting a decline in propagule species richness and abundance with the extent of exposure of these mesohabitats to hydrological processes (e.g. floods and sediment scour).

6. There is one dominant factor that appears to explain propagule bank diversity (abundance and species richness) in the headwater of the Tagliamento River: the quantity and quality of fine sediment containing organic matter, which varies significantly among geomorphological features (mesohabitats) within the active corridor. Large wood jams may be termed a ‘transitional habitat’ due to their retention of fine sediment and propagules on open gravel surfaces. This may have implications for the initial trajectory of vegetation colonisation and the eventual establishment of islands.

In summary, deposited dead large wood accumulations, especially large wood jams, appear to play a pivotal role, directly and indirectly, in maintaining mesohabitat heterogeneity and to a lesser extent floral (propagule and vegetation) diversity across the headwater reach of the Tagliamento River. The natural influences of flood disturbance, deposited dead large wood and the diffuse distribution and establishment of propagules in the lee of dead large wood jams probably influence the subsequent processes of vegetation and islands development on the open gravel surfaces within the active corridor of the headwater of the Tagliamento River. The next chapter investigates the physical properties and propagule bank characteristics of key morphological features and compartments within the single thread, floodplain reach of the Highland Water, New Forest, UK, which is characterised by large wood jams, composed of dead large wood that is very different in its characteristics from that studied in the headwater of the Tagliamento River.

CHAPTER 6

DEAD WOOD JAM AND PROPAGULE BANK STRUCTURE ALONG A SINGLE-THREAD LOWLAND RIVER: THE HIGHLAND WATER, UK

6.1 INTRODUCTION

As outlined in Chapter 2, the dynamics, morphology and geomorphological role of large wood varies with the river type (e.g. Gurnell et al., 2002) and the nature of wood (living or dead) (Gurnell et al., 2001; Gurnell, 2013). This chapter focuses on a relatively small single-thread river, the Highland Water, UK, that is characterised by dead wood accumulations within the active channel. Previous research on large wood along the Highland Water has focused on the dynamics of large wood accumulations and their interactions with channel geomorphology (e.g. Gregory et al., 1985; Gregory and Davis, 1992; Gregory et al., 1994; Gurnell and Sweet, 1998). Research on the geomorphological role of large wood has concentrated on studying the stability of pool-riffle sequences as an important feature of river channels, characteristics of large wood accumulations and their dynamics with changing hydrological regimes, and quantifying the number and size of pools associated with large wood accumulations (Piégay and Gurnell, 1997; Gurnell and Sweet, 1998; Gurnell et al., 2002; Millington and Sear, 2007). Research has also investigated how large wood accumulations influence floodplain sedimentation (Jeffries et al., 2003; Sear et al., 2010) along the Highland Water, focusing on the influence of wood retention on the frequency and duration of overbank and floodplain deposition, formation of multi-channel patterns, and defining the processes and resulting morphology associated with the role of large wood accumulations in the formation and maintenance of floodplain surfaces. However, there is a lack of research into characterising the large wood pieces that constitute large wood accumulations and the possible influence of large wood accumulations on mesohabitat diversity along the Highland Water.

Plant community diversity along the riparian zone of the Highland Water in the New Forest has been recognized to be relatively poor due to intense grazing pressure that prevents regeneration of many woody, grass or herb species (Jeffries et al., 2003). Propagule bank research in other lowland rivers in agricultural catchments with relatively intense grazing pressure has identified spatial and temporal diversity in the propagule bank of different mesohabitats or compartments within the riparian corridor (Goodson et al., 2002; Goodson et al., 2003; Gurnell et al., 2007). In investigating the role of large wood accumulations in the formation of multi-channel patterns, Sear et al. (2010) observed sand and silt splays on the floodplain and large wood accumulation depositional features composed of a complex matrix of seeds, large to fine particulate organic matter, fine sand, silt and clay which are rafted or redistributed into the channel or onto the floodplain during overbank flows. Nilsson and Grelsson (1990) and Andersson et al. (2000) found that the dispersal patterns of small pieces of wood and propagules were strongly correlated. Propagules can stick to floating objects such as small pieces of wood, logs, twigs and leaves and can be stranded in large wood accumulations (Johansen and Hytteborn, 2001). Sear et al. (2010) inferred that seeds retained in the depositional features along the Highland Water are important germination sites for trees and shrubs. Nonetheless, there is a lack of research into the possible relationships between large wood accumulations and propagule and / or plant diversity in lowland rivers in general.

This chapter investigates the physical properties and propagule bank characteristics of wood accumulations and associated mesohabitats within the active channel of the single-thread lowland Highland Water, United Kingdom. The research explores relationships between the type and spatial organisation of deposited dead wood accumulations, and relationships between the sediment characteristics and propagule bank (spring and mid-summer) of key mesohabitats, by addressing following the research questions:

i. What are the types and characteristics of large wood accumulations present within the river?

ii. Are there any associations between large wood accumulations and geomorphological features (mesohabitats)?

iii. Are there any differences in the sediment characteristics of different mesohabitats?

iv. Are there any differences in the propagule bank of different mesohabitats?

v. Are there any significant associations between physical (large wood accumulations and / or sediment) and biotic (propagule bank) characteristics of mesohabitats?

6.2 STUDY SITE

An overview of the research design and research sites included in this thesis was provided in Chapter 3. The research for this chapter was conducted along a third order, low-energy, lowland, gravel-bed, meandering reach of the Highland Water, flowing through the New Forest, Hampshire, UK (Figure 6.1).

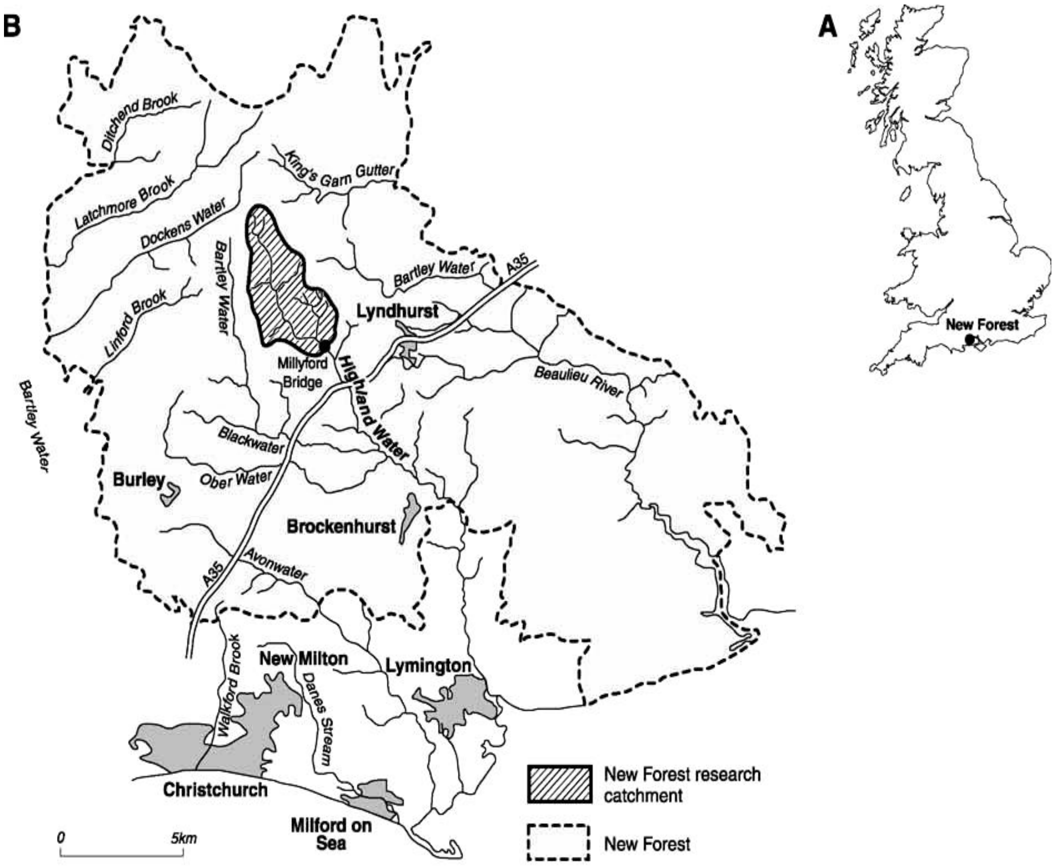


Figure 6.1. Location of Highland Water in (A) South England; and (B) the New Forest and research catchment (Source: Jeffries et al., 2003). (Note that the research reach investigated in this chapter extended downstream from Milyford Bridge to the A35, and so is immediately downstream of the catchment marked on the map).

The 2 km study reach of the Highland Water extends from Milyford Bridge to the bridge crossing of the A35 adjacent to the New Forest Gate House (Figure 6.1B and 6.2). The reach has an average slope of 0.0057 $m.m^{-1}$ and the relatively shallow active channel (approximately 1m to bankfull level) extends to an average width of approximately 3 m (Gurnell and Sweet, 1998; Gurnell et al., 2002; Jeffries et al., 2003). The size of the bed material within the active channel is highly variable, ranging from coarse lag and riffle deposits (D_{50} ~ -5 phi; cobbles) to extensive gravel-pebble deposits (D_{50} ~ -2.5 phi; coarse gravel) to a tightly packed amalgam of alluvial silt, clay and sand within the channel. The banks are composed of cohesive alluvial materials consisting primarily of tertiary sands and clays with fluviogenic gravel lenses (Cox, 1997). The active corridor is characterised by a continually changing mosaic of mesohabitats (including partly and fully submerged sediment mesohabitats (e.g. banks, channel bed, bars, pools, riffles), vegetated mesohabitats (e.g. areas of young sparse seedlings and saplings on moist channel bars and dry bank top surfaces, mature open tree cover on the damp floodplain), and wood-related habitats (e.g. wood piles on the floodplain, large wood pieces and accumulations within the channel, patches of smaller wood pieces and organic matter) (Gurnell and Sweet, 1998; Sear et al., 2010). The varying water levels associated with the river's flashy flow regime disturb sediments and vegetation within the active corridor leading to widespread erosion of banks and bars, and also the deposition and reorganization of sediment and large wood in the active channel and on the floodplain (Gurnell and Sweet, 1998; Jeffries et al., 2003). The river has developed a floodplain across which shallow side channels support surface water flow during high discharge events.

The Highland Water flows through one of the largest areas of relatively unmanaged heathland and woodland in Britain, the New Forest National Park (Figure 6.1B), and its margins and floodplain are mainly covered by mixed woodland. A variety of factors including ownership by the Crown, common rights, and the presence of widespread areas of acidic, relatively infertile soil have all discouraged agricultural and other developments across the New Forest, although the heathland-covered hillslopes are maintained by cutting and burning to prevent encroachment by trees (Tubbs, 1986). The relatively infertile soils and the heavy free-range grazing by ponies, cattle, pigs, donkeys and fallow deer has significantly contributed to the decrease in the density and diversity of the woodland vegetation on the floodplain, probably reducing the number of viable seedlings that reach maturity. The river is bordered by unmanaged, mixed deciduous woodland, dominated by sessile oak (*Quercus petraea*), birch (*Betula pubescens*), ash (*Fraxinus excelsior*), alder (*Alnus glutinosa*) and several *Salix* species (Jeffries et al., 2003), which supply wood to the river channel.

6.3 METHODS

6.3.1 Research Design

Figure 6.2 illustrates the 2 km study reach which was divided into nine contiguous 200 m sub-reaches from upstream to downstream in order to capture any variability along the reach in relation to its sedimentary structure, the character of large wood accumulations within the river channel and some specific mesohabitats and their propagule banks. A survey of the river channel morphology and large wood accumulations was conducted in May 2011. In May and July 2011, samples of sediment and the contained propagule bank were collected using a stratified random sampling design that characterised specific mesohabitats, mainly associated with wood, within each of the 200 m sub-reaches. The latter sampling was conducted in late spring and summer to capture any seasonal differences in the species abundance within the propagule bank of the sampled mesohabitats.

6.3.2 Field Methods

Four types of data and / or samples were collected from the study reach; (i) a detailed geomorphological survey of all nine sub-reaches was conducted; (ii) within all nine sub-reaches, observations and measurements were made of large wood accumulation characteristics and; (iii) within all nine sub-reaches, sediment samples were collected to provide data on sediment calibre, organic content and the plant propagule bank.

(i) Reach geomorphological characterisation

The geomorphology of the study reach was mapped to provide a context for interpreting the other data sets that were collected and also to place them in the context of the study reach as a whole (Figure 6.2). Gurnell and Sweet's (1998) study on the dynamics of large wood and pool habitats was based on field mapping the features along the study reach in 1998. The present study adopted an identical mapping methodology to quantify the recent mesohabitats and active channel features associated with large wood accumulations. The survey focused on the active channel and recorded the location and extent of key mesohabitats (e.g. pools, riffles, and bars), channel bank profiles (e.g. undercutting, vertically eroding), and large wood features (jams and wood pieces). The mapping of the study reach was conducted during low flow conditions. All other field work was conducted with reference to these geomorphological maps.

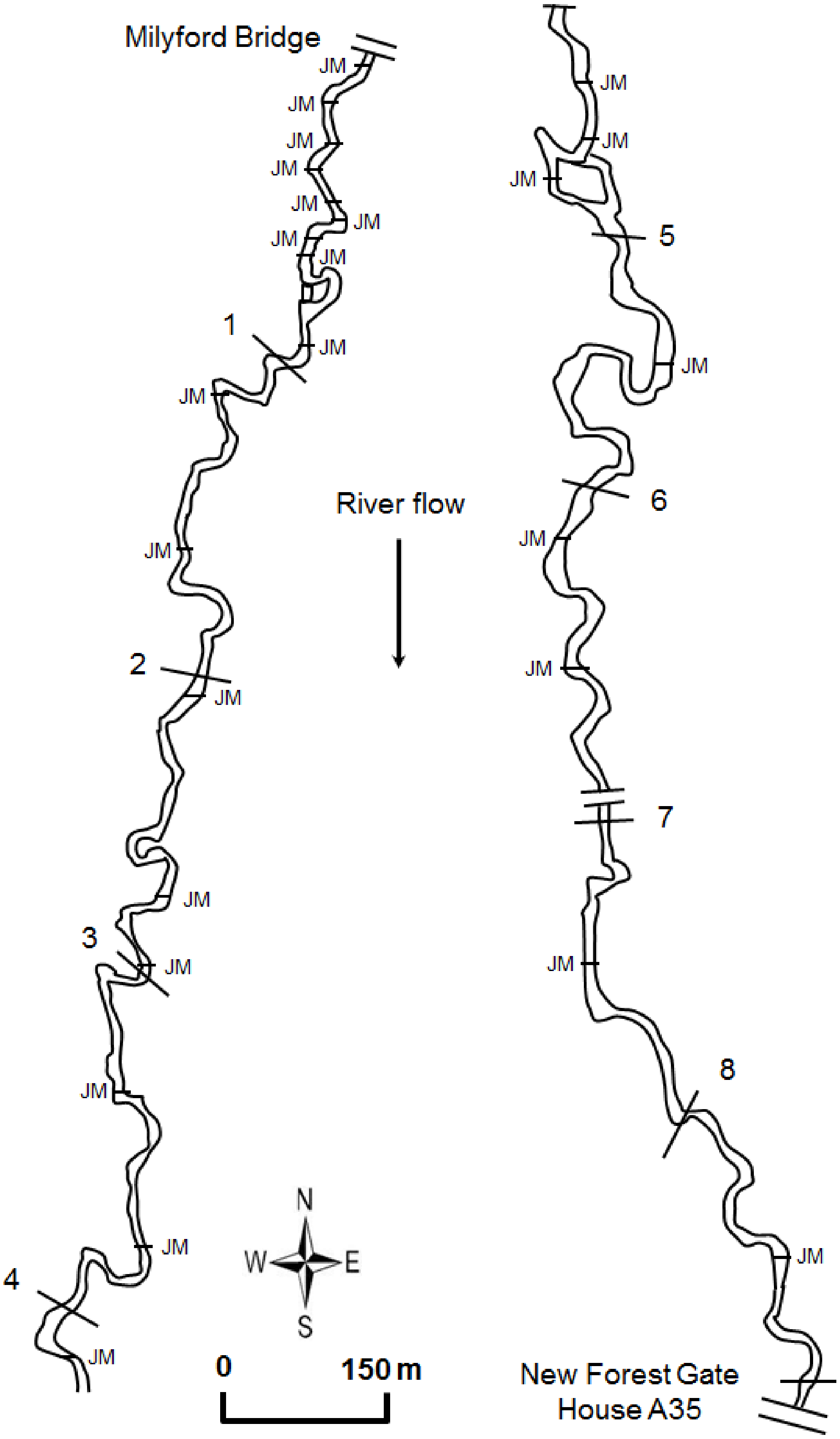


Figure 6.2. The Highland Water study reach, showing the location of the sampling sub-reaches and the investigated jams (JM) from upstream to downstream.

(ii) Large wood accumulation survey

A large wood accumulation survey (details and definitions in Appendix I) was based on the methodology developed by Gurnell and Sweet (1998) with some minor modifications. The survey provides a standardised, repeatable method for recording wood accumulation characteristics and dimensions, channel dimensions in the vicinity of wood accumulations, and the mesohabitats associated with or in the vicinity of wood accumulations. Recordings were based either on visual assessment (e.g. classification of large wood accumulation, identification of mesohabitats) or on measurements of dimensions (e.g. channel, jams, wood pieces).

Since the large wood data relate to a single survey undertaken between 9 and 12 May 2011, they only reflect a snapshot of a very dynamic wood storage regime, which is governed by the magnitude and timing of the most recent major flood event. Each jam was characterised according to jam position, type and decay status (Table 6.1, see Appendix I). Firstly, jams were categorised on the basis of their position with respect to the river planform from downstream to upstream within a sub-reach (jam position); secondly, jams were categorised on the basis of their interaction with river flows and thus impact on channel morphology and mesohabitats (jam class) and; lastly, jams were categorised on the basis of the extent of decay of their wood pieces which is used as an indicator of jam age and stability (jam decay status).

Large wood pieces within jams (> 10 cm in mid-diameter and > 1 m in length) and the dimensions of jams (length, width and depth) were measured using a 30 m tape and 1 m ruler. The volumes of wood pieces (length and diameter) and jams (length, width and depth) were also measured using direct counts and the total wood/air volume method respectively (Gurnell et al., 2000b; Lamberti and Gregory, 2011).

Table 6.1. Characterisation of jams along the Highland Water using three criteria: jam position, jam class and jam decay status.

Criteria	Variables	Definition
Jam position	Upstream of bend	Jams located upstream of bend.
	At bend	Jams located at bend.
	Downstream of bend	Jams located downstream of bend.
Jam class	Active	Tightly stacked wood pieces that completely span the bankfull width of the active channel and are hydraulically effective, causing significant changes to the water surface profile even during low flow.
	Complete	Porous stacks of wood pieces that span the bankfull width of the active channel but do not influence the low flow water surface profile due to their permeability.
	Partial	Stacked wood pieces that span only part of the bankfull width of the active channel and divert flow.
	High	Wood pieces, usually whole trees, suspended across the active channel from the top of the left bank to the right bank and thus causing no change to the water surface profile except during bankfull flow events when they may act to locally deflect water out onto the floodplain.
Jam decay status	Partially decayed xylem	Jams containing wood pieces with partially decayed xylem.
	Bark completely or mostly removed	Jams containing wood pieces with bark completely or mostly removed.
	Bark partly removed showing xylem	Jams containing wood pieces with bark partly removed showing xylem.

(iii) Sediment and propagule bank sampling

Sediment and propagule bank samples were collected using a stratified random sampling design. Sediment samples were collected in each of the nine sub-reaches. Within each sub-reach, sediment samples were collected from five specific mesohabitats: mid-channel bar surfaces (BGB), the sediment retained within jams (JM), the face / toe of banks immediately adjacent or downstream of jams (JB), the surface of unvegetated bare eroding banks between jams (BK) and the bank top / floodplain surface (FP) (Figure 6.3, Table 6.2). The mesohabitats were chosen to investigate the sediment and propagule characteristics of two wood-related habitats (JM and JB) in comparison with three commonly-occurring mesohabitats that were not related to wood accumulations (BGB, BK, FP). A single sample of each mesohabitat type was obtained from each sub-reach, but each sample was a composite of three sub-samples extracted from random, widely-spaced examples of the same mesohabitat type, with the exception of the bulked samples from bar surfaces where four samples were combined to ensure sufficient fine sediment for analysis in these predominantly gravel deposits (Table 6.2). The individual samples were obtained using a cylindrical corer (see Chapter 3, Section 3.5.3). The sub-reaches were sampled in sequence from downstream to upstream in order to minimize contaminating sediment samples.

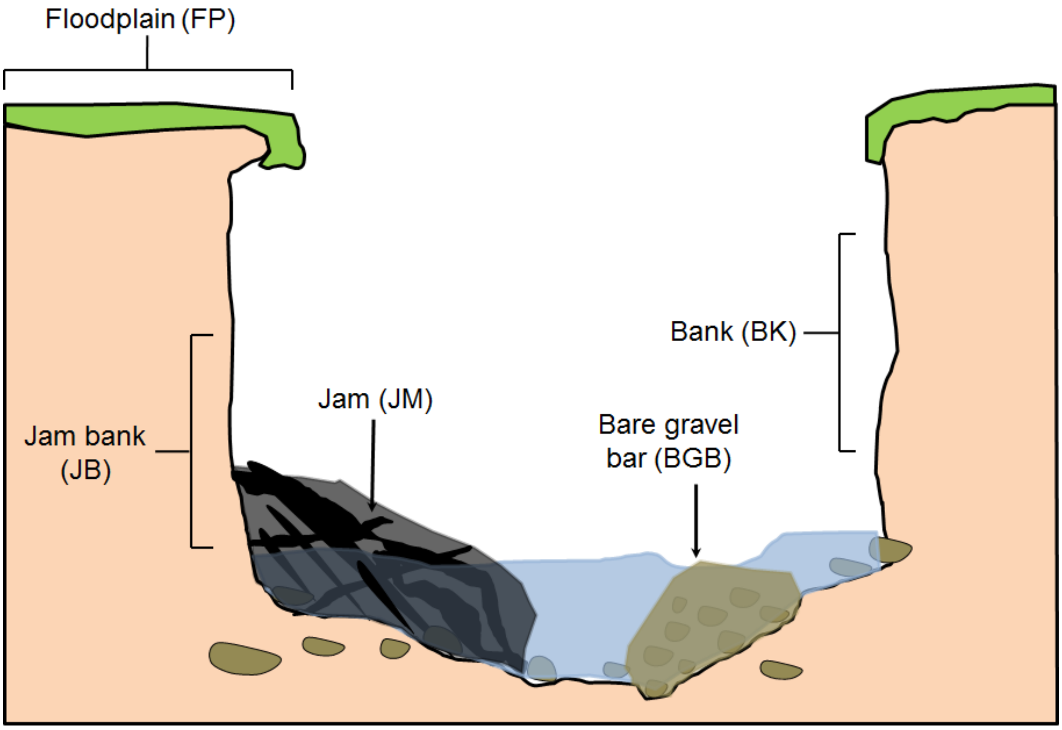


Figure 6.3. Schematic representation of the typical patterning of habitat patches (mesohabitats) representative of the study reach along the Highland Water. The mesohabitats identified within the river corridor along the study reach were bare gravel bar (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP). (Note that the bare gravel bar (BGB), bank (BK) and floodplain (FP) samples were obtained from sites that were not immediately adjacent to jams, but it is not possible to represent this clearly on this cross-sectional diagram).

Since propagule banks vary greatly in time as well as space (Fenner and Thompson, 2005), sediment and propagule bank sampling was undertaken on two separate occasions: (i) in May 2011 (spring (PB1)) following the recession of the major spring floods but prior to the main summer flowering season, to capture the persistent seed bank and; (ii) in July 2011 (mid-summer (PB2)) to capture early summer contributions to the transient seed bank (Schneider and Sharitz, 1986; Richter and Stromberg, 2005).

Table 6.2. The number of bulked samples obtained to characterise mesohabitats along the study reach. Each bulked sample was assembled from 3 replicate samples, apart from bar surfaces where 4 replicate samples* were bulked to ensure sufficient finer sediment for laboratory analysis from these relatively coarse sediments.

Mesohabitats	**Abbreviations**	**Definitions**	**Number of sampled sites**
Bare gravel bar	BGB	Surface sediment of exposed, unvegetated mid-channel bars.	9
Jam	JM	Sediment accumulated within a jam.	9
Bank	BK	Surface of an actively eroding river bank face midway between the bank top and the bank toe.	9
Jam Bank	JB	The face / toe of banks immediately adjacent or downstream of jams.	9
Floodplain	FP	Floodplain surface close to the river channel (i.e. bank top).	9

6.3.3 Laboratory Methods

The laboratory methods of (i) sediment storage and preparation, (ii) sediment analysis and (iii) germination trials used in this study are described in Chapter 3 (Section 3.6).

6.3.4 Data Analysis

Table 6.3 lists the variables investigated in this study and defines how these were derived from the raw field and laboratory measurements. The data generated from these procedures were analysed using a number of descriptive, bivariate and multivariate analysis techniques. For the jam, wood piece, propagule and sediment results, descriptive statistics were used to identify trends in the raw data. Descriptive statistical techniques were used to assess jam characteristics (research question 1) and the associations among jam characteristics and jam-associated mesohabitats (research question 2). Descriptive statistical techniques revealed that most of the variables were not normally distributed and the variables frequently showed differences in variance between jam characteristics or mesohabitats, so non-parametric statistical methods were used for data analysis.

The primary means of assessing research questions 3 and 4 was through comparison of medians of the measured variables, via non-parametric analysis of variance. Kruskal-Wallis (KW) tests or Mann Whitney (MW) tests, as appropriate, were used to explore the differences in sediment and propagule bank variables between the different mesohabitats at different sampling periods. Where KW tests indicated a significant difference ($p < 0.05$) in a particular variable, multiple pairwise comparisons were then performed using Dunn's procedure (Bonferroni corrected significance level) to identify those mesohabitats that exhibited significant contrasts in the variable.

The nature, strength and significance of associations between pairs of variables were explored using the non-parametric Spearman's rank-order correlation coefficient to identify (i) bivariate associations among wood piece and jam characteristics (assessing research question 1); (ii) bivariate associations among sediment and propagule bank characteristics of mesohabitats associated with the respective sampling periods (May (PB1) and July (PB2)).

Multivariate associations were then explored using a combination of ordination methods (Principal Components Analysis (PCA), Detrended Correspondence Analysis (DCA) and Direct Gradient Analysis (DGA) (that is Redundancy Analysis (RDA) or Canonical Correspondence Analysis (CCA) as appropriate). These analyses together with Spearman's rank-order correlation analyses ((ii) outlined above) address research question 5.

PCA was applied to the rank correlation matrix among physical (sediment) variables measured for mesohabitats within the active corridor to identify the principal gradients in the measured physical variables and to explore how these gradients are related to the mesohabitat types. Associations between the gradients defined by the principal components (PCs) and mesohabitats were then explored by (i) producing scatterplots showing PC scores coded by sampling periods and mesohabitat types; and (ii) applying KW and MW tests to PC scores for sampling periods and mesohabitat types, respectively, to assess the statistical significance of any apparent differences observed in scatterplots.

Table 6.3. Variables resulting from field measurements and laboratory measurements of samples collected from study reach.

Variable Abbreviation	**Variable Full Name**	**Description**
Channel variables		
CW	Channel width	The width of a sub-reach at the location of jams measured perpendicular to the river channel axis (m).
Jam and wood piece variables		
FWPJ	Frequency of wood pieces in jam	The total number of individual large wood pieces in sampled jams.
KWPL	Key wood piece length	The total length of the largest wood piece within a jam (m).
KWPD	Key wood piece diameter	The diameter mid-stem of the largest wood piece within a jam (m).
KWPV	Key wood piece volume	The cylindrical volume of the largest wood piece within a jam (m^3).
KWPL/CW	Ratio of key wood piece length to the channel width	The length of key wood pieces relative to the channel width at the location of jam.
WPL	Wood piece length	The average length of wood pieces within a jam (m).
WPD	Wood piece diameter	The average diameter mid-stem of wood pieces within a jam (m).
WPV	Wood piece volume	The cylindrical volume of an average wood piece within a jam (m^3).
JL	Jam length	The longitudinal distance from the base to the top of a wood jam measured parallel to the river channel axis (m).
JW	Jam width	The horizontal width of a wood jam measured perpendicular to the river channel axis (m).
JD	Jam depth	The maximum vertical depth of a wood jam measured above the river bed (m).
JA	Jam area (m^2)	The smallest rectangular area of the ground surface into which a wood jam would fit (m^2).
JV	Jam volume (m^3 or m^3/ha)	The total volume of the smallest rectangular box (of air) into which a wood jam would fit (m^3). Following Gurnell et al. (2000b), the wood+air volumes were adjusted to produce estimates of wood volumes by multiplying the volumes of jams by 0.2.
Propagule bank variables		
T PropSR	Propagule species richness	The total number of propagule species identified in a sample.
HB sp	Number of herb species	The total number of herb species present in a sample.
GS sp	Number of grass species	The total number of grass species present in a sample.

Table 6.3. (Continued)

Variable Abbreviation	Variable Full Name	Description
Propagule bank variables (Continued)		
RH sp	Number of rush species	The total number of rush species present in a sample.
WS sp	Number of woody species	The total number of woody species present in a sample.
T Prop/l	Propagules per litre	The number of viable propagules per unit volume of sampled mesohabitat sediment; Prop/l = Number of viable propagule species in sediment sample x (Total volume of < 4 mm sediment fraction ÷ volume of < 4 mm sediment fraction used in germination trials) x (1000 / Total volume of sediment sample).
HB prop/l	Number of herb propagules	The total number of viable herb propagules per unit volume of sampled mesohabitat sediment.
GS prop/l	Number of grass propagules	The total number of viable grass propagules per unit volume of sampled mesohabitat sediment.
RH prop/l	Number of rush propagules	The total number of viable rush propagules per unit volume of sampled mesohabitat sediment.
WS prop/l	Number of woody propagules	The total number of viable woody propagules per unit volume of sampled mesohabitat sediment.
T Prop/m^2	Propagules per square metre	The number of viable propagules per unit surface area of sampled mesohabitat; Prop/l = Number of samples collected with the corer x pi (3.1416) x (Radius of the corer)^2.
HB prop/m^2	Number of herb propagules	The total number of viable herb propagules per unit surface area of sampled mesohabitat.
GM prop/m^2	Number of grass propagules	The total number of viable grass propagules per unit surface area of sampled mesohabitat.
RH prop/m^2	Number of rush propagules	The total number of viable rush propagules per unit surface area of sampled mesohabitat.
WS prop/m^2	Number of woody propagules	The total number of viable woody propagules per unit surface area of sampled mesohabitat.
Sediment variables		
% OM	% Organic Matter	Percentage organic matter content of bulk mesohabitat sediment sample.
D_{50}	Median particle size (phi units)	Median particle size of bulk mesohabitat sediment sample expressed in phi units.
% G	% Gravel	Percentage of gravel in bulk mesohabitat sediment sample.
% S	% Sand	Percentage of sand in bulk mesohabitat sediment sample.
% ST	% Silt	Percentage of silt in bulk mesohabitat sediment sample.
% C	% Clay	Percentage of clay in bulk mesohabitat sediment sample.

DCA was then applied to the propagule data sets (species presence / absence) in order to investigate whether there were any gradients in propagule species composition that reflected sampling periods and / or mesohabitat types.

Lastly, DGA was applied to the propagule data sets (species presence / absence) in order to investigate the extent to which species presence or absence reflected changes in physical (sediment) variables associated with different mesohabitats, thus building upon the DCA results.

MW tests, KW tests, Spearman’s rank-order correlation and PCA were performed using XLSTAT-Pro software (version 9.1.3, 2009). DCA and DGA were performed using CANOCO v4.5 (ter Braak and Smilauer, 2002).

6.4 RESULTS

6.4.1 Characteristics of Jams

This section describes the characteristics of jams and then presents data on the frequency, volume and dimensions of large wood pieces and jams and their associations along the Highland Water study reach.

A total of 141 large wood pieces (> 10 cm diameter and 1 m length) were found incorporated into 25 major wood jams within the 9 studied sub-reaches of the Highland Water (see Figure 6.2). Table 6.4 presents a summary of characteristics of the 25 jams. The majority of jams were located at river bends (52 %), were complete jams (44 %), and were comprised of large wood pieces with partially decayed xylem (60 %).

Table 6.4. Summary of jam characteristics along the study reach of the Highland Water (n = 25).

Variables	Components	Frequency (Percentage)
Jam Position	Upstream of bend	5 (20)
	At bend	13 (52)
	Downstream of bend	7 (28)
Jam Class	Active	4 (16)
	Complete	11 (44)
	Partial	7 (28)
	High	3 (12)
Jam Decay Status	Partially decayed xylem	15 (60)
	Bark completely or mostly removed	5 (20)
	Bark partly removed showing xylem	5 (20)

Jams and their constituent large wood pieces varied greatly in size along the study reach (Table 6.5). Figure 6.4 shows the relative frequency of the lengths, widths and depths of the 25 wood jams. The average wood volume of jams for the 0.62 ha study reach expressed as cubic meters per hectare of active channel area was 56.7 m^3/ha. The median jam length, width and depth were 3.15 m, 2.5 m and 0.79 m, respectively, but the area and volume of jams varied widely, ranging, respectively, from 0.4 m^3 to 408.0 m^3 (median 6.12 m^3) and 1.04 m^2 to 240 m^2 (median 7.2 m^2) (Table 6.5).

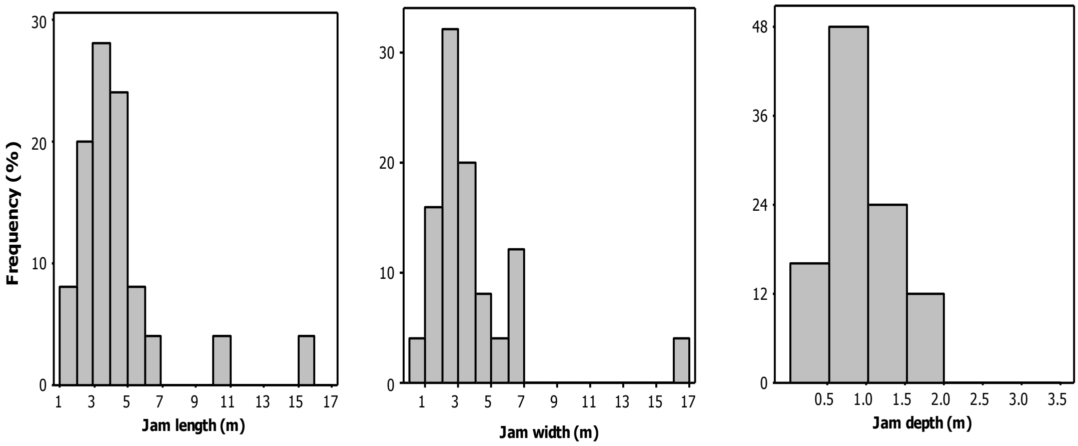


Figure 6.4. Percentage frequency distributions of wood jam dimensions (n = 25) within the study reach: length (m), width (m) and, depth (m).

Table 6.5. Summary statistics for wood jams and key wood pieces (n = 25)*, and individual wood pieces (n = 141).

Variables	Dimensions / Frequency	Mean	Median	Q1	Q3
Jams	Length (m)	4.09	3.50	2.50	4.00
	Width (m)	3.50	2.50	2.00	4.00
	Depth (m)	0.86	0.79	0.54	1.10
	Area (m^2)	19.14	7.20	5.00	11.25
	Volume (m^3)	25.33	6.12	2.75	12.38
Individual wood pieces	Number of wood pieces in jam*	5.64	4.00	3.00	7.00
	Length (m)	3.21	2.50	1.80	4.00
	Diameter (m)	0.21	0.14	0.11	0.23
	Volume (m^3)	0.27	0.04	0.02	0.17
Key wood pieces*	Length (m)	5.38	4.00	3.00	6.50
	Diameter (m)	0.24	0.22	0.13	0.30
	Volume (m^3)	0.45	0.13	0.04	0.32
	Key wood piece length/channel width	1.69	1.38	1.18	2.15

Figure 6.5 shows percentage frequency distributions for the number, dimensions (length and diameter) of individual wood pieces within jams and the ratio of key wood piece length to stream channel width along the study reach. Each jam contained an average of six large wood pieces (median 4). The median wood piece

length and diameter were 2.50 m and 0.14 m, respectively, but wood piece sizes were highly variable with volumes ranging from 0.004 m^3 to 10.804 m^3 (median 0.041 m^3) (Table 6.5). The key wood pieces forming jams were comparatively longer (median length 4.0 m) and larger (median diameter 0.22 m) than average. The median length of the key wood piece within the 25 jams relative to the channel width at the location of the jams was 1.38 (Table 6.5).

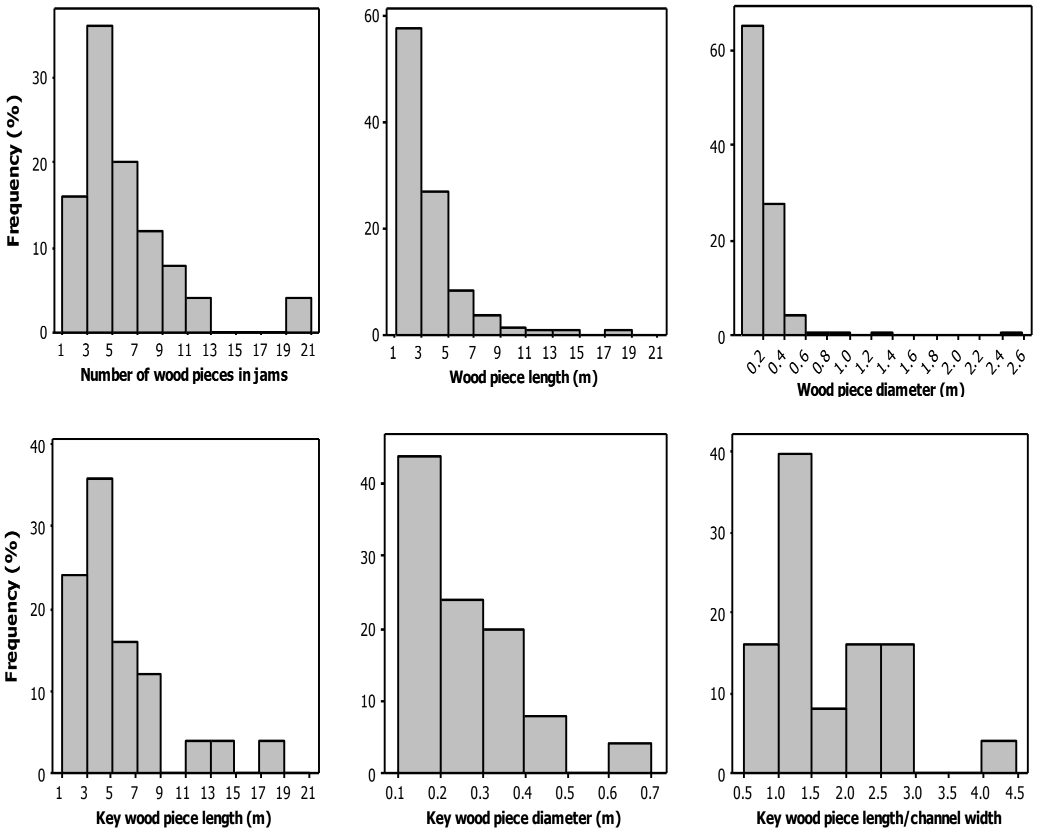


Figure 6.5. Characteristics of individual large wood pieces (n = 141) and key wood pieces (n = 25) within the 25 jams along the study reach of the Highland Water. Top: Percentage frequency distributions of the number (left), the length (m) (middle) and the diameter (m) (right) of large wood pieces found within wood jams. Bottom: Percentage frequency distributions of the length (m) (left) and the diameter (m) (middle) of key wood pieces found within large jams and the ratio of key wood piece length to channel width (right).

To assess the relationships between wood and channel characteristics within the study reach of the Highland Water, associations among jam and wood piece variables and channel width (n = 25, i.e. number of wood jams) were estimated using Spearman's rank correlation (Table 6.6). Overall, key wood piece length, wood piece median length and diameter, and jam width and depth shows a significant positive correlation with channel width. Key wood piece length (and to some extent diameter) shows a significant positive correlation with jam width, depth, volume and area, suggesting that jam size increases with increasingly longer and larger key wood pieces. The ratio of key wood piece length to channel width displays a significant positive correlation with wood piece length and diameter, jam width, volume and area, suggesting jam size and the size of wood pieces within jams significantly increases with an increase in key wood piece length to the channel width ratio.

Table 6.6. Spearman rank correlations among the channel, wood piece and jam variables (n = 25) measured within the nine 200 m sub-reaches of the study reach along the Highland Water (emboldened correlations are statistically significant, $p < 0.05$).

Variables	Abbr.	CW	FWPJ	KWPL	KWPD	KWPL/CW
Channel	CW	**1**	0.2	**0.7**	0.1	0.1
Wood piece frequency and dimension	FWPJ	0.2	**1**	0.1	0.0	0.1
	KWPL	**0.7**	0.1	**1**	0.3	**0.7**
	KWPD	0.1	0.0	0.3	**1**	**0.4**
	KWPL/CW	0.1	0.1	**0.7**	**0.4**	**1**
	WPL	**0.5**	-0.1	**0.8**	0.0	**0.6**
	WPD	0.3	0.0	**0.5**	**0.6**	**0.5**
Jam dimension	JL	0.3	0.4	0.3	0.3	0.3
	JW	**0.6**	0.2	**0.6**	0.2	**0.4**
	JD	**0.5**	0.2	**0.5**	0.4	0.3
	JV	0.4	0.4	**0.5**	**0.4**	**0.4**
	JA	0.3	0.4	**0.4**	**0.4**	**0.5**

Abbr., abbreviations of variables; CW, Channel width; FWPJ, frequency of wood pieces in jam; KWPL, key wood piece length; KWPD, key wood piece diameter; KWPL/CW, ratio of key wood piece length to the channel width; WPL, wood piece median length; WPD, wood piece median diameter; JL, jam length; JW, jam width; JD, jam depth; JV, jam volume; JA, jam area.

6.4.2 Relationship between Jams and Mesohabitats

A total of 107 individual mesohabitats and active channel features were found in the vicinity of the 25 major wood jams within the 9 studied sub-reaches of the Highland Water. Table 6.7 presents a summary of characteristics of the 107 mesohabitats and active channel features that were found in association with the 25 jams. Generally, jams were most frequently associated with pool formation, which accounted for 50 % of all wood-controlled mesohabitats along the Highland Water. The most frequently occurring mesohabitats and active channel features were in-dam pools, marginal pools, unvegetated bars (also described as bar gravel bar (BGB)), vertical eroding banks (also described as bank (BK)) and undercut eroding banks, respectively, whilst the least frequently occurring mesohabitats were riffles and vegetated mid-channel bars.

Table 6.7. Frequency of occurrence of jam-related mesohabitats and active channel features (n = 107).

Jam-Related Mesohabitats	Frequency (Percentage)
In-dam pool	20 (18.7)
Marginal pool	17 (15.9)
Unvegetated bar*	15 (14)
Vertical eroding bank*	14 (13.1)
Undercut eroding bank	14 (13.1)
Dammed pool	11 (10.3)
Plunge pool	6 (5.6)
Vegetated side bar	5 (4.7)
Side channel	3 (2.8)
Riffle	1 (0.9)
Vegetated mid-channel bar	1 (0.9)

* Unvegetated bar and vertical eroding bank are described as bar gravel bar (BGB) and bank (BK), respectively, in Figure 6.3 and Table 6.2.

Table 6.8 presents the frequencies of mesohabitats associated with the characteristics (position and class) of 25 jams within the study reach along the Highland Water. Associations between mesohabitats and jams with particular characteristics were then considered, focusing on those occurring with ≥ 4 % frequency. Considering associations between jam position and the frequency of jam-related mesohabitats, jams located upstream and downstream of bends were associated with more marginal and in-dam pools and unvegetated bars, while jams at bends were associated with more dammed, marginal and in-dam pools, unvegetated bars and vertical and undercut eroding banks. Considering associations between jam classes and the frequency of jam-related mesohabitats, partial jams were associated with more marginal and in-dam pool, unvegetated bar, vertical and undercut eroding banks, complete jams were associated with similar mesohabitats as those related with jams at bends, while active jams were associated with more in-dam pools.

Table 6.8. Frequencies (%) of mesohabitats (n = 107) associated with the characteristics (position and class) of 25 jams within the nine 200 m sub-reaches of the study reach along the Highland Water.

	Jam Position			Jam Class			
Jam-Related Mesohabitats	JDB	JAB	JUB	HJ	PJ	CJ	AJ
FDP	2.8	6.5	0.9	0.9	2.8	4.7	1.9
FPP	1.9	1.9	1.9	0.9	0.9	1.9	1.9
FMP	3.7	7.5	4.7	0.9	4.7	9.3	0.9
FIP	3.7	10.3	4.7	2.8	4.7	7.5	3.7
FRF	0.0	0.9	0.0	0.9	0.0	0.0	0.0
FUB	3.7	6.5	3.7	0.9	4.7	7.5	0.9
FVSB	1.9	0.9	1.9	0.0	1.9	1.9	0.9
FVMB	0.0	0.0	0.9	0.0	0.0	0.0	0.9
FVEB	2.8	7.5	2.8	0.9	4.7	4.7	2.8
FUEB	0.9	9.3	2.8	2.8	3.7	3.7	2.8
FSC	0.9	1.9	0.0	0.9	0.0	0.9	0.9

JDB, jams downstream of bend; JAB, jams at bend; JUB, jams upstream of bend; HJ, high jams; PJ, partial jams; CJ, complete jams; AJ, active jams; FDP, frequency of dammed pools; FPP, frequency of plunge pools; FMP, frequency of marginal pools; FIP, frequency of in-dam pools; FRF, frequency of riffles; FUB, frequency of unvegetated bars; FVSB, frequency of vegetated side bars; FVMB, frequency of vegetated mid-bars; FVEB, frequency of vertical eroding bank; FUEB, frequency of undercut eroding bank; FSC, frequency of side channels.

6.4.3 Sediment Characteristics of the Five Sampled Mesohabitats

The sediment characteristics of five recurring mesohabitats (bare gravel bar (BGB), large wood jam (JM), jam bank (JB), bank (BK) and floodplain (FP)) sampled during two periods (spring 2011 (PB1) and mid-summer 2011 (PB2)) along the Highland Water are presented in Table 6.9. Figure 6.6 presents Box and Whisker plots of the sediment characteristics observed in different mesohabitats at the two sampling times. The characteristics of sediments sampled within the five mesohabitats (n = 9) and during the two sampling periods (n = 2) were compared using KW and MW tests to assess whether they were statistically-significantly different from one another (Table 6.10).

Although sediment characteristics varied notably within the sampled mesohabitats both within and between sampling periods (Figure 6.6, Table 6.9), there were also distinct differences. Mann Whitney tests investigated whether the sediment characteristics of deposited mesohabitat samples were the same overall and within each mesohabitat in both sampling periods. There were significant differences in the % organic matter, % sand, % clay and % silt but no significant difference in % gravel and the median particle size of sediment sampled during the two sampling periods. When the individual mesohabitats were considered, there was considerable variability in % gravel, % sand, % silt, % clay, and the median particle size of sediment from jam (JM) and jam bank (JB) during the two sampling periods. PB1 floodplain (FP) samples were associated with significantly more sand, while PB2 floodplain (FP), jam bank (JB) and jam (JM) samples were associated with significantly higher percentages of organic matter and finer sediments (% silt and clay) than in the other sampling period (Figure 6.6, Table 6.10).

Since the characteristics of sediment deposited across the mesohabitats were significantly different between the sampling periods, the variations in the sediment properties of mesohabitats for the respective sampling periods were analysed separately. For PB1 samples, Kruskal-Wallis tests revealed that jam banks (JB) contained significantly more organic matter than bare gravel bars (BGB). Bank (BK) and floodplain (FP) samples were significantly finer (median sediment particle size) than jam (JM) and bare gravel bar (BGB) samples, particularly bank (BK) samples which contained a significantly higher proportion of finer sediments (% silt and clay). Bare gravel bar (BGB) samples typically contained significantly higher % gravel than floodplain (FP) samples, while floodplain (FP) samples contained significantly higher % sand than bare gravel bar (BGB) samples. For PB2 samples, KW tests revealed that jam (JM) samples contained significantly more organic matter than bare gravel bar (BGB) samples. Floodplain (FP), bank (BK) and jam bank (JB) samples were significantly finer and contained a significantly higher proportion of fine sediments (% silt, clay and sand) than bare gravel bar samples (BGB) which typically contained a significantly higher % gravel than floodplain (FP), bank (BK) and jam bank (JB) samples.

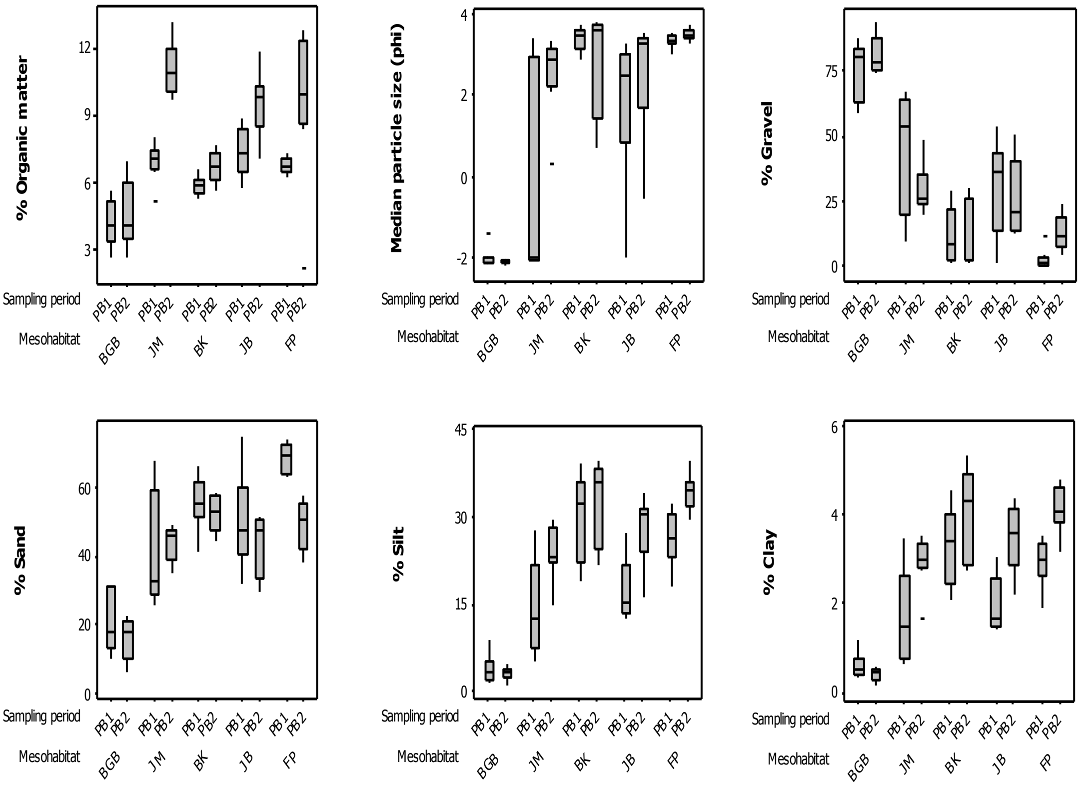


Figure 6.6. Box-whisker plots illustrating contrasts in the sediment properties of samples from bare gravel bar (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) mesohabitats during two different sampling periods (PB1 and PB2). The mesohabitats are ordered along the x-axis from channel bed to floodplain, and thus show a continuum of decreasing hydrological connectivity.

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Table 6.9. Summary of the characteristics of bare gravel bar (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP) sediments sampled within the study reach of the Highland Water. Nine bulk samples were analysed for each mesohabitat (each bulk sample was comprised of 3 replicate samples for JM, BK, JB, FP and 4 replicates for BGB).

Variables	Mesohabitats	Mean	Median	Q1	Q3
Spring samples (PB1)					
% OM	BGB	4.16	4.03	3.33	4.87
	JM	6.90	7.02	6.69	7.35
	BK	5.84	5.88	5.55	6.02
	JB	7.32	7.27	6.88	7.92
	FP	6.68	6.67	6.44	6.97
D_{50}	BGB	-2.06	-2.15	-2.17	-2.05
	JM	0.03	-2.01	-2.06	2.69
	BK	3.36	3.44	3.17	3.47
	JB	1.82	2.49	0.88	2.93
	FP	3.31	3.31	3.25	3.42
% G	BGB	74.84	79.56	63.12	82.31
	JM	41.48	52.71	21.33	61.68
	BK	10.59	7.60	2.31	19.38
	JB	29.65	35.35	24.27	39.55
	FP	1.79	0.15	0.05	1.23
% S	BGB	20.70	18.18	13.69	31.66
	JM	42.87	32.77	30.68	58.98
	BK	55.80	55.35	53.11	59.74
	JB	50.55	47.75	43.40	51.66
	FP	69.04	69.64	64.17	71.30
% ST	BGB	3.90	3.48	2.32	4.48
	JM	14.02	12.40	8.74	17.43
	BK	30.30	32.36	23.25	33.22
	JB	17.82	15.46	13.70	21.54
	FP	26.26	26.48	23.40	29.16
% C	BGB	0.56	0.50	0.33	0.74
	JM	1.63	1.42	0.85	2.24
	BK	3.31	3.43	2.65	3.53
	JB	1.98	1.63	1.52	2.49
	FP	2.91	2.98	2.65	3.28

Table 6.9. (Continued)

Variables	Mesohabitats	Mean	Median	Q1	Q3
Mid-summer samples (PB2)					
% OM	BGB	4.48	4.06	3.61	5.18
	JM	11.07	10.93	10.16	11.99
	BK	6.64	6.66	6.15	7.13
	JB	9.48	9.82	8.59	9.83
	FP	9.81	9.99	8.80	12.05
D_{50}	BGB	-2.14	-2.13	-2.17	-2.12
	JM	2.52	2.87	2.31	3.09
	BK	2.82	3.56	1.77	3.68
	JB	2.51	3.27	2.84	3.37
	FP	3.49	3.47	3.41	3.57
% G	BGB	80.52	78.02	75.13	85.89
	JM	28.98	25.67	24.92	33.22
	BK	9.97	1.96	1.29	23.76
	JB	25.05	20.03	14.13	34.77
	FP	12.36	10.60	7.30	14.51
% S	BGB	16.17	18.39	10.92	21.26
	JM	43.90	46.44	40.45	48.02
	BK	53.16	53.68	48.31	57.08
	JB	43.89	47.65	37.31	50.01
	FP	49.09	51.07	44.22	53.92
% ST	BGB	2.95	3.19	2.81	3.29
	JM	24.19	23.34	22.92	27.07
	BK	32.78	35.94	25.21	37.44
	JB	27.62	30.36	24.84	31.07
	FP	34.40	34.57	32.32	35.59
% C	BGB	0.36	0.42	0.32	0.42
	JM	2.93	2.96	2.87	3.32
	BK	4.09	4.33	2.89	4.94
	JB	3.45	3.59	2.87	4.12
	FP	4.15	4.11	3.88	4.50

Table 6.10. Statistically significant differences in sediment characteristics between samples obtained from five mesohabitats along the study reach of the Highland Water during two sampling periods (PB1 and PB2), identified using Kruskal-Wallis (KW) and Mann Whitney (MW) tests with multiple pairwise comparisons performed using Dunn's procedure with Bonferroni correction.

Variables*	**KW** *p* **value**	**Degrees of freedom**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Spring (PB1) samples			
% OM	< 0.0001	4	JB > BGB
D_{50}	< 0.0001	4	BK, FP > J, BGB
% G	< 0.0001	4	BGB > FP
% S	< 0.0001	4	FP > BGB
% ST	< 0.0001	4	BK > BGB
% C	< 0.0001	4	BK > BGB
Mid-summer (PB2) samples			
% OM	< 0.0001	4	JM > BGB
D_{50}	< 0.0001	4	FP, BK, JB > BGB
% G	< 0.0001	4	BGB > JB, FP, BK
% S	< 0.0001	4	BK, FP, JB > BGB
% ST	< 0.0001	4	FP, BK, JB > BGB
% C	< 0.0001	4	FP, BK, JB > BGB

Variables	**MW** *p* **value**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Spring (PB1) and *Mid-summer (PB2) samples*		
% OM	0.0001	PB2 > PB1
BGB	0.863	n.s.
JM	< 0.0001	PB2 > PB1
BK	0.008	PB2 > PB1
JB	0.004	PB2 > PB1
FP	0.004	PB2 > PB1
D_{50}	0.200	n.s.
BGB	0.931	n.s.
JM	0.094	n.s.
BK	0.666	n.s.
JB	0.136	n.s.
FP	0.031	PB2 > PB1
% G	0.558	n.s.
BGB	0.546	n.s.
JM	0.605	n.s.
BK	0.796	n.s.
JB	0.436	n.s.
FP	0.001	PB2 > PB1

Table 6.10. (Continued)

Variables	**MW** ***p*** **value**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
% S	0.047	PB1 > PB2
BGB	0.605	n.s.
JM	0.730	n.s.
BK	0.489	n.s.
JB	0.489	n.s.
FP	< 0.0001	PB1 > PB2
% ST	0.012	PB2 > PB1
BGB	0.436	n.s.
JM	0.019	PB2 > PB1
BK	0.297	n.s.
JB	0.002	PB2 > PB1
FP	0.001	PB2 > PB1
% C	0.002	PB2 > PB1
BGB	0.190	n.s.
JM	0.024	PB2 > PB1
BK	0.161	n.s.
JB	0.001	PB2 > PB1
FP	0.0003	PB2 > PB1

KW tests were separately performed on the values of each of the variables associated with the mesohabitats within the river corridor to assess the degree to which the sampling period and / or mesohabitats represented statistically significantly different ($p < 0.05$) values of the variables. Multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those sampling periods or mesohabitats that were significantly different from one another ($p < 0.05$). Nine samples* were used in the analyses for each mesohabitat within the study reach; forty-five samples were used in the analyses for each sampling period within the study reach

6.4.4 Propagule Bank Characteristics of the Five Sampled Mesohabitats

The propagule bank characteristics (species richness, propagules per litre and propagule per square metre) of the five mesohabitats (bare gravel bar (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP)) sampled during two periods (spring 2011 (PB1) and mid-summer 2011 (PB2)) are presented in Table 6.11 (a) and (b). The statistical significance of difference in the propagule bank characteristics among the five mesohabitats within and between sampling periods was tested using KW and MW tests (Table 6.12).

In total 184,259 viable propagules of 28 species (2 woody species, 3 rush species, 19 herb species and 4 grass species) were identified in the sampled sediments from the five mesohabitats. Figure 6.7 illustrates the highly variable propagule banks among the five mesohabitats and between the two sampling periods. Mann Whitney tests compared the species richness and abundance of propagule bank samples in the two sampling periods, and found significant differences ($p < 0.05$) with both the species richness and abundance, being higher in the spring (PB1) than the mid-summer (PB2) samples. PB1 and PB2 samples contained a total of 28 and 8 species, respectively, with bank (BK) and jam bank (JB) mesohabitats retaining the most species. Propagule abundance (propagules per litre and propagule per square metre) were higher but also more variable in PB1 compared to PB2 samples, especially for bank (BK) and jam bank (JB) mesohabitats (Figure 6.7). In general, propagule abundance (propagules per litre and propagule per square metre) appear to increase from bare gravel bar (BGB) to jam (JM) to bank (BK) to jam bank (JB) to floodplain (FP) mesohabitats (Figure 6.7). In total, an average of 727 propagules were contained in each PB1 sample in comparison with 31 propagules contained in each PB2 sample, giving a mean of 49 and 3 propagules per litre, respectively, in PB1 and PB2 samples. Most of this difference in propagule abundance was due to much larger quantities of *Juncus effusus*, *Carex pendula* and *Betula pubescens* propagules in PB1 than PB2 samples, and a few other species (*Alisma plantago-aquatica*, *Apium nodiflorum*, *Callitriche hamulata* and *Hypericum humifusum*) being found in a small number of the mesohabitats (jam (JM) and jam bank (JB)) sampled during PB2 (Table 6.11 (a)).

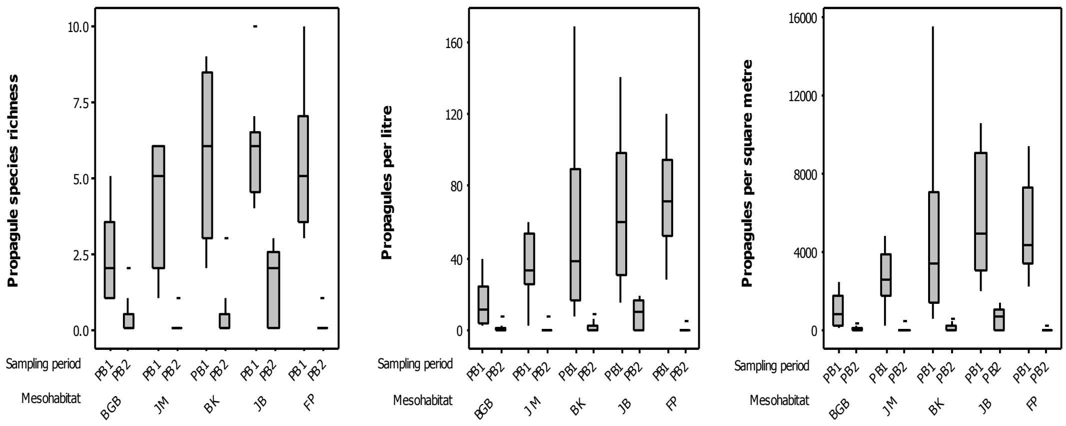

Figure 6.7. Box-whisker plots illustrating propagule species richness, viable propagules per square metre and viable propagules per litre in bare gravel bar (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) mesohabitats associated with two different sampling periods (PB1 and PB2). The mesohabitats are ordered along the x-axis from channel bed to floodplain, and thus show a continuum of decreasing hydrological connectivity.

As the species richness and abundance of viable propagules was very variable and different between the sampling periods, the associations between propagule variables and mesohabitats were analysed separately for the two sampling periods. For PB1 samples, propagule species richness was found to be significantly higher in the sediment samples from jam banks (JB) and banks (BK) compared to bare gravel bar samples (BGB) (Table 6.11 (b) and 6.12). The number of grass and woody species significantly contributed to the differences in propagule species richness between the PB1 mesohabitat samples, with woody species being significantly higher in number in jam (JM) samples compared to bare gravel bar (BGB) samples, and grasses being significantly higher in number in jam bank (JB) samples compared to bare gravel bar (BGB) samples. Propagule abundance (propagules per litre and per square metre) was found to be significantly higher in the sediment samples from jam banks (JB) and floodplains (FP) compared to bare gravel bar (BGB) samples (Table 6.12). The abundance of herb propagules was found to be highest in the sediment samples from floodplains (FP) and lowest in the sediment samples from bare gravel bars (BGB), while the abundance of grass propagules was significantly higher for jam bank (JB) and floodplain (FP) samples compared to bare gravel bar (BGB) samples. The abundance of rush and woody propagules in sediment sampled from the mesohabitats was significantly higher for floodplains (FP) and jam bank (JB), and jam (JM) and floodplains (FP), respectively, compared to bare gravel bars (BGB). For PB2 samples, propagule abundance (propagules per litre and per square metre) and species richness were very low but were found to be significantly higher in the sediment samples from jam banks (JB) compared to both bank (BK) and floodplain (FP) samples (Table 6.11 (b) and 6.12). The number of woody and herb species significantly contributed to the differences in propagule abundance and species richness between the PB2 mesohabitat samples (Table 6.12). The number and abundance (propagules per litre and propagule per square metre) of woody species were significantly higher in jam bank (JB) samples compared to floodplain (FP) samples, while herb species were found to be highest in the sediment samples from jam banks (JB), lowest in the sediment samples from bare gravel bars (BGB), and intermediate in the sediment samples from floodplains (FP) (Table 6.12).

Table 6.11 (a). Propagule species list (and abbreviations (abbr.)) and mean number of propagules per litre and square metre found within the sediment samples from bare gravel bar (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP) mesohabitats during the spring (PB1) and mid-summer (PB2) sampling periods.

		Spring (PB1) samples										**Mid-summer (PB2) samples**									
		Propagules per litre					**Propagules per square metre**					**Propagules per litre**					**Propagules per square metre**				
Species / Mesohabitats	**Abbr.**	**BGB**	**BK**	**JM**	**JB**	**FP**	**BGB**	**BK**	**JM**	**JB**	**FP**	**BGB**	**BK**	**JM**	**JB**	**FP**	**BGB**	**BK**	**JM**	**JB**	**FP**
Agrostis sp.	Agr sp	0.0	0.7	0.0	0.4	0.9	0.0	59.6	0.0	42.0	54.6	0.0	0.0	0.0	2.9	0.5	0.0	0.0	0.0	177.6	21.6
Ajuga reptans	Aju rep	0.4	0.0	0.0	0.0	0.4	23.6	0.0	0.0	0.0	33.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alisma plantago-aquatica	Ali p-a	0.0	2.7	0.2	0.8	1.3	0.0	207.1	21.7	71.6	91.6	0.0	0.0	0.3	0.0	0.0	0.0	0.0	22.0	0.0	0.0
Alnus glutinosa	Aln glu	0.3	0.7	1.4	0.6	0.0	17.2	60.4	136.1	59.4	0.0	0.4	0.9	0.3	1.5	0.0	23.1	48.3	22.0	100.6	0.0
Apium nodiflorum	Api nod	0.0	0.0	0.4	0.0	0.0	0.0	0.0	28.2	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	69.9	0.0
Betula pubescens	Bet pub	0.0	2.9	6.7	3.4	10.0	0.0	241.2	569.2	342.5	713.8	0.7	0.0	0.3	2.6	0.0	49.3	0.0	22.0	177.9	0.0
Callitriche hamulata	Cal ham	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	66.8	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	20.4	0.0
Callitriche stagnalis	Cal sta	0.0	0.7	0.0	0.5	0.4	0.0	60.4	0.0	46.2	27.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cardamine pratensis	Car pra	0.0	0.3	0.0	0.0	0.0	0.0	30.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carex pendula	Car pen	0.7	2.5	0.3	3.3	0.9	34.4	212.0	29.5	278.5	67.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Carex sp.	Carex	1.8	7.5	4.1	12.7	16.9	119.9	660.3	320.1	1200.3	1234.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Digitalis purpurea	Dig pur	0.0	0.8	0.0	0.0	0.4	0.0	61.6	0.0	0.0	32.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epilobium ciliatum	Epi cil	0.9	0.0	0.0	0.0	0.9	52.5	0.0	0.0	0.0	54.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epilobium hirsutum	Epi his	0.2	0.8	0.8	0.3	0.0	17.7	58.3	40.0	24.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Euphorbia sp.	Eup sp	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	29.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Festuca gigantea	Fes gig	0.0	0.7	0.0	0.0	0.9	0.0	59.6	0.0	0.0	54.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hypericum humifusum	Hyp hum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	33.5	0.0
Juncus acutiflorus	Jun acu	0.3	4.7	1.1	3.4	2.2	17.7	428.3	71.8	295.8	151.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Juncus effusus	Jun eff	10.4	21.6	18.6	34.8	32.7	753.8	1750.3	1331.3	2944.7	2357.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Luzula campestris	Luz cam	0.0	0.0	0.3	0.0	0.0	0.0	0.0	18.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Persicaria hydropiper	Per hyd	0.3	0.0	0.0	0.2	0.0	25.4	0.0	0.0	18.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prunella vulgaris	Pru vul	0.0	1.3	0.8	0.0	0.4	0.0	112.3	50.1	0.0	32.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ranunculus repens	Ran rep	0.0	0.2	0.0	0.0	0.0	0.0	28.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sagina procumbens	Sag pro	0.4	8.3	0.4	1.7	3.0	23.6	759.9	21.9	173.7	195.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Senecio vulgaris	Sen vul	0.0	0.8	0.5	1.2	0.9	0.0	65.9	43.2	88.7	58.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sonchus oleraceus	Son ole	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	35.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stachys sylvatica	Sta syl	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Taraxacum officinale agg.	Tar agg	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	18.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Veronica serpyllifolia	Ver ser	0.0	0.8	0.0	0.0	0.0	0.0	55.7	0.0	0.0	0.0	0.0	0.0	0.7	0.5	0.0	0.0	0.0	49.8	25.7	0.0
Total number of propagules		15.7	57.9	35.6	64.8	73.1	1085.5	4911.4	2681.4	5706.4	5224.8	1.1	0.9	1.7	9.2	0.5	72.5	48.3	115.8	605.6	21.6
Number of herb propagules		2.2	16.7	3.1	6.2	8.7	142.6	1439.6	205.1	543.1	590.1	0.0	0.0	1.0	2.3	0.0	0.0	0.0	71.8	149.5	0.0
Number of grass propagules		2.4	11.3	4.5	16.5	19.5	154.3	991.5	349.7	1520.8	1411.5	0.0	0.0	0.0	2.9	0.5	0.0	0.0	0.0	177.6	21.6
Number of rush propagules		10.7	26.3	20.0	38.2	34.9	771.4	2178.6	1421.3	3240.5	2509.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Number of woody propagules		0.3	3.6	8.1	4.0	10.0	17.2	301.6	705.4	402.0	713.8	1.1	0.9	0.6	4.1	0.0	72.5	48.3	44.0	278.5	0.0

Table 6.11 (b). Summary of the propagule bank characteristics of bare gravel bar (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) sediments within the river corridor of the study reach along the Highland Water. Nine bulk samples were analysed for each mesohabitat (each bulk sample was comprised of 3 replicate samples for JM, BK, JB, FP and 4 replicates for BGB).

Variables	Mesohabitats	Mean	Median	Q1	Q3
Spring samples (PB1)					
T PropSR	BGB	2.33	2.00	1.00	3.00
	JM	5.78	6.00	4.00	8.00
	BK	4.33	5.00	3.00	6.00
	JB	5.89	6.00	5.00	6.00
	FP	5.44	5.00	4.00	6.00
T Prop/l	BGB	15.72	11.54	5.26	22.97
	JM	57.91	38.42	17.65	79.99
	BK	35.65	33.69	26.43	52.00
	JB	64.82	59.61	37.12	94.77
	FP	73.08	72.00	60.00	84.26
T Prop/m^2	BGB	1085.50	883.94	317.77	1598.01
	JM	4911.35	3421.67	1661.90	7063.02
	BK	2681.40	2561.81	1931.79	3095.62
	JB	5706.38	4893.37	3306.47	7720.11
	FP	5224.76	4286.71	3799.62	6477.22
Mid-summer samples (PB2)					
T PropSR	BGB	0.33	0.00	0.00	0.00
	JM	0.11	0.00	0.00	0.00
	BK	0.44	0.00	0.00	0.00
	JB	1.56	2.00	0.00	2.00
	FP	0.11	0.00	0.00	0.00
T Prop/l	BGB	1.13	0.00	0.00	0.00
	JM	0.88	0.00	0.00	0.00
	BK	1.65	0.00	0.00	0.00
	JB	9.23	10.44	0.00	16.25
	FP	0.52	0.00	0.00	0.00
T Prop/m^2	BGB	72.48	0.00	0.00	0.00
	JM	48.31	0.00	0.00	0.00
	BK	115.80	0.00	0.00	0.00
	JB	605.61	664.94	0.00	919.59
	FP	21.58	0.00	0.00	0.00

Table 6.12. Statistically significant differences in propagule bank variables between samples obtained from five mesohabitats along the study reach of the Highland Water during two periods (PB1 and PB2), identified using Kruskal-Wallis (KW) and Mann Whitney (MW) tests with multiple pairwise comparisons performed using Dunn's procedure with Bonferroni correction.

Variables*	**KW *p* value**	**Degrees of freedom**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Spring (PB1) samples			
T PropSR	0.009	4	JB, BK > BGB
Number of herbs	0.181	4	n.s.
Number of grass	0.005	4	JB > BGB
Number of rush	0.098	4	n.s.
Number of woody species	0.016	4	JM > BGB
T Prop/l	0.001	4	FP, JB > BGB
Number of herbs	0.033	4	FP = BK = JB = JM = BGB
Number of grass	0.003	4	FP, JB > BGB
Number of rush	0.018	4	FP > BGB
Number of woody species	0.012	4	JM, FP > BGB
T Prop/m^2	0.001	4	JB, FP > BGB
Number of herbs	0.014	4	FP = JB = BK = JM = BGB
Number of grass	0.002	4	JB, FP > BGB
Number of rush	0.005	4	JB, FP > BGB
Number of woody species	0.012	4	JM > BGB
Mid-summer (PB2) samples			
T PropSR	0.018	4	JB > FP, BK
Number of herbs	0.017	4	JB = J = FP = BK = BGB
Number of grass	0.058	4	n.s.
Number of rush	0.385	4	n.s.
Number of woody species	0.013	4	JB > FP
T Prop/l	0.010	4	JB > BK, FP
Number of herbs	0.016	4	JB = J = FP = BK = BGB
Number of grass	0.050	4	n.s.
Number of rush	0.385	4	n.s.
Number of woody species	0.013	4	JB > FP
T Prop/m^2	0.010	4	JB > BK, FP
Number of herbs	0.018	4	JB = J = FP = BK = BGB
Number of grass	0.050	4	n.s.
Number of rush	0.385	4	n.s.
Number of woody species	0.019	4	JB > FP

Table 6.12. (Continued)

Variables^	**MW** ***p* value**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Spring (PB1) and *Mid-summer (PB2) samples*		
T PropSR	< 0.0001	PB1 > PB2
BGB	0.0008	PB1 > PB2
JM	0.0004	PB1 > PB2
BK	0.0002	PB1 > PB2
JB	0.0004	PB1 > PB2
FP	0.0002	PB1 > PB2
T Prop/l	<0.0001	PB1 > PB2
BGB	0.0003	PB1 > PB2
JM	0.0002	PB1 > PB2
BK	< 0.0001	PB1 > PB2
JB	0.0003	PB1 > PB2
FP	0.0002	PB1 > PB2
T Prop/m^2	< 0.0001	PB1 > PB2
BGB	0.0004	PB1 > PB2
JM	0.0002	PB1 > PB2
BK	0.0002	PB1 > PB2
JB	0.0004	PB1 > PB2
FP	0.0002	PB1 > PB2

Mann Whitney and Kruskal-Wallis tests were separately performed on the values of each of the variables associated with the two sampling periods and five mesohabitats to assess the degree to which the sampling period and / or mesohabitats represented statistically significantly different (p < 0.05) values of the variables. Following the Kruskal-Wallis tests, multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those mesohabitats that were significantly different from one another (p < 0.05). Nine samples* were used in the analyses for each mesohabitat; forty-five samples^ were used in the analyses for each sampling period within the study reach

6.4.5 Relationship between Physical and Biotic Characteristics of Mesohabitats along the Study Reach

(i) Spearman's rank correlation analyses

Correlations between sediment and propagule bank variables were explored for all five mesohabitats (9 samples per mesohabitat) for each sampling period separately (45 samples for each sampling period) (Table 6.13).

Table 6.13 presents Spearman rank correlations among sediment and propagule bank variables of mesohabitats for the spring (PB1) sampling period. Generally, total propagule abundance (per litre and per square metre), total species richness, and the number and abundance of herb, grass and rush species display significant positive correlations with indicators of sediment fining such as median sediment particle size (phi), % sand, % silt and % clay, and a significant negative correlation with % gravel. These results indicate a general increase in propagule abundance (per litre and per square metre) and species richness with increasing sediment fining, which is particularly marked for herb, grass and rush species. Total propagule abundance (per litre and per square metre), the abundance of rush (per litre and per square metre), grass (per metre square) and woody (per metre square) propagules, and the number of grass species also display a significant positive correlation with sediment organic matter content.

Table 6.13 also presents Spearman rank correlations between sediment and propagule bank variables of mesohabitats for the mid-summer (PB2) sampling period. The table shows that no significant associations between sediment and propagule bank characteristics were found for PB2 samples indicating that sediment characteristics are not associated with propagule bank characteristics during this mid-summer sampling.

Table 6.13. Spearman rank correlations among sediment and propagule bank variables of mesohabitats (n = 45, for each sampling period) within the riparian corridor of the Highland Water for the spring (PB1) and mid-summer (PB2) sampling periods (emboldened correlations are statistically significant, $p < 0.05$).

		Spring (PB1)						**Mid-summer (PB2)**					
Variables	Abbr.	% OM	D_{50}	% G	% S	% ST	% C	% OM	D_{50}	% G	% S	% ST	% C
Propagules species richness	T PropSR	0.24	**0.36**	**-0.36**	**0.38**	**0.37**	**0.32**	-0.07	-0.09	0.07	-0.05	-0.07	0.03
	HB sp	0.09	0.26	**-0.31**	**0.37**	0.23	0.20	0.16	-0.14	0.14	-0.13	-0.13	-0.03
	GS sp	0.21	**0.36**	**-0.35**	**0.34**	**0.37**	**0.35**	-0.13	0.13	-0.12	0.13	0.11	0.19
	RH sp	**0.35**	0.25	**-0.32**	**0.33**	0.27	0.28	0.00	0.00	0.00	0.00	0.00	0.00
	WS sp	0.25	0.10	-0.02	0.03	0.15	0.08	-0.04	-0.11	0.10	-0.12	-0.08	0.01
Propagules per litre	T Prop/l	**0.37**	**0.47**	**-0.58**	**0.64**	**0.46**	**0.44**	-0.06	-0.07	0.04	-0.02	-0.05	0.06
	HB prop/l	0.15	**0.42**	**-0.51**	**0.54**	**0.38**	**0.36**	0.17	-0.15	0.15	-0.13	-0.14	-0.04
	GS prop/l	0.29	**0.44**	**-0.49**	**0.51**	**0.44**	**0.43**	-0.12	0.12	-0.12	0.13	0.11	0.19
	RH prop/l	**0.35**	**0.43**	**-0.57**	**0.60**	**0.41**	**0.44**	0.00	0.00	0.00	0.00	0.00	0.00
	WS prop/l	0.29	0.20	-0.16	0.20	0.21	0.15	-0.04	-0.07	0.07	-0.08	-0.05	0.04
Propagules per metre	T Prop/m^2	**0.43**	**0.41**	**-0.50**	**0.55**	**0.42**	**0.39**	-0.05	-0.07	0.05	-0.03	-0.05	0.05
	HB prop/m^2	0.20	**0.39**	**-0.46**	**0.50**	**0.37**	**0.34**	0.17	-0.15	0.15	-0.13	-0.14	-0.04
	GM prop/m^2	**0.32**	**0.38**	**-0.42**	**0.44**	**0.39**	**0.37**	-0.12	0.12	-0.11	0.12	0.11	0.19
	RH prop/m^2	**0.41**	**0.35**	**-0.47**	**0.49**	**0.36**	**0.36**	0.00	0.00	0.00	0.00	0.00	0.00
	WS prop/m^2	**0.30**	0.15	-0.10	0.13	0.17	0.11	-0.05	-0.09	0.09	-0.10	-0.06	0.02

Abbr., abbreviations of variables; % OM, organic matter; D_{50}, median sediment particle size (phi); % G, % gravel; % S, % sand; % ST, % silt; % C, % clay; T PropSR, propagule species richness; HB sp, the number of herb species; GM sp, the number of grass species; RH sp, the number of rush species; WS sp, the number of woody species; T Prop/l, propagules per litre; HB prop/l, herb propagules per litre; GM prop/l, grass propagules per litre; RH prop/l, rush propagules per litre; WS prop/l, woody propagules per litre; T Prop/m^2, propagules per metre square; HB Prop/m^2, herb propagules per metre square; GM Prop/m^2, grass propagules per metre square; RH Prop/m^2, rush propagules per metre square; WS Prop/m^2, woody propagules per metre square

(ii) Multivariate analysis and classification of mesohabitat characteristics

Mesohabitat physical characteristics were further explored using Principal Components Analysis (PCA). This was followed by an analysis of the species composition of the sampled propagule banks using Detrended Correspondence Analysis (DCA). The associations between the composition of the propagule bank and the physical (sediment) characteristics of sampled mesohabitats were then investigated using direct gradient analysis (DGA).

Principal Components Analysis (PCA) was used to identify gradients in the sediment variables of sampled mesohabitats (90 samples, 45 for each sampling period, 9 for each mesohabitat) along the study reach and to explore how these are related to period of sampling and mesohabitat type. Because the variables were not normally distributed, PCA was performed on a rank correlation matrix. A reduced set of sediment variables (D_{50}, % OM, % G, % ST + % C) was used to minimise the number of variables included in the analysis, to avoid including sets of variables that summed to 100 %, and also to avoid duplication (e.g. % ST and % C were both highly correlated and so a combined fine sediment variable (% ST + % C) was used).

Table 6.14 lists the sediment variables that were analysed and their loadings on the first two principal components (PCs). The first two PCs explained over 92 % of the variance in the data set (Table 6.14). The variable loadings on PC1 indicate that it describes a gradient of sediment fining (high negative loadings on % Gravel and high positive loadings on D_{50} and % ST + % C). Although PC2 has an eigenvalue that is slightly less than 1, it was retained because it describes a gradient of increasing organic matter content (high positive loadings on % OM) which is informative when the plotting positions of the samples are investigated with respect to PC1 and PC2.

Table 6.14. Eigenvalues, percentage variation explained and variable loadings on the first two components of a PCA performed on mesohabitat sediment variables for the sampling periods of spring (PB1) and mid-summer (PB2) 2011. Results of Kruskal-Wallis (KW) and Mann Whitney (MW) tests applied to the scores of bare gravel bar (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) mesohabitats on the first two PCs.

	PC1	**PC2**
Eigenvalue	3.646	0.973
% variance explained	72.918	19.457
Cumulative variance (%)	72.918	92.375
Loadings		
% Organic Matter	0.398	0.892
Median particle size (D_{50})	0.969	-0.003
% Gravel	-0.963	0.204
% Sand	0.868	-0.338
% Silt + % Clay	0.932	0.148

	MW *p* value	Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)
a - *All samples (comparison of scores of PB1 and PB2 samples)*		
PC1	0.381	n.s.
PC2	< 0.0001	PB2 > PB1
b - *All samples (comparison of scores of PB1 and PB2 samples for each mesohabitat type)*		
PC1		
BGB	0.730	n.s.
JM	0.063	n.s.
JB	0.340	n.s.
BK	0.546	n.s.
FP	1.000	n.s.
PC2		
BGB	0.387	n.s.
JM	< 0.0001	JM2 > JM1
JB	0.004	JB2 > JB1
BK	0.014	BK2 > BK1
FP	0.004	FP2 > FP1

	KW *p* value	Degrees of freedom	Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)
c - *All samples (comparison of scores of samples from the different mesohabitat types)*			
PC1	< 0.0001	4	FP > JM > BGB
PC2	0.0001	4	JM > BK

Kruskal-Wallis (KW) and Mann Whitney (MW) tests were separately performed on the PC scores for samples from the two sampling periods, mesohabitats associated with the sampling periods and all the mesohabitat types along the study reach to assess the degree to which these represented statistically significantly differences ($p < 0.05$). Multiple pairwise comparisons were then performed using the Dunn’s procedure (Bonferroni corrected) to identify those sampling periods and mesohabitats that were significantly different from one another ($p < 0.05$). a = 90 samples (45 for each sampling period) used in the MW analyses, and; b = 9 for each mesohabitat used in the MW analyses; c = 90 samples (18 for each mesohabitat) used in the KW analyses.

The scores of the samples on PC1 and PC2 were investigated to assess whether there were any differences between samples according to sampling periods and mesohabitats (Figure 6.8). Figure 6.8 plots the 90 mesohabitat samples in relation to their scores on PC1 and PC2, and codes them according to (a) sampling periods; (b) mesohabitats; and (c) mesohabitats within each sampling period.

PB2 samples tend to be mainly located in the upper right quadrant of Figure 6.8 (a) while PB1 samples tend to located in the lower left and right quadrants, but there is an overlap between sampling periods. Mann Whitney tests comparing sample scores on PC1 and PC2 showed no significant difference with respect to PC1 (sediment calibre), but a statistically significant difference with respect to PC2 (PB2 sediment samples contain relatively more organic matter than PB1 sediment samples).

When samples from individual mesohabitats are compared (Figure 6.8 (b)), all the bare gravel bar (BGB) samples are clearly separated and distributed to the extreme lower to mid left of most bank (BK) and all floodplain (FP) samples (which overlap), with jam (JM) and jam bank (JB) samples occupying a central position in the plot with respect to PC1 (Table 6.14). Kruskal-Wallis tests applied to the mesohabitat scores on PC1 show statistically significant differences between bare grave bar (BGB), jam (JM) and floodplain (FP) samples (Table 6.14), indicating sediment fining from bare gravel bar (BGB) to jam (JM) to floodplain (FP) samples. Bare gravel bar (BGB) and bank (BK) sediment samples shows little variability in their score on PC2, while jam (JM), jam bank (JB) and floodplain (FP) samples shows high variability in their scores on PC2, although there is a statistically significant difference in the scores of jam (JM) and bank (BK) samples with respect to PC2 (Table 6.14), indicating higher organic content in the former samples.

There also appear to be differences in the scores of the mesohabitat samples with respect to PC1 and PC2 between the two sampling periods (Figure 6.8 (c)). The separation of PB1 and PB2 samples with respect to PC2 appears to be attributable to the different scores of jam (JM), floodplain (FP) and jam bank (JB) samples, and to a lesser extent to contrasts in the scores of bank (BK) samples, whereas gravel bar samples (BGB) show very similar scores for both sampling periods (Table 6.14). This indicates a trend of increasing sediment organic matter content in all but the

BGB mesohabitat from PB1 to PB2, which is also suggested by some of the statistics in Table 6.9.

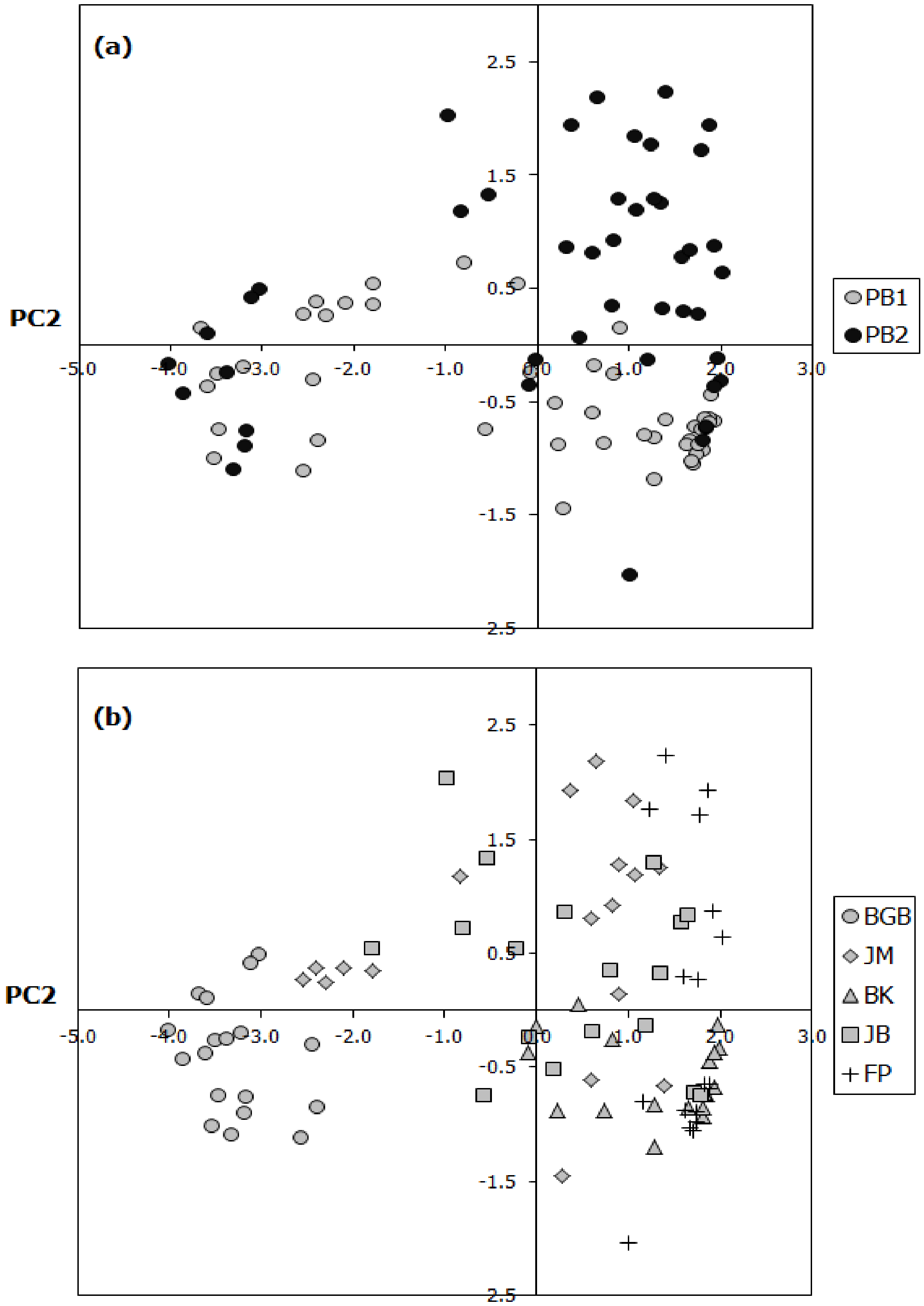

Figure 6.8. Distribution of (a) sampling periods (PB1 and PB2); (b) mesohabitats (amalgamated across sampling periods); in relation to their scores on PCs 1-2 (for meaning of abbreviations see Table 6.1).

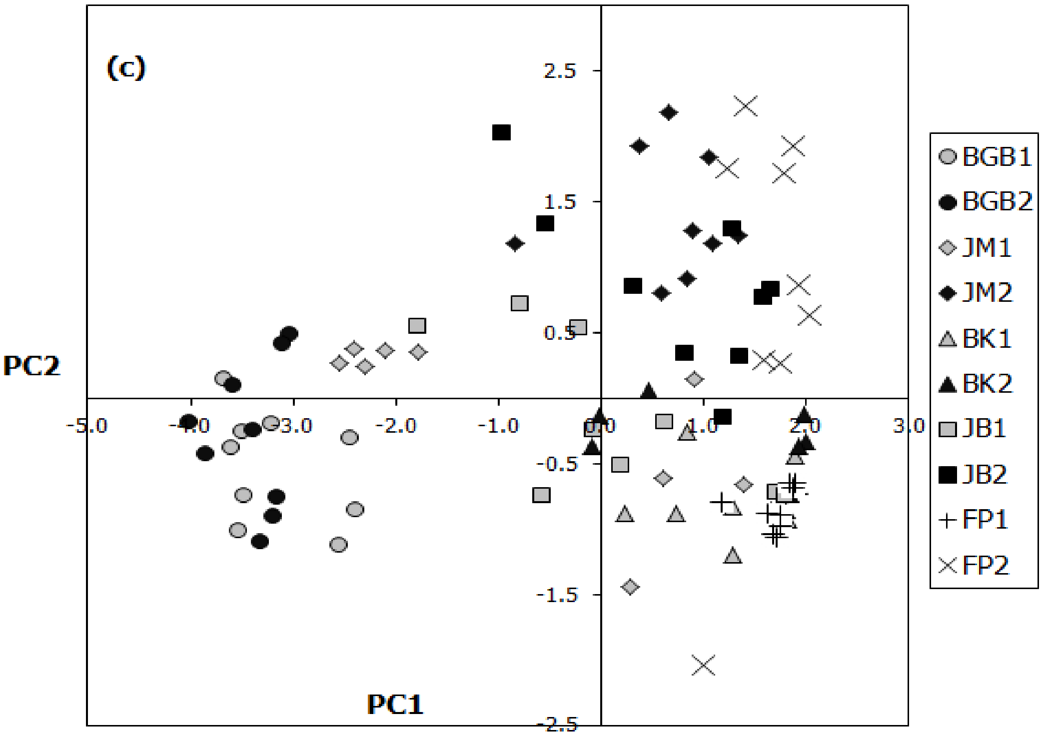

Figure 6.8 (c). Distribution of distinct mesohabitats and sampling period in relation to their scores on PCs 1-2 (for meaning of abbreviations see Table 6.2).

Having established statistically significant contrasts in mesohabitat sediment characteristics using PCA and Kruskal-Wallis tests, the propagule species dataset for the mesohabitats and sampling periods was analysed using DCA to evaluate variations in propagule species composition across the different sampling periods and mesohabitat types. Eigenvalues for the first two axes were 0.556 and 0.431 and the lengths of gradient were 4.787 and 4.360. The cumulative percentage variances within the species data explained by the axes were 9.7 and 17.2 %, respectively.

Figure 6.9 shows the DCA biplot for (a) the propagule species; (b) the samples coded by sampling period; (c) the samples coded by mesohabitat; and (d) the samples coded by sampling period and mesohabitat. All species were included in the analysis and there was no downweighting of rare species. The sampling periods are significantly discriminated according to their species composition with respect to DCA axis 2 (PB1 > PB2, $p < 0.0001$) (Figure 6.9 (b)). Species located within the central area of the species plot (Figure 6.9 (a)) are associated with all mesohabitats and sampling periods, whereas species located towards the ends of axis 2 and beyond the limits of the samples are (often relatively rare) species that are providing discrimination between sampling periods. For instance, PB1 samples were distinguished from PB2 samples by species with low scores on DCA axis 2, including *Ajuga reptans* (*Aju rep*), *Betula pubescens* (*Bet pub*), *Epilobium hirsutum* (*Epi his*), *Euphorbia sp.* (*Eup sp*), *Juncus effusus* (*Jun eff*), and *Sagina procumbens* (Sag pro). Propagule species that are strongly associated with PB2 samples plot towards the top of axis 2 are *Agrostis sp*. (*Agr sp*), *Hypericum humifusum* (*Hyp hum*) and *Veronica serpyllifolia* (*Ver ser*).

Sample scores on DCA axis 1 show significant discrimination between mesohabitats ($p = 0.019$) (Figure 6.9 (c)), especially between floodplain (FP), bare gravel bar (BGB) and jam (JM) samples (see polygons enclosing samples from these mesohabitats in Figure 6.9 (c)). Floodplain (FP) samples plot to the left of jam (JM) samples with bare gravel bars (BGB) samples occupying a central position along axis 1 (Figure 6.9 (b)). However, there appear to be no clear distinctions in the species composition of samples drawn from different mesohabitat types during different sampling periods (Figure 6.9 (d)). From Figure 6.9 (a), floodplain (FP) samples are associated with *Ajuga reptans* (*Aju rep*), *Euphorbia sp.* (*Eup sp*), *Hypericum humifusum* (*Hyp hum*) and *Sonchus oleraceus* (*Son ole*). The propagules of *Juncus effusus* (*Jun eff*) are found in association with bare gravel bar (BGB) samples, while the propagules of *Alnus glutinosa* (*Aln glu*), *Epilobium hirsutum* (*Epi his*) and *Taraxacum officinale agg*. (*Tar agg*) are associated with jam (JM) samples.

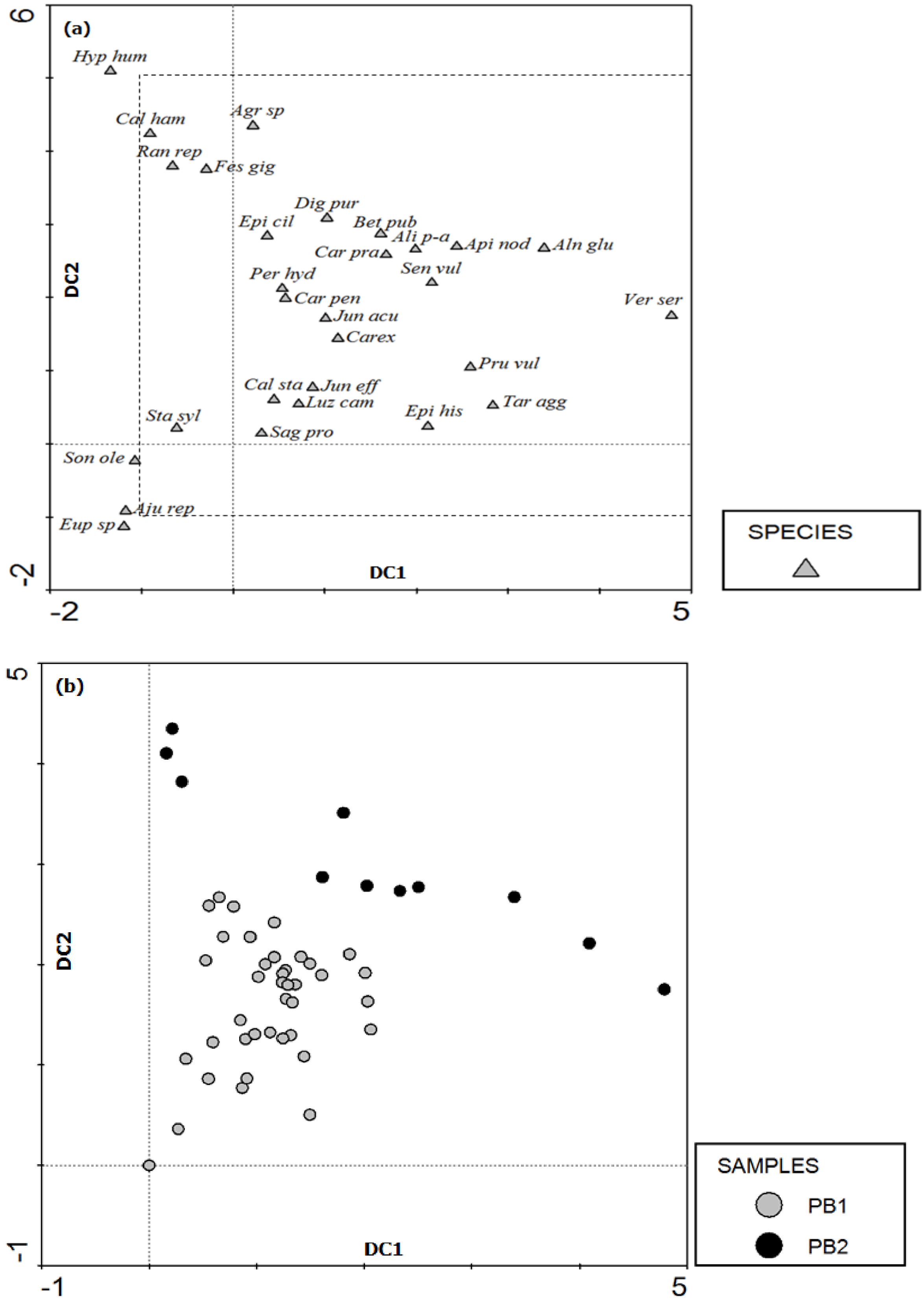

Figure 6.9. DCA Ordination plot of (a) propagule species (for species names associated with abbreviations see Table 6.11 (a)); (b) samples coded by sampling periods.

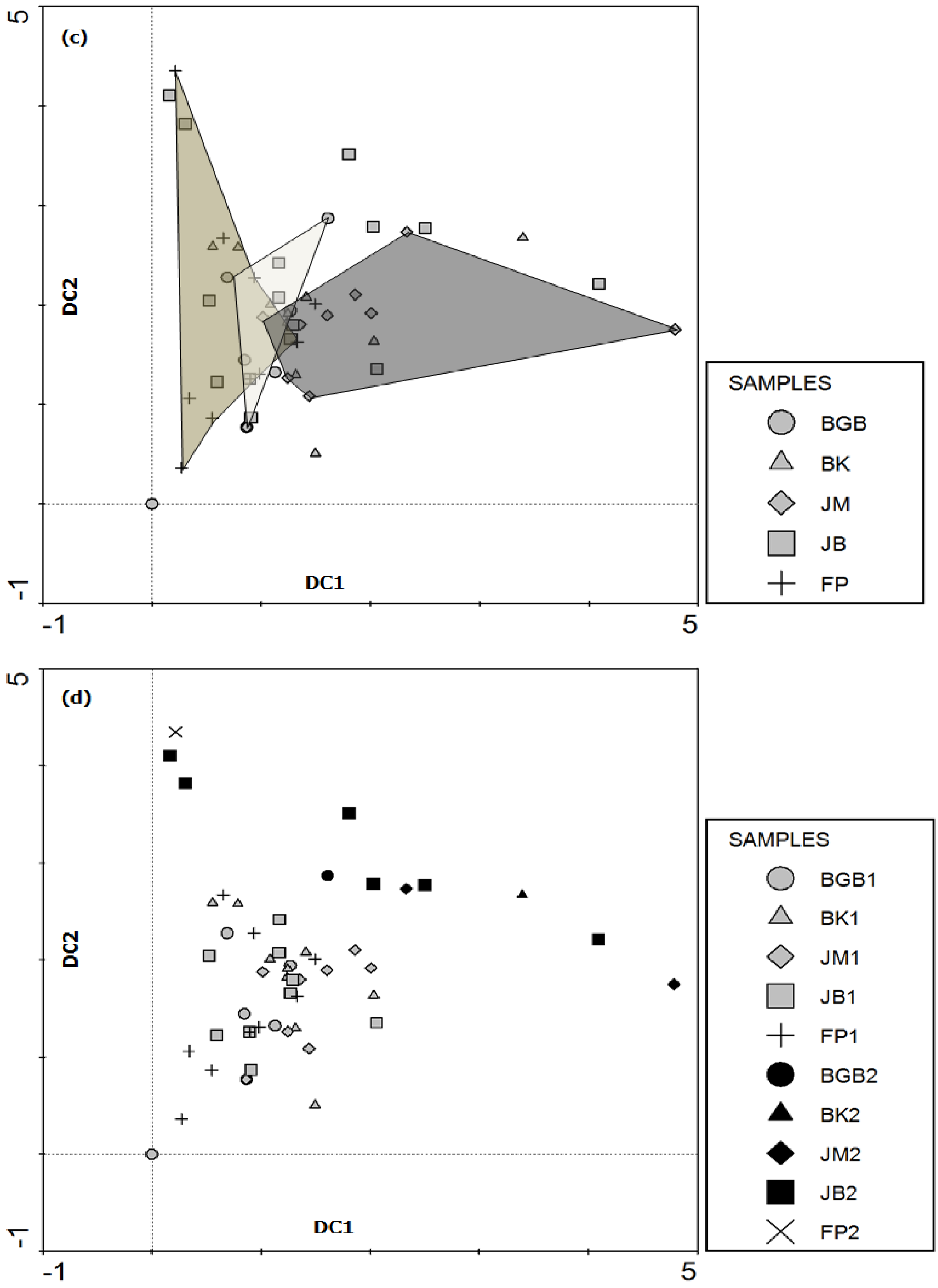

Figure 6.9 (Continued). DCA Ordination plot of (c) samples coded by mesohabitat (the polygons enclose FP (left), BGB (centre) and JM (right) samples); (d) samples coded by mesohabitat and sampling period.

After evaluating the variations in propagule bank species composition across the mesohabitats for the different sampling periods using DCA, the associations between the composition of the propagule bank and the sediment characteristics of sampled mesohabitats were investigated using a direct gradient analysis (DGA) technique. Because the DCA gradient lengths for the propagule bank species dataset was greater than 4 (axis 1 = 4.787 and axis 2 = 4.360), Canonical Correspondence Analysis (CCA) was selected to evaluate relationships between the composition of the propagule bank and the sediment characteristics of the sampled mesohabitats for the two sampling periods (further details of CCA is provided in Chapter 4, Section 4.3.4).

All the sediment variables were included in the CCA, but median particle size and organic matter were the only variables found to be significant ($p = 0.044$ and 0.020, F-ratio = 1.46 and 1.59 respectively; number of permutations = 499) in explaining the variation in the samples after a Monte Carlo permutation test of significance for all the sediment variables. Despite the eigenvalues for the first two axes (0.210 and 0.134) being low (although not exceptional for ecological data), a Monte Carlo permutation test of significance on the first and all calculated axes was significant ($p = 0.040$ and 0.010 respectively). The species-environment correlations were 0.740 and 0.646, showing that there are stronger relationships between the first two CCA axes and the species and sediment data. The cumulative percentage variance explained by the species alone for the first two axes was 3.7 % and 6.0 %, and the cumulative percentage variance explained by the species-environment relationships was 37.9 % and 61.9 %, which shows that a high proportion of the species data variation was explained by the sediment variables. Overall, the propagule species data appear to have a strong association with the characteristics of mesohabitat sediment, particularly median particle size and organic matter.

Figure 6.10 shows the CCA species and sample biplots and the degree to which species and samples are associated with sediment characteristics (arrows). The relative position of the species or samples with respect to the arrows indicates their degree of association with that variable, while the position along the arrow indicates the relative value of the arrow variable that is relevant (i.e. low to high values as the arrow point is approached). Figure 6.10 (a) shows that *Agrostis sp*. (*Agr sp*), *Cardamine pratensis* (*Car pra*) and *Juncus acutiflorus* (*Jun acu*) are associated with increasing sediment calibre and fining, *Apium nodiflorum* (*Api nod*), *Alnus glutinosa* (*Aln glu*), *Epilobium ciliatum* (*Epi cil*) and *Juncus effusus* (*Jun eff*) are associated with increasing organic matter, while *Ajuga reptans* (*Aju rep*) and *Carex sp*. (*Carex*) are associated with increasing % gravel. Figure 6.10 (b) illustrates notable groupings and associations between the sampled mesohabitat types and sediment characteristics. Although floodplain (FP), bare gravel bar (BGB) and jam (JM) samples overlap in their plotting positions, floodplain (FP) samples are generally distributed to the left of jam (JM) samples, with bare gravel bar (BGB) samples positioned in between. Bare gravel bar (BGB) samples plot close to the % gravel vector, most jam (JM) samples plot close to % gravel, % silt and clay and % organic matter vectors, while floodplain (FP) samples plots close to vectors indicating fine sediments (median particle size, % sand and % silt and clay).

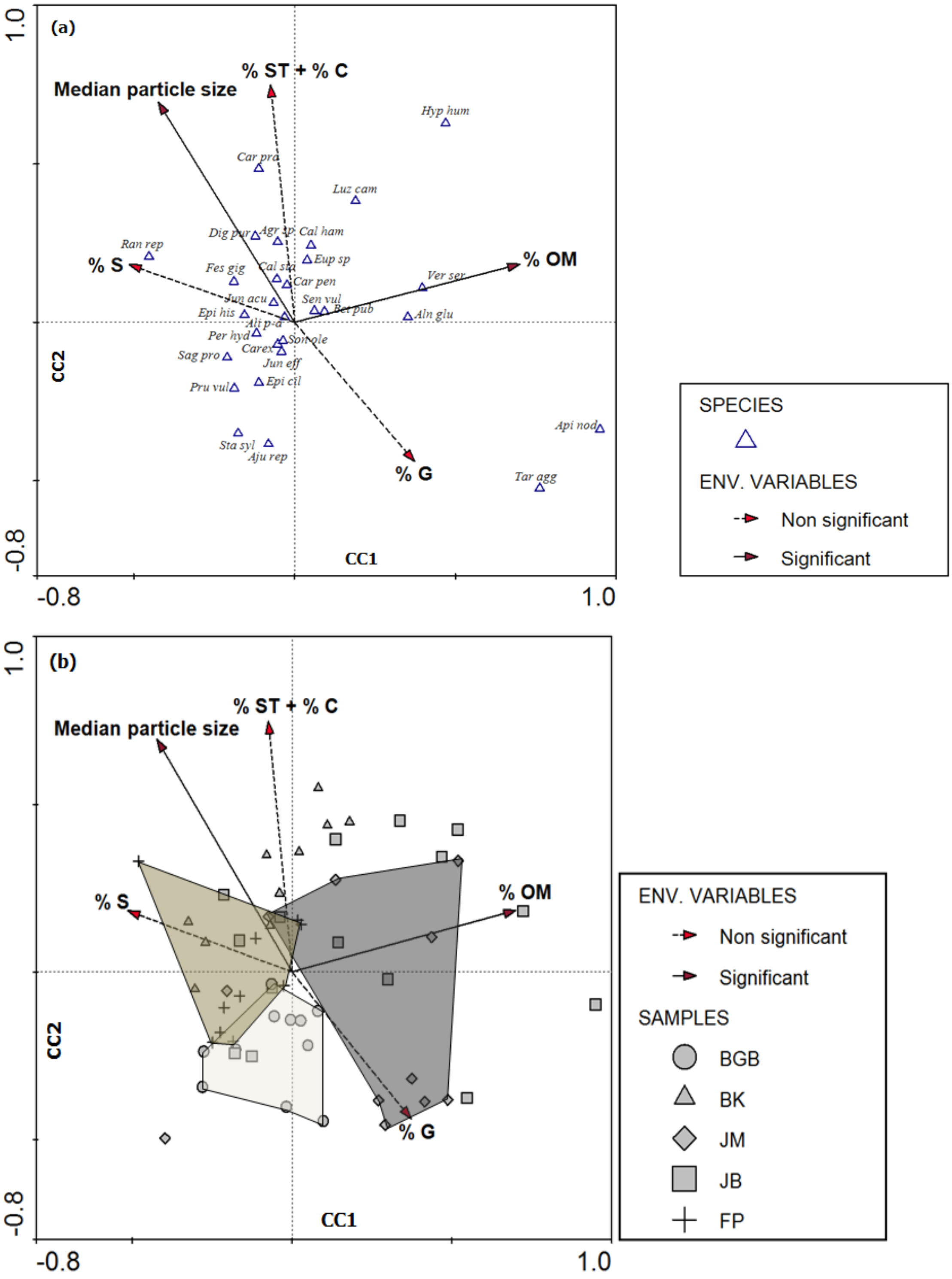

Figure 6.10. CCA ordination plots of (a) propagule species present in the mesohabitat samples in relation to sediment characteristics (arrows) (for species names associated with abbreviations see Table 6.10 (a)); (b) samples coded according to their mesohabitats (amalgamated across sampling periods) in relation to their sediment characteristics (arrows). Polygons enclose samples drawn from floodplains (FP) (left), bare gravel bars (BGB) (centre) and jams (JM) (right).

6.5 DISCUSSION

The discussion is subdivided into five subsections to address the four research questions that were introduced in section 6.1.

6.5.1 What are the Types and Characteristics of Large Wood Accumulations Present within the River?

Some important properties of large wood jams are the number and size of wood pieces (both key and other pieces) in each accumulation, and the size of jams in the river channel (Gurnell et al., 2002; Gurnell, 2013). Overall, key wood piece length, wood piece length and diameter, and jam width and depth were strongly related with channel width. Most of these trends are similar to other catchment studies (Bilby and Ward, 1989; Robison and Beschta, 1990; Abbe and Montgomery, 2003; Chen et al., 2006; Baillie et al., 2008), in spite of the smaller wood piece dimensions compared to the Pacific Northwest and other European rivers that were sampled in these other studies. Along the Highland Water, channel width constrained movement of larger pieces and a high proportion of individual wood pieces and jams spanned the channel width, typical of rivers this size (Keller and Swanson, 1979; Robison and Beschta, 1990; Bilby and Bisson, 1998; Chen et al., 2006). This provides an important structure in the river, critical for the retention of other wood pieces within jams along the channel. The average number of large wood pieces in each jam along this order 3 Highland Water study reach is similar to the order 4 Highland Water reach (Gurnell et al., 2002), although the estimate for the latter was probably too low as considerably less than the entire population of large wood pieces was sampled.

Key wood piece length and diameter and key wood piece length to bankfull width ratio are critical factors in determining jam formation in river systems and the stability of large wood pieces and wood jams, as previously reported by other studies (Braudrick and Grant, 2000, 2001; Martin and Benda, 2001; Gurnell et al., 2002; Abbe and Montgomery, 2003; Gurnell, 2003). As have been previously shown in other Highland Water reaches, key wood piece size and key wood piece length to bankfull width ratio within the study reach are important factors in determining jam size and the size of wood pieces recruited into jams (Gurnell et al., 2002).

Wood storage within the active corridor of rivers provides a basis for drawing comparisons between river systems in terms of the degree to which they reach wood levels for similar forested rivers in unmanaged environments (Gurnell, 2013). The average volume of jams (wood volume of 56.7 m^3/ha) for the present study reach of the Highland Water was typical for rivers bordered by deciduous hardwoods and was relatively high compared to most published data from world rivers (see Gurnell et al., 2002; Gurnell, 2013), expressed as cubic metre per hectare of active channel area. Compared to data from reaches of different order (2nd and 4th) within the Highland Water, U.K., the quantity of wood stored in this study reach is higher than that stored in the second order reach (44 m^3/ha) but lower than that stored in the fourth order reach (88 m^3/ha) (see Gurnell et al., 2002). A further characteristic of the Highland Water jams was that they contained large wood pieces with predominantly partially decayed xylem (60 %), indicating that the majority of wood pieces may have been stored in the river channel for a long time. This suggests that the comparatively large quantity of wood within the study reach of the Highland Water may be a reflection of the long duration of wood piece retention and the characteristics of the riparian deciduous woodland, which are mainly comprised of slow-decaying deciduous hardwood species.

The majority of jams were wedged at river bends (52 %) and completely spanned the river channel (44 %), further illustrating the likely importance of key wood pieces that extend across the river channel for jam development. Baillie et al. (2008) illustrated that larger, longer and more stable than average large wood pieces influence channel morphology and mesohabitat development. Consequently, wood pieces and jams along the Highland Water may likely be considered important structures in controlling rather than responding to the hydrological and sediment transfer characteristics; and thus influencing channel morphodynamics and mesohabitat complexity.

6.5.2 Are There Any Associations between Large Wood Accumulations and Geomorphological Features (Mesohabitats)?

Large wood retained in fluvial systems creates a variety of landforms which enhance the complexity of the physical habitat mosaic of fluvial systems. The impact of large wood jams on flow hydraulics and thus sediment deposition, storage and scouring appears to be considerable along the Highland Water because many different geomorphic features and mesohabitats were in close proximity to the large wood jams surveyed. The most frequently occurring and apparently wood-controlled features were in-dam pools, marginal pools, unvegetated bars, vertical eroding banks and undercut eroding banks, respectively, whilst riffles and vegetated mid-bars were the features that were least frequently observed in association with wood jams. Gurnell et al. (2002) illustrated that 87 % of the in-channel wood accumulations surveyed within the Highland Water were associated with one or more pools and at least one bar or riffle. This association between pool formation and wood jams has been reported by studies in forested river systems (Montgomery et al., 1995; Bilby and Bisson, 1998; Baillie et al., 2008), most especially in relation to the formation of in-dam pools, marginal / backwater pools and plunge pools (e.g. Baillie et al., 2008). The proportion of pools associated with large wood jams within the Highland Water (50 % of all wood-controlled mesohabitats) is similar to observations in other forested river systems by Beechie and Sibley (1997), Baillie and Davies (2002) and Baillie et al. (2008).

The geomorphological role of wood varies widely according to wood accumulation types along the river reach (e.g. Gurnell et al., 2002; Gurnell, 2013). Partial jams containing tightly stacked wood pieces at an angle to channel centre line are hydraulically effective due to the diversion of river flow across the channel, which often causes the lateral scouring and undercutting of banks and the deposition of bar-forming sediment. The damming of the river by channel-spanning complete jams can lead to the scouring of the channel bed through the porous stacks of wood pieces contained within the jam and the deposition of scoured sediment, contributing to the formation of marginal pools, in-dam pools and unvegetated bars. Observations of these features on the Highland Water are in accord with Keller and Swanson (1979) observation of how wood-related sediment storage on low gradient, meandering streams was often in the form of bars downstream of wood-controlled pools. In the

Highland Water, active jams were most strongly associated with the formation of in-dam pools as these jams contain tightly stacked wood pieces, which may lift off the bed (float) during high river flows leading to localised scouring of the channel bed by high velocity threads of water passing under the jams.

Bank vegetation and large wood jam-induced hydrodynamic processes that govern river flow redistribution and the extent of sediment erosion and deposition along single-thread streams are recognised to have a profoundly variable influence on the diversity and distribution of channel geomorphic / mesohabitat features (Thorne and Furbish, 1995; Daniels and Rhoads, 2004; Ottevanger et al., 2012). Observations collected during the present study suggest that large wood jams at river bends are particularly associated with dammed, marginal and in-dam pools and vertical and undercut eroding banks. The force of water tends to erode and undercut river banks on the outside of bends where flow velocities tend to be highest, and this appears to be enhanced by wood jams at bends which frequently show vertical and undercut eroding banks, particularly immediately downstream of the jam, where water plunges over the jam during flood flows. The formation of in-dam, dammed and marginal pools at bends is due to the hydraulic effect of the jam. In particular, active jams cause water to pond upstream, leading to deposition of coarse sediment at the entry to the dammed pool and thus upstream bar development similar to that observed by Abbe and Montgomery (1996). Since the large wood in the Highland Water is less dense than water, it lifts off the bed as water depth increases during high flows, leading to bed scour and the creation in in-dam pools. At the same time water pours over the dam crest at all flows, leading to bed scour downstream and the creation of dam and plunge pools. Since obstructions created by large wood jams at river bends tend to persist on the Highland Water and to be strongly associated with the scour and subsequent deposition of bed sediment, they probably have an important and persistent local influence on bend migration and evolution (Sear et al., 2010). Sediment eroded from around these large jams as the bed and banks are scoured, is deposited downstream where river flow velocities are relatively slower, leading to bar development. Similarly, Keller and Swanson's (1979) observed how wood-related sediment storage on low gradient, meandering streams was often in the form of bars downstream of wood-controlled pools.

6.5.3 Are There Any Differences in the Sediment Characteristics of Different Mesohabitats?

Considerable spatial heterogeneity was observed in the sediment calibre and organic matter content of different mesohabitats sampled in the present study, several of which were wood-related mesohabitats. In addition, there were differences in sediment calibre and organic matter content within the same mesohabitat types on different sampling occasions. The most notable seasonal change in sediment characteristics was that organic matter content was higher in summer than in spring samples, probably due to the addition of organic residue between spring and summer sampling times and the accelerated decomposition during summer of the previous autumn's leaf fall and winter release of dead twigs from the tree canopies. In addition, although there was no general seasonal gradient of sediment fining (D_{50}), summer sediment samples from the sampled mesohabitats contained significantly finer deposits (clay and silt) while spring sediment samples contained significantly more sand. This may reflect the seasonal variability in the intensities of flood disturbance and thus the deposition of relatively finer sediment following the recession of spring floods.

The most notable spatial contrasts in sediment characteristics was significant sediment fining from bars to jams through to floodplains, thus an indication of vertical fining along the riparian zone. Jeffries et al. (2003) observed that the hydrological connection between the channel and the floodplain in the meandering Highland Water was strengthened by the presence of in-channel large wood jams that influenced 41.5 % of overbank ejection of water and sediment during the winter-spring period. Large wood jams characteristically accumulated relatively high amounts of organic matter and intermediate proportions of fine sediments (silt and clay) and gravel. Rivers transport sediment and organic material downstream (Robertson et al., 1999), and roughness elements within the active channel, such as large wood jams, provide sites whose flow resistance allows retention of organic material and sediment of variable calibre. Therefore, the variations in the sediment characteristics of mesohabitat types reflect flow obstruction and associated flow velocity-depth variations that affect the calibre of sediment that can be mobilised, transported and deposited in different locations.

Overall, sediment samples from banks and floodplains were significantly finer, particularly bank samples which contained significantly higher proportion of finer sediments (silt and clay), while floodplain samples were unsurprisingly covered by significantly more sand during spring. Consistent with this study, Goodson et al. (2002), Goodson et al. (2003) and Gurnell et al. (2007) illustrated that floodplain and bank face sediments are usually significantly finer compared to the channel bed, while Sear et al. (2010) similarly observed sand splays on the floodplain during overbank flows typical of the spring season. Together with sediment from floodplains and banks, jam bank samples were significantly finer (silt, clay and sand) than sediment from bars during summer. The complex hydraulic effects of jams induce scouring, transport, deposition and sorting of fluvial sediment (Gomi et al., 2004; Oswald and Wohl, 2008; Gurnell, 2013), including the deposition and storage of fine sediments that was observed on the jam bank during summer. Bars were typically coarser and contained lesser amounts of organic matter regardless of the season as they are subjected to frequent flow disturbance which wash away organic matter and finer sediment. Bank, jam, jam bank and floodplain sediment samples shows considerable variability in organic matter content between the seasons, with jam bank and jam sediment samples retaining significantly more organic matter during spring and summer, respectively. Litter packs are often formed in areas of flow separation or low shear stress, characteristic of jams, and usually decay when stranded in jams following the recession of spring floods during summer, therefore the considerable amount of organic matter in jams during summer. This organic matter may have been accreted onto the bank face / toe immediately adjacent or downstream of jams, explaining the considerable amount of organic matter on the jam bank during spring. Therefore, the between-season trends for mesohabitats within the study reach probably reflect rates of biogeochemical processes (e.g. decomposition rates) and differences in the character of sediments supplied to each mesohabitat by changing hydrological events of the river since the data presented here represent deposition from a sequence of floods of differing timing, duration and magnitude that would be expected to transport sediment of varying calibre and organic content.

6.5.4 Are There Any Differences in the Propagule Bank of Different Mesohabitats?

In all, 28 taxa of viable propagules were identified along the study reach of the Highland Water. The relatively low species diversity along the Highland Water reflects restriction of the species pool to the heavily grazed riparian forest bordering the river. The pressure of grazing, which is the dominant land-use in the New Forest (Jeffries et al., 2003), reduces the number of seedlings that reach maturity, hence heavily retarding regeneration (Douglas and Pouliet, 1997; Clary, 1999; Shaw and Kernot, 2004). This may have significantly affected the composition of the riparian propagule bank and may generally have accounted for the low plant propagule diversity recorded along the Highland Water. Some species, such as *Epilobium hirsutum*, *Juncus effusus*, *Carex pendula* and *Betula pubescens* reflect the mixed woodland and occasional wetlands bordering the Highland Water. Although species poor, the propagule abundance found in the study for the two seasons (22 to 5,706 propagules per square metre) are somewhat higher than those reported for other wooded riparian areas (e.g. Ferris and Simmons, 2000; see Goodson et al., 2001).

In the present study, the statistically significant differences in sediment characteristics between the sampling seasons and mesohabitat types are reflected in differences in the species richness and abundance (in volume and cover) of propagules retained within the river channel and margins. The sediment samples (spring and summer) yielded a significant seasonal pattern in the species richness and abundance of propagules, with spring samples showing higher species richness and abundance than summer samples. The high deposited propagule species richness for the spring period has also been observed by Gurnell et al. (2006a) in a restored reach of the River Cole, West Midlands, UK, and by Gurnell et al. (2008a) in two reaches of the River Frome, Dorset, UK, and a headwater reach of the River Tern, Shropshire, UK. High propagule abundance observed during the spring period in this study is consistent with the findings of Boedeltje et al. (2004) on the low energy Twentekanaal, Netherlands, but contrary to the findings of Gurnell et al. (2006b, 2008a) who observed a summer peak in propagule abundance. However, the studies by Gurnell et al. (2006b, 2008a) focussed mainly on recently river-deposited sediment rather than on the total near-surface seed bank, which was the focus of the present research. Interestingly, although most of the seedlings identified for the spring and summer seasons were from species with a persistent seedbank (that is seeds remain viable for > 1 year) (see Thompson and Grime, 1979; Hodgson et al., 1995; Thompson et al., 1997), the high beta diversity (length of gradient) revealed by Detrended Correspondence Analyses (DCA) suggests that only a few species were shared between the spring and summer samples. Moreover, the flowering periods of the identified species as indicated by Hodgson et al., (1995), suggest that the spring (May) sampling catches the persistent viable seeds and seeds released in the autumn-winter or in the previous summer while the summer sampling in July would have been too early to catch new seeds as most of the species identified in this study (in both seasons) set seeds later in the summer than the July sampling. In which case, seeds from these species would have been produced in the previous year and so many may have lost viability at the time of the July sampling. This may have accounted for the relatively low species richness and abundance of propagules identified during the summer. Also, few of the propagules use water as a primary dispersal mechanism (see Hodgson et al., 1995; Thompson et al., 1997), so they need to be remobilised by water through a secondary dispersal before they are likely to be retained within the channel and margin mesohabitats. The New Forest catchment is usually flooded in winter, but rarely in summer (Peterken and Hughes, 1995). Therefore, propagule retention within the soil propagule bank in and around the river channel was probably comparatively better during spring because of their remobilisation and retention during winter rainfall and floods, while a progressive loss in seed viability (perhaps hastened by desiccation) may be a cause of the relatively impoverished propagule bank in the summer sampling.

Kruskal-Wallis tests and DCA of the riparian propagule bank samples, revealed clear spatial patterns across the river channel and its margins. Hydrochory has been shown to be important for dispersing propagules along rivers and into the riparian corridor (Johansson et al., 1996; Goodson et al., 2003; Gurnell et al., 2007) and transferring propagules from the catchment (upstream) species pool through the river network (e.g. Andersson and Nilsson, 2002; Goodson et al., 2003; Boedeltje et al., 2004). Whereas most of the investigated mesohabitats experienced flood inundation close to the two sampling periods (especially during spring), variable periods of inundation, propagule and sediment trapping by jams and accretion onto the bank toe and face, may have been the factors that significantly influenced the large species richness and abundance of propagules at jam bank mesohabitats. Generally, the difference in the elevational pattern in propagule abundance as shown by the apparent increasing order of propagule abundance from channel habitat (bare gravel bar and jam) to channel bank habitats (bank and jam bank) through to the floodplain is another indicator of the importance of hydrochory along the Highland Water.

Moreover, within each season, spatial patterns were identified for propagule bank diversity. Propagule species richness was significantly higher in the sediment samples from jam banks and banks during spring and in sediment samples from jam banks during summer when these samples were compared to those from bare gravel bars. In relatively less inundated areas, biotic factors such as competition and herbivory (which is intense in the New Forest) are likely to be more important in determining the propagule bank and vegetation composition (Blom et al., 1990; Lenssen et al., 1999). Thus, the low species richness of the floodplain propagule bank is likely a reflection of the relatively low diversity present in the local vegetation communities, irrespective of the season, due to intense herbivory by small and large mammals (e.g. ponies, deer, squirrels) within the New Forest. Propagule abundance was distinctly higher in spring sediment samples from floodplains and jam banks and in summer sediment samples from jam banks. Habitats subjected to alternating drying and flooding conditions, that is floodplains, banks and jam banks during spring and jam banks during summer, have been found to be characterised by higher propagule abundance than permanently flooded habitats such as jams and bars (Combroux and Bornette, 2004) probably due to the build-up of propagules. Therefore, competition, herbivory and seasonal differences in the gradients of flood frequency and magnitude (depth and duration) which consequently influence depositional patterns across the riparian corridor, may have accounted for the spatial heterogeneity between the investigated mesohabitat types.

A more detailed analysis of the propagule vegetative groups within the riparian corridor revealed that propagules are preferentially stored in large quantities in certain mesohabitats during spring and summer, respectively. This seasonal pattern of propagule storage in preferential habitats was also recognised along the River Dove and Cole (Goodson et al., 2004). Depending on their functional attributes such as floating ability, mass, size and their ability to survive and maintain viability within the riparian corridor (i.e. persistence), the propagules of riparian plants of specific vegetative groups can respond to the hydrological attributes of flooding (e.g. timing and duration) in a variety of different ways, resulting in selective deposition (see Hodgson et al., 1995; Thompson et al., 1997). Many riparian monocots such as *Juncus effusus* (rush), *Carex sp.* (grass) and forbs such as *Sagina procumbens* (herb) produce large quantities of seeds and maintain large persistent soil seed banks that enable plants to persist within a habitat as dormant propagules until conditions suitable for their germination and establishment occur (Thompson et al., 1997; Leck and Brock, 2000). This in correspondence with local seed rain from riparian woody species such as *Betula pubescens* and / or the rafting or redistributing of their propagules through runoff or overbank flows during high discharges may have accounted for the large quantity of propagules of woody, herb, rush, grass species been stored on the floodplain during spring. Besides, large flood events usually occurring during winter and spring tend to homogenise riparian vegetation composition, consequently the generally widely distributed propagules of woody, herb, grass and rush species within the floodplain soil propagule bank (Capon, 2003). The stranding of relatively heavier woody propagules of plants such as *Betula pubescens* in jams and the sealing of gaps in the jam by decaying leaves (shed in the autumn) may have accounted for the large quantity of woody propagules in jams during spring. Combroux and Bornette (2004) demonstrated that habitats subjected to frequent inundation such as jams, are characterised by a higher proportion of heavier propagules in the propagule bank as large seeds are likely to move lower in the water column (see Hodgson et al., 1995; Thompson et al., 1997). In simulating the transport and deposition of seeds in a Swedish river by using various-sized wooden cubes, Nilsson et al. (1991) found that seeds with short floating characteristics (i.e. heavier seeds) tended to collect in the same areas where fewer cubes were captured and those with long-term floating ability (i.e. lighter seeds) were found to collect in larger numbers in association with other areas. Consequently, the rafting or redistribution of light-weight grass propagules onto the banks adjacent to jams (jam banks) following winter flooding may have accounted for the large quantities of grass propagules retained on the jam bank during spring. However, during the summer period, propagules of herb and woody species are preferentially stored on the jam bank rather than on the floodplain probably as a function of the deposition of these propagules after seasonal winter-spring floodwaters have receded during summer.

6.5.5 Are There Any Significant Associations between Physical (Large Wood Jams and / or Sediment) and Biotic (Propagule Banks) Characteristics of Mesohabitats?

(i) Are there relationships between sediment and propagule characteristics associated with mesohabitats within the riparian corridor?

The seasonal dynamics and spatial pattern of riparian propagule banks originate from differences in the relative structure of substrates (mineral sediment and organic content) available for propagule deposition or retention. The sediment characteristics of the different mesohabitat types within the riparian corridor of the Highland Water, investigated in this study, accounted for approximately 62 % of the variation in the composition of propagule banks. Most of the variations in propagule bank composition across the mesohabitats, as indicated by the correlation and Canonical Correspondence Analyses respectively, were significantly explained by median particle size and the amount of organic matter, with propagule species richness increasing with increases in the proportion of fine sediment particles and organic matter within the sediment. This was most apparent in the spring sampling, probably reflecting the higher presence of viable proagules at this time. These observations of associations between propagule abundance and sediment properties most probably reflect the fact that hydraulic environments suitable for the deposition of fine sediment particles are also suitable for the deposition of seeds (most of which are light and quite buoyant) and the deposition of organic material, which also has a low density (Gurnell et al., 2008a). Heavier seeds may also collect in association with coarser sediments, particularly on river beds (Gurnell et al., 2007). However, these observations may also support the assertion that the substrate available for propagule deposition or retention might be related to differential propagule retention patterns (Nathan and Muller-Landau, 2000) where elevated concentrations of fine sediment and organic matter even in quite small quantities may increase soil elasticity and porosity and thus support retention of more propagules (Soane, 1990).

Canonical Correspondence Analyses relating propagule bank composition and riparian sediment characteristics also revealed that some of the sampled propagule species and mesohabitats were strongly associated with sediment characteristics, reflecting the overriding importance of the depositional environment for both mineral and organic particles. The propagules of *Ajuga reptans* and *Carex sp.*, which are relatively heavier generally occur in larger densities across the gravel dominated bars of the Highland Water, while the propagules of species such as *Agrostis sp.*, *Cardamine pratensis* and *Juncus acutiflorus* favour relatively fine and seasonally waterlogged soils of woodlands and meadows characteristic of floodplains and jam banks and banks. Besides, the propagules of *Apium nodiflorum*, *Alnus glutinosa*, *Epilobium ciliatum* and *Juncus effusus* generally favour seasonally exposed and disturbed soils in slackwater habitats with relatively high but variable amounts of organic matter and moderate amounts of gravel and fine deposits, typical of large wood jams. As observed by Johansen and Hytteborn (2001) and Sear et al. (2010), large wood jams usually contain litter packs that potentially seal gaps in jams and can serve as floats for plant propagules of varying weights. Due to the variable amounts of propagules (of different vegetative groups), organic matter and fine sediment in large wood jams and its associated habitats, it may therefore be termed a ‘transitional habitat’, providing an important link between channel habitats (bars and channel bed) and the adjacent channel bank habitats (bank and jam bank) and floodplain, and consequently may have implications for the initial trajectory of vegetation colonisation and the eventual development of in-channel and riparian landforms.

(ii) Importance of large wood jams for riparian re-vegetation and landform development

A particularly novel aspect of this study has been that large wood jams within the active channel of the Highland Water are essential in influencing differences in propagule composition and the relative characteristics of substrates (mineral sediment and organic content) available for propagule deposition or retention in large wood jam-related mesohabitats (within jams and the bank face / toe immediately adjacent or downstream of jams (jam banks)). Whilst previous research has identified that open, active river beds can store numerous propagules in preferential sites (that is within the bed and bank toe) and that their species abundance varies in time and space (e.g. Gurnell et al., 2006a, 2007, 2008), the present study has shown that large wood jam-related mesohabitats cumulatively store the largest amount (in terms of species richness and abundance) of viable propagules and also exhibit high seasonal variability.

This present study suggests that during spring and summer, large wood jam-related mesohabitats (jams and jam banks) retained sediments with relatively high amounts of organic matter and intermediate amounts of finer mineral particles. This substrate was favourable for the retention of propagules particularly that of rush, grass and woody species, although floristic diversity in terms of propagule abundance and species richness were vastly variable especially during spring. This supports the assertion that the hydraulic complexity created by large wood accumulations enhances seasonal variations of the relatively abundant and diverse riparian propagule bank, and hence supports vegetation biodiversity within the riparian corridor.

The availability of propagules in the sediment propagule bank is generally assumed to be an important factor for the regeneration and restoration of natural habitats as it functions as a latent plant community (Leck, 1989; Thompson, 1992; Bakker et al., 1996; Goodson et al., 2001). Propagules concentrate in areas of flow separation or low shear stress, characteristic of jams, following depositional processes (Abernethy and Wilby, 1999; Goodson et al., 2001; Andersson and Nilsson, 2002; Tabacchi et al., 2005), and these environments can provide suitable environmental conditions (nutrients, moisture, etc.) for germination. Propagules have been shown to have the ability to germinate or sprout in relatively disturbed habitats (Barrat-Segretain et al., 1999; Barrat-Segretain and Bornette, 2000) typical of mesohabitats associated with large wood jams. Intermittent exposure and drying up of these mesohabitats driven by the seasonal variability in hydrological processes, favours the regeneration process of vegetation via an abundant propagule bank (Capon, 2003; Combroux and Bornette, 2004). Consequently, the progressive deposition and accretion of sediment and propagules (particularly of rush, grass and woody species), sprouting of early-successional germinants and the eventual colonization success of vegetation in the large wood jam-related mesohabitats within the lowland meandering Highland Water may potentially be major factors for determining earlier successional processes and plant diversity (Barrat-Segretain et al., 1998; Pollock et al., 1998; Middleton, 1999; Guilloy-Froget et al., 2002) and may possibly influence the evolutionary sequence of new floodplains (Fetherston et al., 1995; Jeffries et al., 2003; Montgomery and Abbe, 2006; Collins et al., 2012). Therefore, propagule banks within large wood jam-related mesohabitats may not only be important tools in the conservation of plants but also potentially important in the trajectory of floodplain development on lowland meandering rivers.

The next chapter investigates the physical properties and propagule bank characteristics of key morphological features and compartments within the single-thread, restored reach of the River Bure, Norfolk, UK, which is characterised by reintroduced wood (felled trees), that is very different in its characteristics from that studied along the Highland Water.

CHAPTER 7

REINTRODUCED WOOD AND PROPAGULE BANK STRUCTURE ALONG A SINGLE-THREAD RESTORED LOWLAND RIVER: THE RIVER BURE, UK.

7.1 INTRODUCTION

Rivers worldwide are subject to anthropogenic influences that degrade habitat conditions and threaten biodiversity (Malmqvist and Rundle, 2002). Widespread among these impacts are a variety of physical alterations, including straightening, embanking, dredging, and removal of large wood accumulations that homogenize the geomorphological and hydraulic features of the channel which consequently influence river and floodplain ecology (Palmer et al., 2010). Degraded river ecosystems may have their natural regulatory mechanisms altered, reducing their capacity to recover to a fully functioning state (Hobbs and Norton, 2006; Palmer et al., 2010). Since the 1980s, there has been increasing emphasis on the restoration of river form and ecological functions within degraded / disturbed river ecosystems (e.g. Roper et al., 1997; Engel and Parrota, 2003; Harrison et al., 2004; Lepori et al., 2005; Jähnig and Lorenz, 2008; Palmer et al., 2010). Key techniques that have been used to restore or rehabilitate river form and function have included the restoration of meanders to straightened rivers, soft engineering of river banks, introduction of boulders, the construction of artificial riffles and pools, and the installation of protective fencing material, all with the aim of restoring biodiversity by enhancing structural heterogeneity (see Roni et al., 2008; RRC, 2013). More recently, restoration schemes have started to incorporate the reintroduction of large wood to enhance channel structural and hydraulic complexity and thus to re-establish the physical and ecological functions associated with large woody accumulations in undisturbed river systems (Palmer et al., 2010; RRC, 2013).

As outlined in Chapter 2, the dynamics, morphology and geomorphological role of large wood varies with the river type (e.g. Gurnell et al., 2002) and the nature of the wood (living or dead) (Gurnell et al., 2001; Gurnell, 2013). This chapter focuses on a relatively small single-thread river, the River Bure, UK, where felled trees have been introduced into the active channel as part of a restoration scheme. Under natural conditions, large wood in fluvial systems is known to be important for creating sedimentary and morphological / habitat complexity (e.g. Gurnell et al., 2002; Gregory et al., 2003; May and Gresswell, 2003; Gurnell, 2014), storing organic matter and stabilising sediments (e.g. Abbe and Montgomery, 1996; Edwards et al., 1999a), and supporting a variety of plants, aquatic insects and fish (e.g. Tank and Winterbourn, 1996; Benke and Wallace, 2003; Francis et al., 2008a). Research on the geomorphological role of reintroduced large wood has identified significantly more mesohabitat patches per metre channel length and increased frequency of pools (Gerhard and Reich, 2000; Larson et al., 2001; Muotka et al., 2002; Moerke et al., 2004; Muotka and Syrjanen, 2007; Tullos et al., 2009; Palmer et al., 2010). In parallel, ecological research has identified an increase in salmonid abundance, but a variable response in macroinvertebrate species abundance and richness following the addition of large wood (Gerhard and Reich, 2000; Larson et al., 2001; Muotka et al., 2002; Moerke et al., 2004; Muotka and Syrjanen, 2007; Tullos et al., 2009; Palmer et al., 2010). Nonetheless, to date there is a lack of information on the influence of reintroduced large wood on (i) the sediment characteristics of large wood induced mesohabitats and; (ii) relationships between reintroduced large wood and propagule and / or plant diversity in restored river reaches.

This chapter investigates the physical properties of sediments and propagule bank characteristics of reintroduced wood and associated mesohabitats within the active channel of the single-thread lowland River Bure, United Kingdom. The research explores the spatial organisation of reintroduced wood accumulations, and relationships between the sediment characteristics and propagule bank (spring and mid-summer) of key mesohabitats, by addressing the following research questions:

i. What are the characteristics of reintroduced wood?

ii. Are there any associations between reintroduced wood and geomorphological features?

iii. Are there any differences in the sediment characteristics of different mesohabitats?

iv. Are there any differences in the propagule bank of different mesohabitats?

v. Are there any significant associations between physical (reintroduced wood and / or sediment) and biotic (propagule banks) characteristics of mesohabitats?

7.2 STUDY SITE

An overview of the research design and research sites included in this thesis was provided in Chapter 3. The research reported in this chapter was conducted along a third order, low energy, meandering reach of the River Bure, which flows through rural agricultural north-east Norfolk, UK (Figure 7.1).

The 240 m study reach (Figure 7.1B and 7.2) is located on the Blickling Hall estate, near Aylsham (Grid Ref TG161301). The reach has an average slope of 0.005 $m.m^{-1}$ and the relatively shallow active channel extends to an average width of approximately 7.6 m. The bed material within the active channel is gravel but the gravel bed is mainly overlain by a layer of fine sediment (mainly silt). The cohesive banks are composed mainly of sand and clay with occasional gravel lenses. The river is bordered by farmland, parkland and a relatively open, mixed deciduous woodland along much of the river margin, which is dominated by alder (*Alnus glutinosa*) and stinging nettles (*Urtica dioica*).

The silt layer on the river bed results from a combination of silt delivery to the channel from the floodplain (particularly farmland) and historical over-widening of the channel which has reduced flow velocities. Large wood had previously been removed from the reach by fishing clubs and the Environment Agency to improve access for fishing and to mitigate against flood risk. Following concerns raised by the local fishing club regarding habitat quality for wild trout, and a desire to improve the conservation value of the reach, the National Trust site manager designed and implemented a river restoration scheme involving reintroduction of large wood. The wood was reintroduced into the study reach in two phases: within sub-reach A in autumn 2008, and sub-reach B in autumn 2010 (Figure 7.2)

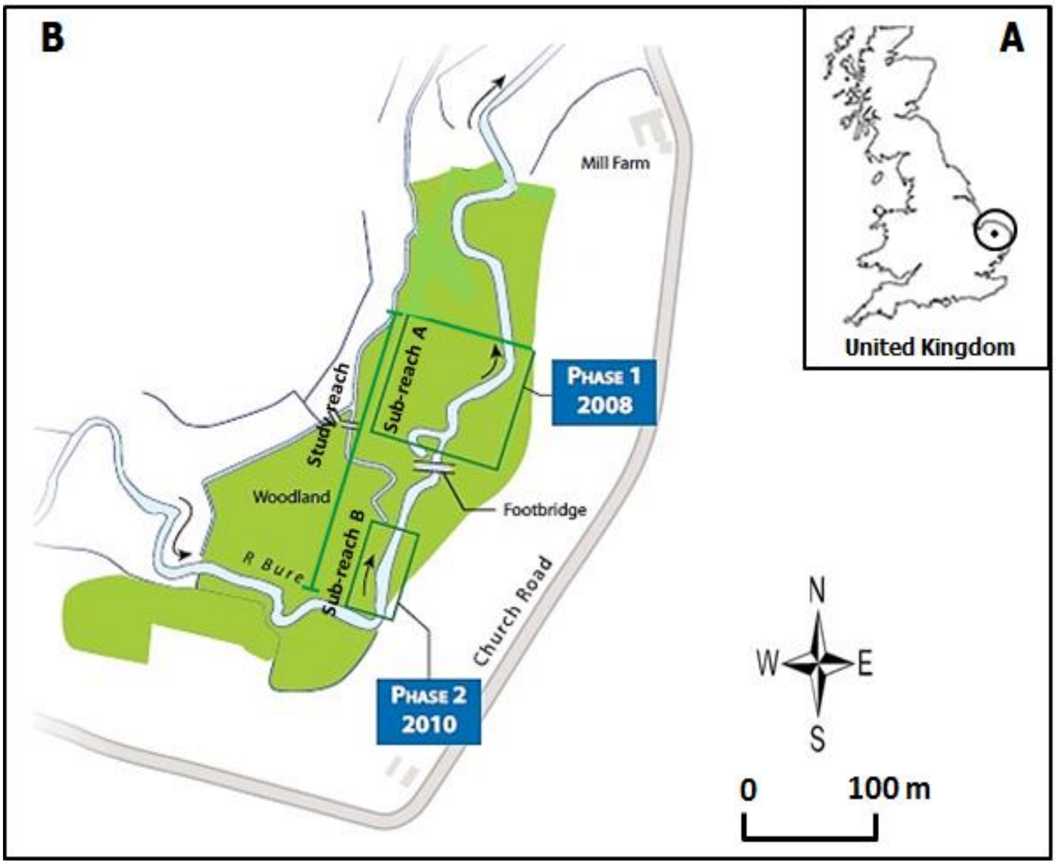

Figure 7.1. (A) Location of the River Bure; (B) the Blickling Hall estate near Aylsham showing the study reach, which includes sub-reaches affected by reintroduction of wood in autumn 2008 (sub-reach A) and autumn 2010 (sub-reach B) (Source: Modified from RRC, 2013).

7.3 METHODS

7.3.1 Research Design

Figure 7.2 illustrates the 240 m study reach along which 12 wood accumulations were introduced in two phases (accumulations 8 to 12 in 100 m long sub-reach A in 2008, accumulations 1 to 7 in 80 m long sub-reach B in 2010). The study reach was sampled from downstream to upstream in order to characterise the reintroduced wood accumulations, explore their relationship with specific mesohabitats of the river's active corridor and capture any variability along the reach in relation to its sediment characteristics and propagule banks. Reintroduced wood accumulations were surveyed in May 2012. Sediment and propagule bank samples were collected in May 2012 and July 2012 in order to investigate the variability in their characteristics along the study reach of the River Bure and to identify any differences between the early- and mid-vegetation growing seasons.

7.3.2 Field Methods

Three types of data and / or samples were collected from all 12 reintroduced wood accumulations within the study reach; (i) observations and measurements were made of the characteristics of each wood accumulation and; (ii) sediment samples were collected for analysis of sediment calibre, organic content and the composition and abundance of the plant propagule bank.

(i) Reach geomorphological characterisation

The geomorphology of the study reach was mapped to provide a context for interpreting the other data sets that were collected and also to place them in the context of the study reach as a whole (Figure 7.2). The survey along the study reach focused on the active channel and adopted the methodology of mapping the location and extent of key mesohabitats and active channel features (e.g. pools and bars), substrate types (fine sediment (clay and silt), sand, and gravel; Nilsson et al., 1989), marginal plants and large wood features. The mapping of the study reach was conducted during low flow conditions.

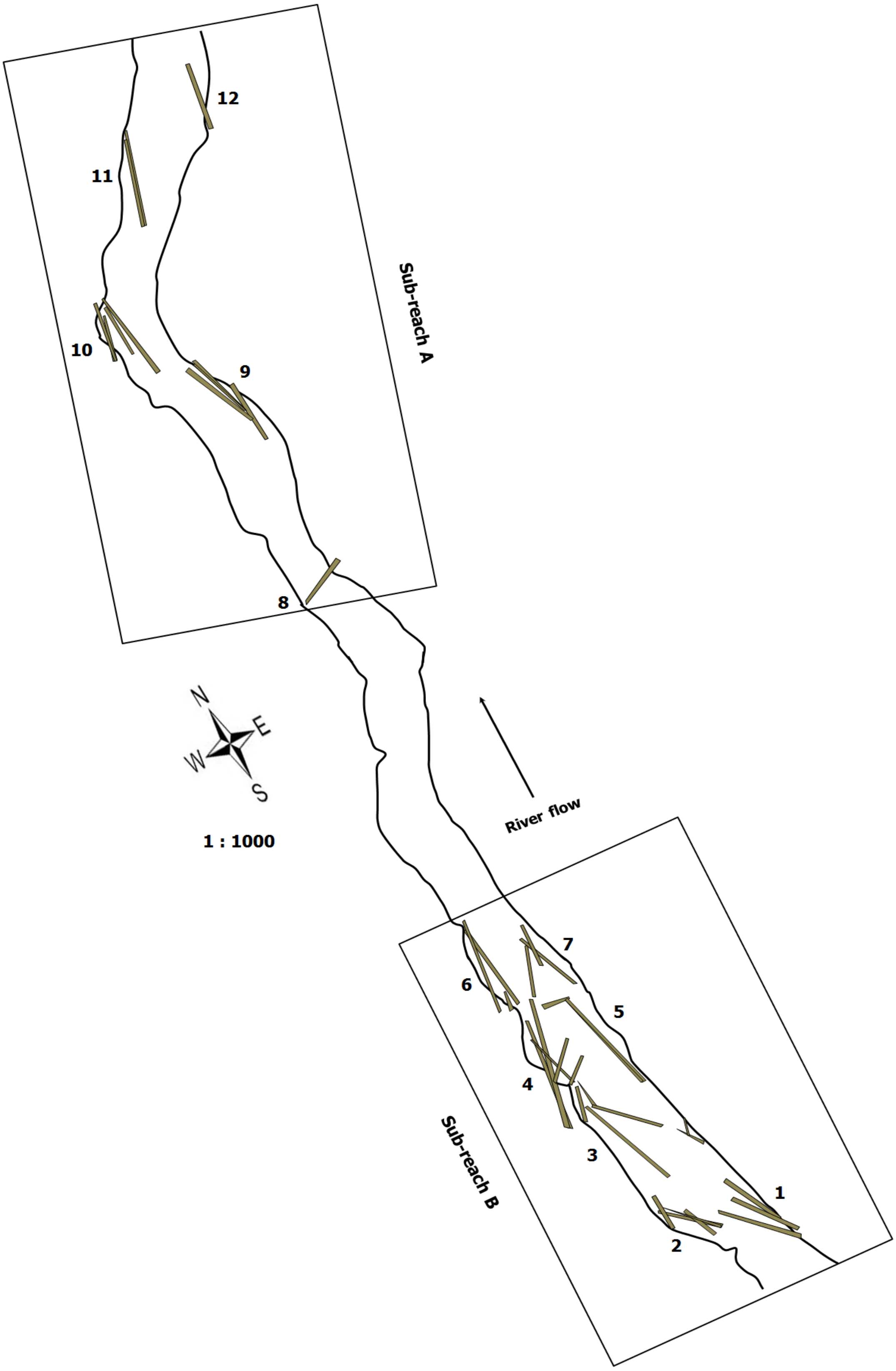

Figure 7.2. The River Bure study reach (located in Figure 7.1B), showing the location of the reintroduced wood accumulations from upstream to downstream. (Note that the wood was reintroduced into sub-reach A in autumn 2008 and into sub-reach B in autumn 2010).

(ii) Large wood accumulation survey

The large wood accumulation survey (details and definitions in Appendix I) along the study reach involved recordings based on either visual assessment (e.g. classification of large wood accumulation type) or on measurements of dimensions (e.g. channel, accumulations, wood pieces). Large wood pieces (> 10 cm in mid-diameter and > 1 m in length) within accumulations (hereafter called jams) and the dimensions of jams were measured (length, width and depth) using a 30 m tape and 1 m ruler. The volumes of wood pieces (length and diameter) and jams (length, width and depth to give a wood/air volume) were also measured (Gurnell et al., 2000b; Lamberti and Gregory, 2011).

(iii) Sediment and propagule bank sampling

Sediment and propagule bank samples were collected using a stratified random sampling design that was similar to that used on the Highland Water (See Chapter 6, Section 6.3.2 (iii)). However, because of differences in the type of wood (mainly very large pieces) and other mesohabitats within the River Bure reach, the location of sampling was slightly modified, although the abbreviations that were used previously are retained. Sediment samples were collected at each of the twelve reintroduced wood jams, where sediment samples were collected from five mesohabitats characteristic of the river corridor (the bare river bed (BGB), the sediment plume retained within and immediately upstream of jams (JM), the bank face and toe adjacent to and immediately downstream of jams (JB), the surface of unvegetated bare eroding banks (BK) and the surface of the floodplain or bank top (FP) (Figure 7.3, Table 7.1). Propagule banks are not only highly variable in space but also through time (Fenner and Thompson, 2005), and so the sediment and propagule bank sampling was undertaken on two occasions: (i) in May 2012 (spring (PB1)), designed to capture the period following the recession of spring floods but prior to the main summer flowering season in order to sample the persistent seed bank and; (ii) in July 2012 (mid-summer (PB2)) following the release of propagules from flowering plants close to the time of sampling to capture the transient seed bank (Schneider and Sharitz, 1986; Richter and Stromberg, 2005).

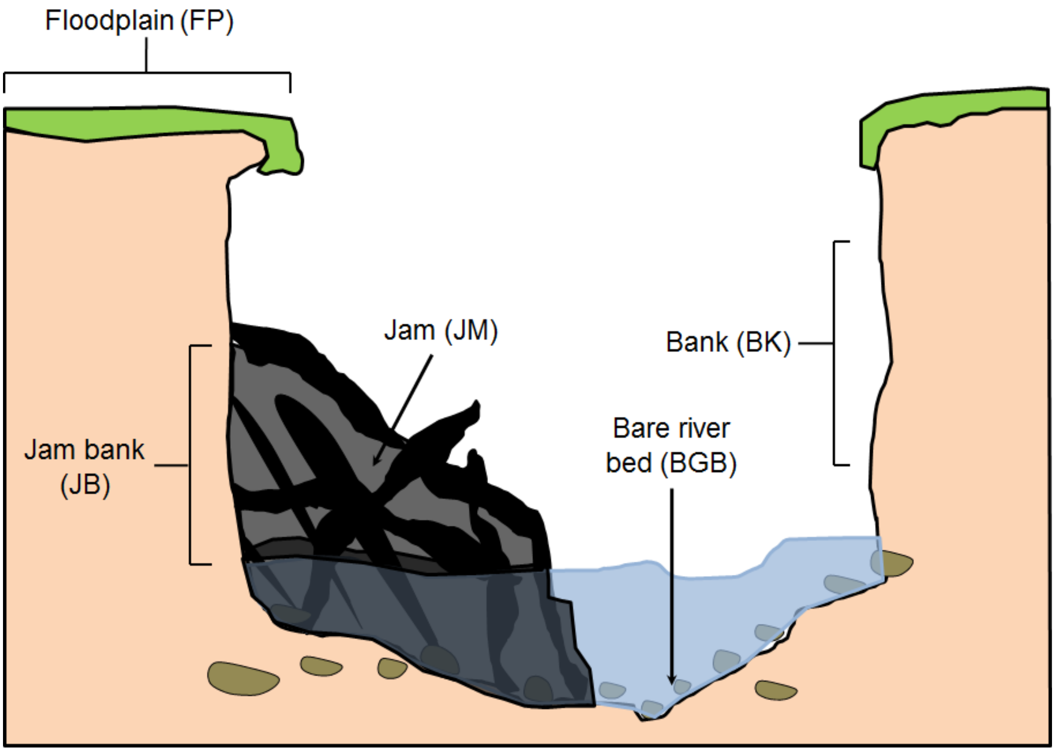

Figure 7.3. Schematic representation of the typical patterning of habitat patches (mesohabitats) representative of the study reach along the River Bure. The mesohabitats identified along the study reach were the bare river bed (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP).

Table 7.1. The number of bulked samples obtained from different mesohabitats along the study reach. Each bulked sample aggregated 3 replicate samples, apart from the bare river bed (BGB) samples where 4 replicate samples were bulked to ensure sufficient finer sediment for laboratory analysis from these relatively coarse bed sediments.

Mesohabitats	**Abbreviations**	**Definitions**	**Number of sampled sites**
Bare river bed	BGB	Sediment on the unvegetated river bed in the areas of highest flow velocity, which were least affected by large wood	12
Bank	BK	Surface of an actively eroding river bank face midway between the bank top and the bank toe	12
Jam	JM	Fine sediment accumulated within or immediately upstream of jam	12
Jam Bank	JB	Sediment on the face / toe of banks immediately adjacent or downstream of jams	12
Floodplain	FP	Floodplain surface close to the river channel (i.e. bank top)	12

Each sample was a composite of three samples extracted from random locations within the sampled mesohabitat, with the exception of the bulked samples from the river bed where four samples were combined to ensure sufficient fine sediment for analysis. The individual samples were obtained using a cylindrical corer (see Chapter 3, Section 3.5.3). Sampling was undertaken, working upstream in order to minimize contamination of sediment samples.

7.3.3 Laboratory Methods

The laboratory methods of: (i) sediment storage and preparation; (ii) sediment analysis; and (iii) germination trials used in this study are described in Chapter 3 (Section 3.6).

7.3.4 Data Analysis

Table 7.2 lists the variables investigated in this study and defines how these were derived from the raw field and laboratory measurements. The results from the above procedures were analysed using a number of descriptive, bivariate and multivariate analysis techniques. For the jam, wood piece, propagules and sediment results, descriptive statistics were used to identify trends in the raw data. Descriptive statistical techniques were used to assess jam characteristics (research question 1). They also revealed that most of the variables were not normally distributed and frequently showed differences in variance when subdivided according to mesohabitats, so non-parametric statistical methods were used for data analysis.

The primary means of investigating research questions 3 and 4 was through comparison of medians of the measured variables, using non parametric analysis of variance. Kruskal-Wallis (KW) tests or Mann Whitney (MW) tests, as appropriate, were used to explore the differences in sediment and propagule bank variables between the different mesohabitats and sampling periods. Where KW tests indicated a significant difference ($p < 0.05$) in a particular variable, multiple pairwise comparisons were performed using Dunn's procedure (Bonferroni corrected significance level) to identify those mesohabitats that exhibited significant contrasts in the variable.

Table 7.2. Variables estimated from field measurements and laboratory measurements of samples collected from the River Bure study reach.

Variable Abbreviation	Variable Full Name	Description
Jam and wood piece variables		
FWPJ	Frequency of wood pieces in jam	The total number of individual large wood pieces in a sampled jam.
WPL	Wood piece length	The average length of a large wood piece (m).
WPD	Wood piece diameter	The average mid-stem diameter of large wood pieces (m).
WPV	Wood piece volume	The cylindrical volume of an average large wood piece (m^3).
JL	Jam length	The longitudinal distance from the base to the top of a wood jam measured parallel to the river channel axis (m).
JW	Jam width	The horizontal width of a wood jam measured perpendicular to the river channel axis (m).
JD	Jam depth	The maximum vertical depth of a wood jam measured above the river bed (m).
JA	Jam area (m^2)	The smallest rectangular area of the ground surface into which a wood jam fits (m^2).
JV	Jam volume (m^3 or m^3/ha)	The total volume of the smallest rectangular box (of air) into which a wood jam would fit (m^3). Following Gurnell et al. (2000b), the wood+air volumes were adjusted to produce estimates of wood volumes by multiplying the volumes of jams by 0.2.
Propagule bank variables		
T PropSR	Propagule species richness	The total number of propagule species identified in a sample.
HB sp	Number of herb species	The total number of herb species present in a sample.
GS sp	Number of grass species	The total number of grass species present in a sample
RH sp	Number of rush species	The total number of rush species present in a sample.
WS sp	Number of woody species	The total number of woody species present in a sample.
T Prop/l	Propagules per litre	The number of viable propagules per unit volume of sampled mesohabitat sediment; Prop/l = Number of viable propagule species in sediment sample x (Total volume of < 4 mm sediment fraction ÷ volume of < 4 mm sediment fraction used in germination trials) x (1000 / Total volume of sediment sample).
HB prop/l	Number of herb propagules	The total number of viable herb propagules per unit volume of sampled mesohabitat sediment.
GS prop/l	Number of grass propagules	The total number of viable grass propagules per unit volume of sampled mesohabitat sediment.
RH prop/l	Number of rush propagules	The total number of viable rush propagules per unit volume of sampled mesohabitat sediment.
WS prop/l	Number of woody propagules	The total number of viable woody propagules per unit volume of sampled mesohabitat sediment.
T Prop/m^2	Propagules per square metre	The number of viable propagules per unit surface area of sampled mesohabitat; Prop/l = Number of samples collected with the corer x pi (3.1416) x (Radius of the corer)^2.
HB prop/m^2	Number of herb propagules	The total number of viable herb propagules per unit surface area of sampled mesohabitat.
GM prop/m^2	Number of grass propagules	The total number of viable grass propagules per unit surface area of sampled mesohabitat.
RH prop/m^2	Number of rush propagules	The total number of viable rush propagules per unit surface area of sampled mesohabitat.

Table 7.2. (Continued)

Variable Abbreviation	Variable Full Name	Description
WS prop/m^2	Number of woody propagules	The total number of viable woody propagules per unit surface area of sampled mesohabitat.
Sediment variables		
% OM	% Organic Matter	Percentage organic matter content of bulk mesohabitat sediment sample.
D_{50}	Median particle size (phi units)	Median particle size of bulk mesohabitat sediment sample expressed in phi units.
% G	% Gravel	Percentage of gravel in bulk mesohabitat sediment sample.
% S	% Sand	Percentage of sand in bulk mesohabitat sediment sample.
% ST	% Silt	Percentage of silt in bulk mesohabitat sediment sample.
% C	% Clay	Percentage of clay in bulk mesohabitat sediment sample.

The nature, strength and significance of associations between pairs of variables were explored using the non-parametric Spearman’s rank-order correlation coefficient to identify (i) bivariate associations among sediment and propagule bank characteristics of mesohabitats associated with the respective sampling periods (May (PB1) and July (PB2)) (ii) bivariate associations among jam and wood piece dimensions, sediment and propagule bank variables for jam-related mesohabitats (jam bank and jams respectively) within the sampling periods (May (PB1) and July (PB2)).

Multivariate associations were then explored using ordination methods (Principal Components Analysis – PCA, Detrended Correspondence Analysis – DCA). These analyses together with Spearman’s rank-order correlation analyses address research question 5.

PCA was applied to the rank correlation matrix among physical (sediment) variables measured for mesohabitats within the active corridor to identify the principal gradients in the measured physical variables and to explore how these gradients are related to the mesohabitat types. Associations between the gradients defined by the principal components (PCs) and mesohabitats were then explored by (i) producing scatterplots showing PC scores coded by sampling periods and mesohabitat types; and (ii) applying KW and MW tests to PC scores for sampling periods and mesohabitat types, respectively, to assess the statistical significance of any apparent differences observed in scatterplots.

DCA was then applied to the propagule data sets (species presence / absence) in order to investigate whether there were any gradients in propagule species composition that reflected sampling periods and / or mesohabitat types.

Unlike previous chapters, the above analyses were not followed by DGA because it was felt that this would add little to interpreting the data set. The rationale for this is explained in section 7.4.5.

MW tests, KW tests, Spearman’s rank-order correlation and PCA were performed using XLSTAT-Pro software (version 9.1.3, 2009). DCA was performed using CANOCO v4.5 (ter Braak and Smilauer, 2002).

7.4 RESULTS

7.4.1 Characteristics of Jams

This section describes the characteristics of jams and then presents data on the frequency, volume and dimensions of large wood pieces and jams and their associations along the River Bure study reach. A total of 74 large wood pieces and trees (> 10 cm diameter and 1 m length) of the species *Alnus glutinosa* were found incorporated into 12 jams studied along the River Bure. All the jams surveyed were partial jams, occupying only part (typically approximately 45 %) of the bankfull width of the active channel.

Jams and their constituent large wood pieces varied greatly in size along the study reach (Figure 7.4, Table 7.3). Figure 7.4 shows the frequency of the lengths, widths and depths of the 12 wood jams. The average wood volume of jams for the 0.23 ha study reach, expressed as cubic meters per hectare of active channel area was 12.59 m^3/ha. The median jam length, width and depth were 15.34 m, 2.87 m and 0.62 m, respectively, but jams varied mostly in length and width (Figure 7.4, Table 7.3). The area and volume of jams varied widely, ranging, respectively, from 0.95 m^3 to 15.13 m^3 (median 3.48 m^3) and 14.16 m^2 to 71.20 m^2 (median 24.97 m^2) (Table 7.3).

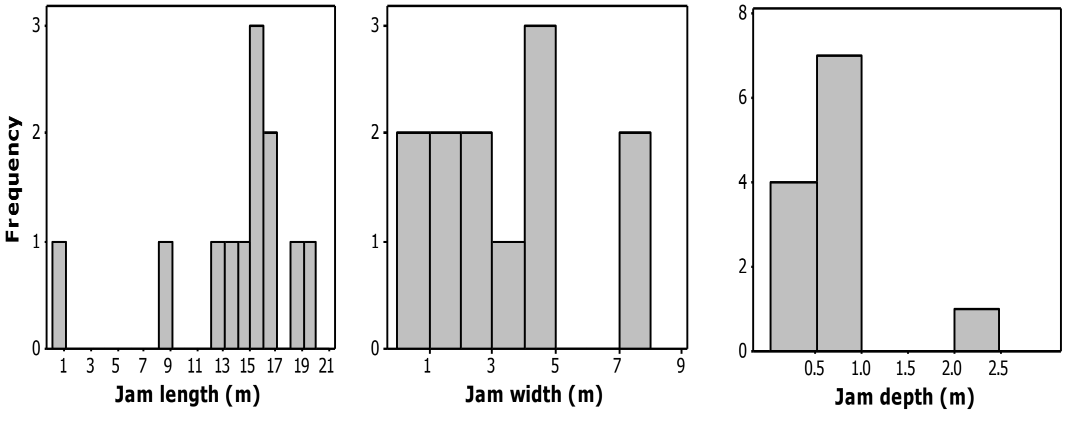

Figure 7.4. Frequency distributions of wood jam dimensions (length (m), width (m) and, depth (m) for the 12 jams) within the study reach.

Figure 7.5 shows frequency distributions for the dimensions (length and diameter) of individual wood pieces within jams along the study reach. The 12 jams contained an average of six large wood pieces (median 5). Some large wood pieces were inaccessible, but it was possible to obtain accurate dimensions for 38 out of the 74 wood pieces that were counted. The median wood piece length and diameter of these 38 pieces were 9.91 m and 0.22 m (Figure 7.5, Table 7.3), respectively, but wood piece sizes were highly variable with volumes ranging from 0.007 m^3 to 8.26 m^3 (median 0.32 m^3) (Table 7.3).

Table 7.3. Summary statistics for jams (n = 12) and wood pieces (n = 74, for the number of wood pieces in jam; n = 38, for the dimensions of the wood pieces).

Variables	**Dimensions**	**Mean**	**Median**	**Q1**	**Q3**
Jams	Length (m)	13.95	15.34	12.95	16.67
	Width (m)	3.39	2.87	1.50	4.78
	Depth (m)	0.72	0.62	0.48	0.79
	Area (m^2)	29.32	24.97	15.51	35.48
	Volume (m^3)	4.57	3.48	1.44	6.90
Wood pieces	Number of wood pieces in jam*	6.17	5.00	3.25	7.50
	Length (m)	8.78	9.91	4.15	11.50
	Diameter (m)	0.26	0.22	0.16	0.31
	Volume (m^3)	0.67	0.32	0.15	0.53

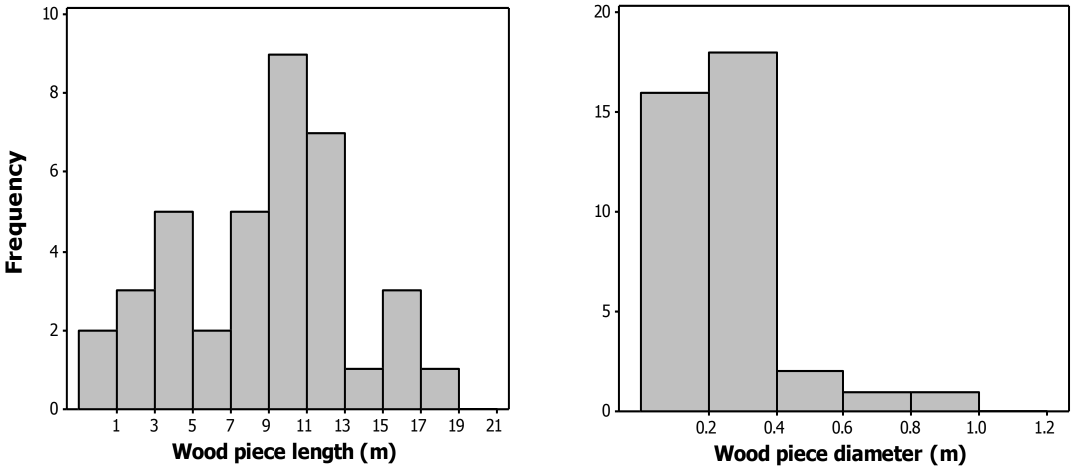

Figure 7.5. Frequency distributions of the length (m) and diameter (m) of wood pieces (n = 38) within the 12 jams along the study reach.

7.4.2 Relationship between Jams, Mesohabitats, and In-Channel Sampling Sites (BGB, JM, JB, BK)

Figure 7.6 presents a geomorphological sketch map of the entire study reach. Several substrate types and mesohabitats (geomorphic features) were found within the reach, particularly in the vicinity of the 12 wood jams. The most frequently occurring geomorphic features were pools and bars which were usually located in close proximity, while three substrate types were identified: gravel, sand and fine sediment (silt and clay). There was an increase in channel depth in areas of the river bed where jams concentrate flow. Finer sediment and sand (which is the dominant substrate type) were mainly observed within jams (JM) and in areas of uniform flow, respectively, and so most BGB samples were sand, whereas most JM and JB samples were finer sediment. Marginal plant species such as *Sparganium erectum, Epilobium hirstutum* and *Phalaris arundinacea* were also observed colonising and trapping fine sediment along the channel margins in proximity to jams, and so in proximity to most JM and some JB samples. Eroding banks, remote from the wood jams and the fine sediment they retained, provided all of the BK samples. The central part of the reach, which had not been subject to wood reintroduction and where there were no wood jams, showed few geomorphic features (a few small pools and bars) and negligible variation in substrate type (a near uniform sand bed, which contributed to some BGB samples). This central part of the reach had much lower morphological and sedimentary complexity than the two restored sub-reaches, which contained all 12 wood jams.

7.4.3 Sediment Characteristics of the Five Sampled Mesohabitats

The sediment characteristics of five recurring mesohabitats (bare river bed (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP)) sampled during two periods (spring 2012 (PB1) and mid-summer 2012 (PB2)) along the River Bure are presented in Table 7.4. Figure 7.7 presents Box and Whisker plots of the sediment characteristics observed in different mesohabitats at the two sampling times. The characteristics of sediments sampled within the mesohabitats (n = 12 sediment samples for each mesohabitat) and during the two sampling periods (n = 60 sediment samples for each sampling period) were compared using KW and MW tests to assess whether they were statistically-significantly different from one another (Table 7.5).

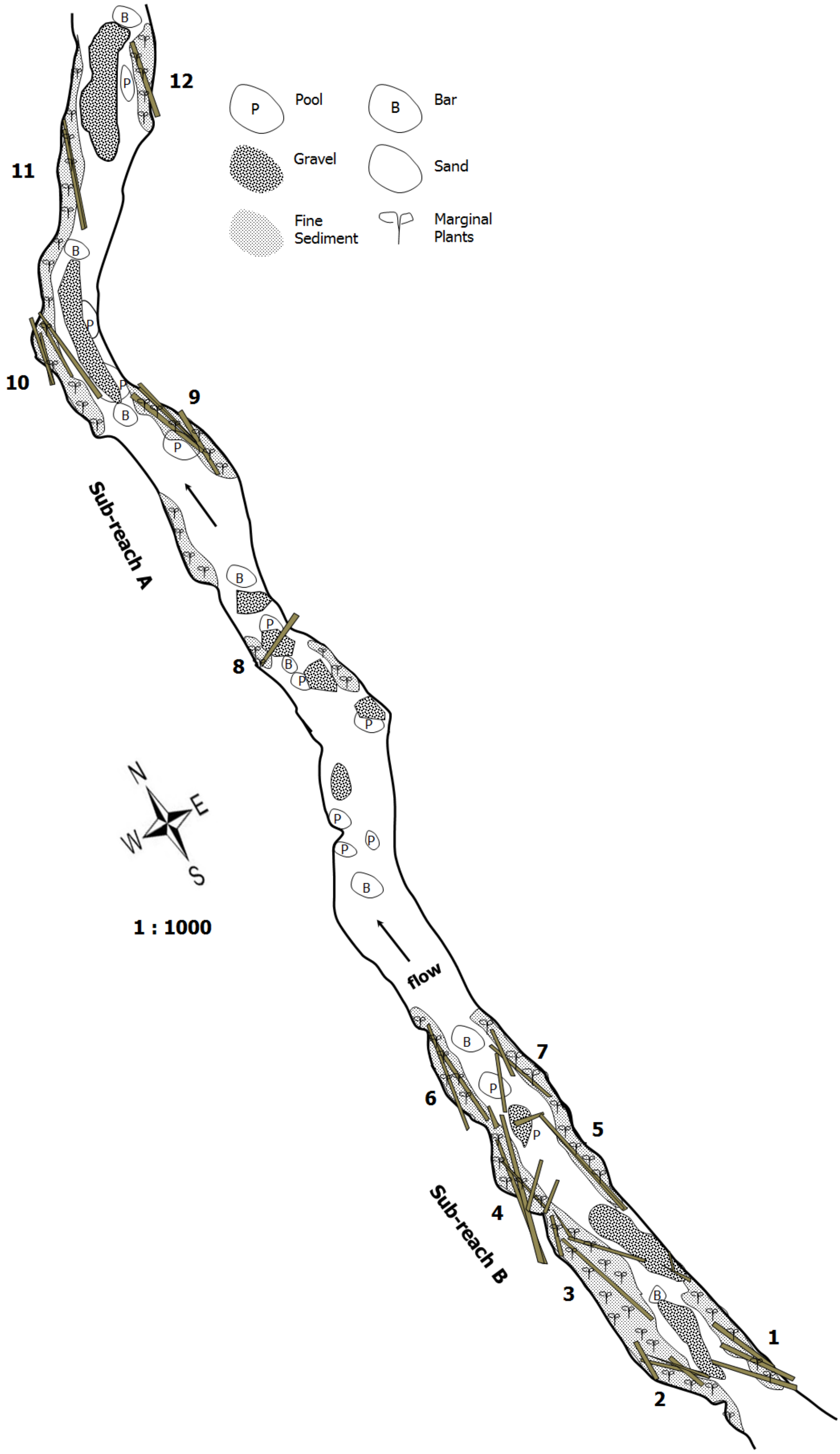

Figure 7.6. Geomorphological sketch map of the study reach, indicating substrate types, geomorphic features, jams and areas colonised by marginal plants.

There was considerable variability in particular sediment properties within sampled mesohabitats in both sampling periods (Figure 7.7). Nevertheless, there were significant differences in the sediment properties of the mesohabitat samples within each sampling period. For PB1 samples, Kruskal-Wallis tests revealed that jam (JM), jam bank (JB), floodplain (FP) and bank (BK) samples were significantly finer (median sediment particle size) than bare river bed (BGB) samples, particularly jam (JM) samples which contained a significantly higher proportion of finer sediments (% silt and clay) and the lowest proportion of % gravel and % sand. Bare river bed (BGB) samples typically contained significantly higher % gravel than jam (JM) samples, while floodplain (FP) samples contained significantly more organic matter than bare river bed (BGB) samples. For PB2 samples, Kruskal-Wallis tests revealed that floodplain (FP), jam bank (JB), bank (BK) and jam (JM) samples again contained significantly more organic matter than bare river bed (BGB) samples. Sediment particle size increased from jam bank (JB) to bank (BK) to jam (JM) to floodplain (FP) through to bare river bed (BGB) mesohabitats. Bare river bed (BGB) samples were significantly coarser than jam bank (JB), bank (BK), jam (JM) and floodplain (FP) samples, particularly jam bank (JB) samples which contained a significantly higher proportion of finer sediments (% silt and clay). Bare river bed (BGB) samples typically contained significantly higher % sand than jam (JM), floodplain (FP), jam bank (JB) and bank (BK) samples. Gravel fractions were highest in the sediment samples from bare river bed (BGB), lowest in the sediment samples from banks (BK), and intermediate in the sediment samples from jam banks (JB). Despite subtle contrasts in these significant differences in the two sampling periods, each period shows a very similar overall pattern, with the BGB samples consistently showing coarser sediment and lower organic matter content, whilst only subtle differences were apparent between the other mesohabitats. Furthermore, when the sediment characteristics of the mesohabitats are compared between the two sampling periods, most differences are not statistically significant. Exceptions are the organic matter content (% OM) in JM and FP samples, which are higher in PB1 than in PB2, and the gravel content (% G) of JM samples, which is higher in PB2 than PB1.

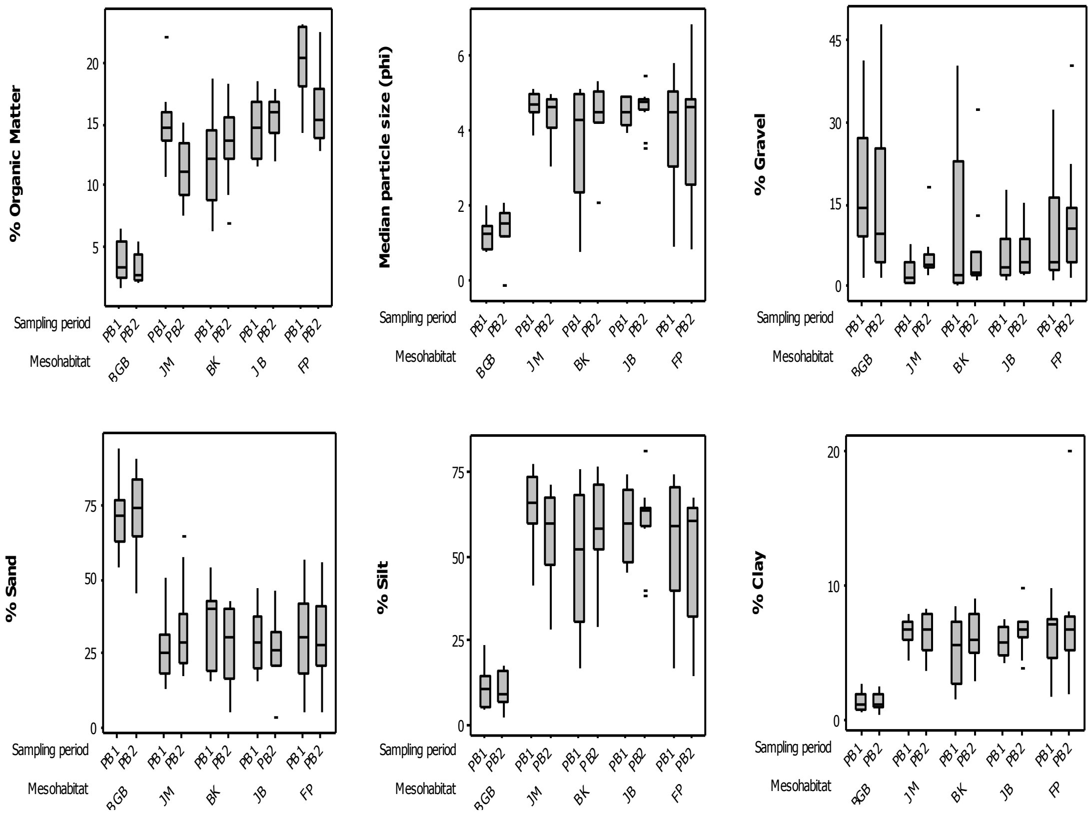

Figure 7.7. Box-whisker plots illustrating contrasts in the sediment properties of samples from bare river bed (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) mesohabitats during two different sampling periods (PB1 and PB2). The mesohabitats are ordered along the x-axis from channel bed to floodplain, and thus show a continuum of decreasing hydrological connectivity.

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Table 7.4. Summary of the characteristics of bare river bed (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP) sediments sampled within the study reach of the River Bure. Twelve bulk samples were analysed for each mesohabitat (each bulk sample was comprised of 3 replicate samples for JM, BK, JB, FP and 4 replicates for BGB).

Variables	Mesohabitats	Mean	Median	Q1	Q3
Spring samples (PB1)					
% OM	BGB	3.78	3.21	2.52	5.16
	JM	14.92	14.76	13.78	15.32
	BK	12.07	12.23	8.82	14.03
	JB	14.67	14.72	12.47	16.23
	FP	20.27	20.49	18.73	22.86
D_{50}	BGB	1.22	1.25	0.87	1.41
	JM	4.69	4.72	4.52	4.97
	BK	3.75	4.31	2.72	4.93
	JB	4.50	4.52	4.20	4.86
	FP	4.06	4.49	3.56	4.96
% G	BGB	17.51	14.18	9.66	26.04
	JM	2.51	1.34	0.58	4.05
	BK	10.44	1.98	0.63	20.60
	JB	5.86	3.42	2.28	7.03
	FP	9.68	4.10	3.39	14.46
% S	BGB	70.83	71.26	63.16	75.40
	JM	25.76	25.24	18.59	29.90
	BK	33.91	39.77	22.17	42.37
	JB	28.78	28.51	20.16	34.52
	FP	30.45	30.56	20.62	36.46
% ST	BGB	10.37	9.98	5.67	12.82
	JM	65.21	65.81	60.02	73.47
	BK	50.50	52.39	32.94	68.01
	JB	59.60	59.54	50.11	67.65
	FP	53.57	59.10	41.59	68.19
% C	BGB	1.29	1.16	0.70	1.75
	JM	6.52	6.61	5.98	7.26
	BK	5.15	5.54	2.89	7.26
	JB	5.75	5.68	4.90	6.77
	FP	6.30	7.11	5.39	7.44

Table 7.4. (Continued)

Variables	**Mesohabitats**	**Mean**	**Median**	**Q1**	**Q3**
Mid-summer samples (PB2)					
% OM	BGB	3.13	2.60	2.26	4.23
	JM	11.20	11.07	9.88	12.90
	BK	13.31	13.51	12.35	14.38
	JB	15.34	15.86	14.25	16.57
	FP	16.17	15.30	14.14	17.31
D_{50}	BGB	1.32	1.51	1.22	1.76
	JM	4.38	4.61	4.22	4.86
	BK	4.46	4.51	4.24	4.99
	JB	4.60	4.74	4.62	4.78
	FP	4.06	4.60	3.56	4.83
% G	BGB	16.59	9.71	5.22	20.72
	JM	5.28	3.92	3.56	5.56
	BK	6.36	2.65	1.96	5.96
	JB	5.61	4.26	2.68	7.25
	FP	12.29	10.77	4.55	13.85
% S	BGB	71.93	74.22	64.23	80.66
	JM	32.65	28.75	21.59	37.65
	BK	27.84	30.08	17.64	39.62
	JB	26.97	26.00	21.52	29.55
	FP	29.54	27.63	21.26	36.57
% ST	BGB	10.12	8.44	6.86	14.88
	JM	55.71	59.91	49.99	67.12
	BK	59.51	58.54	52.19	70.43
	JB	60.90	63.85	60.33	64.72
	FP	50.99	60.50	40.66	63.62
% C	BGB	1.35	1.10	0.98	1.67
	JM	6.36	6.65	5.47	7.51
	BK	6.29	5.99	5.27	7.87
	JB	6.52	6.75	6.19	7.06
	FP	7.18	6.77	5.73	7.23

Table 7.5. Statistically significant differences in sediment characteristics between samples obtained from five mesohabitats along the study reach of the River Bure during two sampling periods (PB1 and PB2), identified using Kruskal-Wallis (KW) and Mann Whitney (MW) tests with multiple pairwise comparisons performed using Dunn's procedure with Bonferroni correction.

Variables	**KW** ***p* value**	**Degrees of freedom**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Spring (PB1) samples			
% OM	< 0.0001	4	FP > BGB
D_{50}	< 0.0001	4	JM, JB, FP, BK > BGB
% G	0.002	4	BGB > JM
% S	< 0.0001	4	BGB > BK, FP, JB, JM
% ST	< 0.0001	4	JM, JB, FP, BK > BGB
% C	< 0.0001	4	JM, FP, JB, BK > BGB
Mid-summer (PB2) samples			
% OM	< 0.0001	4	FP, JB, BK, JM > BGB
D_{50}	< 0.0001	4	JB, BK, JM, FP > BGB
% G	0.026	4	BGB = FP = JB = JM = BK
% S	< 0.0001	4	BGB > JM, FP, JB, BK
% ST	< 0.0001	4	JB, BK, JM, FP > BGB
% C	< 0.0001	4	JM, JB, FP, BK > BGB

Variables	**MW** ***p* value**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
Spring (PB1) and *Mid-summer (PB2) samples*		
% OM	0.174	n.s.
BGB	0.266	n.s.
JM	0.004	PB1 > PB2
BK	0.347	n.s.
JB	0.478	n.s.
FP	0.005	PB1 > PB2
D_{50}	0.701	n.s.
BGB	0.198	n.s.
JM	0.160	n.s.
BK	0.347	n.s.
JB	0.514	n.s.
FP	0.977	n.s.
% G	0.268	n.s.
BGB	0.514	n.s.
JM	0.033	PB2 > PB1
BK	0.630	n.s.
JB	0.478	n.s.
FP	0.378	n.s.

Table 7.5. (Continued)

Variables	**MW** ***p* value**	**Significantly different subgroups (p < 0.05, n.s. if no significant differences)**
% S	0.981	n.s.
BGB	0.590	n.s.
JM	0.198	n.s.
BK	0.198	n.s.
JB	0.977	n.s.
FP	0.799	n.s.
% ST	0.792	n.s.
BGB	0.755	n.s.
JM	0.078	n.s.
BK	0.266	n.s.
JB	0.887	n.s.
FP	0.887	n.s.
% C	0.401	n.s.
BGB	0.630	n.s.
JM	0.932	n.s.
BK	0.319	n.s.
JB	0.160	n.s.
FP	0.843	n.s.

KW tests were separately performed on the values of each of the variables associated with the mesohabitats within the river corridor to assess the degree to which the sampling period and / or mesohabitats represented statistically significantly different (p < 0.05) values of the variables. Multiple pairwise comparisons were then performed using Dunn’s procedure (Bonferroni corrected) to identify those sampling periods or mesohabitats that were significantly different from one another (p < 0.05). Twelve samples were used in the analyses for each mesohabitat within the study reach; sixty samples were used in the analyses for each sampling period within the study reach.

7.4.4 Propagule Bank Characteristics of the Five Sampled Mesohabitats

The propagule bank characteristics (species richness, propagules per litre and propagule per square metre) of the five mesohabitats (bare river bed (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP)) sampled during two periods (spring 2012 and mid-summer 2012) are presented in Table 7.6 (a) and (b). The statistical significance of differences in the propagule bank characteristics among the five mesohabitats within and between sampling periods was tested using KW and MW tests (Table 7.7).

In total 24,484 viable propagules of eight species (1 woody species, 6 herb species and 1 grass species) were identified in the sampled sediments from the five mesohabitats. Figure 7.8 illustrates the highly variable properties of the propagule banks among the five mesohabitats and between the two sampling periods. Mann Whitney tests compared the species richness and abundance of propagule bank samples in the two sampling periods, and found significant differences ($p < 0.05$), with both the species richness and abundance being higher in the spring (PB1) than the mid-summer (PB2) samples (Table 7.7). PB1 and PB2 samples contained a total of 8 and 7 species, respectively, with floodplain (FP) and jam bank (JB) mesohabitats retaining the most species, followed by jam (JM) samples. Propagule abundance (propagules per litre and propagule per square metre) were higher but also more variable in PB1 compared to PB2 samples, especially for jam (JM) and jam bank (JB) mesohabitats (Figure 7.8). In general, propagule abundance (propagules per litre and propagule per square metre) appear to increase from bare river bed (BGB) and bank (BK) to jam (JM) to jam bank (JB) to floodplain (FP) mesohabitats (Figure 7.8). There were also distinct differences in propagule characteristics of the sediment sampled from particular mesohabitats across the two sampling periods (Table 7.7). Propagule species richness was significantly higher in PB1 jam bank (JB) samples, while propagule abundance was significantly higher in PB1 jam bank (JB) and jam (JM) samples, whereas in PB2 only floodplain (FP) samples showed higher propagule species richness and abundance than the other mesohabitat types (Figure 7.8, Table 7.7).

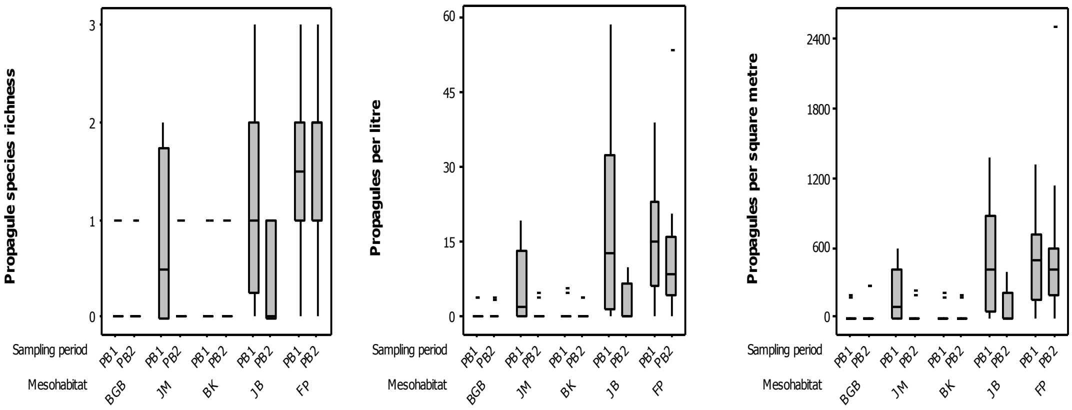

Figure 7.8. Box-whisker plots illustrating propagule species richness, viable propagules per square metre and viable propagules per litre in bare river bed (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) mesohabitats associated with two different sampling periods (PB1 and PB2). The mesohabitats are ordered along the x-axis from channel bed to floodplain, and thus show a continuum of decreasing hydrological connectivity.

In relation to the propagule types found in PB1 samples, the number and abundance of herb and grass propagules in sediment sampled from the floodplain (FP) was significantly higher compared to banks (BK) and bare river bed (BGB) samples. For PB2 samples, propagule abundance and species richness was found to be significantly higher in the sediment samples from floodplain (FP) compared to jam bank (JB), jam (JM), banks (BK) and bare river bed (BGB) samples (Table 7.6 (b) and 7.7). The number and abundance of herb and grass propagules in sediment sampled from the floodplain (FP) was significantly higher compared to jam bank (JB), jam (JM), banks (BK) and bare river bed (BGB) samples (Table 7.7). The most frequently found species was *Urtica dioica* (particularly present on the floodplain). Some species appear constrained to particular mesohabitats: *Alnus glutinosa* was found only within jam (JM) samples in spring (PB1) and within jam bank (JB) samples in mid-summer (PB2); *Plantago major* was found only within jam bank (JB) samples in spring (PB1) and within the floodplain (FP) samples in mid-summer (PB2) (Table 7.6 (a)).

Table 7.6 (a). Propagule species list (and abbreviations (abbr.)) and mean number of propagules per litre and square metre found within the sediment samples from bare river bed (BGB), jam (JM), jam bank (JB), bank (BK) and floodplain (FP) mesohabitats during the spring (PB1) and mid-summer (PB2) sampling periods.

		Spring (PB1) samples										**Mid-summer (PB2) samples**									
		Propagules per litre					**Propagules per square metre**					**Propagules per litre**					**Propagules per square metre**				
Species / Mesohabitats	**Abbr.**	**BGB**	**BK**	**JM**	**JB**	**FP**	**BGB**	**BK**	**JM**	**JB**	**FP**	**BGB**	**BK**	**JM**	**JB**	**FP**	**BGB**	**BK**	**JM**	**JB**	**FP**
Agrostis spp.	Agr sp	0.0	0.0	0.3	5.3	2.7	0.0	0.0	15.2	145.7	104.8	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	62.1
Alnus glutinosa	Aln glu	0.0	0.0	1.2	0.0	0.0	0.0	0.0	36.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	18.1	0.0
Callitriche hamulata	Cal ham	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	17.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Callitriche stagnalis	Cal sta	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	16.8	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	16.9
Conyza sp.	Cony sp	0.0	0.5	1.2	2.0	4.5	0.0	17.0	36.0	69.4	141.5	0.0	0.0	0.0	0.8	0.9	0.0	0.0	0.0	31.9	44.4
Epilobium hirsutum	Epi his	0.0	0.0	0.5	0.0	0.0	0.0	0.0	16.4	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	46.3
Plantago major	Plan ma	0.0	0.0	0.0	3.8	0.0	0.0	0.0	0.0	94.2	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	29.9
Urtica dioica	Urt dio	0.6	0.4	2.9	6.8	7.8	30.7	14.7	82.9	192.6	250.6	0.6	0.6	0.7	1.0	7.6	46.0	31.0	33.9	43.2	354.9
Total number of propagules		0.6	0.9	6.3	18.2	15.5	30.7	31.8	186.5	518.7	514.0	0.6	0.6	0.7	2.4	11.7	46.0	31.0	33.9	93.3	554.5
Number of herb propagules		0.6	0.9	4.7	13.0	12.8	30.7	31.8	135.3	373.0	409.1	0.6	0.6	0.7	1.8	10.5	46.0	31.0	33.9	75.2	492.4
Number of grass propagules		0.0	0.0	0.3	5.3	2.7	0.0	0.0	15.2	145.7	104.8	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	62.1
Number of rush propagules		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Number of woody propagules		0.0	0.0	1.2	0.0	0.0	0.0	0.0	36.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	18.1	0.0

Table 7.6 (b). Summary of the propagule bank characteristics of bare river bed (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) sediments within the river corridor of the study reach along the River Bure. Twelve bulk samples were analysed for each mesohabitat (each bulk sample was comprised of 3 replicate samples for JM, BK, JB, FP and 4 replicates for BGB).

Variables	**Mesohabitats**	**Mean**	**Median**	**Q1**	**Q3**
Spring samples (PB1)					
T PropSR	BGB	0.17	0.00	0.00	0.00
	JM	0.75	0.50	0.00	1.25
	BK	0.17	0.00	0.00	0.00
	JB	0.17	1.00	0.75	2.00
	FP	1.42	1.50	1.00	2.00
T Prop/l	BGB	0.63	0.00	0.00	0.00
	JM	6.25	2.09	0.00	12.89
	BK	0.89	0.00	0.00	0.00
	JB	18.24	12.56	4.96	23.76
	FP	15.01	14.95	6.38	22.23
T Prop/m^2	BGB	30.65	0.00	0.00	0.00
	JM	186.49	91.10	0.00	396.92
	BK	31.79	0.00	0.00	0.00
	JB	518.69	414.15	157.90	828.22
	FP	496.97	493.02	172.92	692.64
Mid-summer samples (PB2)					
T PropSR	BGB	0.17	0.00	0.00	0.00
	JM	0.75	0.00	0.00	0.00
	BK	0.17	0.00	0.00	0.00
	JB	0.33	0.00	0.00	1.00
	FP	1.58	2.00	1.00	2.00
T Prop/l	BGB	0.61	0.00	0.00	0.00
	JM	0.73	0.00	0.00	0.00
	BK	0.64	0.00	0.00	0.00
	JB	2.44	0.00	0.00	4.83
	FP	12.20	8.37	4.86	13.10
T Prop/m^2	BGB	45.98	0.00	0.00	0.00
	JM	33.94	0.00	0.00	0.00
	BK	31.05	0.00	0.00	0.00
	JB	93.30	0.00	0.00	178.21
	FP	571.46	418.14	197.85	556.47

Table 7.7. Statistically significant differences in propagule bank variables between samples obtained from five mesohabitats along the study reach of the River Bure during two periods (PB1 and PB2), identified using Kruskal-Wallis (KW) and Mann Whitney (MW) tests with multiple pairwise comparisons performed using Dunn's procedure with Bonferroni correction.

Variables*	**KW *p* value**	**Degrees of freedom**	**Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)**
Spring (PB1) samples			
T PropSR	0.0003	4	FP, JB > BK, BGB
Number of herbs	0.002	4	FP > BK, BGB
Number of grass	0.120	4	n.s.
Number of woody species	0.087	4	n.s.
T Prop/l	< 0.0001	4	FP, JB > BK, BGB
Number of herbs	0.001	4	FP > BK, BGB
Number of grass	0.107	4	n.s.
Number of woody species	0.087	4	n.s.
T Prop/m^2	< 0.0001	4	FP, JB > BK, BGB
Number of herbs	0.001	4	FP > BK, BGB
Number of grass	0.107	4	n.s.
Number of woody species	0.087	4	n.s.
Mid-summer (PB2) samples			
T PropSR	< 0.0001	4	FP > JB, JM, BK, BGB
Number of herbs	0.0001	4	FP > JB, JM, BK, BGB
Number of grass	0.087	4	n.s.
Number of woody species	0.406	4	n.s.
T Prop/l	< 0.0001	4	FP > JB, JM, BK, BGB
Number of herbs	< 0.0001	4	FP > JB, JM, BK, BGB
Number of grass	0.087	4	n.s.
Number of woody species	0.406	4	n.s.
T Prop/m^2	0.0001	4	FP > JB, JM, BK, BGB
Number of herbs	< 0.0001	4	FP > JB, JM, BK, BGB
Number of grass	0.087	4	n.s.
Number of woody species	0.406	4	n.s.

Table 7.7. (Continued)

Variables^	**MW** ***p* value**	**Significantly different subgroups ($p < 0.05$, n.s. if no significant differences)**
Spring (PB1) and *Mid-summer (PB2) samples*		
T PropSR	0.082	n.s.
BGB	0.727	n.s.
JM	0.086	n.s.
BK	0.863	n.s.
JB	0.025	PB1 > PB2
FP	0.700	n.s.
T Prop/l	0.019	PB1 > PB2
BGB	0.863	n.s.
JM	0.039	PB1 > PB2
BK	0.727	n.s.
JB	0.010	PB1 > PB2
FP	0.310	n.s.
T Prop/m^2	0.052	n.s.
BGB	0.727	n.s.
JM	0.063	n.s.
BK	0.863	n.s.
JB	0.007	PB1 > PB2
FP	0.832	n.s.

Mann Whitney and Kruskal-Wallis tests were separately performed on the values of each of the variables associated with the two sampling periods and five mesohabitats to assess the degree to which the sampling period and / or mesohabitats represented statistically significantly different ($p < 0.05$) values of the variables. Following the Kruskal-Wallis tests, multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those mesohabitats that were significantly different from one another ($p < 0.05$). Twelve samples* were used in the analyses for each mesohabitat; sixty samples^ were used in the analyses for each sampling period within the study reach

7.4.5 Relationship between Physical and Biotic Characteristics of Mesohabitats along the Study Reach

(i) Spearman's rank correlation analyses

Correlations between sediment and propagule bank variables were explored across all five mesohabitats for each sampling period separately (60 samples for each sampling period) (Table 7.8).

Table 7.8 presents Spearman rank correlations among sediment and propagule bank variables of mesohabitats for the spring (PB1) sampling period. Generally, total propagule abundance (per litre) shows a significant positive correlation with % silt, while the number and abundance (per litre and per square metre) of herb species display a significant negative correlation with % gravel, and a positive correlation with % silt. These correlations although weak indicate a general increase in propagule abundance (per litre and per square metre) and species richness with increasing sediment fining, which is particularly marked for herb species. Total propagule abundance (per litre and per square metre), total species richness, and the number and abundance of herb species also display a significant weak positive correlation with sediment organic matter content.

Table 7.8 also presents Spearman rank correlations between sediment and propagule bank variables of mesohabitats for the mid-summer (PB2) sampling period. The table shows that total propagule abundance (per litre and per square metre), total species richness, and the number and abundance of herb species reveal a significant weak positive correlation with sediment organic matter content, similar to the observation for the spring (PB1) samples.

Table 7.8. Spearman rank correlations among sediment and propagule bank variables of mesohabitats (n = 60, for each sampling period) within the active corridor of the River Bure for the spring (PB1) and mid-summer (PB2) sampling periods (emboldened correlations are statistically significant, $p < 0.05$).

		Spring (PB1)						Mid-summer (PB2)					
Variables	Abbr.	% OM	D_{50}	% G	% S	% ST	% C	% OM	D_{50}	% G	% S	% ST	% C
Propagules species richness	T PropSR	**0.39**	0.20	-0.20	-0.16	0.23	0.19	**0.33**	0.10	0.14	-0.12	0.10	0.16
	HB sp	**0.38**	0.20	**-0.26**	-0.13	0.22	0.18	**0.28**	0.09	0.16	-0.12	0.10	0.15
	GS sp	0.19	0.00	0.13	-0.07	0.03	0.07	0.19	-0.03	0.19	0.00	-0.08	0.06
	WS sp	0.03	0.15	-0.08	-0.15	0.16	0.11	0.18	0.08	-0.12	-0.03	0.06	0.06
Propagules per litre	T Prop/l	**0.46**	0.25	-0.20	-0.23	**0.28**	0.24	**0.37**	0.12	0.13	-0.15	0.12	0.17
	HB prop/l	**0.44**	**0.26**	**-0.27**	-0.21	**0.28**	0.25	**0.32**	0.10	0.16	-0.14	0.11	0.16
	GS prop/l	0.19	0.00	0.12	-0.08	0.04	0.07	0.19	-0.03	0.19	0.00	-0.08	0.06
	WS prop/l	0.03	0.15	-0.08	-0.15	0.16	0.11	0.18	0.08	-0.12	-0.03	0.06	0.06
Propagules per metre	T Prop/m^2	**0.43**	0.22	-0.18	-0.19	0.25	0.21	**0.32**	0.08	0.15	-0.11	0.09	0.14
	HB prop/m^2	**0.42**	0.23	**-0.27**	-0.18	0.25	0.23	**0.28**	0.07	0.18	-0.11	0.08	0.14
	GM prop/m^2	0.19	0.00	0.13	-0.08	0.03	0.06	0.19	-0.03	0.19	0.00	-0.08	0.06
	WS prop/m^2	0.03	0.15	-0.08	-0.15	0.16	0.11	0.18	0.08	-0.12	-0.03	0.06	0.06

Abbr., abbreviations of variables; % OM, organic matter; D_{50}, median sediment particle size (phi); % G, % gravel; % S, % sand; % ST, % silt; % C, % clay; T PropSR, propagule species richness; HB sp, the number of herb species; GM sp, the number of grass species; WS sp, the number of woody species; T Prop/l, propagules per litre; HB prop/l, herb propagules per litre; GM prop/l, grass propagules per litre; WS prop/l, woody propagules per litre; T Prop/m^2, propagules per metre square; HB Prop/m^2, herb propagules per metre square; GM Prop/m^2, grass propagules per metre square; WS Prop/m^2, woody propagules per metre square

To assess the variability and the degree of dependency of jam-related mesohabitats characteristics on jam and wood piece features during different sampling periods along the River Bure, correlations between wood, sediment and propagule bank variables were explored for jam-related mesohabitats (jam and jam bank) for each sampling period separately (24 samples for each sampling period) (Table 7.9).

Table 7.9 presents Spearman rank correlations among wood, sediment and propagule bank variables associated to the jam-related mesohabitats for the spring (PB1) and mid-summer (PB2) sampling periods. Considering correlations between wood variables and PB1 sediment and propagule variables, indicators of jam size such as jam area and volume show a significant positive correlation with % gravel and the number and abundance (per litre and per square metre) of woody species, and a significant negative correlation with % silt and % clay, while jam width displays a significant negative correlation with total propagule abundance (per litre and per square metre). These results suggest that during spring (PB1), there is a general increase in gravel proportions and the number and abundance of woody species with increasing jam size, although total propagule abundance (per litre and per square metre) decreases with increasing jam width. Wood piece length shows a significant positive correlation with total propagule abundance (per litre and per square metre) and the number and abundance (per litre and per square metre) of herb species, while wood piece diameter shows a significant positive correlation with median sediment particle size, % silt and % clay, and a significant negative correlation with % sand. This suggests that during spring (PB1), there is a general increase in fine sediment (% silt and % clay) retention and propagule abundance (per litre and per square metre), mainly herb species, in jams containing larger wood pieces.

Considering correlations between wood variables and PB2 sediment and propagule variables (Table 7.9), jam area displays a significant positive correlation with % gravel and % sand, and a significant negative correlation with indicators of sediment fining such as median sediment particle size (phi), % silt and % clay, while jam depth and wood piece diameter shows a significant negative correlation with % sand and % gravel, respectively. These results suggest that during mid-summer (PB2), there is a general decrease in fine sediment retention with increasing jam size, while the proportion of coarse sediment increases with decreasing jam depth and wood pieces size within jams. However, the table also shows that there are no significant associations between other wood, sediment and propagule bank variables in PB2 samples indicating that most wood characteristics are not associated with sediment and propagule bank characteristics during this mid-summer sampling.

Table 7.9. Spearman rank correlations among wood variables and sediment and propagule bank characteristics related to the jam associated mesohabitats (jam and jam bank) (n = 24 samples for each sampling period) within the active corridor of the River Bure for the spring (PB1) and mid-summer (PB2) sampling periods (emboldened correlations are statistically significant, $p < 0.05$).

		Spring (PB1)								Mid-summer (PB2)							
Variables	Abbr.	FWPJ	JL	JW	JD	JA	JV	WPL	WPD	FWPJ	JL	JW	JD	JA	JV	WPL	WPD
Sediment	% OM	-0.25	0.23	0.03	-0.02	-0.08	0.15	0.21	0.28	-0.05	0.04	-0.21	-0.04	-0.20	-0.17	0.01	0.08
	D$_{50}$	-0.28	-0.07	-0.14	0.00	-0.38	-0.09	0.16	**0.53**	-0.09	-0.02	-0.29	0.39	**-0.48**	-0.17	0.21	0.33
	% G	0.07	0.01	0.31	-0.29	**0.54**	0.31	**-0.43**	-0.23	0.07	0.07	0.36	-0.07	**0.48**	0.08	-0.20	**-0.55**
	% S	0.29	0.02	0.10	0.02	0.32	0.06	-0.10	**-0.52**	0.16	-0.02	0.28	**-0.46**	**0.42**	0.16	-0.27	-0.21
	% ST	-0.26	-0.03	-0.19	0.06	**-0.42**	-0.11	0.21	**0.51**	-0.09	0.04	-0.30	0.38	**-0.49**	-0.16	0.29	0.31
	% C	-0.22	-0.07	-0.14	0.00	**-0.45**	-0.16	0.22	**0.49**	-0.19	0.09	-0.26	0.32	**-0.54**	-0.20	0.38	0.33
Propagule species richness	T sp	-0.19	0.35	-0.38	0.12	0.04	0.14	**0.51**	0.06	0.28	0.03	-0.14	0.15	-0.20	-0.08	0.20	-0.03
	HB sp	-0.05	0.25	-0.34	0.12	-0.19	-0.05	**0.64**	0.00	0.19	0.10	-0.10	0.33	-0.10	0.07	0.37	-0.10
	GS sp	-0.16	0.19	-0.10	0.02	0.26	0.16	-0.16	0.03	-	-	-	-	-	-	-	-
	WS sp	-0.13	0.09	-0.09	0.04	0.31	**0.44**	-0.07	0.24	0.21	-0.15	-0.09	-0.33	-0.21	-0.33	-0.33	0.15
Propagules per litre	T prop/l	-0.16	0.34	**-0.45**	0.15	-0.01	0.15	**0.49**	0.15	0.33	-0.02	-0.15	0.13	-0.22	-0.11	0.14	-0.01
	HB prop/l	-0.01	0.29	-0.34	0.21	-0.25	-0.07	**0.67**	0.01	0.23	0.07	-0.12	0.31	-0.12	0.06	0.34	-0.09
	GS prop/l	-0.19	0.19	-0.13	0.01	0.26	0.17	-0.18	0.06	-	-	-	-	-	-	-	-
	WS prop/l	-0.12	0.09	-0.08	0.06	0.30	**0.44**	-0.05	0.24	0.21	-0.15	-0.09	-0.33	-0.21	-0.33	-0.33	0.15
Propagules per metre square	T prop/m^2	-0.22	0.35	**-0.43**	0.16	0.02	0.15	**0.49**	0.10	0.33	-0.01	-0.17	0.14	-0.23	-0.12	0.18	-0.02
	HB prop/m^2	-0.05	0.32	-0.30	0.21	-0.19	-0.03	**0.65**	-0.02	0.24	0.07	-0.13	0.30	-0.14	0.03	0.35	-0.09
	GS prop/m^2	-0.19	0.19	-0.13	0.01	0.26	0.17	-0.18	0.06	-	-	-	-	-	-	-	-
	WS prop/m^2	-0.12	0.09	-0.08	0.06	0.30	**0.44**	-0.05	0.24	0.21	-0.15	-0.09	-0.33	-0.21	-0.33	-0.33	0.15

Abbr., abbreviations of variables; % OM, organic matter; D$_{50}$, median sediment particle size (phi); % G, % gravel; % S, % sand; % ST, % silt; % C, % clay; FWPJ, frequency of wood pieces in jam; JL, jam length; JW, jam width; JD, jam depth; JA, jam area; JV, jam volume; WPL, wood piece length; WPD, wood piece diameter; T PropSR, Propagule species richness; HB sp, the number of herb species; GM sp, the number of grass species; WS sp, the number of woody species; T Prop/l, Propagules per litre; HB prop/l, herb propagules per litre; GM prop/l, grass propagules per litre; WS prop/l, woody propagules per litre; T Prop/m^2, Propagules per metre square; HB Prop/m^2, herb propagules per metre square; GM Prop/m^2, grass propagules per metre square; WS Prop/m^2, woody propagules per metre square

(ii) Multivariate analysis and classification of mesohabitat characteristics

Mesohabitat physical (sediment) characteristics were further explored using Principal Components Analysis (PCA). This was followed by an analysis of the species composition of the sampled propagule banks using Detrended Correspondence Analysis (DCA) and an analysis of the associations between the composition of the propagule bank and the physical (sediment) characteristics of sampled mesohabitats using direct gradient analysis (DGA).

Principal components analysis (PCA) was used to identify gradients in the sediment variables of sampled mesohabitats (120 samples, 60 for each sampling period and 12 for each mesohabitat) along the study reach and to explore how these are related to period of sampling and mesohabitat type. Because the variables were not normally distributed, PCA was performed on a rank correlation matrix. A reduced set of sediment variables (D_{50}, % OM, % G, % ST + % C) was used to minimise the number of variables included in the analysis, to avoid including sets of variables that summed to 100 %, and also to avoid duplication (e.g. % ST and % C were both highly correlated and so a combined fine sediment variable (% ST + % C) was used).

Table 7.10 lists the sediment variables that were analysed and their loadings on the first two principal components (PCs). The first two PCs explained over 92 % of the variance in the data set (Table 7.10). The variable loadings on PC1 indicate that it describes a gradient of increasing sediment organic matter (high positive loadings on % OM) and sediment fining (high negative loadings on % Gravel and % Sand and high positive loadings on D_{50} and % Silt + % Clay). Although PC2 has an eigenvalue that is slightly less than 1, it was retained because it describes a gradient of increasing sediment coarsening (high positive loadings on % Gravel) which is informative when the plotting positions of the samples are investigated with respect to PC1 and PC2.

Table 7.10. Eigenvalues, percentage variation explained and variable loadings on the first two components of a PCA performed on mesohabitat sediment variables for the sampling periods of spring (PB1) and mid-summer (PB2) 2012. Results of Kruskal-Wallis (KW) and Mann Whitney (MW) tests applied to the scores of bare river bed (BGB), jam (JM), bank (BK), jam bank (JB) and floodplain (FP) mesohabitats on the first two PCs.

	PC1	**PC2**
Eigenvalue	3.859	0.767
% variance explained	77.190	15.342
Cumulative variance (%)	77.190	92.531
Loadings		
% Organic Matter	0.831	0.257
Median particle size (D_{50})	0.978	0.029
% Gravel	-0.587	0.803
% Sand	-0.946	-0.234
% Silt + % Clay	0.986	-0.008

	MW *p* value	Significantly different subgroups (p < 0.05, n.s. if no significant differences)
a - *All samples (comparison of scores of PB1 and PB2 samples)*		
PC1	0.764	n.s.
PC2	0.788	n.s.
b - *All samples (comparison of scores of PB1 and PB2 samples for each mesohabitat type)*		
PC1		
BGB	0.755	n.s.
JM	0.060	n.s.
JB	0.713	n.s.
BK	0.347	n.s.
FP	0.590	n.s.
PC2		
BGB	0.514	n.s.
JM	0.551	n.s.
JB	0.478	n.s.
BK	0.887	n.s.
FP	0.977	n.s.

	KW *p* value	Degrees of freedom	Significantly different subgroups (p < 0.05, n.s. if no significant differences)
c - *All samples (comparison of scores of samples from the different mesohabitat types)*			
PC1	< 0.0001	4	JB, FP, JM, BK > BGB
PC2	0.0003	4	FP > JM, BGB

Kruskal-Wallis (KW) and Mann Whitney (MW) tests were separately performed on the PC scores for samples from the two sampling periods, mesohabitats associated with the sampling periods and all the mesohabitat types along the study reach to assess the degree to which these represented statistically significantly differences (p < 0.05). Multiple pairwise comparisons were then performed using the Dunn's procedure (Bonferroni corrected) to identify those sampling periods and mesohabitats that were significantly different from one another (p < 0.05). a = 120 samples (60 for each sampling period) used in the MW analyses, and; b = 12 for each mesohabitat used in the MW analyses; c = 120 samples (24 for each mesohabitat) used in the KW analyses.

The scores of the samples on PC1 and PC2 were investigated to assess whether there were any differences between samples according to sampling periods and mesohabitats (Figure 7.9). Figure 7.9 plots the 120 mesohabitat samples in relation to their scores on PC1 and PC2, and codes them according to (a) sampling periods; (b) mesohabitats; and (c) mesohabitats within each sampling period.

With respect to PC1 and PC2, there were no clear contrasts in the scores of PB1 and PB2 samples (Figure 7.9 (a)) and the scores of mesohabitat samples between the two sampling periods (Figure 7.9 (c)). Mann Whitney tests comparing scores of PB1 and PB2 samples and mesohabitat samples between the two sampling periods on PC1 and PC2 showed no significant difference with respect to PC1 (sediment fining and increasing organic matter) and PC2 (sediment coarsening), confirming the visual impressions obtained from Figure 7.9 (a) and Figure 7.9 (b).

When samples from individual mesohabitats are compared (Figure 7.9 (b)), all the bare river bed (BGB) samples are clearly separated and distributed to the extreme upper and lower left of all jam bank (JB), floodplain (FP), bank (BK) and jam (JM) samples (which overlap) with respect to PC1. Kruskal-Wallis tests applied to the mesohabitat scores on PC1 reveal that jam bank (JB), floodplain (FP), jam (JM) and bank (BK) samples are significantly different from bare river bed (BGB) samples (Table 7.10), indicating that bare river bed (BGB) samples are coarser and have lower organic matter content than all other samples. In relation to PC2, jam bank (JB) and bank (BK) sediment samples shows little variability in their scores on PC2, while bare river bed (BGB), jam (JM) and floodplain (FP) samples shows high variability in their scores (Figure 7.9 (b)). Floodplain (FP) samples have statistically significant higher scores on PC2 than jam (JM) and bare river bed (BGB) samples (Table 7.10), indicating that once the broad sediment calibre differences explained by PC1 are removed, FP samples tend to contain more gravel than other samples. This appears to reflect less variability and few low scores in FP samples in relation to PC2 (Figure 7.9 (b)).

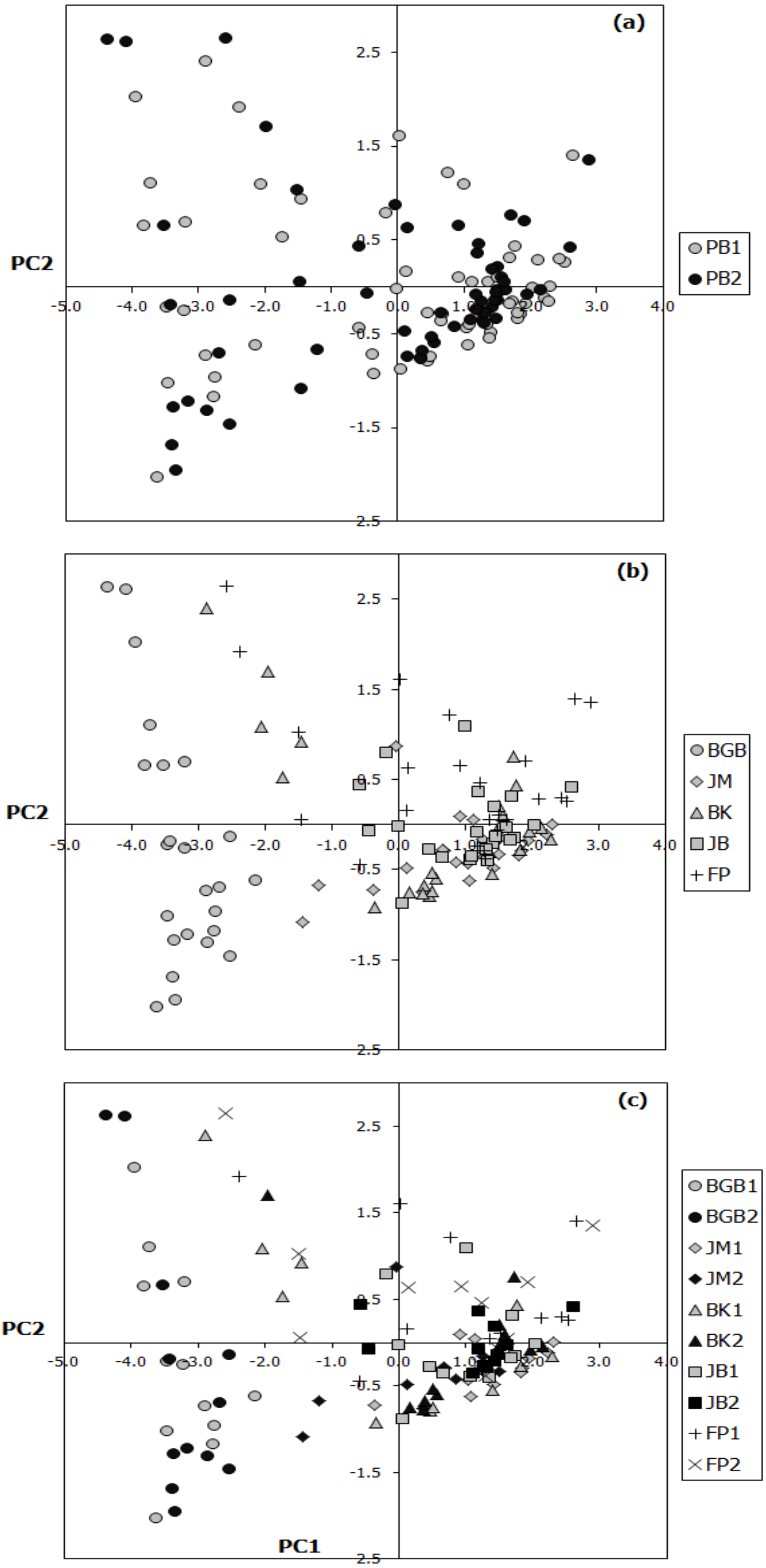

Figure 7.9. Distribution of (a) sampling periods (PB1 and PB2); (b) mesohabitats (amalgamated across sampling periods); and (c) distinct mesohabitats and sampling period; in relation to their scores on PCs 1-2 (for meaning of abbreviations see Table 7.1).

The propagule species dataset for the mesohabitats and sampling periods was analysed using DCA to investigate whether there were variations in propagule species composition across the different sampling periods and mesohabitat types. Eigenvalues for the first two axes were 0.818 and 0.527 and the lengths of gradient were 4.977 and 5.719. The cumulative percentage variances within the species data explained by the axes were 21.1 and 34.7 %, respectively.

Figure 7.10 shows the DCA biplot for (a) the 8 propagule species and the samples coded by sampling period; (b) the samples coded by mesohabitat and (c) the samples coded by sampling period and mesohabitat. All species were included in the analysis and there was no downweighting of rare species. There were no apparent contrasts in the samples scores along axes 1 and 2 for the two sampling periods (Figures 7.10 (a)), mesohabitats sampled during the sampling periods (Figures 7.10 (c)) and the different mesohabitat types (Figures 7.10 (b)). However, the almost complete absence of propagule species in BGB and BK samples means that the plots are only comparing species data for three mesohabitats, JM, JB and FP, and for a total of only 8 species.

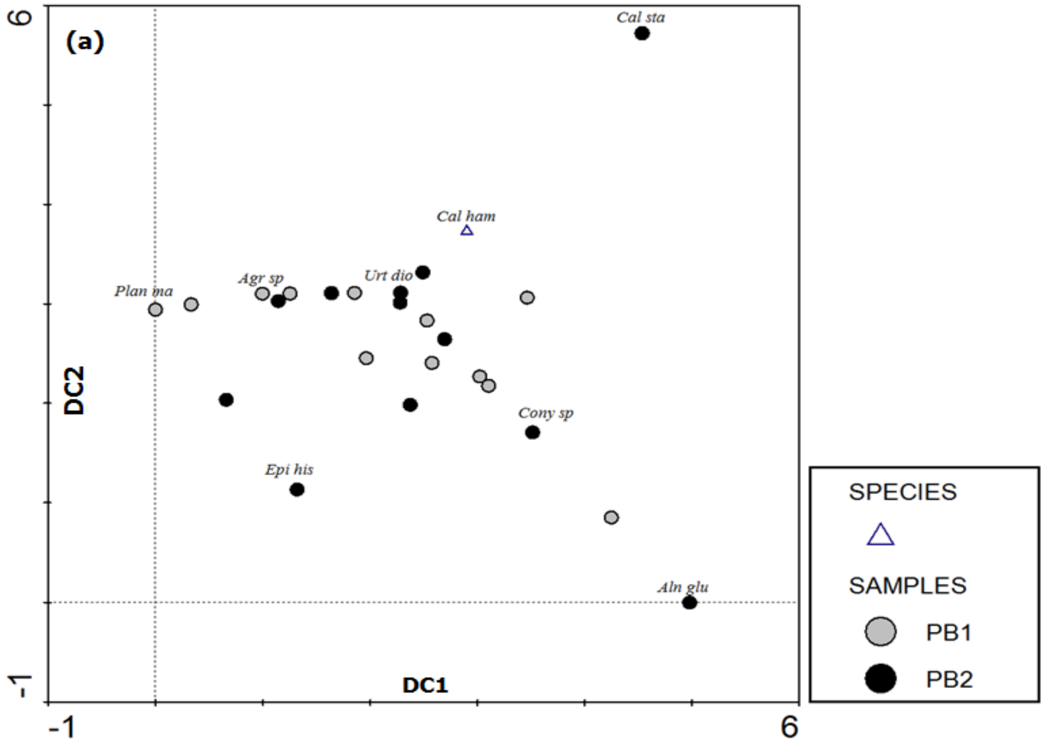

Figure 7.10. DCA Ordination plot of (a) propagule species and samples coded by sampling period (for species names associated with abbreviations see Table 7.6 (a)).

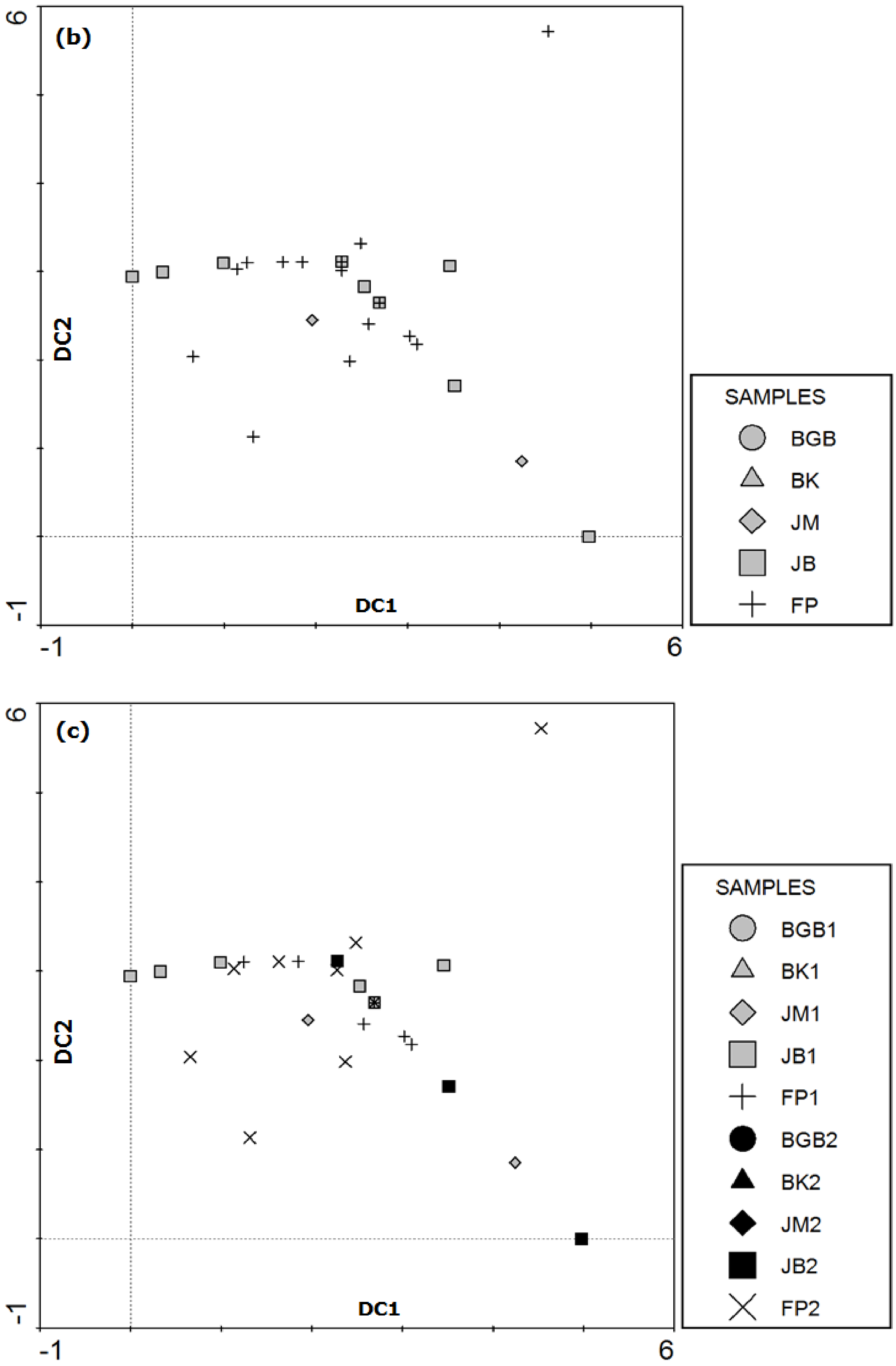

Figure 7.10 (Continued). DCA Ordination plot of (b) samples coded by mesohabitat; (c) samples coded by mesohabitat and sampling period.

Given the poor discrimination between mesohabitats and sampling periods in relation to most sediment and propagule properties, with only the BGB samples clearly discriminated by sediment properties and with propagules almost completely represented by three mesohabitats (JM, JB, FP), the associations between the composition of the propagule bank and the sediment characteristics of sampled mesohabitats at the River Bure site was not pursued further using a direct gradient analysis (DGA) technique. However, from the ordination and correlation analyses that have been presented, it is clear that propagule species are found in predominantly fine sediments with relatively high organic content, which are characteristic of JM, JB and FP mesohabitats.

7.5 DISCUSSION

The discussion is subdivided into five subsections to address the four research questions that were introduced in section 7.1.

7.5.1 What are the Characteristics of Reintroduced Wood?

Wood storage within the active corridor of rivers provides a basis for drawing comparisons between river systems in terms of the degree to which they reach wood levels for similar river systems (Gurnell, 2013). Compared to most published data of natural wood loading in river reaches bordered by deciduous hardwoods, the quantity of wood stored in this restored study reach (average wood volume of 12.97 m^3/ha) is lower than would be expected in reaches subject to a natural supply of large wood (see Gurnell et al., 2002; Gurnell, 2013).

Some important properties of large wood jams are the size (length and diameter) of wood pieces in each accumulation and the size of jams in the river channel (Gurnell, 2013). Wood pieces and jams were relatively large along the restored reach of the River Bure compared to most published wood data for river reaches with a natural wood supply (Gurnell, 2013). These large wood pieces and jams partially spanned the river channel, diverting flow and consequently forming important structures in controlling sediment transfer and storage characteristics; and thus contributing to channel morphodynamics and mesohabitat complexity. However, the accumulations contained relatively small numbers of wood pieces, and so remain quite open structures unlike those found in more natural settings, such as the Highland Water reach (Chapter 6).

7.5.2 Are there Any Associations between Reintroduced Wood and Geomorphological Features?

Under natural conditions, large wood retained in fluvial systems is important for creating sedimentary complexity and enhancing the diversity of mesohabitats (e.g. Gurnell et al., 2002; Gregory et al., 2003; Gurnell, 2014). The impact of large wood jams on flow hydraulics and thus sediment deposition, storage and scouring was apparent along the restored reach because there was an increase in the diversity of substrate calibre types and geomorphic features in close proximity to the large wood jams surveyed. The most frequently occurring and apparently wood-controlled geomorphic features were pools and bars. This association between pool and bar formation and wood jams has been reported by studies in forested river systems (e.g. Montgomery et al., 1995; Beechie and Sibley, 1997; Bilby and Bisson, 1998; Baillie and Davies, 2002; Gurnell et al., 2002; Baillie et al., 2008).

Large wood jams improve hydraulic diversity through local redistribution of flow energy and flow patterns, driving the sorting and redistribution of sediment of differing particle size on the river bed (Gurnell, 2013). Along the River Bure restored reach, the partial wood jams diverted flow away from the banks, hence reducing bank erosion and leading to the redistribution of sediment and the scouring of the river bed, locally increasing channel depth and revealing the true gravel bed. Although sand was the most prevalent substrate material along the reach, the river's underlying coarse gravel bed was exposed in a few areas where flow was concentrated by large wood, while a finer substrate (silt and clay) was mostly found within large wood jams, particularly along the channel. This sorting of sediment induced by the large wood, is leading to aggradation of the bed around the reintroduced trees and along the channel margins between the reintroduced trees, both of which were suitable for colonisation by marginal plant species such as *Sparganium erectum*, *Epilobium hirstutum* and *Phalaris arundinacea*. These species are able to trap and stabilise fine sediments in low energy rivers such as the Bure, leading to channel migration, or where the channel is over-widened, channel narrowing (Gurnell et al., 2006b, 2014).

Thus it appears that large wood is already leading to channel adjustment within the restored reach of the River Bure and this is leading to channel narrowing and may eventually reinstate the higher flow velocities, capable of moving fine sediment through the reach. However, at the present time, the widespread burial of the river's gravel bed by sand and finer sediments, and the lack of geomorphic features such as bars and riffles formed of the true river bed material (gravel), suggests that there is a long way to go before the wood achieves its full hydraulic effect and induces significant sediment sorting and morphological complexity. Such effects are only likely to occur when some of the accumulations develop into complete or active jams that span the channel and are less permeable than the current wood structures. The probability of this occurring will increase as the channel narrows.

7.5.3 Are there Any Differences in the Sediment Characteristics of Different Mesohabitats?

Overall, the River Bure reach was dominated by sand and finer sediments. Sediment properties showed high variance within sampling periods and mesohabitat types. However, there were some statistically significant differences between mesohabitat types, with the bare river bed sediments (BGB) being consistently coarser and containing less organic matter than other mesohabitats. This variability was supported by the Principal Components Analysis of sediment properties. There was also significantly higher organic matter content in jam and floodplain samples and significantly lower gravel in jam samples in the first (spring) than in the second (summer) sampling period. However, the complex hydraulic effects of jams that induce very significant and patchy scouring, deposition and sorting of fluvial sediment, which has been observed in other studies (e.g. Gomi et al., 2004; Oswald and Wohl, 2008; Gurnell, 2013), were not observed on the River Bure. This may reflect the low energy of the river's flow regime, coupled with the over-widened channel. However, there was clear evidence of fine sediment retention around the jams and along the channel margin in the restored reach (represented by jam and jam bank samples). There was also a clear increase in the variability in bed sediment calibre between those parts of the reach containing reintroduced wood (ranging from gravel through sand to silt patches) and the central section of the reach, where no wood was present, and where a smooth sand layer completely covered the gravel bed. These observations support a broad difference in sediment calibre between habitats associated with jams (jam and jam bank) and those not associated with jams (bank, bare bed) within the channel at this early stage of mesohabitat development following restoration.

7.5.4 Are there Any Differences in the Propagule Bank of Different Mesohabitats?

Overall, the active corridor along the study reach was observed to have a propagule bank that was poor in abundance and species richness. This may not be surprising as riparian conditions (i.e. cleared or wooded) have been found to have a strong influence on propagule bank composition and structure, with wooded reaches containing relatively less species and lower total number of germinable propagules (Williams et al., 2008). However, the very sparse propagule banks of the River Bure mesohabitats are poor even when compared to the observations on the heavily wooded Highland Water reach (Chapter 6).

Propagule abundance was lowest in the bare river bed (BGB) and eroding bank (BK) samples, where a propagule bank was almost non-existent, and was highest in the wood-related (jam (JM), jam bank (JB)) and floodplain habitats. The increase in abundance of propagules in the wood and vegetation associated habitats concurs with observations by Gurnell et al. (2007) on the rivers Frome and Tern.

The samples (spring and summer) obtained across the active corridor of the restored reach showed a significant change in the propagule bank characteristics between sampling periods, with the spring samples showing higher species richness and abundance than the summer samples. As with the Highland Water study, the mid-summer (July) sampling may have been too early to reflect summer propagule production and may have been affected by a loss in seed viability (perhaps hastened by desiccation) following the spring (May) sampling. Furthermore, of the 8 species identified in the germination trials, one of the most frequently identified, *Alnus glutinosa*, produces seed between February and May (Hodgson et al., 1995), so is most likely to be found in the spring (May) samples.

Overall the propagule banks observed on the River Bure were impoverished, but the presence of wood-related mesohabitats appeared to be important both in retaining propagules and also in providing colonisation sites for emergent aquatic plants such as *Sparganium erectum* and *Phalaris arundinacea*, that largely propagate vegetatively from rhizome fragments that are too large to have been sampled using the sampling techniques employed in this study.

7.5.5 Are there Any Significant Associations between Physical (Reintroduced Wood and / or Sediment) And Biotic (Propagule Banks) Characteristics of Mesohabitats?

Mesohabitats associated with large wood were finer, contained more organic matter and had a richer and more abundant propagule bank than other in-channel mesohabitats. These associations were demonstrated consistently by all of the analyses that were applied to the data set collected on the River Bure. However, there were no strong differences between the different wood-related habitat samples and those from the floodplain. Hence, large wood-related habitats exhibit an environment suitable for the growth of propagules and consequently essential for the regeneration of floodplain forest (Hughes et al., 2005).

Mesohabitats in the restored reach of the River Bure are responding to wood reintroduction, but the response is subdued. Fine sediment containing organic matter and propagules is accumulating around the large wood, and the channel is beginning to show evidence of more widespread sediment sorting and landform development that can be attributed to the large wood. However, none of these wood-related effects match what would be expected in a reach subject to a long term, natural supply of wood (e.g. the Highland Water reach, Chapter 6).

Thus, the River Bure reach is recovering its wood-related complexity slowly, and the recovery is likely to accelerate as the channel narrows and more wood, particularly smaller pieces, are supplied to support the development of complete and truly active wood jams. These larger and less porous wood structures should be more effective in retaining plant propagules as well as in creating hydraulic diversity, so that a more substantial propagule bank comprising both long- and short-lived species should start to develop in the wood-related mesohabitats.

7.6 SYNOPSIS

Based on the results of the study presented in this chapter, the following conclusions can be drawn:

1. The reintroduced wood, although characteristically diverse in dimensions and size (volume and area), formed relatively simple porous large jams that only partially spanned the active channel of the River Bure restored reach.

2. The enhancement of hydraulic diversity by reintroduced wood, and the consequent redistribution of flow energy and flow patterns has driven some differential scouring, sorting and deposition of sediment, and has induced an increase in geomorphic and sedimentary complexity along the restored sections of the River Bure reach in comparison with the central section, which does not contain wood. Geomorphic features in close proximity to reintroduced wood were pools and bars, while the major substrate types along the restored reach were gravel, sand and finer sediment (silt and clay) which were respectively located in places of flow concentration, places of uniform flow and within jams.

3. The sediments sampled from five recurring mesohabitats within the River Bure reach show considerable heterogeneity both within and between mesohabitats. However, floodplain and jam-related habitats were associated with finer, more organic rich sediments than river bed and eroding bank habitats. The retention of fine sediments around the large wood and intervening channel margins, and its colonisation by aquatic vegetation, indicates a process of channel narrowing induced by the reintroduced wood in this over-widened channel. Furthermore, the exposure of the true gravel bed in some small areas of the reach where wood has been introduced is a further indication of the recovery of the channel to its form and structure prior to over-widening.

4. The propagule bank of mesohabitats within the River Bure restored reach showed a low abundance of viable propagules and they were generally species poor. Propagule species richness and abundance of mesohabitats

within the active corridor varies in time and space, with large wood jam-related mesohabitats cumulatively storing the largest amount (in terms of species richness and abundance) of viable propagules. However, these propagule banks are poorly developed, and may not recover significantly, until the wood recovers to form complete and active jams that are likely to be more retentive.

5. The dominant factor that appears to explain propagule bank diversity (abundance and species richness) along the River Bure restored reach were the quantity and quality of fine sediment containing organic matter, which varies significantly among mesohabitats within the active corridor. Large wood jam-related mesohabitats may be termed a ‘transitional habitat’ between the channel bed and the river margins (bank and floodplain) due to their high retention of fine sediment, organic matter and propagules. On the River Bure, these habitats are also probably transitional in time, reflecting the gradual development of naturally-functioning wood accumulations. This suggests that the restored channel is on a ‘trajectory to recovery’ and may have implications for the initial trajectory of vegetation colonisation, the narrowing of the active channel and the eventual development of more complex channel banks and riparian habitats.

The next chapter brings together the main findings from this chapter and previous chapters in relation to the research aims and questions identified early in this thesis (Chapter 2, Section 2.7), drawing together some general conclusions.

CHAPTER 8

CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

8.1 INTRODUCTION

This chapter draws together the main findings in relation to the research questions identified early in this thesis (Chapter 2, Section 2.7), in order to draw some general conclusions (Section 8.2, 8.3 and 8.4). A number of research gaps are then identified for future research, which may permit further refinement of the results reported in this thesis or which may address some of the additional questions that have been identified during the course of this research (Section 8.5).

Following a review of the literature, Chapter 2 concluded that despite the existence of a sizeable body of research concerning large wood in riparian zones, several notable research gaps existed. One gap concerned variations in large wood, sediment retention and landform development in riparian zones across different styles and sizes of river, with a particularly notable lack of information on large, multi-thread rivers. The review also indicated that there has been very little plant ecological research related to riparian wood; most notably a lack of consideration of interactions between large wood and propagules. Lastly, the potential contribution of large wood to river restoration had received limited research attention. With these research gaps in mind, the following research questions were identified:

1. What are the types and characteristics of large wood accumulations present within the riparian corridor of different styles of river systems?

2. Does deposited large wood within riparian corridors influence sediment structure, landform and physical habitat development and thus the geomorphology of different river systems?

3. Do large wood-related habitats retain plant propagules within the riparian corridor of different river systems and does propagule retention vary in space

(within- mesohabitats / river reaches) and through time (age / seasonally / in relation to restoration)?

Considerable progress has been achieved in addressing these three research gaps through investigations carried out within rivers of different size and style. The four research chapters (Chapters 4, 5, 6, and 7) have each investigated and discussed findings relating to these research gaps, and so a brief overview is provided here in order to draw some general conclusions.

8.2 WHAT ARE THE TYPES AND CHARACTERISTICS OF LARGE WOOD ACCUMULATIONS PRESENT WITHIN THE RIPARIAN CORRIDOR OF DIFFERENT STYLES OF RIVER SYSTEM?

To augment the literature that currently exists on large wood in different river systems, the types and characteristics (e.g. quantity, size) of large wood in both single- and multi-thread river reaches were investigated and discussed in this thesis.

Investigations across the four study sites revealed dissimilarities in the nature and types of large wood accumulations present. Large wood within two wide, island-braided reaches of the Tagliamento River was widely dispersed but preferentially retained on the top and edges of gravel bars, where it had snagged during the falling limb of floods. However, the features produced by the wood were quite different in the two reaches. In the headwater reach, several different types of large wood accumulation were identified including uprooted trees (entire, uprooted trees), large wood jams (condensed accumulations of logs, shrubs, trees, root masses and other wood pieces), individual logs (individual, unbranched trunks or large unbranched pieces of wood), uprooted shrubs (entire, uprooted shrubs) and root boles (root mass of a tree plus a portion of the trunk). Individual logs and large wood jams were significantly more frequent than the other types and large wood jams accounted for the greatest quantity (i.e. volume) of large wood. The majority of these were dead wood accumulations, which became incorporated into islands by protecting tree seedlings that grew to produce a canopy that was capable of retaining further dead wood, sediment and propagules. In the middle reaches of the Tagliamento River, wood was deposited in similar locations and forms to the headwaters, although whole uprooted trees were more frequent than in the headwaters. In addition, much of the deposited wood was capable of sprouting. In particular, deposited uprooted trees, because of their size and internal resources, grew rapidly to form a canopy that retained sediment, additional wood and propagules, evolving into pioneer and eventually large, established islands. In contrast, in the narrow single-thread Highland Water, the main type of large wood accumulation was jams, with the majority being complete jams, located at river bends, and comprised of large dead wood pieces with partially decayed xylem. Lastly, wood emplaced in a restored reach of the River Bure showed less decay than in the Highland Water and was mainly comprised of individual felled trees that were quite open structures and only partly spanned the active channel. The lack of large wood pieces around the felled trees and limited evidence of wood decomposition illustrate that wood in the River Bure had yet to develop the properties of the long-term wood supply and storage evident in the Highland Water.

This thesis has also provided field measurements of the quantity of large wood stored in three of the study reaches (Tagliamento headwaters, Highland Water, River Bure). Large wood storage within the riparian corridor is widely estimated as a basis for drawing comparisons between river systems (Gurnell, 2013). Comparisons of wood storage between the three study sites reported in this thesis showed relatively similar wood loadings (wood volumes) for the braided headwater reach of the Tagliamento River (average wood volume 55.64 m^3/ha) and the single-thread lowland Highland Water reach (average wood volume 56.7 m^3/ha) but lower levels for the single-thread River Bure restored reach (average wood volume 12.97 m^3/ha). This is a further indication that the River Bure restoration requires a period of natural wood supply to achieve the levels of wood storage that might be expected in naturally-functioning wood reaches.

The dimensions (length, diameter, height / width) of the different types of large wood accumulation found within rivers are an important factor in determining their stability and their potential to influence channel morphology (Abbe and Montgomery, 2003; Gurnell, 2003). The dimensions of the large wood accumulations observed within the four study reaches were characteristically diverse. The dimensions of large wood accumulations in the two reaches of the Tagliamento

River, were small relative to the channel width, but were large in absolute terms, particularly the uprooted trees observed in the middle reach, which often exceeded 17 m in length. In contrast, most large wood jams spanned the channel width of the narrower Highland Water reach, despite the small size of the key pieces relative to those observed on the Tagliamento River. The size of key wood pieces relative to bankfull width is an important factor that determines the style and stability of wood accumulations. Despite the wide range in wood piece and accumulation sizes observed, they were all small in comparison with those reported from some other environments (e.g. Pacific Northwest) where riparian trees reach much larger dimensions because of differences in climate, species, stand age, and forest management history.

Evidence of longitudinal trends in the distribution and characteristics of large wood accumulation types can be tentatively inferred from the three naturally-functioning study sites (Highland Water, Tagliamento headwater, Tagliamento middle reach). These trends relate to the widening of channels which typically occur in a downstream direction within single-thread river systems, although the expected downstream reduction in channel gradient associated with channel widening is not reflected across all the three naturally-functioning study reaches, since the middle-width Tagliamento headwater reach is much steeper than the narrow Highland Water reach. Nevertheless, the dominance of channel-spanning accumulations in the Highland Water would be expected in small headwater channels whose width is much smaller than the height of the riparian trees, whereas the dispersed, discrete accumulations observed in the other two reaches are characteristic of multi-thread channels whose width greatly exceeds the height of the riparian trees. At a reach scale, the hillslope-confined headwater reach of the Tagliamento River, also showed some downstream trends, indicating local influences on wood dynamics. The total frequency of large wood accumulations decreased from upstream to downstream, with some anomalies, while large wood jams and individual logs, which contributed enormously to the total number of large wood accumulations, also appeared to decrease from upstream to downstream. The quantity of uprooted trees also decreased from upstream to downstream. The discrepancies in wood distribution along the river can be tentatively attributed to differences in wood delivery and retention processes along the reach. Local bank undercutting, wind throw and / or hillslope instability may have accounted for the trends in uprooted trees, which are probably quickly broken up into smaller pieces during transport, while the downstream change in the frequency of islands, which are important wood retention sites, may also have accounted for the trends in the total frequency of large wood accumulations, large wood jams and individual logs. The association between wood accumulations and the presence of retention structures was echoed in the Highland Water reach where key wood piece length and diameter, and wood jam width and depth were strongly, significantly positively-correlated with channel width.

8.3 DOES DEPOSITED LARGE WOOD WITHIN RIPARIAN CORRIDORS INFLUENCE SEDIMENT STRUCTURE, LANDFORM AND PHYSICAL HABITAT DEVELOPMENT AND THUS THE GEOMORPHOLOGY OF DIFFERENT RIVER SYSTEMS?

The evaluation of the nature of large wood (living or dead) and differences in wood quantity and accumulation types within the contrasting river reaches studied in this thesis has offered the opportunity to gain an in-depth understanding of two components of its influence on river geomorphology: sediment calibre and composition, and landform development. The research has clearly illustrated that the retention of large wood within river channels impacts sediment dynamics (retention, erosion, sorting), and mesohabitat or landform development.

8.3.1 Substrate Diversity along Different Styles of River Systems and their Associations with Large Wood

Sediment heterogeneity was identified across sampled mesohabitats at all four study sites. Significant spatial heterogeneity was observed in sediment calibre and organic matter content, showing contrasts within and between wood-related and other mesohabitats. Within the island-braided reach of the Tagliamento River, root bole sediment deposits and sediment plume deposits, which are mesohabitats associated with deposited trees that form the nucleus of early-stage pioneer islands, were finer and contained more organic matter than the adjacent gravel bar sediment deposits. Similar to observations for intermediate- and later-stage pioneer islands in the middle reach of the Tagliamento River, established islands in the active channel of the headwater reach were covered by significantly finer sediments (including clay and silt) that contained more organic matter than the adjacent gravel bars. Along the single-thread Highland Water, the most notable spatial contrasts in sediment characteristics was significant sediment fining from bars to jams through to floodplains, and for the single-thread restored River Bure reach, bare river bed sediments in the centre of the channel were consistently coarser and contained less organic matter than other (floodplain, banks and wood-related) mesohabitats. These variations in the sediment characteristics among mesohabitat types, irrespective of river styles, reflect the hydraulic changes induced by flow obstructions that affect the calibre of sediment that can be mobilised, transported and deposited in different locations.

Significant temporal (seasonal and age) variations were also observed in sediment characteristics of sampled mesohabitats. Within the island-braided reach of the Tagliamento River, as pioneer islands increased in age, the proportion of organic matter retained within their sediment plumes and the proportion of fine sediment retained within and between open bars associated with islands increased significantly. On the Highland Water, the most notable seasonal (between mid-summer and spring) change in sediment characteristics was that organic matter content was significantly higher in summer than in spring samples. Notable temporal variations in the organic matter content for specific mesohabitats were also observed, with wood-related mesohabitats (jam banks and jams) retaining significantly more organic matter during spring and summer, respectively. Although there was no general seasonal gradient of sediment fining, summer sediment samples (particularly floodplain, bank, jam bank samples) contained a significantly higher proportion of finer particles (clay and silt) while spring sediment samples (particularly floodplain samples) contained a significantly higher proportion of sand. However, on the River Bure reach, there was no apparent seasonal variation in sediment characteristics, although jam and floodplain samples contained a significantly higher proportion of organic matter and there was a significantly lower proportion of gravel in jam samples in the spring than in the summer sampling period. These apparent temporal trends probably reflect seasonal changes in the delivery of organic matter and / or biogeochemical processes (e.g. decomposition rates) and differences in the character of sediments mobilised and deposited by hydrological events, particularly floods.

Sediment that accumulated within large wood structures and related mesohabitats exhibited variable characteristics among the study reaches. Along the headwater reach of the Tagliamento River, large wood jams accumulated sediment containing a relatively higher proportion of sand and intermediate proportions of organic matter, fine sediments (silt and clay) and gravel in comparison with island surface and open bar surface samples, although the proportion of sand and organic matter associated with wood deposits was highly variable. Large wood jams (represented by jam and jam bank samples) within the active channel of the Highland Water, characteristically accumulated relatively higher amounts of organic matter and intermediate proportions of fine sediments (silt and clay) and gravel in comparison with samples from other mesohabitats. On the River Bure, there was clear evidence of fine sediment retention around the introduced large wood, but also generally along the channel margin, such that sediment associated with wood jams did not show significantly different characteristics from all of the mesohabitats that were not directly influenced by large wood. Nevertheless, there was a clear increase in the variability in bed sediment calibre in those parts of the reach containing reintroduced wood (ranging from gravel through sand to silt patches) in comparison with those parts where no wood was present. In the wood free sections, the gravel river bed was covered by a near-homogeneous sand layer. Therefore, once again the restored River Bure can be discriminated from the other three study reaches, since it shows some response to the restoration with wood, but as yet the wood-related mesohabitats do not show significantly different sediment characteristics from all other sampled mesohabitat types as was observed on the other reaches.

8.3.2 Geomorphic Features Associated with Large Wood in Different Styles of River Systems

Large wood retained in fluvial systems creates a variety of mesohabitats and / or landforms which enhance the complexity of the physical habitat mosaic. The hydraulic impact of large wood accumulations leads to variability in the erosion, sorting and deposition of fluvial sediments, and as a consequence the creation of particular landforms and associated mesohabitats.

In the two braided reaches of the Tagliamento River, large wood was observed to have an important influence on the retention and accretion of finer sediment on gravel bar surfaces, eventually leading to the development of islands. The wood-related mechanisms involved in island development varied according to whether the wood was capable of sprouting and also the type of accumulation. Within the middle reach of the Tagliamento River, sprouting of deposited trees lead to the development of early-stage pioneer islands that are highly variable in length and width, but show significantly lower surface elevation relative to the adjacent gravel bar surface compared to intermediate- and later-stage pioneer islands. Although there is a clear trend of increasing length, width and surface elevation with island age, the variability in pioneer island morphology (i.e. height, width and length) at the intermediate and later stages of development suggest highly variable rates of sediment accretion, reflecting local contrasts in interactions between the islands and inundating river flows. Other geomorphic features associated with pioneer island development, particularly during the early stages, is the presence of large accumulations of wood and crescent-shaped scour holes / pools of varying depths around the root boles of the deposited trees. In the headwater reach of the Tagliamento River, wood jams were the most frequent form of wood accumulation and these were often associated with lee-side deposition of fine sediment, which aggraded with vegetation colonisation and the retention of additional wood.

In the two single-thread river reaches, large wood accumulations that extend partially or across the entire width of the active channel were important features driving sediment and organic matter retention, whereas wood that partially spanned the channel also retain fine sediment and organic matter, but as part of a more general pattern of sediment retention along the channel margins. The impact of large wood jams on flow hydraulics and thus sediment deposition, storage and scouring appears to have induced considerable patch scale geomorphic heterogeneity along the Highland Water compared to the River Bure. The most frequently-occurring, wood-related features along the single-thread river reaches were pools and bars. Pools (mostly in-dam pools and marginal pools) were observed in association with 50 % of all wood accumulations along the Highland Water. Partial jams were frequently associated with the formation of marginal pools, unvegetated bars, and eroding banks; complete jams were frequently associated with the formation of marginal pools, in-dam pools and unvegetated bars; while active jams were most strongly associated with the formation of in-dam pools. Large wood jams at river bends are particularly associated with dammed, marginal and in-dam pools and vertical and undercut eroding banks, while jams located upstream and downstream of bends were frequently associated with marginal and in-dam pools and unvegetated bars. On the River Bure reach no such wood-related geomorphic features were observed, but the increase in patchiness in bed sediment calibre suggests that restoration with large wood is leading to some channel adjustment but more time is needed for the development of distinct wood-related landforms.

The research also demonstrated that geomorphic features along large rivers may profoundly influence the retention of large wood. Within the headwater reach of the Tagliamento River, the main geomorphic structures associated with wood retention were the surfaces and margins of islands, the crests of bars and strand lines at the edges of channels. The largest frequency and quantity (volume or mass) of large wood accumulations, mostly jams, were associated with sites where island development was extensive. These observations support the hypothesis of Gurnell et al. (2000a) that geomorphological style of a river is an indicator of wood retention and availability potential.

8.4 DO LARGE WOOD-RELATED HABITATS RETAIN PLANT PROPAGULES WITHIN THE RIPARIAN CORRIDOR OF DIFFERENT RIVER SYSTEMS AND DOES PROPAGULE RETENTION VARY IN SPACE (WITHIN- MESOHABITATS / RIVER REACHES) AND THROUGH TIME (AGE / SEASONALLY / IN RELATION TO RESTORATION)?

In exploring the dependence of plant communities (propagule bank and / or colonising vegetation) on large wood within the riparian zones of different river reaches, mesohabitats associated with large wood structures were compared with other mesohabitats. The results of this research is summarised in relation to the following themes: (i) the temporal and spatial variation in riparian propagule banks and / or colonising vegetation; (ii) the associations between the physical characteristics (large wood and sediment) of mesohabitats and their standing vegetation and / or propagule banks. Key controls and interactions relevant to these two themes and the degree to which they are supported by results presented in this thesis are summarised in Figure 8.1.

8.4.1 Temporal and Spatial Variation in Riparian Propagule Banks and / or Standing Vegetation

The research presented in this thesis shows that riparian plant community (propagule bank and / or colonising vegetation) composition is highly variable between and within the four studied river reaches. Within the middle reach of the Tagliamento River, where both the propagule bank and colonising vegetation were studied, pioneer islands were found to support distinct vegetation and propagule communities at each stage of development. Generally, the species richness of the standing vegetation was high but propagule bank species richness and abundance were low. The latter partly reflects the species present in the standing vegetation, many of which produce short-lived propagules, but it also probably reflects the fact that the propagule bank samples had to be stored at very low temperatures, which may not have suited some of the propagule species present in this Mediterranean environment. In the headwater reach of the Tagliamento River, propagule bank abundance and species richness were also low, but at this location this probably reflected the relatively species poor standing vegetation, the low natural longevity of many of the propagule species, the harsh physical environment, and the low proportion of fine sediments available to contribute to propagule bank development (Richter and Stromberg, 2005) rather than the mode of sample storage, which was more appropriate to the alpine conditions of this reach. Along the Highland Water, the relatively low species diversity recorded in the propagule bank is not unexpected, given the intense grazing pressure within the riparian forest bordering the river and the restricted species pool in this mature woodland setting. Nevertheless, when compared to the Highland Water reach, the riparian propagule bank of the River Bure was extremely impoverished, further suggesting that the recovery of natural function following wood emplacement is at a very early stage.

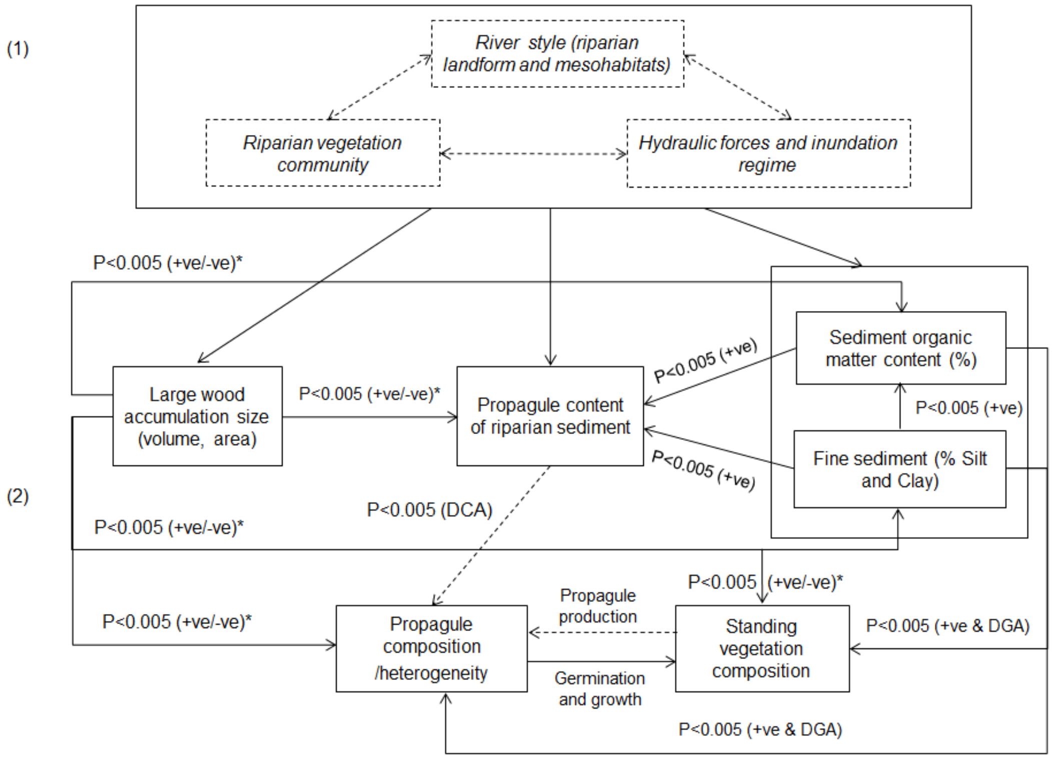

Figure 8.1. Flow chart illustrating key controls and process interactions relating to the role of large wood in riparian systems with, where relevant, the statistical strength of the process interactions identified in this thesis. (1) The three groups of interacting controls on large wood, sediment and propagules, which provided the environmental context for each of the four study reaches; and (2) process interactions and linkages between large wood, physical processes and vegetation that operated within the study sites. The broken boxes represent the three interacting sets of controls on large wood, sediment and propagules, unbroken boxes represent the variables investigated in the research, unbroken arrows represent the process linkages investigated (and where relevant the statistical strength of those linkages), and broken arrows show linkages that were not explicitly investigated. *The nature of these process interactions depends on the river style, age / season and the size of large wood structures.

Temporal variations were observed in riparian plant community (propagule bank and / or colonising vegetation) characteristics within three of the studied reaches. Within the middle reach of the Tagliamento River, the propagule bank and standing vegetation were studied within pioneer islands of different age. Standing vegetation height, cover, and species richness gradually increased from early- to intermediate-to later-stage pioneer islands. There was also high variability in propagule bank characteristics among the different mesohabitats associated with islands of different ages but no significant differences in abundance or species richness were found in association with island age. Research on the Highland Water and River Bure involved sampling on two separate occasions in spring and early summer. In both reaches, significant seasonal differences were observed in the richness and abundance of propagules, with spring samples showing higher species richness and abundance than early summer samples. This can largely be explained by the timing of flowering and seed production in many of the recorded species, which in most cases post-dated the early summer sampling. This suggests that while the propagules of some species persisted through the winter to the spring sampling, some lost viability and were not replaced by newly-formed propagules in the intervening period between spring and early summer sampling.

Statistical analysis of the properties of propagule bank samples from the different study reaches revealed clear spatial patterns across the sampled mesohabitats, several of which were wood-related. Within the middle reach of the Tagliamento River, root boles and sediment plumes on early stage pioneer islands had a higher propagule abundance and species richness than the adjacent gravel bars, although the difference was not statistically significant. However, contrasts in the propagule bank between island sediment plumes and gravel bar sediment associated with intermediate- and later-stage islands showed very high variance and no statistically significant differences. In particular, the intermediate-stage islands, which were very closely spaced, showed relatively high propagule abundance and species richness on intervening open gravel bar sediments, indicating propagule retention in the small gaps between the pioneer islands. In the headwater reach of the Tagliamento River, propagule richness and abundance were generally found to be highest in the sediment samples from established islands, lowest in the sediment samples from bare gravel bars and intermediate in the sediment samples from large wood jams although there was high variance among samples within each of these groups and thus the differences were not statistically significant. On the Highland Water, wood-related (jam and jam bank) mesohabitats exhibited significantly higher propagule abundance and species richness than other mesohabitats, reflecting the impact of wood jams on flow hydraulics and thus deposition and retention of these organic particles. No such distinction was found on the River Bure, further indicating the early stage of recovery of natural function in this restored reach. Overall, it appears that spatial heterogeneity observed in the riparian propagule bank structure of the four study sites may be linked to a combination of propagule traits (timing of production and dispersal, size, and weight), hydraulic characteristics of the mesohabitats in which they are found, the degree of exposure of mesohabitats to propagule transport processes (e.g. flow pulses), and in some cases, the cold storage of the samples.

8.4.2 Associations between the Physical Characteristics (Large Wood and Sediment) of Mesohabitats and their Standing Vegetation and / or Propagule Banks

The temporal and spatial variations observed in propagule bank abundance and species composition associated with different landforms / mesohabitats, were strongly associated with variations in the calibre of the substrate, suggesting that hydraulic processes affecting mobilisation, transport and deposition are the central cause of these spatio-temporal variations. In particular, propagule bank abundance and species richness were generally found to be significantly (positively) associated with fine (silt and clay) sediments with relatively high organic matter content, and thus landforms / mesohabitats associated with fine sediments with relatively high organic matter content also contained relatively abundant and species rich propagule banks.

Landforms / mesohabitats associated with large wood, especially those sampled along small, single-thread river reaches (jam and jam bank), were finer, contained more organic matter and had a richer and more abundant propagule bank than the other riparian mesohabitats investigated. Although most marked in relation to the small, single-thread Highland Water reach, these associations were demonstrated consistently by statistical analyses applied to the data sets collected along all three naturally-functioning reaches. In general, large wood structures in the active channel of the different river styles were found to be important for retaining fine sediment and propagules and thus potentially driving sedimentary, propagule and / or standing vegetation diversity within the reaches. Only the restored River Bure showed a weak response of sedimentary complexity and propagule retention to wood emplacement. Overall, large wood structures may be termed ‘transitional habitats’ due to their retention of fine sediment and propagules within active river channels, providing an important link between the channel habitats (bars and channel bed) and the adjacent relatively elevated and / or established habitats (established islands, banks and floodplain). The progressive deposition and accretion of sediment and propagules (particularly of grass and woody species), successful germination, growth and eventual colonization of vegetation on large wood-associated mesohabitats may be important tools in the conservation of plants and also the morphological evolution of the channel. The latter process is crucial to the use of wood in river restoration.

8.5 IMPLICATIONS OF RESEARCH FINDINGS FOR RIVER MANAGEMENT

8.5.1 Utilisation of Large Wood in River Restoration and Conservation Efforts

Recently, restoration schemes have started to incorporate large wood to enhance river channel structural and hydraulic complexity and thus to re-establish the physical and ecological functions associated with large woody accumulations in undisturbed river systems (Palmer et al., 2010; RRC, 2013). The value of large wood as a resource for river restoration and recovery has been demonstrated by research relating habitat complexity to fish and macroinvertebrate community indices (e.g. Crispin et al., 1993; Sotir, 1998; MacNally et al., 2001; Lester and Boulton, 2008; Nagayama et al., 2008). This thesis has demonstrated that single-thread rivers respond to wood reintroduction, with wood accumulations improving hydraulic diversity through local redistribution of flow energy and resultant flow patterns, driving widespread sediment sorting and redistribution, landform development on the river bed, and the retention of fine sediment, organic matter and propagules; thus providing colonisation sites suitable for emergent aquatic and wetland plants.

Some important properties of large wood accumulations for sediment and propagule retention and for the formation of geomorphic features, as identified in this thesis, are the number and size of wood pieces (both key and other pieces) in each accumulation, and the size of accumulations in the river channel. Comparing rivers of similar size (e.g. 5 - 15 m wide) under natural conditions (the Highland Water) and under restoration (River Bure), large wood pieces in the naturally functioning single-thread system varied widely in size, and predominantly formed channel spanning accumulations anchored by a few large key pieces. These complex structures, comprised of interlocking wood pieces of various sizes, created significant sedimentary and morphological physical habitat complexity (the wood jam and associated pools and bars), stored large amounts of organic matter, trapped and stabilised fine sediments, and supported a more substantial propagule bank, comprising both long- and short-lived species, than the wood in the restored river. The restoration on the River Bure, involved the reintroduction of large wood pieces, as is typical of many restoration schemes (RRC, 2013) but in the case of the Bure, the wood pieces were particularly large, taking the form of sizeable felled trees. These trees formed large open partial accumulations, reflecting the limited supply of wood pieces of other sizes to the river. As a result, relatively slow recovery of wood-related mesohabitat complexity and channel narrowing and adjustment were observed. To accelerate channel morphodynamics (channel narrowing and adjustment) and mesohabitat complexity during the implementation of river restoration using wood, catchment managers are advised to subject river reaches to an ongoing supply of wood pieces (whether natural or artificially supplied) and to ensure a range of piece sizes including smaller pieces, to mimic wood supply processes on natural rivers (e.g. Highland Water). This would support the development of less porous complete and truly active wood jams, which would be relatively more effective at retaining sediment and plant propagules (both long- and short-lived species) as well as creating hydraulic diversity and thus contributing to the significant development of geomorphic features (e.g. pools, riffles and bars) and wood-related mesohabitats that are essential for supporting a diverse fauna (aquatic insects and fish) and flora, and for the regeneration of floodplain forest. Consequently, the conservation of fauna and flora demands optimizing the quantity and sustaining the quality of large wood biomass in fluvial systems.

As conservation funds are limited, conservation actions must be strategic and cost-effective. The maintenance and / or reintroduction of large wood structures, which are a natural, renewable and cheap resource, into the riparian zones of European rivers appears to be a very promising tool for maintaining and restoring ecosystem function including the morphodynamics of river reaches.

8.5.2 Catchment Management Approaches and Climate Change

Naturally-functioning riparian zones are biodiversity 'hotspots' with exceptional concentrations of endemic species, but they have experienced exceptional loss of habitat over recent decades (Myers et al., 2000; Johnson, 2002), and thus represents a critical opportunity for conservation. The conservation of riparian landscapes encompassing mosaics of protected areas, unprotected areas of conservation interest, and varying forms of human settlement and use, usually involves the design and implementation of different management interventions and the engagement of policy-makers at the local, national and international levels on issues such as climate change that have wider and long-term implications. As the efforts to conserve ecosystems increase to encompass previously overlooked habitats (e.g. large wood structures) supporting distinct assemblages of natural communities whose ecological interactions are critical for their long-term persistence, the issues of climate change and / or its effects, probably compounded by management actions, have come to the forefront of the global debate. Therefore, based on the findings of this thesis, the sections below consider present management actions or decisions adopted in the respective research sites that are influenced by natural wood loading (Highland Water and Tagliamento River) and proposes possible scenarios and alternative management actions, aimed at delivering biodiversity and ecosystem outcomes at different scales.

(i) The Highland Water, New Forest

The European Commission and United Nations designations of Special Protection Area (SSSI / SAC) and Wetlands of International Importance (International Convention on the Conservation of Wetlands), respectively, impose international as well as national conservation responsibilities on the managers of the New Forest National Park (New Forest Association, 2011; Ramsar, 2013). It is believed that the many demands from grazing, tourism, recreation and infrastructure development (e.g. roads, gravel extraction) are exceeding what some habitats within the New Forest can sustain (Denton, 2006; Rotherham, 2013) and that as a result there is the potential for damage of these natural habitats and associated wildlife.

The New Forest streams, including the Highland Water, have been undergoing human modification since the 1870's to improve ground conditions for forestry and grazing (Tubbs, 1986; New Forest Association, 2011). These modifications have encompassed the removal of large wood structures from the Highland Water channel and controlled grazing in its floodplain forest. Large wood structures along the Highland Water are not only important in maintaining considerable geomorphological and ecological diversity, but also contribute to the function and condition of some SSSI / SAC habitats on the floodplain, notably riparian woodland, mires, wet grassland and bog woodland, through their impact on seasonal floods. Seasonal flooding of the floodplain is particularly important as it contributes to the supply of fine sediment and propagules, essential for the survival of one of the finest floodplain forest in Britain, which sustains several plant species that are rare, vulnerable, endangered or nationally scarce (Ramsar, 2013). However, the management of large wood structures along the Highland Water has been a contentious issue over the years, as these structures have often been indiscriminately removed by the Environmental Agency (Forestry Commission, 2009). This management action has the potential to reduce river channel dynamics, which construct the floodplain, and the opportunity for natural flooding of the floodplain, thus (i) concentrating flow energy within the river channel resulting in increased erosion, transport of gravel, the potential for channel bed incision (as has been obeserved in some reaches) and consequently reducing morphological complexity, and (ii) reducing the possibility for the exchange of fine sediment and propagules between the channel and the floodplain, and the seeding of floodplains through hydrochory, thus potentially resulting in a decline in riparian floral diversity. Further, pressures from overgrazing by livestock (e.g. cattle, pig, New Forest ponies) have caused a decline in floral diversity on the floodplain (European Commission, 2003; Rare Breeds Survival Trust, 2014), an observation confirmed by the relatively low species diversity recorded in the propagule bank. This has led to the radical decision to progressively limit the number of ponies, which has had a counterintuitive effect, leading to a considerable decline in the population of New Forest ponies in a short period of time (Ramsar, 2013; Rare Breeds Survival Trust, 2014). Therefore, there is the need for managers of the New Forest to maintain an optimal livestock population and supply of large wood to the stream channel. If both are kept in a state of equilibrium, this may produce desirable effects and favourable conditions critical to maintaining and controlling plant community dynamics in the different SSSI / SAC habitats along the Highland Water as well as securing the long-term viability of grazing animals in the New Forest.

In the South East of the UK, where the New Forest is located, climate change is likely to lead to hotter and drier summers, milder and wetter winters, and increased flood risk and soil erosion (New Forest National Park Authority, 2007). These apparent temporal trends in temperature and flow rates may intensify the seasonal changes in the delivery of organic matter and / or biogeochemical processes (e.g. decomposition rates), and differences in the character of sediments mobilised and deposited by hydrological events, particularly floods. As large wood structures significantly store relatively more fine sediment, organic matter and propagules (i.e. carbon sinks) and provide suitable colonisation sites for emergent aquatic and wetland plants, a reduction in river flow rates and an increase in temperature during the drier summers may lead to the rapid proliferation and establishment of vegetation within and around large woods structures, resulting in the likely development of new floodplain habitats. This increase in vegetation, is of course dependent on light penetration of the forest canopy, which may also be affected by climate (or grazing) change. In either case, the development of increased shade from aquatic plants or tree shading may contribute to a cooling of water temperature that may in part counteract rising summer water temperatures induced by climate change. An increase in river flow rates during the wetter winters may lead to increased flooding and thus seeding of a larger area across the riparian forest, probably resulting in changes to the natural structure and species composition of woodlands such as the loss of species (local extinction) due to changes in or loss of habitats and the widespread distribution of some flora due to an expansion of the spatial range of their habitats. Therefore, for the New Forest to survive for future generations, there is the need for managers to firmly plan for these potential impacts and adapt sustainable land management actions aimed at primarily minimising the adverse effects of climate change or taking advantage of any potential benefits at different scales to improve biodiversity.

(ii) The Tagliamento River

The Tagliamento River, a proposed reference river for the European Alps (Ward et al., 1999) with connectivity between landscape elements crucial for sustaining functional processes, and physical and biological diversity, is a river of good status as defined by the Water Framework Directive. The whole Tagliamento basin is subject to severe threats, primarily sediment (sand and gravel) mining, water withdrawal and infrastructure development (e.g. hydropower installations, and high-voltage power line and highway construction) (Bertoldi et al., 2008), that have both direct (e.g. sediment mining) and indirect (e.g. flow regulation, highway construction) effects on channel morphology and ecological dynamics. As demonstrated in this thesis, the continual interactions between large wood and sediment in braided rivers influences the ecological engineering of a suite of landforms such as islands. Consequently, to maintain the ecological integrity and the self-restoration capacity of the Tagliamento river, anthropogenic activities must be properly managed to sustain the supply of wood and coarse and fine substrate to the braidplain, in order to drive positive ecological-physical feedbacks that reflect the provision of numerous water management benefits, in the form of biodiversity conservation, flood amelioration, nutrient management and aquifer recharge.

IPCC assessments of the effects of climate change on precipitation and temperature in the Friuli region of Italy, where the Tagliamento River is located, indicates an increase in temperatures by approximately 5°C, especially during the summer season, and an increase in snowfall-snowmelt processes and subsequent river discharge variations (TRUST, 2011; Gunawardhana and Kazama, 2012) by the end of the 21st century compared to the present climate. Precipitation, thus river flow, is predicted to increase in the winter and decrease in the summer, spring and autumn seasons (Gunawardhana and Kazama, 2012), with implications on the Tagliamento River’s aquifer recharge. The projected spring-summer-autumn decrease poses a risk of water deficit for surface- and ground-water interactions, that are likely to be exaccerbated by irrigation pressures with the potential for increased nitrate pollution of groundwater. Simulations of climate change scenarios show that by the end of the 21st century, annual aquifer recharge in the Friuli region is anticipated to decrease by 11 %, reducing the available annual groundwater volume by 335 Million m^3 and consequently reducing groundwater available for irrigation by 10 - 15 % (TRUST, 2011). These pending threats to water resources (surface and groundwater), both in relation to quantity and quality, and their associated implications for biodiversity need to be addressed through planning and practical management in compliance with the European Water Framework Directive (2000/60/EC) and the Groundwater Directive (2006/118/EC).

Within the headwater and island-braided reaches of the Tagliamento River, large wood structures were observed to have an important influence on the retention and accretion of finer sediment on gravel bar surfaces, eventually leading to the development of pioneer islands that were found to support distinct propagule and vegetation communities. In testing the effectiveness of Managed Aquifer Recharge techniques, it has been shown that an increase in vegetation cover on habitats such as islands within the riverine landscape could restore groundwater by 70 % of the groundwater deficit induced by climate changes in the Friuli region (TRUST, 2011). Therefore, practical management strategies that safeguard the steady delivery and subsequent storage of wood within the active corridor of the Tagliamento River need to be adopted as this influences the development of a mosaic of vegetated island patches that not only ensure the recharge of groundwater but also the storage and uptake of carbon, essential for the Tagliamento River ecosystem to cope with changing climate conditions.

8.6 RESEARCH GAPS

At least eight specific research gaps arise directly from the research reported in this thesis and provide starting points for further research:

1. Relatively few seedlings of different species emerged in the germination trials reported in this thesis in comparison to other published data. In the present research, sediment samples were stored in cold storage before germination trials in order to ensure comparability in the results of the trials regardless of the time of storage. Nevertheless, this method of storage probably caused the loss of propagule viability in some species. Therefore, to be able to comprehensively evaluate the viable riparian propagule bank, sediment samples collected for future research should be immediately germinated to reduce the risk of losing propagule viability, with further treatments (e.g. scarification, chilling, freezing) then applied to break dormancy in those species that have very specific germination requirements.

For this approach to be feasible, it would be necessary to study reaches in a single environment at any one time in order to minimise the time and distance involved in transporting samples prior to germination.

2. Considerable spatial heterogeneity was observed in sediment calibre and organic matter content of different mesohabitats sampled in the present study, several of which were large wood-related mesohabitats. Active river channels and their floodplains exhibit numerous geomorphic and microtopographical features including levees; abandoned channels; back swamps; floodplain side channels; scroll bars, ridges and swales; pools; riffles; and bars. While some wood-related mesohabitats / landforms were the focus of the present research, other wood-related mesohabitats / landforms (as stated above) may also be hotspots for riparian forest regeneration. Therefore, research focussing on a wider range of wood-related fluvial landforms and related processes is a potentially fruitful area that is at present under-researched.

3. The observations reported in this thesis support the assertion that large wood accumulations moderate mobilisation, transportation and deposition of mineral sediment and organic particles including plant propagules. However, no direct observations of these processes were made. Little research has been devoted to this theme, but an understanding of the processes could contribute to improved design of wood emplacement in restoration schemes in terms of its ability to trap sediment and propagules and drive landform development and turnover.

4. Since the present research demonstrates that large wood structures are important reservoirs for propagules, it may be of interest to undertake experiments that compare the effectiveness of seeding riparian areas (hydrochory) in rivers with and without large wood structures respectively, as this may potentially be important for rapid colonisation and stabilisation of river bank and floodplain soil surface. The findings of this research may influence the management and economic choice of artificial seeding or natural stage-controlled seeding of cleared riparian areas over the long term.

5. The present research identified propagules and standing vegetation of different vegetative groups associated with different wood-related mesohabitats. Although a reasonable diversity of propagules and standing vegetation were observed in association with large wood accumulations, knowledge of the bio-engineering and life-history traits of these species (e.g. root architecture, canopy uprooting and flow resistances, growth rates, regeneration capacity) that might directly or indirectly influence substrate erosion resistance, a property critical for landform development and relevant to river self-restoration, remains limited.

6. Riparian zones of rivers in relatively undisturbed and disturbed (particularly urban) environments are particularly susceptible to invasion by alien or exotic plants due to a combination of disturbances that reduce competition and create (i) an early successional environment that is ripe for invasion, and (ii) the hydrochorous transport of propagules that are conveyed to suitably moist riparian areas in which germination may proceed (Décamps et al., 1995; Hood and Naiman, 2000). Some significant questions that follow from the above are: what proportion of propagules trapped in large wood accumulations are from non-native plants? What are the dynamics (spatial and temporal) of the propagules of these non-native species in relation to large wood characteristics and hydrological disturbance (e.g. flooding)?

7. Standing vegetation richness and cover was found to increase as island landforms developed within the active corridor of the braided Taglaimento River. The different stages of a plant's life cycle are important for their successful establishment and growth, and play a critical role in shaping vegetation communities of landscapes such as islands because they fluctuate through different stages of their developmental cycle (vegetation succession) including aging, dying back, and regenerating (McPherson and DeStefano, 2003). However, this fluctuation through the different stages of vegetation succession on islands within the braidplain has not been comprehensively

demonstrated empirically in this thesis and needs to be addressed in future studies.

8. Lastly, standing vegetation on islands sheds propagules that can germinate or become buried in the soil and accumulate in a propagule bank, whose characteristics have been found to be highly variable within and around evolving islands. This thesis has established that over time, the composition of standing vegetation and the propagule bank on islands changes. However, it would be of interest to emphatically and properly quantify the contribution of large wood-related propagule banks to the overall composition of standing vegetation as the propagule bank buffers plant populations against environmental and stochastic variability (Thompson, 2000) by influencing the effective population sizes and community dynamics of plants (e.g. Vitalis et al., 2004; Fenner and Thompson, 2005).

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APPENDIX I

Wood Accumulation Recording Sheet for Single-Thread Reaches

Preamble

The locations of large wood inputs, volumes of large wood stored in different reaches and number of jams along a reach is causally related to the morphological processes and local channel geometry. The accumulation type is a function of the size of large, key elements of large wood in the accumulation in relation to the channel width. The accumulation could be composed of single large wood pieces or a build-up of large wood pieces (jam). The classification of large wood jams aids in determining appropriate management strategies, according to their location within the drainage basin.

Information for this accumulation recording sheet was compiled from Angela Gurnell (pers. com.) and from the following data sources (in alphabetical order): Abbe and Montgomery (2003); Gregory et al. (1993); Guby and Dobbertin (1996); Gurnell and Sweet (1998); Gurnell et al. (1995); Gurnell, et al. (2000b); Gurnell et al. (2002); Gurnell (2003); Gurnell et al. (2005); Gurnell (2013); Wohl and Goode (2008, 2009); Wohl and Jaeger (2009); and Wohl et al. (2010).

Definition of Terminologies on Wood Accumulation Recording Sheet

Accumulation number: Number accumulations in sequence along the reach starting from downstream (to minimise disturbance).

Accumulation Character

Record relevant codes or values in the recording sheet box

Position	1	Within 2 channel widths upstream of bend
	2	At bend
	3	Within 2 channel widths downstream of bend
Class	1	Active (completely spans channel and causes change in water surface level during low flow)
	2	Complete (completely spans channel but does not affect water surface level at low flow)
	3	Partial (does not completely span channel)
	4	High (bridges channel from bank top to bank top)
Wood source	1	Unknown (source of wood cannot be determined)
	2	Riparian (sources of wood appears to be valley bottom adjacent to the channel)
	3	Hillslope (wood originates from a steeper landform adjacent to the valley bottom; either a depositional feature such as a moraine, or the valley wall)
	4	Floated (fluvial transport from upstream)

5 Hillslope mass movement/debris flow
6 Bank Undercutting
7 Other (other clearly defined source such as debris flow; explained in comments section).

Accumulation Dimensions

Record relevant measured values in the correct units in the recording sheet box

Jam % orientation to channel centre line	% of channel width (perpendicular to banks) occupied by a partial jam to nearest 10 %
Upstream-downstream width	Width of accumulation from most extreme downstream to upstream extent measured parallel to the banks (nearest 0.1 m)
Bank to bank width	Width of accumulation from bank to bank measured parallel to the accumulation crest (nearest 0.1 m)
Base to top accumulation depth	Depth of accumulation from bottom (usually river bed except for high accumulations) to top (nearest 0.1 m)

Accumulation Structure

Record relevant measured values in the correct units in the recording sheet box

No. wood pieces	Number of wood pieces > 1 m long and 0.1 m in diameter contained within the accumulation
Length of largest key wood piece and other wood pieces	Length of wood pieces which appear critical to supporting the accumulation and the length of other wood pieces in accumulation (nearest 0.1 m)
Diameter of largest key wood piece and other wood pieces	Diameter (mid-point of cylinder measured at both ends and averaged) of wood pieces which appear critical to supporting the accumulation and the diameter of other wood pieces in accumulation (nearest 0.05 m)

Orientation (Angle with Respect to Downstream Flow)

Horizontal orientation of large wood piece	Deviation of orientation from channel centre line to nearest 15 degrees

Repeat above for second and third largest wood pieces if present.

Decay Status

Degree of decay	1	Living wood (green or brown needles/leaves still attached, very fresh piece of wood, tree may appear to be living).
	2	Bark intact (all bark intact (no decay), a relatively new piece of wood)
	3	Bark completely or partly removed showing the xylem with limbs still attached
	4	Partially decayed xylem (moderately soft wood that cannot be pulled apart easily)
	5	Completely decayed xylem/rotten (very soft wood that can be pulled apart easily by hand)

Accumulation-Associated Channel Features

All features have some overlap with a zone extending to 1 channel width upstream or downstream of the accumulation. If any of the following are present, enter 'X' in the recording box and measure dimensions

Dammed pool	Pool immediately upstream of accumulation
Plunge pool	Pool immediately downstream of accumulation (scoured by water spilling from accumulation at high flows)
Marginal pool	Pool to side of accumulation (usually associated with partial jams)
In-dam pool	Pool scoured under the accumulation structure by underflows during high flows
Riffle	Raised area of channel bed comprised of coarse sediment, associated with highly disturbed shallow water at low flow
Unvegetated bar	Raised area of channel bed comprised of unvegetated sediment which protrudes above the water surface at low flow
Vegetated side bar	Raised area of vegetated channel bed located at the bank toe which protrudes above the water surface at low flow
Vegetated mid-channel bar	Raised area of vegetated channel bed located in the channel which is surrounded by and protrudes above the water surface at low flow
Vertical eroded bank	Bank with a vertical eroding face across part or all of the bank profile
Undercut eroding bank	Bank excavated at its base so that the toe is set back well beyond the upper part of the bank profile
Side channel	Secondary channel cut in the channel bank and floodplain by water diverted around the accumulation.

Riparian Variables

Dominant species on the floodplain	E.g., deciduous versus coniferous; dominant plant species

Wood Accumulation Recording Sheet

Survey date: ....

Observer (s): ....

Stream: ....

Start location (Cordinates): .... End location (Cordinates): ....

Reach No.: .... Reach Length: ....

Flow Velocity: .... Stream Stage Condition: ....

Notes:..

....

....

....

....

....

....

....

....

Accumulation (acc.) Number										
Channel Dimensions										
Channel width in m to nearest 0.5 m (1 channel width upstream of acc.)										
Max channel depth to bank tops in m to nearest 0.1 m (1 channel width upstream of acc.)										
Channel width in m to nearest 0.5 m (1 channel width downstream of acc.)										
Max channel depth to bank tops in m to nearest 0.1 m (1 channel width downstream of acc.)										
Accumulation Character										
Position										
Class										
Wood source										
Accumulation Dimensions										
Jam % orient. to channel centre line										
Upstream-downstream width (m)										
Bank to bank width (parallel to acc)(m)										
Base – top depth (m)										

Accumulation (acc.) Number										
Accumulation Structure										
No. wood pieces										
Total length of largest key wood piece										
Length within bankfull										
Length with the riparian										
Length 2nd largest wood piece										
Length 3rd largest wood piece										
Length 4rd largest wood piece										
Length Nth largest wood piece										
Diameter 1st largest wood piece										
Diameter 2nd largest wood piece										
Diameter 3rd largest wood piece										
Diameter 4rd largest wood piece										
Diameter Nth largest wood piece										
Orientation (Angle With Respect To Downstream Flow)										
Hor. Orient. 1st largest piece										
Hor. Orient. 2nd largest piece										
Hor. Orient. 3rd largest piece										
Hor. Orient. 4th largest piece										
Hor. Orient. Nth largest piece										
Decay Status										
Degree of decay										
Accumulation-Associated Channel Features (Within 1 Channel Width Of The Acc.)										
Dammed pool										
Plunge pool										
Marginal pool										
In-dam pool										
Riffle										
Unvegetated bar										
Vegetated side bar										
Vegetated mid-channel bar										
Vertical eroding bank										
Undercut eroding bank										
Side channel (induced by acc. blockage)										
Riparian Variables										
Dominant species										

APPENDIX II

The Presence / Absence List of Established Vascular Plant Species on Pioneer Islands at Sites I, II and III

				Site I					**Site II**					**Site III**				
Plant species (latin names)	**Abbreviations**	**Life form**	**Life-history**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Achillea millefolium	Achi mi	Herb	Perennial	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Aethusa cynapium	Aet cyn	Herb	Annual	0	0	0	0	0	1	1	1	1	0	0	1	1	1	1
Agrostis canina	Agro ca	Grass	Perennial	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0
Agrostis setacea	Agro se	Grass	Perennial	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0
Agrostis stolonifera	Agro sto	Grass	Perennial	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Alnus incana	Alnus i	Woody	Perennial	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0
Alopecurus geniculatus	Alop g	Grass	Perennial	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Amorpha fruticosa	Amor f	Woody	Perennial	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
Angelica vulgaris	Ange v	Herb	Perennial	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1
Artemisia vulgaris	Artem v	Herb	Perennial	0	0	0	1	0	1	1	1	1	1	0	1	0	0	1
Aster novi-belgii	Aster n	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Buddleja davidii	Buddl d	Woody	Perennial	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1
Calamagrostis epigejos	Cala epi	Grass	Perennial	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0
Calamagrostis stricta	Cala str	Grass	Perennial	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1
Campanula rotundifolia	Camp ro	Herb	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Centaurea nigra	Cent n	Herb	Perennial	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0
Centaurea sp.	Cent sp	Herb	Perennial	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1
Cirsium arvense	Cirsi a	Herb	Perennial	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Clematis vitalba	Clem v	Woody	Perennial	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1

				Site I					**Site II**					**Site III**				
Plant species (latin names)	**Abbreviations**	**Life form**	**Life-history**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Convolvulus arvensis	Convo a	Herb	Perennial	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0
Conyza canadensis	Cony ca	Herb	Annual	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cornus sanguinea	Corn s	Woody	Perennial	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Coronilla emerus	Coro e	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Corylus avellana	Cory a	Woody	Perennial	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Crataegus monogyna	Crata m	Woody	Perennial	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Crepis paludosa	Crep p	Herb	Perennial	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dactylorhiza sp.	Dact sp	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Datura stramonium	Datu s	Herb	Annual	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0
Daucus carota	Dauc c	Herb	Biennial	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Descurainia sophia	Desc s	Herb	Annual	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Diplotaxis muralis	Diplo m	Herb	Annual	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Diplotaxis tenuifolia	Diplo t	Herb	Perennial	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1
Echium vulgare	Echi v	Herb	Biennial	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Elymus caninus	Elym c	Grass	Perennial	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Elymus farctus	Elym f	Grass	Perennial	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0
Elytrigia sp.	Elyt sp	Grass	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Epilobium montanum	Epi mo	Herb	Perennial	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Epilobium sp	Epi sp1	Herb	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Equisetum sp	Epi sp2	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Eupatorium cannabinum	Eup ca	Herb	Perennial	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1
Euphorbia cyparissias	Eup cy	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Euphrasia nemorosa	Eup ne	Herb	Annual	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Filipendula ulmaria	Filip u	Herb	Perennial	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0

				Site I					**Site II**					**Site III**				
Plant species (latin names)	**Abbreviations**	**Life form**	**Life-history**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Frangula alnus	Frang a	Woody	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Fraxinus excelsior	Frax es	Woody	Perennial	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Galium mollugo	Gali m	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Galium saxatile	Gali s	Herb	Perennial	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Galium verum	Gali v	Herb	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Glyceria maxima	Glyc m	Grass	Perennial	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Gypsophila repens	Gyps r	Herb	Perennial	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1
Hedera helix	Hede h	Woody	Perennial	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Hieracium lingulatum	Hier l	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hieracium perpropinquum	Hier p	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hypericum perforatum	Hyp p	Herb	Perennial	0	0	0	0	0	1	0	1	1	0	1	1	1	0	1
Hypochaeris glabra	Hypo g	Herb	Perennial	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Leontodon taraxacoides	Leon t	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ligustrum vulgare	Lig v	Woody	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Lotus corniculatus	Lot c	Herb	Perennial	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0
Lithospermum sp.	Lyth sp	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Melilotus albus	Meli a	Herb	Biennial	0	0	1	1	1	0	0	1	0	1	0	1	1	1	1
Mentha aquatica	Men a	Herb	Perennial	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Molinia caerulea	Moli c	Grass	Perennial	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1
Origanum vulgare	Orig v	Herb	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ostrya carpinifolia	Ostr c	Woody	Perennial	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Pedicularis sp.	Ped sp	Herb	Annual	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

				Site I					**Site II**					**Site III**				
Plant species (latin names)	**Abbreviations**	**Life form**	**Life-history**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Petasites hybridus	Peta h	Herb	Perennial	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1
Peucedanum palustre	Peu p	Herb	Biennial	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Picris echioides	Pic e	Herb	Annual	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1
Picris hieracioides	Pic h	Herb	Biennial	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Platanus sp.	Plane	Woody	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Plantago lanceolata	Plan l	Herb	Perennial	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1
Plantago major	Plan m	Herb	Perennial	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Poa palustris	Poa pa	Grass	Perennial	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1
Poa pratensis	Poa pr	Grass	Perennial	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Poa trivialis	Poa tr	Grass	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polygonum persicaria	Poly p	Herb	Annual	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Populus nigra	Pop n	Woody	Perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Reseda lutea	Res l	Herb	Perennial	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0
Robinia pseudo-acacia	Rob p	Woody	Perennial	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Rubus caesius	Rub c	Herb	Perennial	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Salix alba	Sal a	Woody	Perennial	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0
Salix elaeagnos	Sal e	Woody	Perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Salix purpurea	Sal p	Woody	Perennial	0	1	1	1	1	1	1	1	0	1	0	0	1	0	1
Salix sp.	Sal sp	Woody	Perennial	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1
Salix triandra	Sal t	Woody	Perennial	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Sanguisorba minor	San m	Herb	Perennial	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0
Scabiosa columbaria	Sca c	Herb	Perennial	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1

				Site I					Site II					Site III				
Plant species (latin names)	**Abbreviations**	**Life form**	**Life-history**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Sedum reflexum	Sed re	Herb	Perennial	0	0	1	0	1	1	1	1	1	0	0	1	0	1	0
Senecio aquaticus	Sen a	Herb	Biennial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Senecio sp.	Sen sp	Herb	Biennial	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Serratula tinctoria	Sera t	Herb	Perennial	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Solidago canadensis	Soli c	Herb	Perennial	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Sonchus arvensis	Son a	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Succisa pratensis	Suc p	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Taraxacum officinale	Tar off	Herb	Perennial	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0
Teucrium chamaedrys	Teu c	Herb	Perennial	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Thymus serpyllum	Thy se	Herb	Perennial	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Trifolium campestre	Tri c	Herb	Annual	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tripleurospermum maritimum	Tri m	Herb	Perennial	1	1	1	0	0	1	0	0	1	0	1	0	1	0	1
Tussilago farfara	Tus f	Herb	Perennial	0	1	1	1	1	0	0	0	0	0	0	0	1	0	1
Verbascum sp.	Ver sp	Herb	Biennial	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Vicia cracca	Vic c	Herb	Perennial	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1

	Site I					**Site II**					**Site III**				
Summary of variables investigated / Pioneer Islands	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Diversity															
Species richness	12	22	27	23	12	26	33	35	26	19	25	24	30	33	43
Vegetation cover	5	10	10	10	5	80	80	95	90	95	100	95	100	100	100
Life form															
Number of herb species	6	11	15	14	6	12	20	23	18	8	15	13	19	21	30
Number of grass species	0	4	5	5	2	5	6	4	5	2	2	5	2	3	5
Number of woody species	6	7	7	4	4	9	7	8	3	9	8	6	9	9	8
% Herb species	50	50	56	61	50	46	61	66	69	42	60	54	63	64	70
% Grass species	0	18	19	22	17	19	18	11	19	11	8	21	7	9	12
% Woody species	50	32	26	17	33	35	21	23	12	47	32	25	30	27	19
Life-history															
Number of annual species	1	1	3	2	0	2	4	2	1	0	1	1	1	2	4
Number of biennial species	0	0	2	2	1	1	1	1	0	1	1	1	2	2	4
Number of perennial species	11	21	22	19	11	23	28	32	25	18	23	22	27	29	35
% Annual species	8	5	11	9	0	8	12	6	4	0	4	4	3	6	9
% Biennial species	0	0	7	9	8	4	3	3	0	5	4	4	7	6	9
% Perennial species	92	95	81	83	92	88	85	91	96	95	92	92	90	88	81