Aquatic vegetation processes in a floodplain-river system and the influence of lateral dynamics and connectivity

Antoine A. Keruzoré

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Supervisors:
Dr. Nigel Willby
Prof. Dave Gilvear

UNIVERSITY OF
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STATEMENT OF ORIGINALITY

I hereby confirm that this PhD thesis is an original piece of work conducted independently by the undersigned and all work contained herein has not been submitted for any other degree.

All research material has been duly acknowledged and cited.

Signature of Candidate

Antoine A. Keruzoré

Date: 16th of August 2012

GENERAL ABSTRACT

In river ecology the description and understanding of near-natural ecosystem functionality is a difficult task to achieve as the majority of river floodplains have been intensively impacted by human activities. This work addresses ecological functionality of a relatively unimpacted large river system, focussing on the lateral dynamic and connectivity mechanisms driving aquatic vegetation processes. Macrophytes were found to be very patchily distributed at the riverscape scale, being mainly confined to low energy lateral habitats in the floodplain, such as backwaters. Backwaters provided favourable conditions for plants to colonise and recruit and contributed highly to species diversity and productivity at the floodplain scale. Differences between backwaters were attributed to the frequency of connectivity with the main channel during flood events. Nevertheless, the ecological mechanism driving diversity through flooding appears not to be related to flow disturbance. Biomass produced in backwaters was found to remain stable after potentially scouring floods. Therefore the hypothesis that flood disturbances promote species diversity through the removal and destruction of biomass and rejuvenate communities such that species coexistence is increased was rejected. Rather, it appears that diversity in backwaters increases along a temporal gradient as a response to the input of colonists and their accumulation overtime through successive flood inputs. Despite the apparently non-destructive effect of floods on macrophyte biomass, backwaters appear to have a significant role in exporting large amounts of plant propagules from the site of production. Backwaters represented a net source of propagules which highly enriched the main channel pool of potential colonists. However, whereas propagules could be dispersed for long distances in flood flows the probability for them to reach a suitable downstream habitat was extremely low. This work showed that dispersal at baseflow and entry to backwaters through the downstream end after short dispersal drift provided a greater chance of successful colonisation despite the individually much shorter distance moved. Backwaters were demonstrated to be rather isolated aquatic habitats, even though they experience hydrological connectivity, suggesting that primary colonisation of these sites is a limiting step. Instead, colonisation was shown to rely primarily on propagules generated internally by established plants. Whereas colonisation could occur via internal re-organisation of existing plant propagules, the backwater seed bank could also contribute to the macrophytes species established in backwaters. Such contribution was consistently low to medium along a gradient of disturbances and connectivity and showed independence from such river flow processes. Species richness was found to be higher in the established species than in the seed bank, suggesting that asexual reproduction is prioritised by aquatic vegetation in riverine backwaters. The occurrence or persistence of macrophyte species in backwaters depends upon rhizome and plant shoot regeneration. The lack of influence of connectivity revealed that plants may originate from both in situ and externally waterborne vegetative propagules derived from other upstream backwaters. This research demonstrated that the lateral dynamic and associated connectivity are major components of river floodplain ecology which generate a wide spectrum of habitats and have a controlling effect on vegetation processes. Therefore a naturally dynamic ecological state is required to support ecosystem functionality in large river floodplains and especially to maintain a high level of species diversity, productivity and colonisation of backwaters by macrophytes.

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CHAPTER I.

GENERAL INTRODUCTION

I.1. SCIENTIFIC BACKGROUND

I.1.1. *River floodplain structure and dynamic*

Riverine floodplains have a unique position in lotic freshwater ecosystems. Indeed they are located at the lowest topographic point in a landscape and consist of a spatially dynamic mosaic of aquatic habitats organised along a main linear feature extending from the headwaters to the sea (Tockner *et al.* 2010). Such elements of the landscape expand and contract accordingly with flow variations. Floodplain elements are interconnected and dependent on adjacent surface and subsurface habitats as hydrological exchange occurs along longitudinal, lateral and vertical dimensions.

I.1*.2. Flow regime, disturbances and connectivity*

Natural floodplain-river systems present a dynamic flow regime. Flow pulses, with fluvial deposition and lateral planform instability, generate a wide spectrum of waterbodies, as secondary channel, backwaters, ponds, swamp areas and are a product of lateral dynamics (Ward *et al.* 2002). In this work, we will focus on riverine backwaters. We refer to 'backwater' as former river channel that lost its upstream connection through alluvial or woody debris deposition associated with lateral migration or channel instability. However, backwaters keep a permanent downstream connection to river channel (Bornette *et al.*, 1998a). As a result backwaters fulfil the lotic part of the riverscape with standing water conditions met at low flow. During flood flows with increasing water levels, the connection to the river corridor is briefly but fully restored overflowing the upstream part of backwaters and potentially creates disturbing and scouring conditions associated with high water velocities.

In river floodplains connectivity refers to “a permanent and episodic links between the main course of a river and various waterbodies lying in the alluvial floodplain” as during flood (Lasne *et al.*, 2007). In river floodplains floods are the main hydrological disturbances (Henry *et al.*, 1996). Flood related disturbances are recognised to increase spatial and temporal heterogeneity of riverine ecosystems (Poff & Ward 1990; Parsons *et al.* 2005). Therefore both connectivity and disturbances are closely related and interconnected. The degree and frequency of connectivity in river floodplains is controlled by the elevation differences and distance between disconnected waterbodies and river corridor as well as flood amplitude (Ward & Tockner, 2001; Tyser *et al.*, 2002). Connectivity, as with flood flow regime, can be characterised in terms of amplitude, duration, frequency and timing (Tyser *et al.*, 2002; Ward *et al.*, 2002).

I.1.3. *River floodplain diversity*

Natural river floodplains are among the most complex, biodiverse and productive ecosystems in the world (Tockner *et al*., 2002). Nevertheless 90% of the area of original river floodplains have been reduced or have disappeared through channel straightening and embankment (Tockner *et al.*, 2002) mainly for flood control, navigation, hydropower and agricultural expansion (Scholten *et al.*, 2005). However, the variability of natural flow regime in driving ecological processes and diversity of rivers is a deterministic structural feature of such ecosystems.

Indeed, in 2002 Amoros & Bornette recognized that connectivity, as experienced during flood disturbances, affects habitat heterogeneity. The variety of habitats and conditions forms a repetition of heterogeneous patches and niches (Santamaria, 2002) that favours and drives high species diversity in rivers and their associated lateral floodplain waterbodies. However, according to the Intermediate Disturbance Hypothesis (Grime, 1973; Connell, 1978), disturbances remove biomass and create gaps thus enabling new species to emerge and establish (Roxburgh *et al.*, 2004). At extreme disturbance intensity only the most resistant species can tolerate extreme conditions. Low disturbance is assumed to lead to competitive exclusion by a few dominant species monopolising resources. At intermediate level of disturbance intensity plays a major role in regulating competition by removing sufficient biomass for a maximum of species to coexist (Figure 1.2).

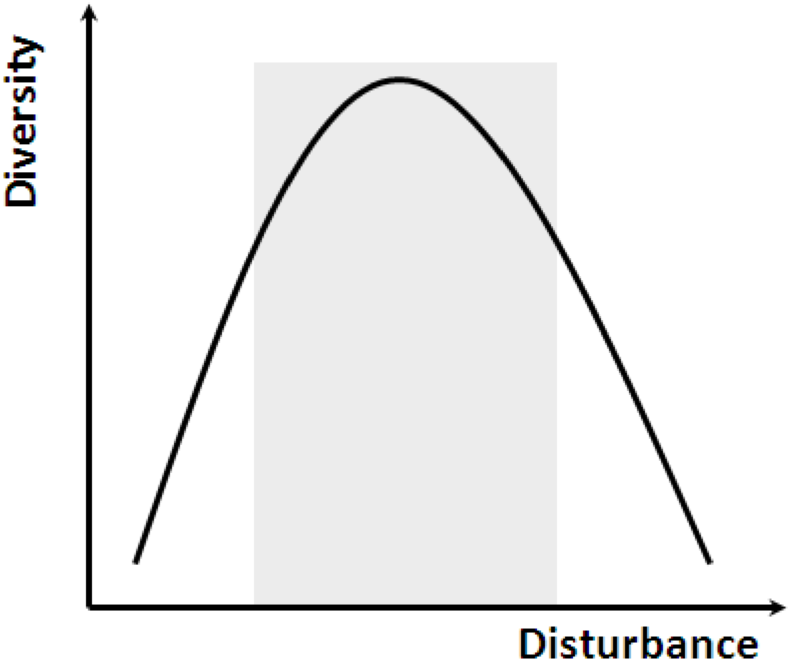


Figure 1.1. Intermediate Disturbance Hypothesis model representing species diversity along a gradient of disturbance. Grey area represents highest species diversity found at medium disturbance regime.

I.1.4. *Dynamics of macrophytic vegetation in riverine backwaters*

The term macrophyte refers to any aquatic plant that can be determined, usually to species level, by the naked eye (Janauer, 2001). Aquatic plants include all plants that occur permanently or seasonally in aquatic or wet environments (Barrett *et al.*, 1993). Macrophytes grow near or in the water and can be emergent, submergent, or floating.

In lowland rivers, macrophytes are controlled by flow disturbances (Franklin *et al.*, 2008). Indeed, the most important abiotic variables controlling macrophytes include discharge and velocity of the flow regime experienced that exerts hydrodynamic forces on plants. At the community level, aquatic plant species richness can reach a maximum value when flood scouring is of intermediate frequency and/or intensity (Bornette *et al.*, 1998a). At an individual level, whereas macrophytes may undergo plant breakage or uprooting, this will depend on the relative intensity of the hydrodynamic forces and/or the capacity of plants to resist or avoid damages (Schutten *et al.*, 2005). Some species have evolved the ability to maximise the anchorage strength. Also the reconfiguration of above-ground parts, such as plant placement or leaf orientation in the water column with increasing velocity (through flattening, alignment of shoots with flow direction and compaction or streamlining of leaves (O'Hare *et al.*, 2007)) seem to be important adaptations to resist mechanical damages (Bornette & Puijalon, 2010).

Exclusive competition through plant succession is another major driver of macrophyte diversity along rivers (Bornette & Puijalon, 2010). Successional patterns of macrophytes are driven by the age, nutrient concentration and disturbance patterns experienced in waterbodies (Van Geest *et al.*, 2005; Padial *et al.*, 2009; Sarbu *et al.*, 2011). Young waterbodies experience colonisation from pioneer species (*Chara spp.*, *Juncus bulbosus*, *Callitriche sp.*), whereas in ageing sites the dominance of more competitive species (e.g. nymphaeids) leading to terrestrialisation over decades, if not centuries and the replacement of strictly aquatic plants by emergent species (e.g. *Typha latifolia*). In eutrophic systems, higher productivity may lead more rapidly to the dominance of competitive species and accelerated plant succession (Khan & Ansari, 2005). Nevertheless, at patch or habitat scale flood disturbances may modify successional stage by resetting plant succession by removing macrophyte biomass at a local or wider scale (Pollock *et al.*, 1998).

In lowland and meandering rivers, backwaters present restricted connectivity aside from flood flows, and offer favourable flow conditions supporting extensive growth of macrophytes (Willby & Eaton, 1996). Indeed backwaters are usually accepted to be reservoirs of species diversity and productivity, as for macrophytes (Abernethy & Willby, 1999). Comparatively, the main stems of rivers are under constant flow velocity pressure and relatively devoid of macrophytes. Lateral habitats therefore concentrate vegetation and contrast with the main river corridor which is naturally almost devoid of vegetation. The metacommunity of macrophyte species at the riverscape level is therefore composed of several physically disconnected communities.

A key determinant of the vegetation dynamic (Figure 1.3) is the probability of reaching and colonising a suitable habitat (Pickett & McDonell, 1989; Bullock *et al.*, 2002). In the present context it supposes that colonisation will occur within the site of production or, after dispersal from the site of production, to downstream backwaters. Water movement is a significant vector for the dispersal of seeds or vegetative fragments of aquatic plants (Johansson *et al.*, 1996; Nilsson *et al.*, 2010). In river systems, propagule dispersal is commonly described as flood-induced and mediated (Sculthorpe, 1967; Okada *et al.*, 2009). Indeed high flows are able to generate plant fragments by breaking aquatic vegetation. Some species break and produce viable shoot fragments able to disperse over both short and long distances. Also seed release or remobilisation from sediments seems to be higher under increased flows (Boedeltje *et al.*, 2004). Once retained in an appropriate habitat for growth, dispersed propagules may successfully colonise and recruit new individuals near the parent plant, in distant empty patches or downstream habitats (Cellot *et al.*, 1998).

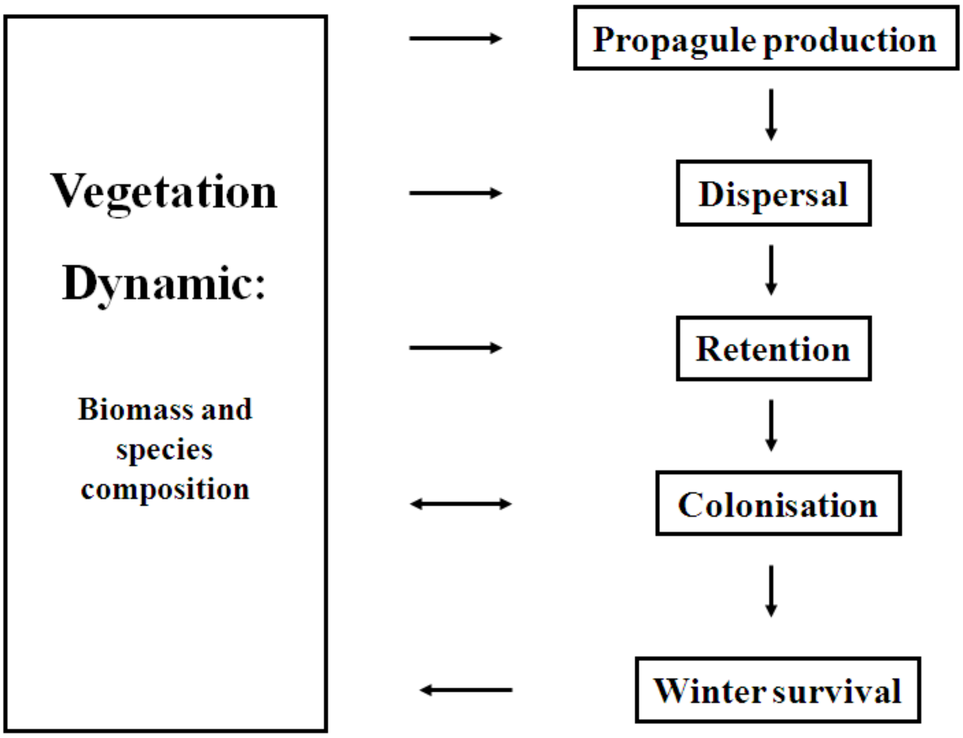


Figure 1.2. Vegetation dynamic model (modified from Riis, 2008).

I.2. GENERAL BACKGROUND AND OBJECTIVES

In 2000 The European Commission adopted the Water Framework Directive 2000/60/EC with the objective to achieve a sustainable management of all surface waters and groundwaters in EU Member States and in the UK. The directive requires EU members to reach good status of all inland and coastal waters by 2015 and to define how this should be achieved through the establishment of ecological objectives. Setting environmental quality objectives to reach a good status involves assessment of the present ecological status of water bodies.

At present large river assessments remain rare and only partially consider river systems mostly due to practical issue. Channel dimensions, water velocity, depth and turbidity constitute challenging and limiting factors in surveying and gathering records. Ecological knowledge is therefore partial and targets limited types of aquatic habitats (Franklin *et al.*, 2008). In addition ecological assessments in large rivers are potentially unreliable as they commonly omit interconnected aquatic habitats found in the floodplain based. Finally current assessments are predominantly representative of the ecological conditions of disturbed and modified river floodplains (Thorp *et al.*, 2006). In this respect, assessments of ecological conditions of a relatively unimpacted large river system remain rare and difficult to achieve. However, such scientific knowledge is required to provide a balanced assessment of the ecological status of large rivers relative to pristine conditions and to advise appropriate restoration measure for degraded sites.

This work was designed to understand the role of natural mechanisms, such as lateral dynamic and connectivity, in driving and maintaining natural ecological processes.

Lateral connectivity is one element of hydromorphological integrity that is highlighted by the Water Framework Directive but the linkage between hydromorphology and aquatic ecology remains poorly understood. This work particularly focused on riverine backwater habitats found in the floodplain of large rivers as a product of river dynamic, and fluvial aquatic vegetation community in order to assess the role and potential importance of such habitats and their contribution to floodplain-river system ecology.

I.3. STUDY SITES

In 2002 Ward *et al.* developed a general and simple representation of a river floodplain in sub-dividing it into three distinct reach sections as follows:

i) Steep headwaters present constrained channel migration with high energy flows and are characterised by coarse substratum and a narrow floodplain;

ii) Medium-gradients of a floodplain present multiple braided or meandering channels with medium energy flows. The particular landform characteristics of these gradients include river bars, islands, oxbows and backwaters;

iii) Low-gradients of a floodplain present channel laterally stabilised by erosion-resistant banks of fine cohesive alluvium and low energy flows.

The present work mainly took place in the River Tay catchment, along River Tay and its major tributary the River Tummel in Perthshire, Central Scotland (Figure 1.3). These rivers are among the largest in the UK and have a predominantly upland catchment and are characterised by semi-natural floodplains and by gravel-bed main channels. This work focused on the backwaters of medium-gradient reaches of these rivers and their aquatic vegetation.

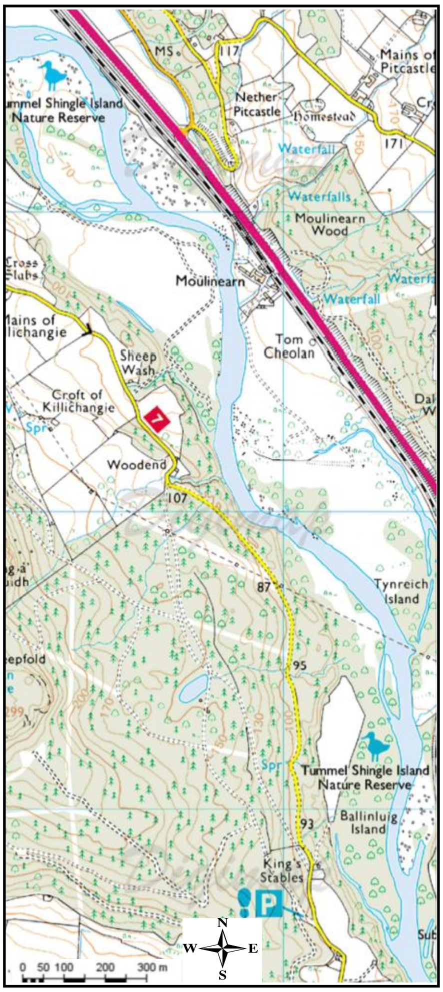
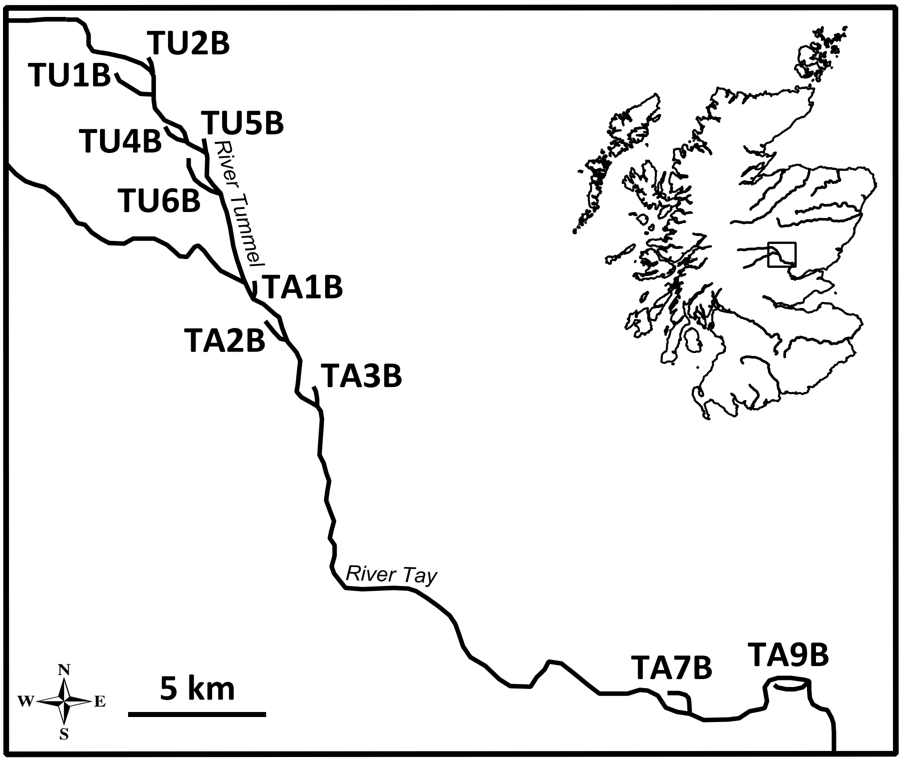


Figure 1.3. River Tummel reach and associated riverine backwaters, from Pitlochry to Ballinluig, Perthshire, Central Scotland (Source: Digimap®).

The River Tay discharges from Ben Lui, Western Scotland, to the Firth of Tay, South of Dundee. It has a catchment area of 5 200 km^2 and is the largest river in the UK by discharge (mean: 170 m3/s). It is the longest river in Scotland and the seventh longest in the UK. The River Tummel discharges from its source in Stob Ghabbar, Western Scotland, to the confluence with River Tay at Logierait after a course of 93 km (Figure 1.4). The River Tummel has a catchment area of 1670 km^2. The work concentrated specifically on a 33 km river reach (5.2 km on River Tummel and 27.8 km on River Tay) from Pitlochry to Haugh of Kercock (Figure 1.6 and 1.7) which is in a semi-natural condition and supports a high density of backwaters.



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In total 10 backwaters were assessed for this work with five backwaters distributed on River Tummel (TU1B, TU2B, TU4B, TU5B and TU6B) and Tay (TA1B, TA2B, TA3B, TA7B and TA9B) (Figure 1.8 and 1.9). These riverine backwaters are remains of former river channel and displayed a gradient of connectivity with the main channel (0.5 to 14 times per year). The river reach was surveyed from 2009 to 2011 according to the objectives described in more details in the methods sections of the subsequent chapters in this thesis.

A smaller part of the present work took place along the River Spey in the Scottish Highlands, Northeast Scotland. The River Spey discharges from Loch Spey to Moray Firth. It has a catchment area of 3 008 km^2, is the second longest and the fastest-flowing river in Scotland and has an average discharge of 64 m^3.s^{-1}. The work concentrated specifically on a 25 km river section from Newtownmore to Aviemore presenting semi-natural condition and also supports a high density of backwaters. Height backwaters were surveyed on River Spey (Figure 1.5).

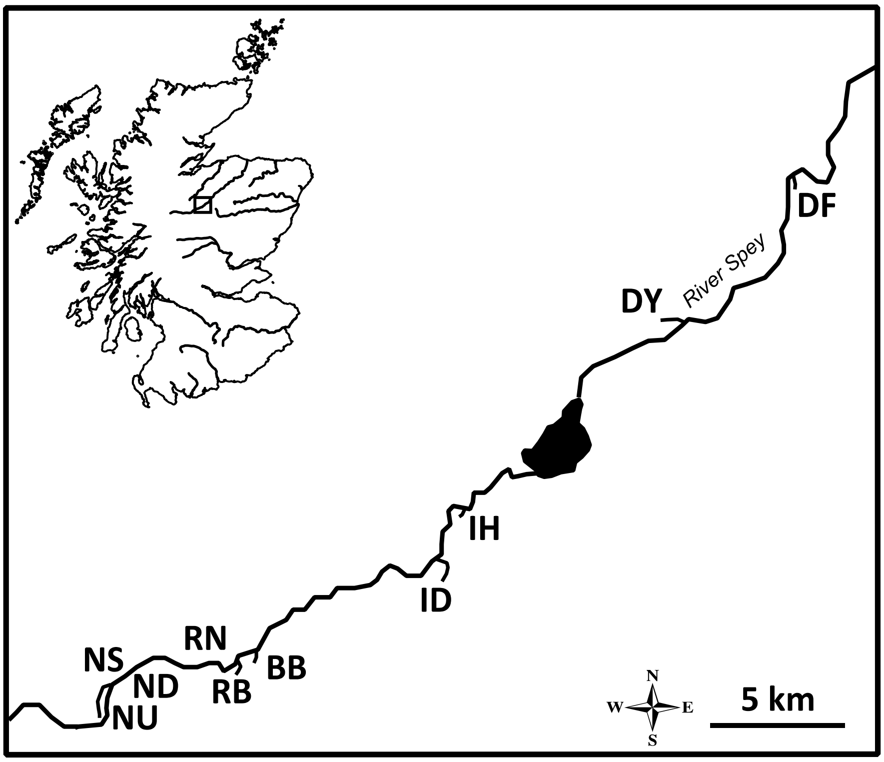

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Figure 1.8. Photograph of Tomdachoille backwater, River Tummel (© Antoine A. Keruzoré).

Figure 1.9. Photograph of Balmacneil backwater, River Tay (© Antoine A. Keruzoré).

I.4. SPECIFIC OBJECTIVES

1. The first objective was to survey macrophyte distribution, diversity and production at the floodplain scale and to identify the major environmental drivers. The study was specifically designed to cover a gradient of lateral connectivity and to compare main channel and floodplain waterbodies in order to determine the role of lateral dynamic and the ecological value of backwaters in a river floodplain.

2. The second objective was to determine the mechanisms responsible for driving species diversity in lateral aquatic habitat such as backwaters. Specifically it sought to test the relevance of the Intermediate Disturbance Hypothesis and whether coexistence of high species richness depends upon removal of biomass and the creation of by flood diturbance. It also aims to identify if connectivity and disturbance processes are joined mechanisms disrupting macrophyte communities in riverine backwaters.

3. The third objective was to assess the influence of flooding and connectivity in plant dispersal and colonisation. It sought to model empirically the dispersal of macrophytes produced in backwaters and the probability of propagules reaching and colonising suitable habitats, with a particular focus on dispersal to downstream habitat from site of production.

4. The fourth objective was to measure differences between established vegetation and seed bank species composition in backwaters along a gradient of disturbance. It was planned to assess the influence of disturbance regime in driving changes in similarity of both species richness and composition as mean of judging the relative importance of recruitment from the seed bank versus external inputs.

I.5. RESEARCH RESULTS RESTITUTION

The results gathered for this work are contained in this PhD thesis as a series of four research manuscripts organised as chapters as follow:

Chapter 2. The role of lateral connectivity in the maintenance of macrophyte diversity and production in large rivers.

Chapter 3. Aquatic vegetation in large rivers: do flood-related disturbances matter?

Chapter 4. Simulated plant dispersal and colonisation in large rivers; the influence of floods and connectivity.

Chapter 5. Seed banks and established vegetation in riverine backwaters: the influence of connectivity and fluvial disturbance.

CHAPTER II.

The role of lateral connectivity in the maintenance of macrophyte diversity and production in large rivers

Antoine A. Keruzoré[1], Nigel J. Willby[1], David J. Gilvear[1]

[1]School of Natural Sciences, Biological and Environmental Sciences, University of Stirling, Scotland, UK

Contact: antoine.keruzore@stir.ac.uk

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II.1. ABSTRACT

Large European river floodplains have been intensively reduced through human activities over several millennia. Ecological assessments of natural large river systems remain rare and potentially flawed with regards to the ecological status of the overall riverscape since they typically omit either the main channel of the river or, more commonly, aquatic habitats that occur naturally in the floodplain of dynamic systems. Surveys were conducted over a longitudinal and lateral gradient to assess distribution, richness and production of macrophytes along two little-disturbed large upland rivers in Scotland. Lateral dynamics, through the creation of backwaters, underpinned the occurrence, abundance and production of macrophytes in these rivers Indeed backwaters, despite representing only 5% of the total area of aquatic habitat, supported a significantly higher concentration of species (65% of species recorded at the riverscape scale were unique to backwaters) than the main channel. The frequency with which backwaters were connected to the main channel during flood flows influenced their species richness. Highest species richness in backwaters was typically found at low connectivity. Standing crop in backwaters was 150 times higher per unit area than in the main channel, while at the riverscape scale backwaters accounted for an average 89% of aquatic plant biomass. The highest plant biomass was found at low and medium connectivity with the main channel. Backwaters thus appear to be crucial habitats in maintaining macrophyte diversity and production in large river ecosystems. These results emphasise the importance of river hydrodynamics and lateral connectivity in maintaining macrophyte community diversity along large rivers. Additionally such results illustrate the potentially very significant role of backwaters as source habitats supplying propagules and organic matter to downstream reaches. We argue that the entire riverscape (floodplain plus main channel) must be considered in the holistic

assessment of such systems, while protection of this resource requires greater recognition of linkages within and across habitats, both aquatic and terrestrial, to be effective.

II.2. INTRODUCTION

Natural river floodplains are among the most biodiverse and productive ecosystems in the world (Tockner *et al*., 2002). Nevertheless, floodplains have been heavily reduced by human activities. At present in Europe at least 90% of the area of floodplains has disappeared through channel straightening and embankment (Tockner *et al.*, 2000). The main drivers for such reductions are flood control, navigation, hydropower and agricultural expansion (Scholten *et al.*, 2005). For instance, in Germany more than 76% of the Elbe floodplain has been converted into agriculture (Scholten *et al.*, 2005). In the UK no such figures exist but it is widely acknowledged that floodplains have been modified very extensively for agriculture (Bailey *et al.*, 1998). River flow regulation and reduction dictate that channel and flow dynamics are increasingly disconnected from floodplain ecosystems. Thus, near-natural examples of large ecologically intact rivers have become very rare (Bornette & Amoros, 1991; Nicolas and Pont, 1997; Yager *et al.*, 2011).

Natural river floodplains present a mosaic of habitats generated by fluvial deposition and lateral instability in planform associated with a dynamic flow regime. Such processes lead to the formation of a variety of waterbodies or backwaters within the riverscape that are almost lotic in character. In this paper, the term ‘backwater’ refers to a former river channel that has lost its upstream connection with the main stem through alluvial or woody debris deposition, but retains a downstream connection to the river channel (Bornette *et al.*, 1998a). During flood flows the upstream connection between backwater and main stem is briefly restored thus creating full continuity with the river corridor.

The restricted connectivity of backwaters to the river is believed to play a key role in providing refuge, reproduction and nursery habitats for various aquatic biota (Boedeltje *et al.*, 2001; Amoros & Bornette, 2002; Nunn *et al.*, 2007). Backwaters may therefore be seen as reservoirs of diversity and to be a significant lateral component of river floodplains (Tockner *et al.*, 2000). Despite this biological assessments of large rivers are typically confined to the main river channel only, or backwaters separately (Thorp *et al.*, 2006). Thus, assessments commonly fail to consider the contribution of floodplain waterbodies to the biodiversity, production and ecology of the overall riverscape or ignore the potential interactions between different aquatic habitat types. Even for some of the most studied large rivers in Europe, such as the Danube and Rhine rivers, little comparative quantitative information exists (Tockner & Stanford, 2002; Sarbu *et al.*, 2011). Also, in many large lowland rivers the main channel is no longer free-flowing due to impoundments for navigation or power generation which may reduce the contrast in physical character between the main channel and lateral aquatic habitats (Hohensinner *et al.*, 2004). At a larger scale, synoptic surveys of aquatic vegetation, from which criteria for conservation evaluation have been developed (e.g. in the UK, Palmer *et al.*, 1992; Holmes *et al.*, 1998), have ignored floodplain water bodies because they do not sit comfortably in conventional definitions of lacustrine or riverine habitats.

Macrophyte surveys of rivers generally focus on small wadeable channels due to the practical difficulty of surveying macrophytes in large rivers. The channel dimensions, water velocity, depth and turbidity of large rivers demands a fundamentally different survey approach to that used in small rivers. As a consequence knowledge of macrophyte ecology in large rivers is still limited (Franklin *et al.*, 2008). A sensible and realistic approach to monitor macrophytes in large river systems is needed to encompass more accurately the ecological relationships between the main river channel and its backwaters.

The aim of this research was to determine the role of lateral connectivity in driving the distribution, diversity and production of macrophytes in large rivers using as a case study two of the largest rivers in the UK (Tummel and Tay). This study first compares the distribution of macrophytes in main channel and backwaters using richness, composition and biomass to characterise the aquatic vegetation. Secondly, it analyses the response of vegetation in backwaters to various environmental variables including connectivity to the main channel. We hypothesised that: 1) backwaters will concentrate macrophytes and will be highly productive compared to the river corridor; 2) macrophyte richness and production will vary between backwaters as a function of their connectivity to the hydrologically dynamic main stem, as well as other factors, such as their fertility. From a conservation and methodological aspect this study aims to quantify the importance of riverine backwaters as aquatic habitats for macrophytes at the riverscape scale, whether they merit specific protection, and how they can contribute to the ecological assessment of large rivers.

II.3. MATERIALS AND METHODS

II.3.1. Study sites

Assessment of macrophytes took place along the Rivers Tummel and Tay between Pitlochry and Perth in Perthshire, Scotland (Figure 2.1). The Rivers Tummel and Tay are amongst the largest rivers in the UK (Tummel catchment: 1670 km^2, average discharge: 73 m^3.s^{-1}, maximum discharge: 706 m^3.s^{-1}; Tay catchment: 4991 km^2, average discharge: 169 $m^3.s^{-1}$, maximum discharge: 1554 $m^3.s^{-1}$). The river reach assessed was 33 km long (5.2 km on River Tummel and 27.8 km on River Tay). A total of 10 backwaters were monitored, five on each river. Backwaters were typically 200-500 m in length and, within the 33 km study reach, had a combined surface of 0.15 km^2 compared to a main channel surface area of 2.75 km^2.

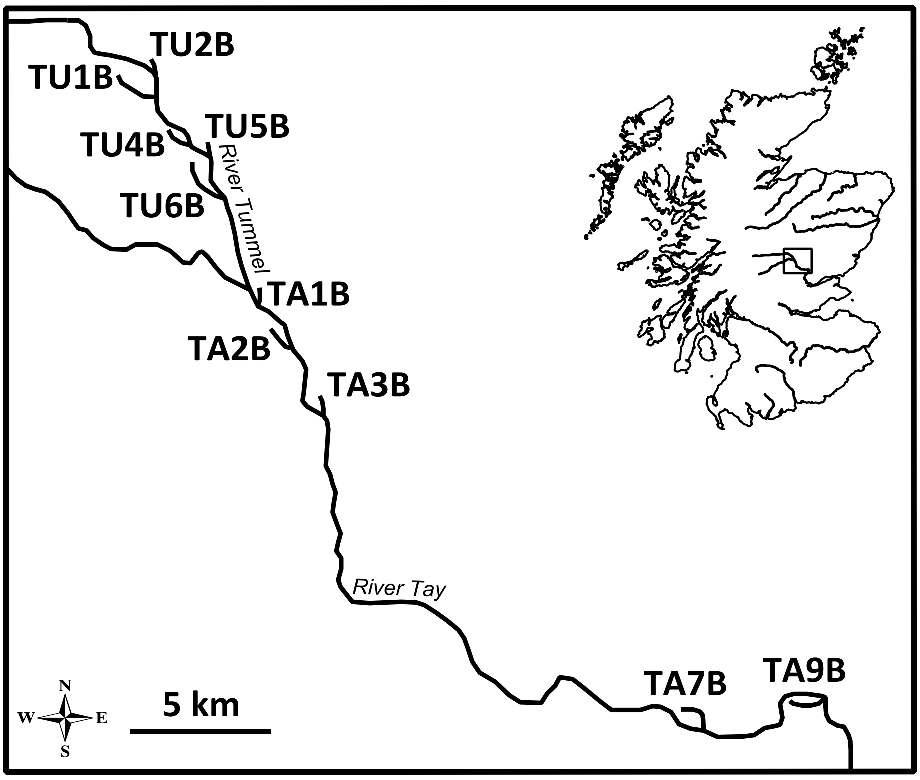

Figure 2.1. Map of Rivers Tummel and Tay river floodplains showing the position of the two rivers in Scotland and the assessed riverine backwaters.

II.3.2. Paired backwater and main channel macrophyte sampling

Backwaters and the main channel were surveyed in total on five occasions distributed over the growing season (May to September) of the years 2009-2011. Abundance of all aquatic macrophytes (subdivided into hydrophytes and helophytes) and their total biomass were recorded on each date. Backwaters and main channel were monitored using six transects established perpendicular to the channel. In backwaters these transects were equidistant in order to subdivide the site equally. Transects in the main channel were located adjacent to the relevant backwater by extending transects towards the river channel (Figure 2.2). Sampling effort was thus similar between backwaters and between backwaters and main channel. Presence of macrophytes was recorded in a 5 metre wide zone centred on each transect. Plant taxa were classified as either hydrophyte (submerged + floating leaved taxa) or helophyte (emergent taxa). Macrophyte biomass was collected in a 30 x 30 cm quadrat at three equally spaced points along each transect.

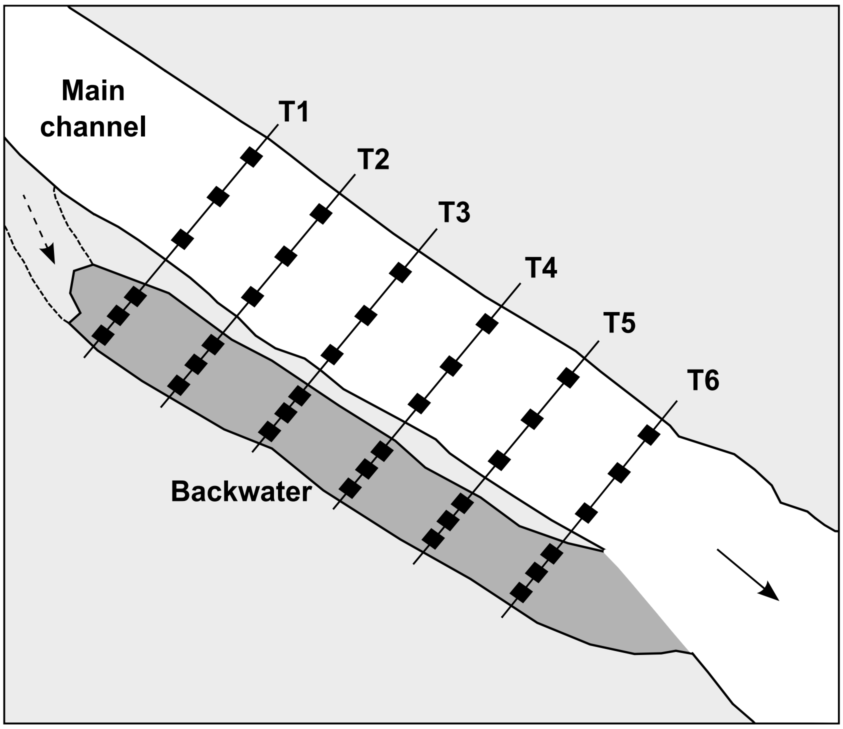

Figure 2.2. Macrophyte sampling methodology in backwaters and main channel. Lateral transects (T1 to T6) were equally distributed in backwaters and along the adjacent main channel sections. Dark grey colour represents the backwater area; white colour represents the main channel area. Species richness was surveyed along a 5 m wide strip centred on each transect (labelled T1 to T6) and biomass was measured at 18 sampling points (black squares) in main channel and backwater. Dashed section and arrow at the upstream part of the backwater represent connection with the main channel and backwater flow entering in flood.

Thus on each sampling occasion biomass was collected at 180 sampling points over all backwaters (10 x 6 x 3). In total 1800 quadrats were sampled in the backwaters (900 samples) and main channel (900 samples). For safety reasons (flow velocity > 1 ms^{-1} and water depth > 3 metres) some intended sampling sites in the main channel could not be physically sampled but when this was the case snorkelling and kayaking confirmed that these sites were extremely sparsely -or un-vegetated.

II.3.3. Laboratory processing

After collection samples were stored in a fridge at 4º Celsius and processed within 5 days of collection. For each sample biomass was separated into its component species. Samples were carefully washed to remove sediment and detritus, and then oven-dried at 80º Celsius for 48 hours and weighed to determine the dry weight.

II.3.4. Environmental parameters

For each backwater sinuosity, length, width, water depth and sediment size were recorded. For each sampling point in main channel and backwaters water temperature, dissolved oxygen concentration (LDO HQ20 dissolved oxygen meter) and light intensity at water surface (SKP 2200 light meter – SKP 210 PAR sensor) were recorded. Also, once per month over the growing season, three water samples per backwater and one in the main channel upstream from each backwater were collected for analysis of major nutrients. Nitrate (cadmium reaction), nitrite (sulphanilamide/N-1-naphthylethylene reaction) and ammonium (Berthelot reaction) were determined with a Bran Luebbe autoanalyser 3. Total phosphorus (antimony/molybdate reaction), was read at 690 nm with a Cecil Aquarius 7000 spectrometer. Connection frequency of backwaters with the main channel during flood flows was calculated by coupling levelling data for each backwater transect with hydrological data supplied by the Scottish Environment Protection Agency from 01/01/2000 to 31/12/2010 (station 15012 at Pitlochry (Tummel) and station 15006 at Ballathie (Tay)). By comparing water level and the sill elevation at the upstream end of each backwater the increase of water level required to initiate an upstream connection during flood events could be determined. The number of connections in the last 10 years was calculated for each backwater. In this study connection frequency refers to the average number of discrete connection events per year over the last 10 years.

II.3.5. Data analysis

Analyses were performed using the R statistical package (R Development Core Team, 2011). A Wilcoxon test was used to compare species richness and standing crop between backwaters and main channel. Differences between backwaters, and the effect of timing of sampling were assessed using the multiple comparisons Kruskal-Wallis test. Generalised Linear Models were performed to test the significance of environmental variables in explaining variation in plant richness and biomass in backwaters. Biomass data was root squared transformed prior to analysis. A log link function with Poisson distribution was used to model species richness. Environmental variables were treated as the fixed effect with site and transect as a nested random effect. Species composition in backwaters and main channel was compared using a non-metric multidimensional scaling (NMDS) ordination. Environmental determinants of vegetation composition in backwaters were tested using a canonical correspondence analysis (CCA).

Floodplain plant species richness was estimated using a sample-based rarefaction analysis to allow richness in different aquatic habitat types to be compared when sampling effort is standardised (R package Vegan). Floodplain standing crop was estimated using the paired measurements of the standing crop in backwaters and main channel over the three year survey period. These figures were then applied to the water surface areas of both habitat types obtained from a GIS analysis to estimate the proportional contribution of different habitats to production at the riverscape scale.

II.4. RESULTS

II.4.1. Environmental characteristics of backwaters

Main physical and chemical characteristics of surveyed backwaters and adjacent main channel sections are presented in Table 2.1 and 2.2. These tables were obtained using data collected from June 2009 to September 2011.

Table 2.1. General physical characteristics among surveyed main channel sections and paired backwaters.

					Sediment (% cover)			
	Sinuosity	Width (m)	Depth (m)	Velocity (m.s-1)	Silt	Sand	Gravel	Cobble
Main channel								
Average	1.1	71	2.1	1.6	0.0	1	8	91
Min.	1	51	0.6	0.6	0.0	0.0	3	88
Max.	1.2	105	9	3.5	0.0	1.5	12	100
Backwaters								
Average	1.2	17	0.75	0.0	21	17	11	51
Min.	1.1	5	0.36	0.0	0.0	0.05	6	0.0
Max.	1.6	32	1.1	0.01	88	90	35	99.9

Table 2.2. General chemical characteristics among surveyed main channel sections and paired backwaters.

Site	NO_3^- (mg.l^{-1})		NH_3^+ (mg.l^{-1})		Total P (mg.l^{-1})		pH		Conductivity (µS.cm^{-1})	
	Main channel	Backwater	Main channel	Backwater	Main channel	Backwater	Main channel	Backwater	Main channel	Backwater
TU1	0.148 ± 0.081	0.119 ± 0.099	0.009 ± 0.005	0.030 ± 0.045	0.011 ± 0.005	0.008 ± 0.003	7.3 ± 3.3	6.7 ± 0.1	39.0 ± 18.0	51.2 ± 8.9
TU2	0.153 ± 0.088	0.475 ± 0.318	0.012 ± 0.006	0.014 ± 0.010	0.009 ± 0.005	0.003 ± 0.008	7.4 ± 3.8	7.1 ± 0.2	42.3 ± 22.5	184.7 ± 106.5
TU4	0.156 ± 0.087	0.597 ± 0.299	0.013 ± 0.004	0.012 ± 0.008	0.007 ± 0.003	0.008 ± 0.012	7.4 ± 3.8	7.2 ± 2.0	41.2 ± 21.3	98.1 ± 26.2
TU5	0.168 ± 0.099	0.154 ± 0.097	0.007 ± 0.004	0.012 ± 0.008	0.011 ± 0.006	0.008 ± 0.004	7.5 ± 3.9	7.2 ± 3.3	41.4 ± 22.1	40.3 ± 19.7
TU6	0.137 ± 0.074	0.306 ± 0.225	0.011 ± 0.004	0.042 ± 0.024	0.009 ± 0.004	0.022 ± 0.008	7.6 ± 3.9	6.9 ± 0.3	40.6 ± 21.4	142.7 ± 17.8
TA1	0.157 ± 0.092	0.316 ± 0.240	0.006 ± 0.003	0.020 ± 0.025	0.009 ± 0.004	0.014 ± 0.006	7.4 ± 3.8	6.9 ± 0.2	40.7 ± 21.1	108.2 ± 79.4
TA2	0.204 ± 0.116	0.180 ± 0.135	0.004 ± 0.003	0.004 ± 0.003	0.010 ± 0.005	0.006 ± 0.002	7.3 ± 3.7	7.1 ± 0.2	43.2 ± 22.2	58.8 ± 18.2
TA3	0.190 ± 0.112	0.268 ± 0.165	0.009 ± 0.005	0.007 ± 0.005	0.008 ± 0.004	0.007 ± 0.003	7.4 ± 3.8	7.3 ± 0.1	42.5 ± 22.4	83.8 ± 41.9
TA7	0.150 ± 0.164	0.188 ± 0.169	0.014 ± 0.007	0.031 ± 0.014	0.011 ± 0.006	0.028 ± 0.015	7.5 ± 3.7	7.5 ± 0.4	45.8 ± 22.9	133.3 ± 61.9
TA9	0.241 ± 0.139	0.555 ± 0.319	0.017 ± 0.008	0.023 ± 0.013	0.010 ± 0.006	0.008 ± 0.004	7.5 ± 3.4	7.0 ± 2.9	41.5 ± 19.4	87.7 ± 43.8

II.4.2. Species richness analysis

II.4.2.1. *Comparison between river channel and backwaters*

Over two years of macrophyte surveys 65 species were recorded (30 hydrophyte taxa; 35 helophyte taxa). Many fewer species were recorded in the main channel (All taxa: 21 sp.; 4 hydrophytes, 17 helophytes.) than in backwaters over the same reach (All taxa: 63 sp.; 28 hydrophytes; 35 helophytes) (Figure 2.3). At the floodplain scale 5% of species (3 sp.) were recorded only in the main channel, 30% (20 sp.) were found in both main channel and backwaters and 65% (42 sp.) were unique to backwaters. Two of the hydrophyte taxa found in the main channel (*Ranunculus fluitans* and *Fontinalis antipyretica*) were also found in backwaters, whereas *Racomitrium aciculare* and *Lemanea fluviatilis* were found only in the main channel. Nine percent of main channel species (3 sp.) were found only there whereas 91% (20 sp.) were also common to backwaters. In backwater habitats 34% of species (20 sp.) were also recorded in the main channel whereas 66% of species (42 sp.) were only recorded in backwaters.

A full listed of recorded taxa in backwater and main channel habitats is given in Appendices 2.1 and 2.2. No relationship was found between richness and distance downstream along the 33 km studied reach for either main channel ($R^2 = 0.017$; p-value = 0.96) or backwaters ($R^2 = -0.214$; p-value = 0.55).

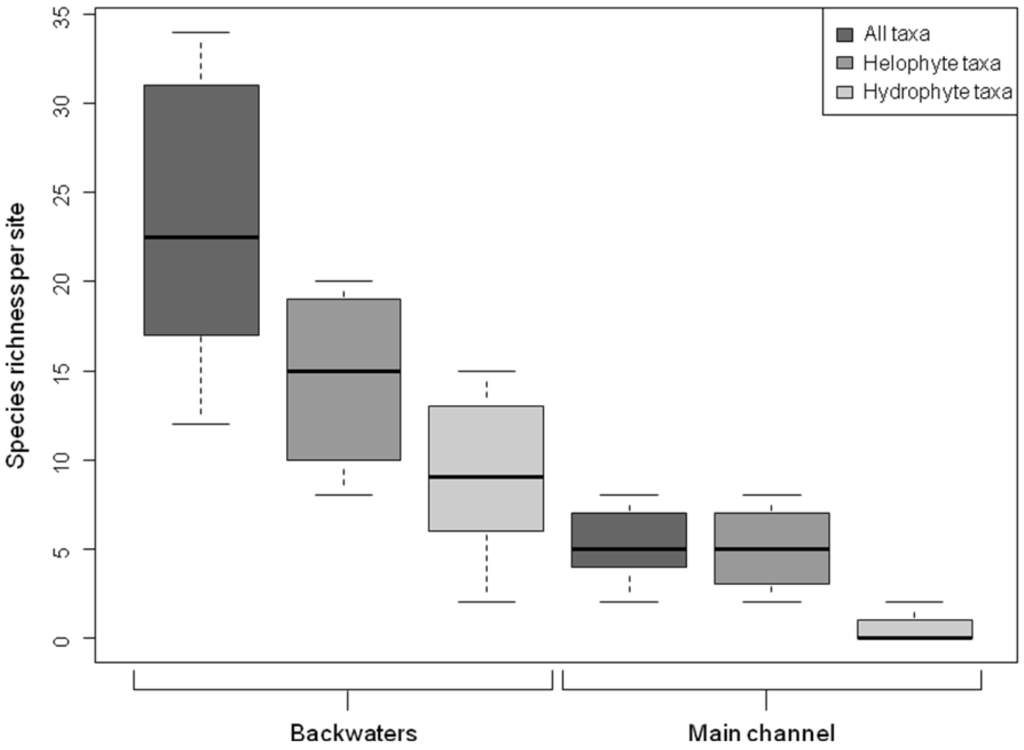

Figure 2.3. Species richness (all, helophyte and hydrophyte taxa) per site between and among surveyed main channel sections and paired backwaters.

Over all taxa recorded, richness was significantly higher in backwaters than in the main channel (Wilcox: W = 2500; p-value < 0.0001). Helophytes and hydrophytes showed higher richness in backwaters than in the main channel (helophytes: Wilcox: W = 2476; p-value < 0.0001; hydrophytes: Wilcox: W = 2461.5; p-value < 0.0001). Across plant groups differences in species richness between main channel and backwaters were independent of the timing of sampling (All taxa: Kruskal Wallis = 0.8821; df = 2; p-value = 0.64; Hydrophytes: Kruskal-Wallis = 0.2238; df = 2; p-value = 0.89; Helophytes: Kruskal-Wallis = 0.9097; df = 2; p-value = 0.63).

Analysis of compositional data by NMDS showed a clear partition between river channel and backwaters (Figure 2.4). No spatial pattern of similarity could be found between paired backwater-main channel sites at the floodplain scale. The Sørensen index of similarity between composition in backwaters and main channel ranged from 5% and 52% for all taxa, from 0% and 36% for hydrophytes and from 8% and 58% for helophytes. Values of the Sørensen index were not significantly correlated with connectivity for any plant groups.

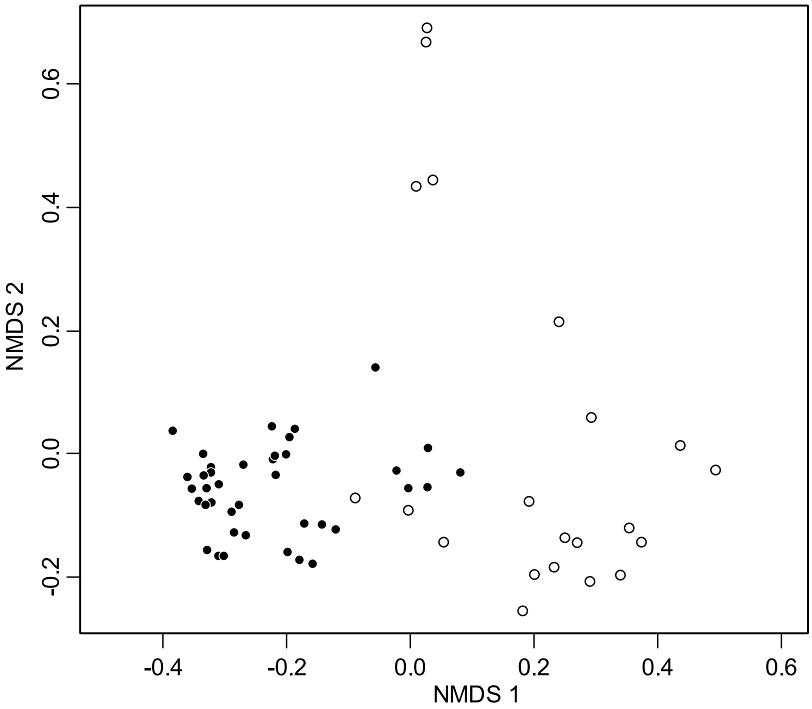

Figure 2.4. Non-metric multidimensional scaling ordination (NMDS) plot of species composition comparing main channel (o) and backwaters (•) distribution along the Rivers Tummel and Tay (stress = 0.16).

Richness within individual backwaters showed no evidence of the accumulation of species between successive transects that might be expected due to flow (All taxa: Kruskal-Wallis = 7.1839; df = 5; p-value = 0.21; Hydrophytes: Kruskal-Wallis = 6.8495; df = 5; p-value = 0.23; Helophytes: Kruskal-Wallis = 6.0324; df = 5; p-value = 0.30).

II.4.2.2. *Comparison between backwaters*

Total species richness in backwaters ranged from 9 to 34. The number of hydrophytes ranged from 1 to 15 and helophytes from 7 to 20. Richness varied significantly between sites (Kruskal-Wallis, $p < 0.0001$). Differences in richness between sites were independent of the timing of sampling (Kruskal-Wallis, $p > 0.05$). The CCA analysis showed that species composition of backwaters was related significantly (p-value = 0.01) to the frequency of connection to the main channel (Figure 2.5). Generalised Linear Models showed that species richness in backwaters was influenced significantly by connectivity with the main channel for all taxa and for hydrophytes (p-value < 0.05). Water depth was also a significant factor but of lower importance (all taxa: p-value < 0.05). No significant explanatory variables were detected for helophytes.

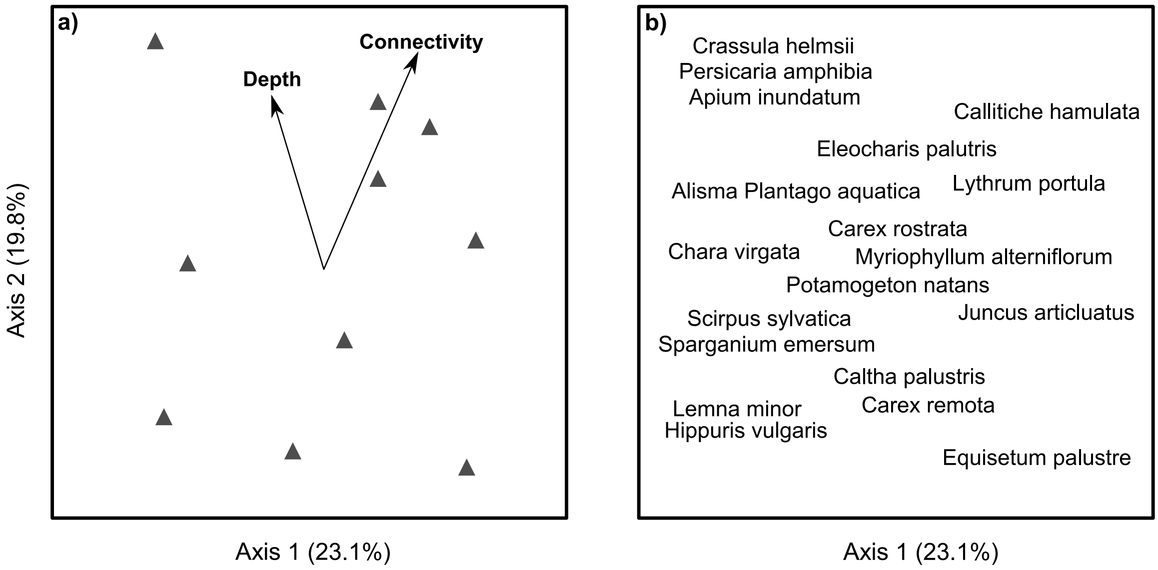

Figure 2.5. CCA ordination of backwaters by connection frequency categories. a) Ordination plot with connectivity as first axis and water depth as second axis; b) species plot showing the most common species recorded in surveyed backwaters.

II.4.2.3. *Floodplain species richness estimation*

Species richness estimation at the floodplain scale using a species accumulation curve constructed by randomised resampling demonstrated a consistently higher number of species in backwaters than in the main channel (Figure 2.6).

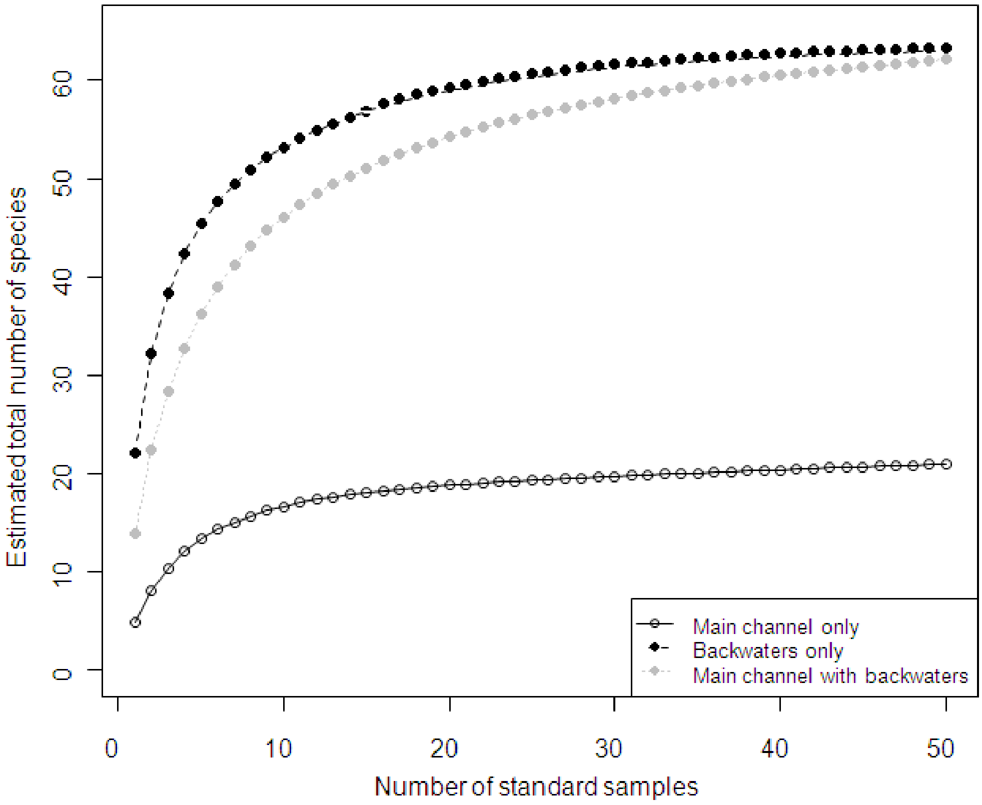

Figure 2.6. Species rarefaction curve (samples based rarefaction analysis) for main channel only, backwaters only and main channel with backwaters showing species accumulation with increasing numbers of individuals sampled.

Once sampling effort exceeded 25 standard samples the estimated species richness was asymptotic and was three times higher in backwaters (60 species) than in the main channel (20 species). An aggregate sample derived from a combination of backwaters and main channel was slightly less species-rich than backwaters alone due to the small number of unique species associated with the main channel compared to backwaters, but this aggregate ultimately converged at the same richness of 60 species. The differential between the channel only species pool, versus paired main channel plus backwaters together provides an indication of the scale of undersampling that will occur in large rivers if surveys are restricted to the main stem. Equally it indicates the potential scale of species loss if backwater habitats are disconnected from the main channel by engineering or flow regulation or degraded by drainage or infilling.

II.4.3. Standing crop

II.4.3.1. *Comparison between river corridor and sampled backwaters*

Plant biomass was significantly higher in backwaters than in the river corridor (Wilcox: W = 534047; p-value < 0.0001). Mean biomass produced in the main channel was 0.3 g m^{-2} compared to 40.3 g m^{-2} in backwaters. Biomass in backwaters was thus, on average, 150 times higher than in the main channel. Biomass in backwaters was generally a result of production by 2 to 4 species per sampling point (most commonly *Potamogeton natans*, *Myriophyllum alterniflorum*, *Carex rostrata* and *Callitriche hamulata*), whereas in the main channel it was a result of 1 or 2 species maximum. Timing of sampling did not influence the difference in biomass between river channel and backwaters (Figure 2.7); biomass was always significantly higher in backwaters than in the main channel (May: W = 44 566, p-value < 0.0001; July: W = 27 460, p-value < 0.0001; September: W = 21 779, p-value < 0.0001).

No relationship was found between biomass and distance downstream on the 33 km studied river reach for either main channel (R^2 = -0.148; p-value = 0.68) or backwaters (R^2 = -0.110; p-value = 0.76).

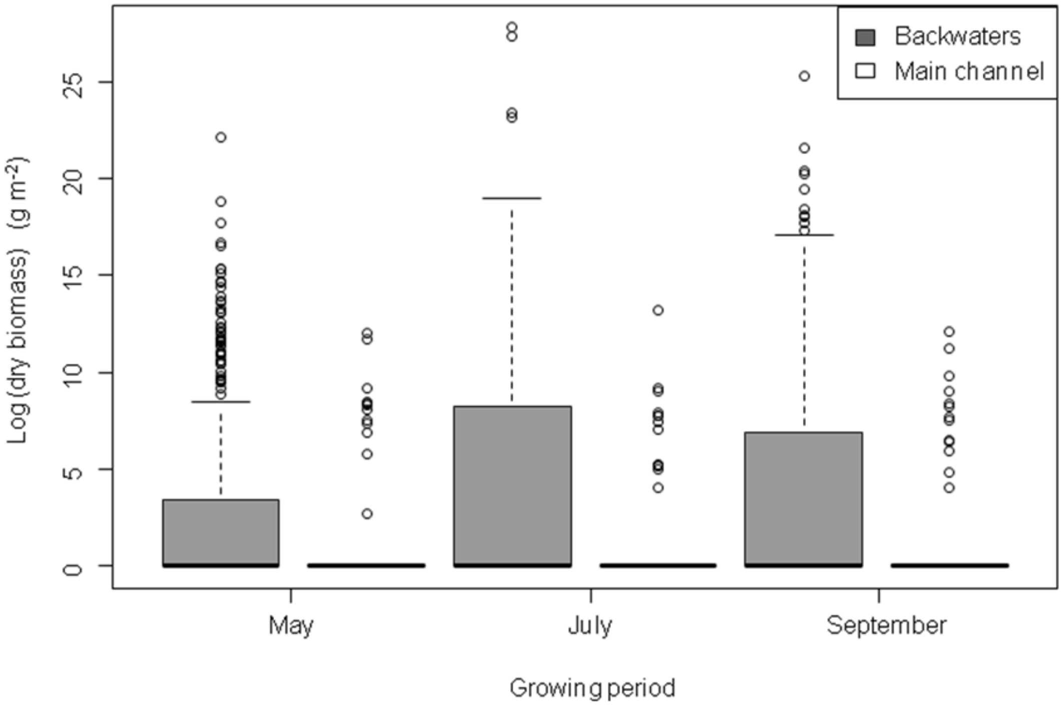

Figure 2.7. Variation of productivity along a seasonality gradient in backwaters and main channel.

II.4.3.2. *Comparison between backwaters and main channel transects*

Biomass was highly variable between backwaters (min < 0.1 g m^{-2}; max = 168.6 g m^{-2}) and significantly different between sites (Kruskall Wallis = 776.1; df = 9; p-value < 0.0001). Timing of sampling had a significant effect on biomass recorded in backwaters (df = 2, p-value < 0.0001) but not in main channel sections (df = 2, p-value = 0.61). Lowest biomass was found in May (27.2 g m^{-2} in backwaters and 0.2 g m^{-2} in the main channel), reaching a peak in backwaters in July (50.6 g m^{-2}) but remaining stable in main channel (0.2 g m^{-2}). In September biomass decreased in backwaters (45.8 g m^{-2}) and remained similarly low in the main channel (0.3 g m^{-2}). Differences in biomass were found along the longitudinal gradient within backwaters (Kruskal Wallis = 13.962; p-value = 0.016; df = 5). Biomass was significantly higher at transects located mid-way along backwaters whereas both upstream and downstream ends supported less biomass, suggestive of the effects of increased physical disturbance.

General Linear Models showed that biomass in backwaters was not influenced by connectivity with the main channel (p-value > 0.05). No significant explanatory variables were detected to explain biomass. However, sites with intermediate connectivity with the main channel presented the highest production (80.9 g m^{-2}; 168.6 g m^{-2}).

II.4.3.3. *Contribution to standing crop at the floodplain scale*

At the floodplain scale, along the 33 km reach of the rivers Tummel and Tay surveyed, backwaters and main channel accounted for 5% and 95% respectively of the total area of aquatic habitat. Visual inspection of maps for large rivers in Europe and North America suggests that this figure is fairly normal in natural systems. Based on this relative proportion, backwaters made a substantially larger contribution to floodplain standing crop than the main channel. Averaged across the growing season backwaters accounted for 89 % (2073 kg) of the standing crop in aquatic habitats at the floodplain scale compared to just 11 % (264 kg) in the main channel (Table 2.3).

Table 2.3. Distribution of dry weight standing crop in a standard unit of floodplain aquatic habitat (km^{-2}).

	Area of floodplain aquatic habitat	Percentage of floodplain aquatic habitat	May		July		September	
	(km^2)	%	kg	%	kg	%	kg	%
Main channel	2.75	95	234	15	233	8	325	12
Backwaters	0.15	5	1369	85	2545	92	2306	88
Total	2.90	100	1603	100	2779	100	2631	100

II.5. DISCUSSION

II.5.1. Macrophyte distribution

The occurrence and distribution of macrophytes in the floodplain had a strong lateral dimension. A profound difference was found between the river channel and backwaters (Figure 2.3 and 2.4). Macrophytes were principally recorded in backwaters since the standing water conditions were favourable for colonisation and growth (Bornette *et al.*, 1998a). Differences were even more pronounced with regards to strictly aquatic species. Recent studies of European large rivers (e.g. Danube) have underlined the presence of multiple macrophytes species in their main channel (Breugnot *et al.*, 2008; Janauer *et al.*, 2010) contrasting with the present results. However, many major European rivers are heavily impacted by eutrophication and impoundment which may lead to more favourable, albeit unnatural, conditions for growth of macrophytes in the main channel (Birk *et al.*, 2012). In previous studies of the distribution of riverine macrophytes velocity, flow regime, water depth and sediment size have all proved to be significant factors (Chambers *et al.*, 1991; Riis *et al.*, 2001; Demars & Harper, 2005; Riis & Biggs, 2003; Makkay *et al.*, 2008; Capers *et al.*, 2009).

In backwaters, macrophyte species richness was primarily influenced by connectivity with the main channel, as also reported by Robach *et al.* (1997), whereas water depth was of secondary importance. Species richness was negatively correlated with increasing connectivity (or disturbance intensity). Thus, aquatic vegetation will likely experience major abiotic constraints in establishing in the main channel. The interaction of these environmental factors strongly discriminates between macrophyte distribution in the river channel and backwaters. Accordingly, the estimated number of species at a floodplain scale (Figure 2.6) indicates that backwaters will contribute highly to diversity (65% of species in this study) and that the loss of lateral connectivity and aquatic habitats associated with human activities will therefore severely impact biodiversity in large river systems (Ward & Tockner, 2001). Spatial turnover of species between backwaters themselves was also relatively high contributing to a high overall species pool as backwaters covered a wide range of connectivity (Figure 2.5; 2.9; 2.10 and 2.11), whereas the main channel was relatively uniform with respect to factors that define viable habitat for macrophytes (Figure 2.8) and consequently different sites in the main channel accumulated species at a very low rate.

Figure 2.8. Photograph of River Tummel main channel (facing upstream) at Ballinluig, Perthshire, Scotland (© Nigel Willby).

Plant species composition and abundance has remained stable in these backwaters across several years, even though connectance, via major flood events, has occurred on multiple occasions. More detailed investigation is therefore required to identify which aspects of connectivity, such as physical flow disturbance, mediation of dispersal, or other ecological processes, are driving species richness and biomass production.

II.5.2. Productivity by macrophytes at the river floodplain scale

Bornette *et al.* (1998a) hypothesised that floodplain productivity would be mainly supported by backwaters. This is confirmed by the present study. On average, and across the growing season, main channel biomass was 0.3 g m^{-2} compared to 40.3 g m^{-2} in backwaters. Standing crop was therefore 150 times higher in backwaters than in the main river. However, biomass in backwaters was mainly driven by habitat variability in the floodplain and not by connectivity (Roberston *et al.*, 2001). As in Amoros and Bornette (2002) highest biomass occurred at medium disturbance regime, which might reflect an optimal equilibrium for production between physical disturbance at high connectivity, versus tree shading, potential nutrient depletion and competitive exclusion by floating-leaved species with low submerged biomass (e.g. nymphaeids or lemnids) at low connectivity. In the studied backwaters, and unlike some previous studies, nutrient concentrations did not control biomass (Bedford *et al.*, 1999; Hilton *et al.*, 2006) possibly because the nutrient concentrations were consistently low in most sites. Differences in biomass between backwaters and main channel were independent of the timing of sampling with respect to the growing season (Figure 2.7). At a larger scale backwaters presented a very high contribution to floodplain standing crop, accounting for 89% of aquatic plant biomass produced across the growing period (Table 2.3). A peak of production was reached in July where 92% of biomass was produced in backwaters. Previous quantitative assessments of production in different components of the floodplain are rare but this result is likely to be typical of undisturbed systems.

In the River Continuum Concept (RCC) production within the main stem of medium sized and lowland rivers is viewed as being mainly supported by in situ vascular hydrophytes and phytoplankton and algal production (Vannote *et al.*, 1980). The RCC has been applied to upstream reaches and large regulated rivers but is inappropriate for natural river floodplains as it only values the main river channel and ignores the importance of production in lateral habitats (Thorp *et al.*, 2006). In the flood pulse concept Junk *et al.*, (1989) drew attention to the significant lateral component of energy inputs to extensive floodplains and the ecological consequences of episodic flood pulses. Since then several workers have demonstrated that lateral habitats in large rivers are responsible for driving structural and functional processes in riverine ecosystems, such as production and nutrient cycling (Hein *et al.*, 2003; Preiner *et al.*, 2007). The present study demonstrates that lateral habitats associated with low energy flows, higher transparency of the water column and nutrient inputs from the main channel (Preiner *et al.*, 2007) produce favourable conditions for primary production by higher plants.

II.5.3. Nested functional role of backwaters in river floodplain ecology

This research illustrates the significant production occurring in backwaters and its potential contribution to the river floodplain ecosystem (Thorp *et al.*, 2006). Equally, Battle & Mihuc (2000) stressed the importance of backwater vegetation in decomposition and nutrient recycling. During high flow disturbances fresh plant material and propagules (Henry *et al.*, 1996), as well as inorganic matter, are exported from backwaters (Tockner *et al.*, 1999) which are thus key source habitats in large river systems (Cellot *et al.*, 1998). It is therefore tempting to say that backwaters are critical for nutrient recycling or for fish reproduction in large rivers, and thus for the wider ecosystem services that rivers provide. However, for nutrients or organic inputs, as well as passive propagule dispersal, their fate in downstream reaches and water bodies of the floodplain is uncertain (Cellot *et al.*, 1998). Therefore it may be unwise to generalise the influence that backwaters may exercise over floodplain functioning or downstream colonisation.

II.5.4. Implications for assessment of large rivers

The present survey provides a guiding image (Willby, 2011) of the distribution of macrophytes along a large natural upland river. The main channel itself is highly unrepresentative of macrophyte diversity and production at the riverscape scale, especially for hydrophyte taxa. A significant contrast between main channel and backwaters should be expected when surveying similar natural large rivers. Backwaters should therefore be considered as an inclusive part of the river system and not disregarded due to convenience or convention (Bornette *et al.*, 1998b). Recognising the contribution of floodplain water bodies to biodiversity at a riverscape scale requires well designed sampling protocols. Across backwaters, surveys should concentrate on covering a gradient of connectivity (Figure 2.9; 2.10; 2.11). Anthropogenic activities such as channel engineering, flow regulation, floodplain drainage and agricultural intensification will severely impair interactions between the main channel and floodplain aquatic habitats with knock-on effects on ecosystem functioning due to restrictions on the flow of biota and organic matter (Tyser *et al.*, 2001; Ward *et al.*, 2002). This investigation highlights the importance of a naturally dynamic flow regime since the associated processes of lateral instability and alluvial deposition promote the formation and turnover of lateral aquatic habitats in unconstrained reaches (Gilvear & Winterbottom, 1992) and regulate exchanges between main stem and backwaters. Therefore the existence of backwater habitats, their physical diversity, and the biota they support may yet prove to be the best guide to the integrity of large rivers, while the comparative ease of sampling backwaters may offer a partial solution to the practical difficulties of sampling main channel environments. Nevertheless, for an integrated assessment of the ecological quality of large rivers, the main stem cannot be ignored altogether.

Figure 2.9. Photograph of backwater experiencing high connection frequency with the main river channel, River Tay, Perthshire, Scotland (© Nigel Willby).

Figure 2.10. Photograph of backwater experiencing intermediate connection frequency with the main river channel, River Tummel, Perthshire, Scotland (© Antoine Keruzoré).

Figure 2.11. Photograph of backwater experiencing low connection frequency with the main river channel, River Tay, Perthshire, Scotland (© Nigel Willby).

II.5.5. Conservation perspectives for macrophytic vegetation of river floodplains

This study underlines the high value of backwaters in preserving macrophyte diversity and production in river floodplains. Therefore it is critical to adequately protect residual backwaters as they remain a reservoir of a large majority of the macrophytes that could occur in the lowland reaches of large rivers (Tockner & Stanford, 2002). However, backwaters are also used as reproductive and refuge areas for various life stages of a large range of other species (macro invertebrates, fish, amphibians, birds and mammals) (Amoros & Bornette, 2002) which increases their overall value. Barta *et al.* (2009) suggested that a gradient of flow conditions and connectivity of floodplain waterbodies to the main channel will maintain a higher diversity of species. Thus, at the floodplain scale, river systems containing backwaters with a range of connection frequencies to the main channel should support the highest diversity of aquatic vegetation and associated species (van der Nat *et al.*, 2003) and their protection should be prioritised.

Conservationists are by no means oblivious to the significance of floodplain aquatic habitats and there is an extensive literature on the importance of lateral river habitats for fish. Some of the most famous ornithological sites in Europe are associated with huge floodplain wetlands covered by Ramsar site designation, which effectively protects an entire wetland complex containing a variety of aquatic habitats, although fish are increasingly being cited in Ramsar designations. However, birds aside, floodplain water bodies themselves are not generally renowned for supporting large populations of rare species and as a habitat they do not feature in Annex 1 of the HD. Similarly, while the EU WFD places considerable emphasis on the assessment of both biological and hydromorphological quality elements in determining the ecological status of water bodies it fails to even mention the terms ‘floodplain’ or ‘lateral connectivity’, opting instead to highlight longitudinal continuity and connectivity to groundwater. Backwaters, as with many other freshwater habitats, therefore risk falling through the cracks – neglected by multiple key pieces of environmental legislation (Boon & Lee, 2005) and succeeding in achieving protection only when large enough to support major populations of qualifying bird species.

In reality floodplain backwaters themselves may be rather ill-suited to specific legal protection since this tends to pigeon-hole habitats and species, rather than recognising the connectivity between populations, life stages and habitats. Also, being the product of channel mobility, backwaters are rarely static features around which site boundaries can be neatly drawn. Most sites considered in the present study were in fact protected, either via designation under the Habitats Directive as Special Areas of Conservation (SAC), through being aligned with the Annex I priority habitat ‘alluvial forests of alder, ash and white willow’ (Habitat Type: H91E0), or by national designations as Sites of Special Scientific Interest due to the presence of mobile gravel bed islands supporting nationally important bird species. Elsewhere in the UK (e.g. on the Rivers Spey, Conon and Eden) or in other parts of Europe (e.g. France and Austria), floodplain aquatic habitats have also received international protection indirectly through association with alluvial forest (which is frequently associated with important heron colonies in continental Europe thus attracting additional protection as a Special Protection Area for birds). Alternatively, they have been included within sites qualifying as ‘Oligotrophic to Mesotrophic standing waters with vegetation of *Littorellion uniflorae* (H3130)’, as a component of ‘Transition mires and quaking bog (H7140)’ or ‘Water courses of plain to montane level with Batrachian *Ranunculus* vegetation (H3260)’. In other cases sites have benefitted from European protection through hosting or being attached to rivers which host Habitats Directive Annex 2 species, such as pearl mussel, river and brook lamprey, salmon, otter or beaver, or aquatic plants, such as *Luronium natans* or *Marsilea quadrifolia*. Backwater habitats, such as secondary channels are considered an essential element of functional floodplain wetlands but are difficult and costly to reinstate during restoration schemes (Buisje *et al.*, 2002). Therefore including backwaters as part of the designation of larger areas is a more effective way of protecting floodplain integrity and maintaining the fluvial processes that create and transform backwater habitats. Nevertheless, backwaters are commonly overlooked and would benefit from a more explicit recognition of their various roles, whether in river ecosystem functioning, provision of nursery habitat for fish, in the maintenance of populations of rare species, or in natural flood management. This will rely on valuing connectivity within and between terrestrial and aquatic habitats more highly.

ACKNOWLEDGMENTS

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Appendix 2.1. Hydrophyte species list recorded among surveyed main channel sections and paired backwaters.

Species Latin name	Main channel	Backwaters
Apium inundatum		√
Callitriche sp.		√
Callitriche hamulata		√
Callitriche stagnalis		√
Chara virgata		√
Crassula helmsii		√
Eleocharis acicularis		√
Elodea canadensis		√
Elodea nuttallii		√
Fontinalis anti	√	√
Juncus bulbosus		√
Lemanea fluviatilis	√	
Lemna minor		√
Littorella uniflora		√
Lythrum portula		√
Myriophyllum alterniflorum		√
Nitella flexilis		√
Persicaria amphibia		√
Potamogeton alpinus		√
Potamogeton berchtoldii		√
Potamogeton crispus		√
Potamogeton natans		√
Potamogeton obtusifolius		√
Potamogeton polygonifolius		√
Racomitrium aciculare	√	
Ranunculus fluitans	√	√
Sparganium angustifolium		√
Sparganium emersum		√
Sparganium natans		√
Subularia aquatica		√

Appendix 2.2. Helophyte species list recorded among surveyed main channel sections and paired backwaters.

Species Latin name	Main channel	Backwaters
Agrostis stolonifera		√
Alisma plantago-aquatica		√
Caltha palustris		√
Cardamine hirsuta		√
Cardamine pratensis		√
Carex nigra	√	√
Carex remota	√	√
Carex rostrata	√	√
Carex vesicaria		√
Carex viridula		√
Eleocharis palustris	√	√
Epilobium palustre		√
Equisetum arvense	√	√
Equisetum fluviatile		√
Equisetum palustre		√
Fallopia japonica	√	√
Filipendula ulmaria	√	√
Galium palustris	√	√
Glyceria fluitans	√	√
Hippuris vulgaris		√
Iris pseudacorus		√
Juncus acutiflorus		√
Juncus articulatus	√	√
Juncus bufonius		√
Juncus effusus	√	√
Mentha aquatica	√	√
Mimulus guttatus	√	√
Myosotis scorpioides	√	√
Phalaris arundinacea	√	√
Ranunculus flammula	√	√
Ranunculus repens	√	√
Scirpus sylvatica		√
Solanum dulcamara		√
Sparganium erectum		√
Typha latifolia		√

CHAPTER III.

Aquatic vegetation in large rivers: do flood-related disturbances matter?

Antoine A. Keruzoré[1], Nigel J. Willby[1], David J. Gilvear[1]

[1]School of Natural Sciences, Biological and Environmental Sciences, University of Stirling, Scotland, UK

Contact: antoine.keruzore@stir.ac.uk

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III.1. ABSTRACT

Theory suggests that disturbance events will promote species diversity through the removal of biomass such that coexistence is increased. This hypothesis was tested using a diverse assemblage of aquatic vegetation growing in a backwater in the lower reaches of a large upland river in Scotland where frequency of connection to the main river channel controls exposure to potential mechanical disturbance by floods. An in situ experiment was set up in which four macrophyte species were grown in plastic trays and exposed to flooding. Trays were distributed between an adjacent non-flooded control and the intermittently flooded backwater that only differed with the occurrence of floods. After flooding, biomass was compared between control and backwater. At community level the biomass of aquatic vegetation displayed surprising stability to flood disturbance, including large events with recurrence intervals of 10-30 years. The four species showed different responses to flooding but none experienced a significant biomass reduction. Despite an intermediate level of exposure to floods our study demonstrated that disturbance at this site was insufficient for significant biomass removal and thus could not account for the high observed diversity, as predicted by the Intermediate Disturbance Hypothesis. Instead we suggest that diversity is maintained by a complex interaction of various ecological processes, such as input of propagules, retention, competition and recruitment which change in a non-linear manner over time as connectivity and exposure to flood disturbance decreases.

III.2. INTRODUCTION

Understanding the mechanisms which drive species diversity remains a focus of research in ecology. Disruptions associated with various forms of disturbance have long been implicated in the maintenance of diversity and the Intermediate Disturbance Hypothesis (IDH) is one of the most widely cited hypotheses to explain the deterministic effects of environmental factors on diversity. According to the IDH an extreme disturbance regime allows only tolerant species to persist or pioneer species to colonise while a low disturbance regime promotes loss of species through interspecific competition. An intermediate disturbance is tolerable by the largest spectrum of species and is thus expected to support maximum diversity. More specifically the IDH designates disturbance as an agent of biomass loss which therefore opens up space and resources thus supporting the establishment of new species (Roxburgh *et al.*, 2004). At a medium intensity of disturbance the level of biomass removal is sufficient to reduce competitive exclusion and optimise coexistence.

In river systems floods are the major disturbance. Floods entail extreme and fast changing flow conditions and are characterised by timing, frequency, duration and amplitude in both discharge and velocity. In river floodplains flood pulses are responsible for structuring and modifying both morphological and biological features (Ward *et al.*, 1999). More generally the hydrological dynamic promotes lateral instability and drives the formation or destruction of floodplain habitats, such as oxbows and palaeo-channels (Amoros & Bornette, 2002). In this paper we use the term 'backwaters' to refer to former river channels in which upstream connection to the river is progressively lost through alluvial and woody debris deposition (Petts & Amoros, 1996). Backwaters therefore provide almost standing water conditions in a fluvial environment. At base flow, backwaters only keep a downstream connection to the river corridor (Van Der Nat *et al.*, 2003). This restricted connectivity to the main river, where flows are stronger and more variable, presents ideal conditions for aquatic plant colonisation and growth. Indeed backwaters seem to accumulate macrophytes along large rivers and to represent a major reservoir of floodplain biodiversity. However, during flooding, complete connection to the main channel is temporarily restored with flow entering at the upstream end. Then, with profound and rapid change in water velocity, formerly sheltered backwaters supporting an abundance of aquatic vegetation are exposed to sporadic and potentially very damaging flow conditions. Floods can be a major environmental factor structuring backwater macrophyte communities due to destruction of biomass (Henry *et al.*, 1996), whilst flood disturbances may arrest successional processes thus rejuvenating aquatic ecosystems and their plant communities (Bornette *et al.*, 1998).

Recent works have mainly examined macrophyte response to flow disruption focusing on species diversity by comparing pre/post flooding status (Strausz & Janauer, 2007), biomass allocation response to water-logging and submergence (Blanch *et al.*, 1999; Deegan *et al.*, 2007) or morphological plasticity along a gradient of flow velocity (Puijalon *et al.*, 2008). In ecosystems where water movement exerts a constant stress two strategies, resistance or avoidance, are used to minimize the negative impact of stressful conditions (Puijalon *et al.*, 2011). Avoidance allows plants to escape unfavourable conditions by preventing the negative effects of disturbance. Resistance leads plants to experience unfavourable conditions but without significant biomass loss. Either strategy will drive distribution, morphological adaptation and biomass allocation to minimise the effects of disturbance. Nevertheless, the biomass allocation response of aquatic vegetation to highly episodic, intense and mechanically stressful changes in flow conditions, as induced by flood flows, and its ecological implications, have rarely been addressed (Barrat-Segretain, 2001; Fritz, 2004; Strausz & Janauer, 2007).

This paper assesses the biomass response of aquatic vegetation to flood disturbance as a means of understanding the drivers of macrophyte diversity in riverine backwaters. Our main hypothesis is that flood disturbances will significantly reduce biomass thus reducing competitive exclusion and thereby accounting for high observed diversity. The sub-hypothesis are that 1) established macrophytes will show a lower overall biomass in the flooded backwater due to flood disturbance relative to a non flooded control; 2) flooding effects will differ spatially in the exposed backwater along longitudinal and a lateral gradients consistent with differences in the intensity of disturbance, and 3) responses will differ between macrophyte species according to their growth habit.

III.3. MATERIAL AND METHODS

III.3.1. Study sites

The study was carried in a backwater in the Tummel Shingle Island Nature Reserve located four kilometres downstream from the town of Pitlochry on the River Tummel, Perthshire, Scotland (56º40’33”N; 3º41’43”W). On average this backwater connects with the main channel six times per year (range for backwaters on the Tay-Tummel floodplain = 0.5 to 14) and supports a high diversity of aquatic plant species (15 species) relative to other sites in the floodplain (range = 2 to 15). For the experiment the control site consisted of a pond located next to the backwater that did not connect to the river. The exposed site was a backwater that was fully connected to the river during floods. The backwater was 500 meters long with an average width of 25 meters. Both sites were characterised by large particles (pebbles). No gradient in sediment size was recorded along the flooded backwater.

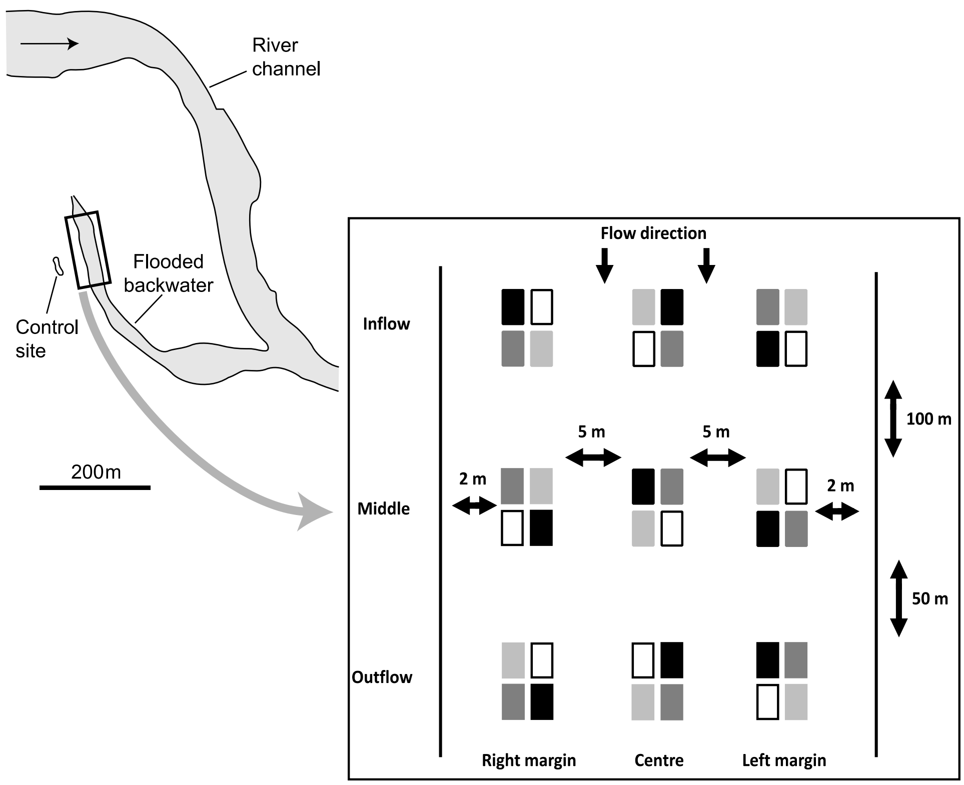

Figure 3.1. Trays arrangement in flooded backwater with: □ *Myriophyllum alterniflorum*; ░ *Potamogetons natans* ; ▓ *Ranunculus flammula* ; ■ *Mentha aquatica*.

III.3.2. Tray preparation

In this study four macrophytes species were studied: the amphibious *Mentha aquatica* and *Ranunculus flammula*, and the fully aquatic *Potamogeton natans* and *Myriophyllum alterniflorum*. Plants were grown in plastic trays (length: 60 cm; width: 30 cm; height: 10 cm). To reproduce the substrate conditions found in the backwater each tray was prepared by filling it with locally sourced large pebbles (90%) and a well-mixed matrix of finer sediments (10%: sand, silt, organic matter) sourced from the flooded backwater. In total 48 trays were prepared (12 trays per species). For each species plant shoots were collected from populations found in the backwater. All collected shoots had fully developed roots and leaves and were of the same approximate size (15 to 20 cm length). A total of 120 plants were collected per species and were transplanted as 10 evenly distributed shoots per tray. All trays were then left in the control site for an acclimation period of five weeks. No flood occurred during the five weeks of acclimation.

III.3.3. Trays settlement

After the acclimation period trays were distributed between control and backwater. Three trays per species remained in the control site and nine trays per species were evenly dispersed in the backwater (Figure 3.1). Trays were levelled with the sediment of the backwater to complete the similarity with the natural bed and pinned to the bed with four 60 cm long metal stakes to secure anchorage during floods. In the week following relocation of trays to the backwater several checks were made to ensure that all plants were still rooted to the sediment. If missing or uprooted, plants were replaced or replanted.

III.3.4. Post-flood plant sampling

One day after a flood, trays in both control and flooded site were inspected. Three plants were harvested from each of the 48 trays (36 plants in total in control, 9 plants per species; 108 plants in total in flooded backwater, 27 plants per species). Sampled plants were brought back to the laboratory and stored in a fridge at 4 degrees Celsius.

III.3.5. Laboratory processing

Before processing plants were carefully cleaned with water to remove sediment particles, organic matter, and filamentous algae. Plant material was divided between:

leaves, stems and root system. All measurements were completed within 5 days of collection. Plant material was then dried for 48 hours at 80 degrees Celsius before weighing.

III.3.6. Environmental parameters

For both control and backwater site physical and physicochemical parameters were measured in order to assess differences that could stimulate or inhibit plant growth and thus interfere with biomass comparison between treatments. Water depth, temperature, pH, dissolved oxygen and conductivity were measured at each tray at fortnightly intervals during the period of the assessment. Water samples were collected from the exposed backwater (3 samples per date) and the control site (1 sample per date) to determine the concentration of nitrogen and phosphorus over the growing season (May to September).

III.3.7. Data analysis

Data analysis was performed using the R statistical package. In the analysis vegetation was differentiated at three levels: the overall plant community, at growth form level as aquatic versus amphibious species and at the level of each of the four species. Plant biomass was considered in terms of above-ground dry biomass (stems + leaves biomass); below-ground dry biomass (root biomass); total biomass (above-ground dry biomass + below-ground dry biomass).

Differences in biomass were tested between: 1) between control and flooded site using Wilcoxon test; 2) within flooded site (between positions on the longitudinal or lateral gradient) using ANOVA. On the longitudinal gradient trays were grouped as: inflow, middle and outflow. On a lateral gradient trays were grouped as: left margin, middle and right margin (Figure 1). Data on environmental variables were compared using T-test between control site and the exposed backwater to assess differences that could influence biomass growth. Biomass data was normalised prior to analysis by fourth root transformation.

III.4. RESULTS

III.4.1. Flood characteristics

During the experiment two floods connected the backwater to the river corridor of the River Tummel (August and November 2009). Amplitudes of the two floods differed with peak of discharge of 433 m^3/s in August (equivalent to a summer discharge of Q0.2; i.e. the flow that would on average be exceeded for 0.2% of the time in the previous 50 years of data) and 600 m^3/s in November (equivalent to a winter discharge of Q0.04), compared to a long term mean base flow of 74 m^3/s (Figure 3.2).

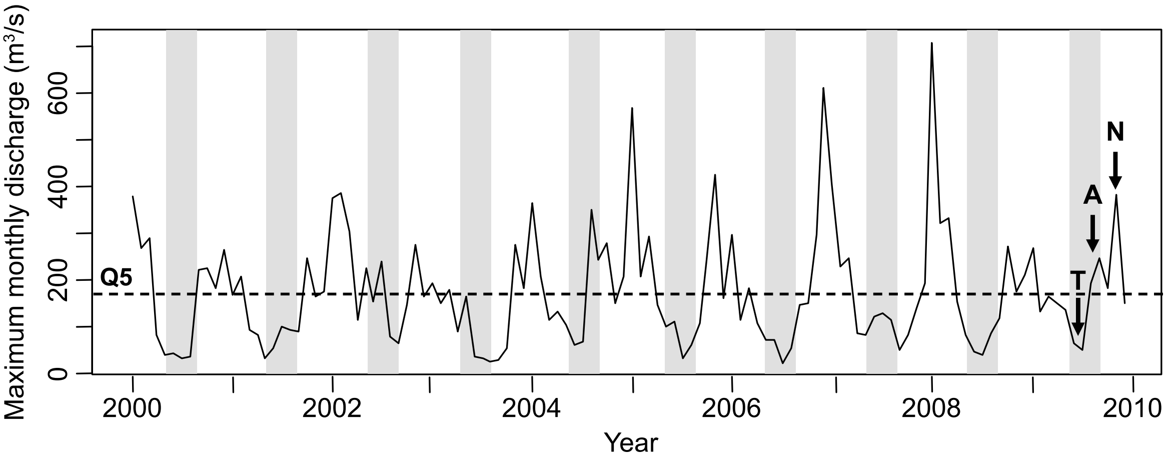

Figure 3.2. River Tummel hydrology graph (data recorded at Pitlochry, station 15012, 1 mile upstream from study site) representing maximum monthly discharge (m^3/s) from 2000 to 2010. Honrizontal dashed line represents Q5 (flow exceeded on average for 5% of the time in the previous 50 years of data). Black arrows represent August (**A**) flood; November (**N**) flood and (**T**) tray settelment. Shaded areas represent macrophytes growing period (from May to September). August flood was the second highest summer flood in the last decade. November flood was the fourth highest winter flood in the last decade.

III.4.2. Environmental parameters

Analysis of environmental parameters only showed significant difference between non-flooded control and flooded backwater in the dissolved oxygen concentration (T-test; $p < 0.05$) being 3.9 ± 0.7 mg/l in the flooded backwater and higher in the control (5.1 ± 0.5 mg/l). We therefore consider that growing conditions in the control and exposed site were similar in all important respects with the exception of exposure to flooding.

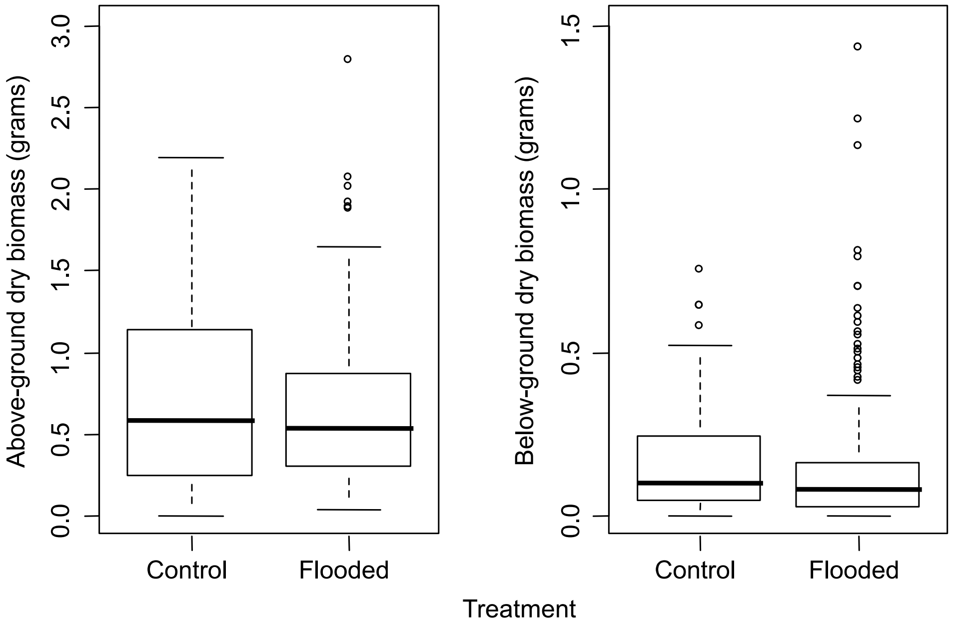

Figure 3.3. Above-ground and below-ground dry biomass of ramets of all species in control site and flooded backwater.

III.4.3. Control vs. backwater comparison

III.4.3.1. *Above-ground biomass*

At plant community level above ground biomass was not different between control and backwater (Wilcoxon test; $p > 0.05$) (Figure 3.3). At the growth form level aquatic plant species biomass showed a significant difference being higher in the flooded backwater (Wilcoxon test; $p < 0.05$). Amphibious plant species showed no significant differences between control and backwater (Wilcoxon test; $p > 0.05$). At the species level, above-ground biomass of *Potamogeton natans* did not differ between control and backwater (Wilcoxon test; $p > 0.05$). The other three species showed significant but contrasting differences (Figure 3.4). *Mentha aquatica* presented significantly lower biomass in the flooded backwater (Wilcoxon test; $p < 0.05$). Higher above-ground biomass was displayed in the backwater for *Myriophyllum alterniflorum* (Wilcoxon test; $p < 0.05$) and *Ranunculus flammula* (Wilcoxon test; $p < 0.05$).

III.4.3.2. *Below-ground biomass*

Below-ground biomass analysis showed no significant differences between control and backwater at any plant functional type or species level (Figure 3.4). No uprooting was recorded in any trays after flooding.

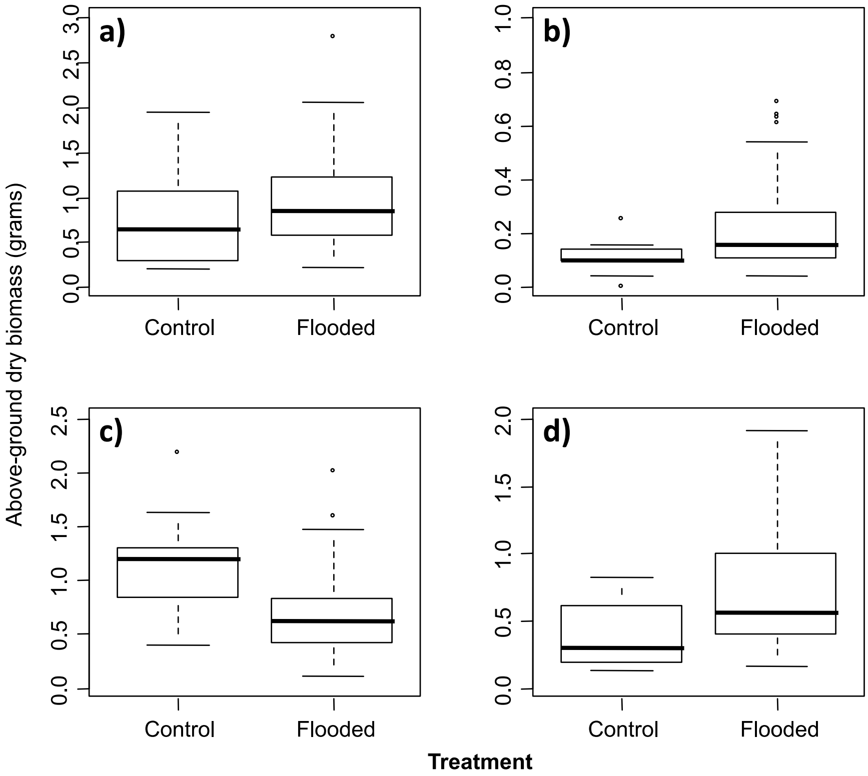

Figure 3.4. Above-ground dry biomass of ramets in control site and flooded backwater; **a)** *Potamogetons natans*; **b)** *Myriophyllum alterniflorum*; **c)** *Mentha aquatica*; **d)** *Ranunculus flammula*.

III.4.4. Within backwater assessment: longitudinal gradient

III4.4.1. *Above-ground biomass*

Above-ground biomass at plant community level did not show differences between longitudinal positions in flooded backwater (ANOVA, F = 2.16, P > 0.05) (Figure 3.5). Plant functional type level presented different responses to longitudinal position in the backwater (Figure 3.5). No significant differences was found for the aquatic plant species group (ANOVA, F = 0.06, P > 0.05) but amphibious plant species group showed significant differences between the inflow position versus the middle and outflow position (ANOVA, F = 12.7, P < 0.05). At species level no significant difference were found for *Potamogeton natans* (ANOVA, F = 1.14, P > 0.05) and *Myriophyllum alterniflorum* (ANOVA, F = 0.4, P > 0.05). Conversely, *Mentha aquatica* (ANOVA, F = 9.8, P < 0.05) and *Ranunculus flammula* (ANOVA, F = 4.38, P < 0.05) showed differences in relation to longitudinal position. For both species a lower above-ground biomass was found at the inflow position in the flooded backwater compared with the next two positions along the longitudinal gradient.

III4.4.2. *Below-ground biomass*

Below-ground biomass analysis showed no significant differences between longitudinal positions at any plant functional type or species level.

III.4.5. Within backwater assessment: lateral gradient

III.4.5.1. *Above-ground biomass*

Above-ground biomass results only displayed significant differences on the left margin for *Myriophyllum alterniflorum* with lower above-ground biomass (ANOVA, F = 6.64, P < 0.05). No difference was found for any other plant functional type or species level along the lateral gradient.

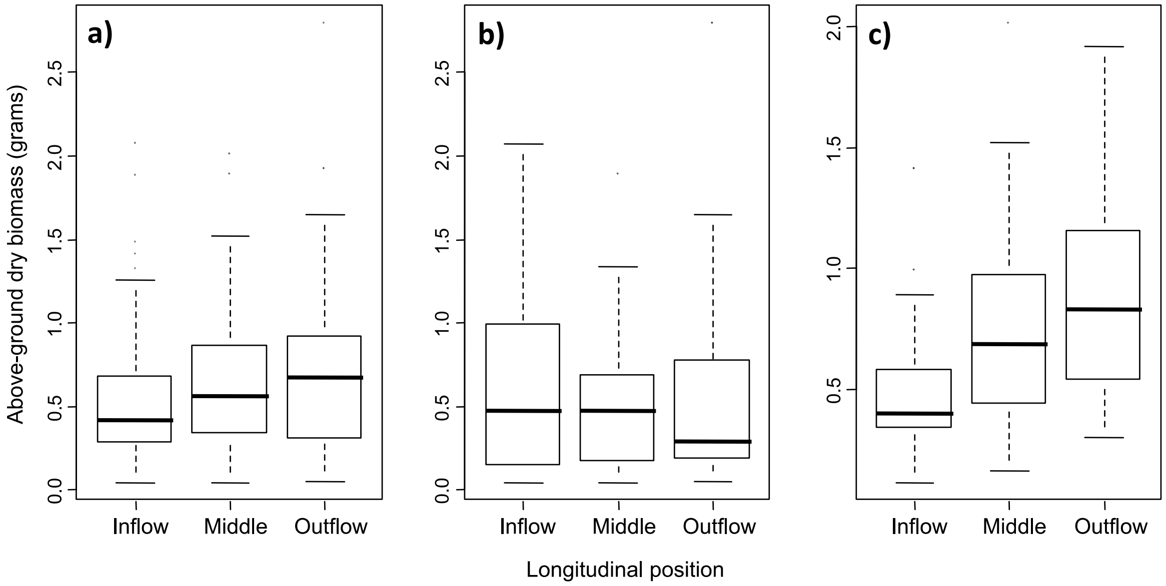

Figure 3.5. Above-ground dry biomass of ramets along a longitudinal gradient in the flooded backwater; **a)** all species; **b)** aquatic species and **c)** amphibious species.

III.4.5.2. *Below-ground biomass*

Below-ground biomass analysis showed no significant differences between lateral positions at any plant functional type or species level.

III.5. DISCUSSION

III.5.1. Macrophyte biomass response to flooding

Flooding disturbances are generally considered to reduce macrophyte biomass (Henry *et al.*, 1996). Our results failed to reveal the biomass reduction expected after flooding. No evidence of apical shoot destruction, abrasion or stem breakage was recorded. Also plant uprooting did not occur as confirmed by counts of plants per tray after flooding. Indeed community biomass was not significantly reduced and was surprisingly insensitive to exposure to flooding.

The most impacted compartment was above-ground biomass. However, the impact of flooding was still very limited. Both aquatic and amphibious plant communities did not experience biomass reduction in response to flooding. Only *Mentha aquatica* displayed reduced above-ground biomass in the backwater after floods whereas Jung *et al.* (2009) described it as being flood-tolerant. While amphibious species can show adaptation to fast flow (Boeger & Poulson, 2003) our results suggest such species may be more sensitive to flooding. Amphibious species typically present more rigid stems and leaves which increases drag (Bal *et al.*, 2011). Purely aquatic species are more compressed, often have a streamlined shape and, because of the reduced need for supporting structural tissue can easily bend as flow increases (Miler *et al.*, 2012). Unexpectedly, *Myriophyllum alterniflorum* and *Ranunculus flammula* presented higher above-ground biomass in the flooded backwater. Plant dimension and biomass increase were already documented (Puijalon *et al.*, 2008) but represent a rare response to change in increasing hydrodynamic. A second possibility is that nutrient limitation in infertile environments is relieved in connected sites during floods or via seepage through alluvial substrates (Tockner *et al.*, 1999) or that growth in flood exposed sites benefits from the removal of epiphytic algae by scouring (Hilton *et al.*, 2006). *Potamogeton natans* stems were previously showed to be more resistant in standing waters (Bociag *et al.*, 2009) but here they did not endure flooding effects as both above and below-ground biomass compartments were similar whether plants were exposed to flooding or not (Zmeja & Gałka, 2008). Both *Myriophyllum alterniflorum* and *Potamogeton natans* can withstand high water velocities in open upland river channels (up to ~1.2m/s) and their growth form presumably therefore bestows a high level of resistance to high flows in otherwise standing water environments.

Across the four species the least impacted compartment was below-ground biomass. Results showed almost no differences across every levels of analysis. Unlike Fritz (2004) below-ground biomass compartment was not higher in the hydrologically disturbed environment. The absence of below-ground overdevelopment in the flooded backwater indicates no strengthening of the anchorage structures to resist flooding (Puijalon *et al.*, 2011). However, oxygen stress (as in the control site) may negatively influence plant growth (Blanch *et al.*, 1999) and may explain the absence of biomass difference in our results. Riis *et al.* (2004) suggested that high flows do not result in biomass removal by increasing current velocity but rather through increased bed mobility.

Our study emphasises biomass stability and the limited effect of flooding over the course of our experiment in an exposed backwater compared to a non-flooded control. Previous works have indicated morphological adaptations such as small to intermediate size and high plasticity in biomass allocation in response to stress factors (Puijalon *et al.*, 2008), but in our case no differences in biomass allocation were evident. Field observations revealed that plants were flattened to the sediment surface immediately after flooding indicating that they can bend without breaking (O'Hare *et al.*, 2007) and thus effectively avoid flow disturbance. A similar result was found in the Danube after a significant flood in 2002 (Strausz & Janauer, 2007). It is arguable that larger (and thus even rarer) floods might be expected to cause larger biomass reductions at our site but there is little evidence even for this. In the immediate aftermath of the August 2004 flood, the largest growing season flood in the last 50 years on the River Tummel, Willby (unpublished) observed that in the same backwater there was only small and localised damage to some beds of *Potamogeton natans* and *Juncus bulbosus* caused by the traction of large woody debris over the bed, and slight abrasion of leaf filaments of *Myriophyllum alterniflorum* in the most exposed locations. Within a few weeks of occurrence no evidence of these effects could be found. Therefore, for our study context, we reject our main hypothesis that an intermediate level of biomass removal caused by flood disturbance contributes to high observed diversity.

III.5.2. Macrophyte biomass response along spatial gradients

Although several studies have examined macrophyte distribution in large rivers (Breugnot *et al.*, 2008; Sarbu *et al.*, 2011), to our knowledge no study has really tried to relate spatial variation in flooding effects on macrophyte biomass to hydraulic factors. The most affected compartment in our study was above-ground biomass. Amphibious species were the most sensitive to floods with lower biomass in the flooded backwater in the area of upstream connection where it is assumed that disturbance intensity is highest. In contrast to purely aquatic plants amphibious species exhibit aerial structures and may lack stem flexibility and streamlining (O'Hare *et al.*, 2007). Consequently they might suffer more easily from mechanical disturbance during high flow.

Breugnot *et al.* (2008) noted that in a large river aquatic vegetation displayed a strongly marginal distribution while the mid-channel was un-vegetated. Increasing water depth and velocity disturbances were negatively correlated with aquatic vegetation presence. Barrat-Segretain (2001) suggested that biomass allocation could be an adaptation to the spatial variability in disturbance intensity experienced by vegetation. In our case values did not differ between the margins and centre of the flooded backwater across all biomass compartments and plant groups and species. Consequently we generally reject our sub hypothesis that flooding effects will differ spatially in the exposed backwater both along longitudinal and lateral gradients and between species, although there is some evidence that biomass of amphibious plants can be reduced in upstream areas of greatest disturbance.

III.5.3. Implications in relation to the Intermediate Disturbance Hypothesis

According to the Intermediate Disturbance Hypothesis flood disturbances are expected to remove biomass and thus maintain diversity through a reduction in competitive exclusion which would otherwise take place. In contradiction with the IDH our in situ experiment showed the stability and tolerance of macrophytic vegetation in a backwater exposed to flooding. While widely used to explain patterns in species diversity the IDH remains under debate (Roxburgh *et al.*, 2004). It has recently been presented as "an elegant but oversimplified representation of a complex knot of concepts: that many events can both augment or erode diversity through various linked processes at a range of scales" (Sheil & Burslem, 2003). In other words, and in contradiction with the IDH, diversity is not always controlled through biomass removal and gap formation. Our investigation supports the hypothesis that disturbances do not affect plant biomass but that various ecological interactions are responsible for driving species diversity.

Here we propose an alternative model to explain changing macrophyte diversity in riverine backwaters for which connectivity and disturbance are dissociated into independent mechanisms. From backwater formation and along a gradient of age, alluvial and woody debris accumulate at the upstream part of backwaters (Petts & Amoros, 1996). Consequently over the lifetime of a backwater progressively higher water levels are needed to connect with the river during high flows and so connection frequency must decline. Connection to the river will control the frequency and intensity of key ecological processes including the input and retention of plant propagules (Moggridge *et al.*, 2009), recruitment and competition (through natural succession) (Amoros & Bornette, 1999). In our model we do not propose that floods create gaps; instead we suggest that diversity reflects the expression of species along a successional gradient that is aligned with connectivity. Species accumulation and colonisation of backwaters from water borne seed rain and the sediment propagule bank will drive the change in composition and richness (Abernethy & Willby, 1999), the latter reaching a maximum when optimal ecological conditions are met for the greatest number of species to emerge and establish. A low connectivity will lead to dominance and progressive exclusion by the most competitive species and will decrease diversity. At the highest connectivity only the best adapted species can tolerate nearly constant flow pressure and opportunities for establishment are rare, even though propagule inputs may be high. An intermediate connectivity regime satisfies the largest spectrum of both early and late successional species and will naturally occur in sites of intermediate age. The main difference with the IDH is that, in line with our results, flood disturbances are not required to arrest succession by biomass removal and thus prevent exclusion of poorer competitors.

III.6. CONCLUSION

Our in situ experiment revealed stability of macrophyte biomass in a backwater exposed to potential flood disturbances. Evidently aquatic plants can effectively avoid or resist the effects of high flows associated with flooding through a range of strategies (Puijalon *et al.*, 2011). Even where reductions are observed at the level of individual species, increased growth by other species will likely buffer changes in biomass at a community level. Our results demonstrate that mechanical flood disturbances did not cause significant biomass removal and therefore this mechanism cannot account for high community diversity in backwater vegetation. Instead, we suggest that species diversity is driven by connectivity and a number of correlated processes. We propose that diversity depends on the interaction between the input and retention of propagules and their recruitment which changes predictably with connectivity (Bornette *et al.*, 2008). There is a strong temporal dimension to changes in the relative importance of these processes since connectivity inevitably decreases with time, although probably in a non-linear manner reflecting the influence of floods of different magnitude.

This conclusion does not detract from the importance of a fluvial dynamic in driving a gradient of connectivity (Amoros & Bornette, 2002) and in generating a mosaic of backwaters of different ages (Van Geest *et al.*, 2003), ranging from the newly created and frequently connected through to the mature and permanently disconnected, which is required to maintain the diversity of macrophytes at a floodplain level.

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CHAPTER IV.

Simulated plant dispersal and colonisation in large rivers; the influence of floods and connectivity

Antoine A. Keruzoré[1], Nigel J. Willby[1], David J. Gilvear[1]

[1]School of Natural Sciences, Biological and Environmental Sciences, University of Stirling, Scotland, UK

Contact: antoine.keruzore@stir.ac.uk

IV.1. ABSTRACT

In large temperate rivers macrophytes naturally concentrate in low energy backwaters while the main channel is largely devoid of vegetation. Dispersal is widely believed to be driven by water movement, especially flood flows. Dispersing plant propagules are therefore expected to originate from backwaters and their establishment downstream is dependent on entering other backwaters. This hypothesis was tested by studying the dispersal of tracers in a 33 km reach of the Tay-Tummel river system in Scotland. 44 000 tracers made from small colour-coded bamboo sticks were released under flood flows (when lateral backwaters can be entered from both upstream and downstream directions) and 19 800 tracers at base flow (when backwaters can only be entered at their downstream end via backflow). The distribution of deposited tracers was used to establish patterns of dispersal between backwaters of varying connectivity under contrasting flows. Results demonstrated that the most probable route of backwater colonisation was through retention within the site of origin. Woody debris and riparian vegetation contributed most to retention. Export from backwaters contributed to the main river drift from which > 95% (in flood) and > 92% (at baseflow) of tracers were lost. The major bottleneck for backwater connectivity was the exchange of tracers between backwaters (the major source in this river system) under both flood and base flows when < 0.015% and < 0.27% respectively of tracers released upstream entered downstream backwaters. However, under base flow tracers had a 20 fold higher probability to enter downstream backwaters than under flood flows. Backwaters are shown to be rather isolated at the floodplain scale despite their physical inter-connectance. Since the receipt of external water-borne inputs was very rare we infer that the colonisation and maintenance of vegetation in riverine habitats must rely mainly on in situ sources. Colonisation of submerged habitat is also more likely through

step-wise movement of propagules over short distances and under base flow. Our findings offer a mechanistic understanding of dispersal in large rivers and emphasise the importance of different elements of the flow regime for the dispersal of biota between habitat patches. They also demonstrate the significance of floodplain aquatic habitats as a net source of potential colonists and as a contributor of organic input to riverine ecosystems.

IV.2. INTRODUCTION

In natural large river floodplains the dynamics of aquatic vegetation are driven by environmental extremes related to river corridor dimensions, water depth and velocity. Whereas the main river channel is expected to be largely devoid of macrophytes under near-natural conditions lateral aquatic habitats (e.g. backwaters) contribute greatly to floodplain species diversity and productivity (Keruzoré, *et al.* in press). While the main channel represents a hostile habitat for aquatic plants due to high water velocity, depth and turbidity, backwaters offer a low energy environment suitable for many macrophyte species (Willby & Eaton, 1996; Bornette *et al.*, 1998). Macrophyte populations in large rivers are therefore constrained along river channels and geographically isolated in patches of favourable habitat associated with backwaters. In such a context the population dynamics of plants should involve 1) propagule production in backwaters; 2) dispersal of propagules from backwaters; 3) retention of propagules within or in downstream backwaters; 4) recruitment of retained propagules; 5) resistance to disturbances after colonisation. A key deterministic element in the dynamics of vegetation is the probability for propagules to reach and colonise available habitats (Pickett & McDonell, 1989; Bullock *et al.*, 2002; Riis, 2008). In rivers it relates to internal colonisation (i.e. local to the source of production) and/or to the connectivity to downstream aquatic habitats via the dispersion of propagules liberated from upstream sites. Connectivity in riverine environments refers to permanent or episodic links between surface and subsurface waters of the river and various waterbodies lying in the alluvial floodplain (Ward *et al.*, 1999). As examples of former river channels backwaters have lost their upstream connection to the main river through alluvial deposition or the accumulation of large woody debris but retain a permanent downstream connection at base flow. However, as water levels increase during high flows upstream connection is temporarily restored and backwaters experience full connection to the river. Connectivity is commonly accepted to be a major driver of species diversity in river floodplains, via propagule dispersion within and between habitats (Amoros & Bornette 2002).

Macrophyte reproductive organs include sexual (seed or spores) or asexual propagules. Asexual propagules are either vegetative shoots with roots and leaves which detach passively from the parent plant, or are derived from allofragments (stem or rhizome fragments formed by mechanical breakage during flow disturbances). The relative success of colonisation via seeds or vegetative propagules of aquatic plants is much debated. Successful sexual reproduction is often considered to be constrained through biotic (e.g. intra and interspecific competition, herbivory (Elger *et al.*, 2009)) or abiotic factors (e.g. water depth) (Abernethy & Willby, 1999; Okada *et al.*, 2009). Conversely, vegetative propagules are believed to have a higher chance of successfully colonising new habitats as they often already possess roots and leaves (Boedeltje *et al.*, 2007). However, whereas sexual propagules were previously showed to be produced in larger numbers, asexual propagules displayed a higher role in successful colonisation of habitats (Barsoum, 2002; Boedeltje *et al.*, 2004). In both cases, once dispersed, propagules that establish can generate new individuals and hence populations (Cellot *et al.*, 1998).

Dispersion is a process of transportation of propagules. In river systems water flow, and especially disturbance by flooding, act as the main dispersal vector (Sculthorpe, 1967; Bornette & Amoros, 1996; Bornette *et al.*, 1998; Cellot *et al.*, 1998; Boedeltje *et al.*, 2004; Okada *et al.*, 2009). Water-assisted dispersal into backwaters can be achieved in two ways: (i) via flooding, since full connection is achieved at both upstream and downstream ends or, (ii) through downstream connection at base flow, when drifting propagules may enter by backflow or the action of wind (Figure 4.1). In flood-disturbed habitats, such as backwaters, flood-assisted dispersal was shown to be an important mechanism in aquatic macrophyte colonisation (Henry & Amoros, 1996; Henry *et al.*, 1996; Vogt *et al.*, 2006).

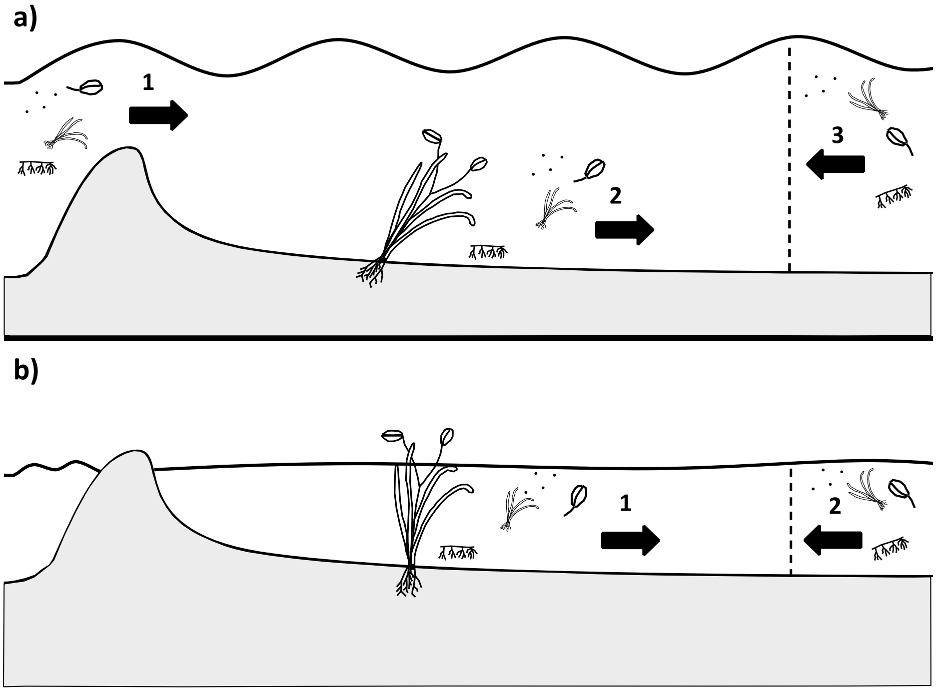


Figure 4.1. Theoretical model of macrophytes species dispersal in riverine backwaters at flood flow (**a**) and base flow (**b**). Sediment accumulation on the left side of the figure marks the separation between backwater and main channel at the upstream end. Dashed line on the right side of the figure marks the separation between backwater and main channel at the downstream end. (**a**): At flood flow, **1.** represents potential external propagule inputs from upstream sources; **2.** represents potential propagule export from backwaters; **3.** represents potential propagule inputs entering site at the downstream end. (**b**): At base flow, **1.** represents potential propagule export from backwaters; **2.** represents potential inputs entering site at the downstream end.

Dispersal studies indicate greater potential for seeds to travel long distances compared to shoots and rhizomes as seeds tend to have a higher buoyancy and lower roughness (Bacles *et al.*, 2006). However, it is also argued that some seeds will drift shorter distances due to lower buoyancy or higher roughness (Barrat-Segretain, 1996). Dispersal is reported to be constrained by various factors including: river sinuosity, channel complexity, buoyancy of material, retention success (Schneider & Sharitz, 1988; Johansson & Nilsson, 1993). Assessment of propagule dispersal, through population genetic analyses, illustrates the large range of distances travelled by propagules, from a few meters to several kilometres, extending up to 75 kilometres (Fer & Hroudova, 2008).

Our investigation aimed to establish if flood disturbances are the main driver of dispersal that interconnects patches of floodplain aquatic habitat. The main hypothesis of the present study was that connectivity facilitates colonisation of backwaters and that inputs of propagules occur primarily during flooding rather than at base flow. We also wished to test if backwaters function as a net source of propagules exported via the main river channel rather than a sink of propagules drifting in the main channel. The present paper presents a mechanistic model of plant dispersal and colonisation in large river floodplains. This model predicts the routes by which plants colonise backwaters along large rivers and examines whether connectivity has a controlling effect on colonisation processes.

IV.3. MATERIAL AND METHODS

IV.3.1. Study site

The study took place on the Rivers Tummel and Tay in Perthshire, Central Scotland, UK. The Tay is the largest river in the UK by mean discharge (170 m^3/s) and is a relatively unimpacted gravel-bed river with a predominantly upland catchment (catchment area: 5200 km^2). Dispersal under flood flows was modelled over a 33 km river reach: 5.2 km of the Tummel (before confluence with the Tay) and 27.8 km on the Tay (below confluence with Tummel) (Figure 4.2); and was assessed over ten backwaters, five on each river. Base flow dispersal was modelled over a 4.1 km river reach of the River Tay (Figure 4.2); and was assessed over three backwaters. In the reaches studied channel widths ranged from 50 to 80 metres.

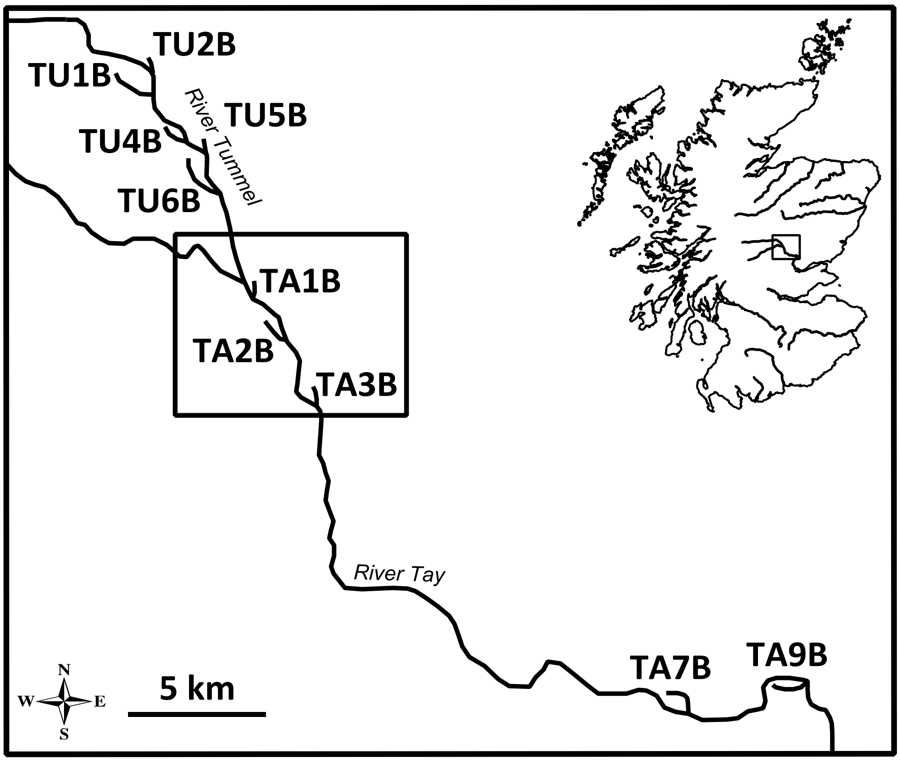


Figure 4.2. River Tummel and Tay, from Pitlochry to Haugh of Kercock, Perthshire, Central Scotland. Flood dispersion experiment took place from backwater TU1B to TA9B). Base flow experiment took place from backwater TA1B to TA3B (section in black box on river reach).

IV.3.2. Drift material and dispersal simulation

Dispersal was simulated using small tracers (bamboo sticks) to represent macrophyte fragments. Tracers were 6 cm long with a mean diameter of 8 mm. Wood propagule mimics were previously found to strongly reproduce the dispersal pattern of plant propagules (Nilsson & Grelsson, 1990; Andersson *et al.*, 2000). To identify the site of origin tracers were colour-coded using water-resistant spray paint with one colour per site. In our experimental design water flow was the only means of tracer dispersal. At the floodplain scale, under both flow conditions, the dispersal pathway was identified and modelled as: (i) direct dispersal (i.e. directly from one backwater to another) and (ii) indirect dispersal (i.e. from the main channel to backwaters) (Figure 4.3).

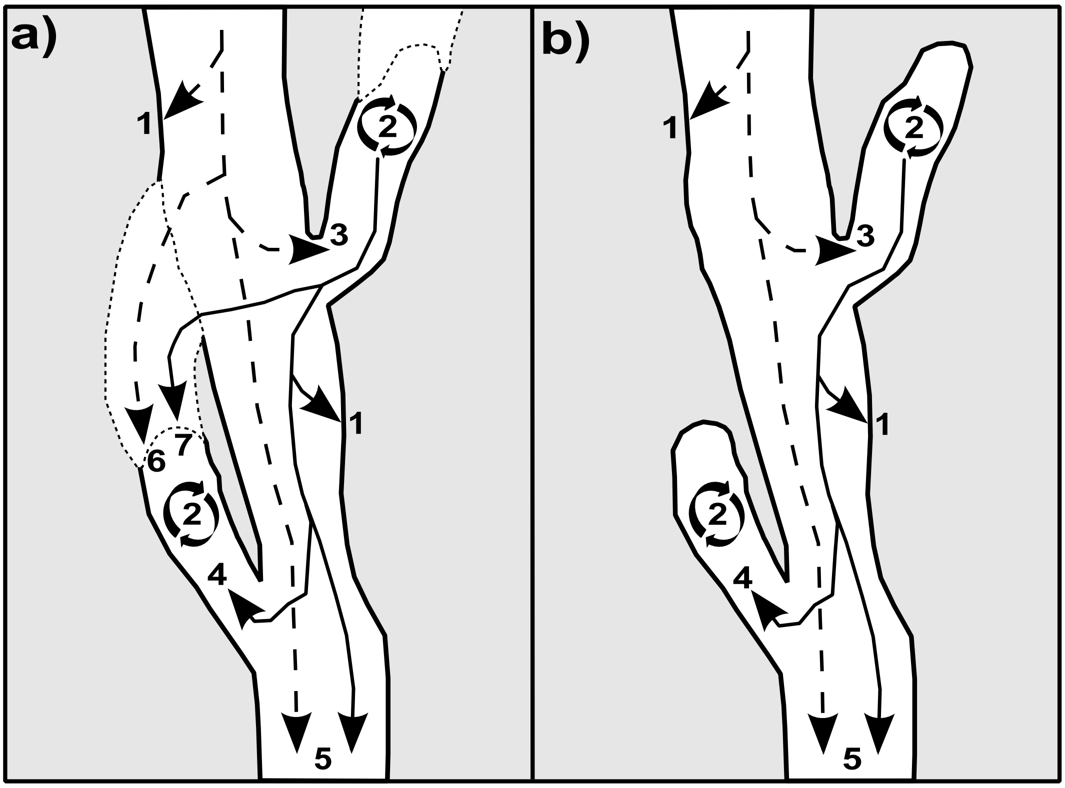


Figure 4.3. Landscape dispersal model in riverine floodplain in **a)** flood flows; **b)** base flow. Grey shaded area represents terrestrial habitat. White coloured area represents aquatic habitat. Dashed backwater sections of the **a)** model represent full connection of backwaters in flood flows. Dashed arrow line represents pathway of propagules originating from the main channel. Solid arrow line represents pathway of propagules originating from backwaters. Codes on the figure refer to: 1) retention of propagules along the main channel; 2) internal retention within backwaters; 3) input of propagules originating from the main channel (indirect connectivity) into a backwater at its downstream end; 4) input of propagule originating from one backwater (direct connectivity) into a different backwater at its downstream end; 5) propagules lost in drift; 6) input of propagules originating from the main channel (indirect connectivity) into a backwater at its upstream end; 7) input of propagules originating from one backwater (direct connectivity) into a different backwater at its upstream end.

At the backwater scale dispersal was modelled within sites to assess the retention and export of material. A tracer retrieval success trial was undertaken before flood and base flow experiments in which it was found that > 90% of tracers were successfully retrieved by the surveyor.

IV.3.3. Flooding flow simulation

The investigation of dispersal by flood flow consisted of releasing a total of 44 000 tracers distributed over 11 sites (4 000 tracers per site). Two sites were located in the main channel and nine sites in backwaters. Within-backwater retention was modelled using 500 tracers released at their upstream part. Downstream dispersal from backwaters was modelled with 3500 tracers left at the downstream part of each backwater. Indirect dispersal was modelled with 4000 tracers placed at each of two sites on the riverbank. The first of these sites was upstream of the first backwater (TU1B) on the River Tummel and the second site was upstream of the first backwater (TA1B) on the River Tay (Figure 4.2). High water flows were the only means to remove and disperse tracers in both main channel and backwaters. After the flood event the main channel and backwaters were intensively searched by two people for 10 days to retrieve tracers. 85% of the river reach was searched. The remaining 15% could not be searched for reasons of inaccessibility and safety (steep or eroded banks) but due to its topography retention of tracers was considered to be very unlikely. However, all backwaters were intensively searched. Tracers were searched for from the water level up to the trash line. The origin and position of all retrieved tracers were recorded on maps as well as information on retention features. No flood occurred during the period over which sticks were searched for. The combination of buoyancy and bright spray paint colours ensured a high rate of detection of retained material. Average data for backwaters and for main channel position was used in the flood flow model.

IV.3.4. Base flow simulation

A total of 18 600 bamboo tracers (6 200 in each of three replicates) were released over six release sites. For each replicate one release position was in the main channel and three positions were in backwaters. Within-backwater retention was modelled using 200 tracers released at their upstream part. Direct dispersal from backwaters was modelled with 1400 tracers released at their downstream part. Indirect dispersal was modelled with 1400 tracers released in the main channel at the top of the studied reach, upstream of all the backwaters. Water movement was the only means by which to disperse tracers in both main channel and backwaters. After releasing the tracers, a period of 3 hours was allowed to elapse for dispersion. The backwaters and main channel were then intensively searched to retrieve tracers and assess dispersion distances, retention and connection. The origin and position of retrieved sticks were recorded on maps along with information on retention features. No change in water level occurred between the release of material and the searching period. During base flow all backwaters were only connected to the river at their downstream end. Average data of the three replicates was used in the base flow model.

IV.3.5. Data analysis

Data analysis was based on recovered tracers. Data treatment consisted of quantifying dispersal pathways as either (i) dispersal along the river reach, (ii) retention within backwaters or in the main channel and finally (iii) direct and indirect dispersal from upstream sources (channel or backwaters) into downstream backwaters (Figure 4.3). Dispersal analysis aimed to illustrate drifting distances. Retention analysis aimed to assess both success and type of retention. Connectivity analysis aimed to test the influence of flood duration and measure indirect and direct exchanges of tracers between the main channel and backwaters, as well as between individual backwaters. Backwater flooding duration was calculated by coupling levelling data for each backwater transect with hydrological data gathered from the Scottish Environmental Protection Agency from 03/02/2011 to 05/02/2011 (station 15012 at Pitlochry on river Tummel and station 15006 at Ballathie on River Tay). By comparing water level and the sill elevation at the upstream end of each backwater, the increase of water level required connecting backwaters to the main channel during flood and the duration of connection was calculated. Correlation was used to test the influence of flood duration on tracers export and import in backwaters. Connection success was considered at an ecological level by discriminating between strictly aquatic and marginal zones in which tracers were retrieved according to the species requirements (Figure 4.4).

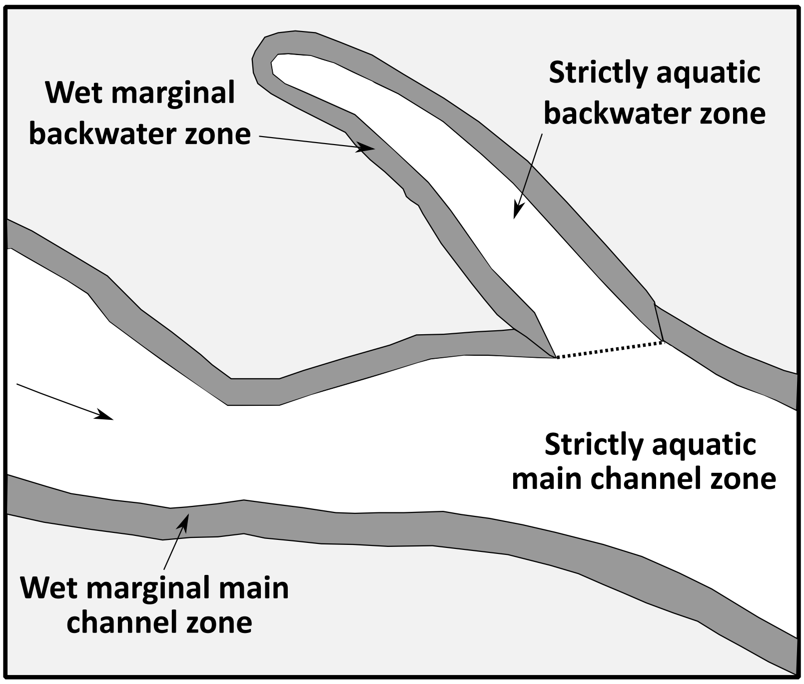


Figure 4.4. Details of floodplain zones considered in dispersion processes. Strictly aquatic zone corresponds to the zone where propagules of strictly aquatic macrophytes species have a possibility to establish either in backwaters or main channel. Wet marginal zone corresponds to the buffer zone between strictly aquatic and terrestrial habitats where propagules of amphibious macrophyte species have a chance to establish either in backwaters or main channel. Stipples represent terrestrial zones. Dashed line marks the separation between backwater and main channel.

Successful connection referred to the deposition of tracers in the appropriate zone for establishment. For instance, strictly aquatic species connection and colonisation can only be successful if sticks were found in the strictly aquatic backwater zone. For amphibious species connection and colonisation can only be successful only in the wet marginal backwater zone where soil saturation is sufficient to exclude most terrestrial plant taxa but permanent inundation does not occur. When tracers were found deposited outside either of these two zones, they were considered to be non-viable propagules.

In this investigation colonisation success could obviously not be directly addressed due to the inert material used to model dispersal. Nevertheless Riis, Madsen & Sennels (2009) established the regeneration success of allofragments as being 60% (after an average 27.5 days) for strictly aquatic species growing in standing water conditions comparable to those seen in our backwaters. Also Michelan *et al.* (2010) recorded an average success of regeneration of 61% of amphibious species after air exposure (after a maximum of 26 days). Therefore we used a figure of 60% to estimate colonisation success and thus complete our model. Here regeneration refers to the emergence of sprouts and new roots sufficient for rooting in sediment (Barrat-Segretain & Bornette 2000).

IV.4. RESULTS

IV.4.1. Flood flow simulation

IV.4.1.1. *Flood characteristics*

The flood occurred on the 4th of February 2011. At the peak of the flood discharge reached 481 m^3/s on River Tummel and 903 m^3/s on River Tay. All backwaters along the river reach fully connected to the main channel and interconnected to each other during the flood. This was the highest recorded flow on the Tay-Tummel system in the previous 36 months and the fourth highest flow since the year 2000.

IV.4.1.2. *Within backwaters*

IV.4.1.2.1. *Dispersion*

100% of tracers placed in backwaters were moved under flood flow. Tracers dispersed on average 160 m from their original position (range 1 to 450 m) (Table 4.1). In both models (Figure 4.5 & 4.6), on average 83% of tracers were exported out of backwaters into the main channel (varied from 0 to 100%). The proportion of tracers retained was related to the duration of flood exposure in backwaters, (controlled by the height of the upstream sill) although the significance of this relationship was borderline (r = 0.656; p-value = 0.055). Backwaters that connected for the longest period of time thus exported the highest proportion of tracers (i.e. retained the least).

Table 4.1. Dispersal distances of tracers (km) in flood and base flow models before retention in aquatic and wet marginal zones.

	Flood flow model			Base flow model		
	Strictly aquatic zone	Wet marginal zone	All zones	Strictly aquatic zone	Wet marginal zone	All zones
Within backwater	0.19	0.14	0.16	0.04	0.06	0.045
Backwater exported	3.20	12.20	12.20	1.78	1.57	1.45
Within main channel	-	3.50	3.50	1.44	1.50	1.7
In downstream backwater						
Direct connection	21.80	19.40	19.10	0.65	1.10	0.67
Indirect connection	-	7.90	7.90	0.23	-	0.23

IV.4.1.2.2. *Retention*

Of 17% tracers retained, 20% of retained tracers were deposited in the strictly aquatic backwater zone; 70.4% were in the wet marginal backwater zone; and 9.6% were retained out the zone of viable habitat for macrophyte survival. Therefore estimated success rate in retention in aquatic zones reached 3.4% and was higher for wet marginal with 12% retention (Figure 4.5 & 4.6). The retention of tracers in the strictly aquatic zone was mainly a result of woody debris (53%) and riparian vegetation (32%). Existing aquatic vegetation accounted for a lower proportion (15%). The retention of tracers in the wet marginal zone was mainly caused by deposition amongst riparian grasses (71.5%) or by woody debris (28.1%) (Table 4.2).

Table 4.2. Flood flow model retention percentages in the different habitats and considering the different origins of tracers. Grey shaded columns are results for tracers reaching aquatic zones, white coloured columns are results for tracers reaching wet marginal zones.

					In downstream main channel		In downstream backwater			
	Within backwater		Within main channel		From backwater		From backwater		From main channel	
Woody debris (%)	53	28.1	-	1.3	75	20	-	71	-	-
Aquatic vegetation (%)	15	-	-	-	-	-	100	-	-	-
Riparian vegetation (%)	32	-	-	-	-	-	-	-	-	-
Riparian grasses (%)	-	71.5	-	94.7	25	61	-	3	-	100
Bare sediments (%)	-	0.2	-	-	-	-	-	-	-	-
Bare rock substrate (%)	-	0.2	-	4	-	19	-	26	-	-

IV.4.1.2.3. *Estimated colonisation*

In backwaters 2% of the initial in situ production was estimated to successfully colonise aquatic habitat compared with 7,2 % tracers reaching marginal habitat (Figure 4.5 & 4.6).

IV.4.1.3. *Within main channel*

IV.4.1.3.1. *Dispersion*

100% of tracers left in the main channel were dispersed from their original position. Tracers were on average dispersed over 3.5 km (Table 4.1). However, the distance travelled ranged from a minimum of 7 m to a maximum of 20.8 km. 94% of tracers did not reach the aquatic main channel zone after dispersal and 98% of tracers did not reach the wet marginal zone as they were never retrieved. Tracers exported from backwaters were retained after 12.2 km drift on average (range: 12 m to 31.1 km) (Table 4.1). In the downstream main channel section, once exported out of backwaters, 99% of tracers (82% of original backwater pool) and 90% of tracers (74% of original backwater pool) respectively did not reach the aquatic main channel zone and the wet marginal zone were never retrieved and were considered moribund given the very limited availability of suitable habitat downstream of the study reach (Figure 4.5 & 4.6).

IV.4.1.3.2. *Retention*

Retention success rate of tracers in the main channel was null as no sticks were found in the main channel after flooding (i.e. all retained sticks were deposited outside the aquatic favourable zones). Retention on the banks was equivalent to 9.6% of tracers released directly in the main channel. However, 63% of these retained tracers were moved a long way above the main channel (up to 25 m on river banks) and outside the wet marginal zone (6.1% of original production). Ultimately only 3.5% first retained tracers could experience retention in the wet marginal zone (Figure 4.5 & 4.6). Retained tracers in the wet marginal zone were mainly deposited on riparian grass vegetation type (Table 4.2).

Once exported from backwater, respectively 0.1% (0.08% of original pool) and 5.6% of tracers (4.6% of original pool) were retained downstream in the strictly aquatic main channel and wet marginal zone. Retention in the aquatic zone was mainly by woody debris and grass while in the amphibious zone retention was due mainly to riparian grasses, woody debris and rock substrate (Table 4.2).

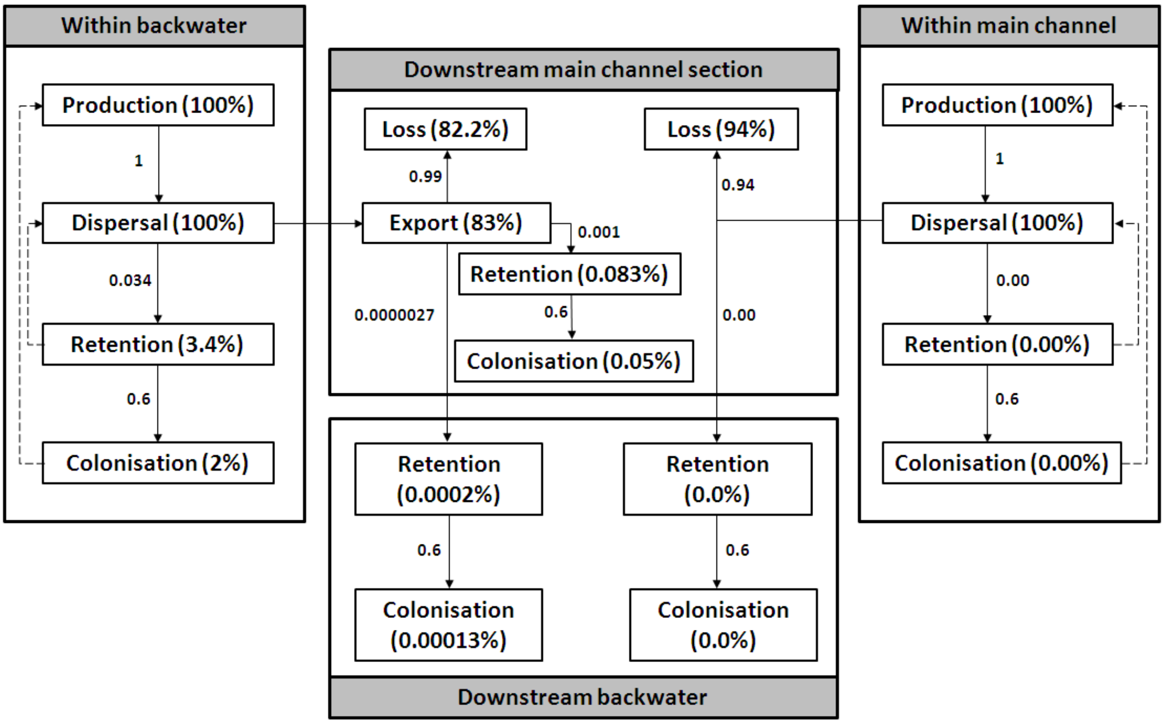


Figure 4.5. Flood flow dispersal model from and to strictly aquatic zones within and between both backwaters and main channel. Numbers in the process boxes are the proportion of the initial release of tracers to successfully complete that process. Numbers between the process boxes are probabilities of successfully completing the process indicated. The retention process boxes only relate to retention within viable habitat for the tracers type concerned.

IV.4.1.3.3. *Estimated* colonisation

Of the tracers originally left in the main channel 2.1% were estimated to establish successfully in amphibious habitat bordering the main channel. Colonisation success of tracers in an aquatic zone was estimated to be zero. In the downstream main channel section 0.05% and 2.8% of tracers produced and exported respectively from backwater aquatic and wet marginal zones successfully colonised into the main channel (Figure 4.5 & 4.6).

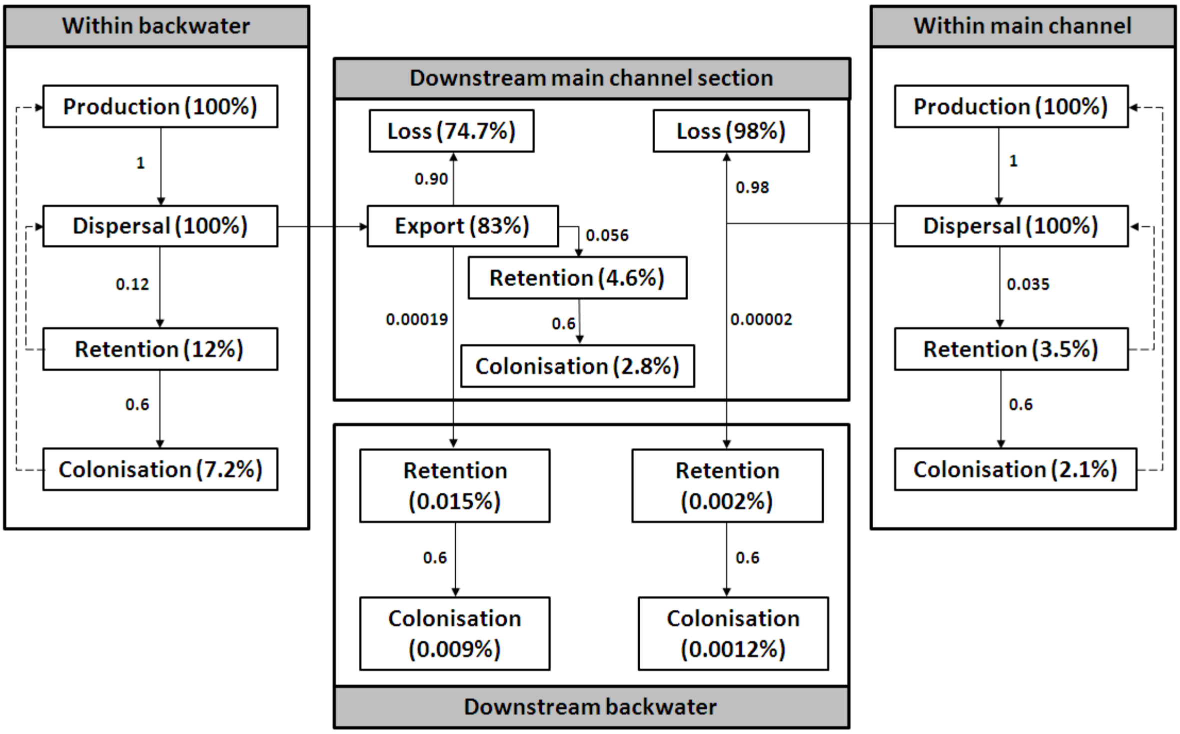


Figure 4.6. Flood flow dispersal model from and to wet marginal zones within and between both backwaters and main channel. Numbers in the process boxes are the proportion of the initial release of tracers to successfully complete that process. Numbers between the process boxes are probabilities of successfully completing the process indicated. The retention process boxes only relate to retention within viable habitat for the tracers type concerned.

IV.4.1.4. *In downstream backwaters - from main channel*

IV.4.1.4.1. *Retention*

Retention of tracers in aquatic zones was zero as no tracers left originally in the main channel were recovered in the strictly aquatic backwater zone after dispersal. Retention of tracers in wet marginal zones was slightly higher but still very low with only 0.002% retained (Figure 4.5 & 4.6). All retention was associated with riparian grasses. Mean dispersal distance before retention was 7.9 km (Table 4.1). The probability of entering a backwater for tracers originating in an upstream section of main channel origin was unrelated to the duration of flooding of backwaters (i.e. the time for which they maintained an upstream connection to the main channel) (r = 0.165; p-value = 0.671).

IV.4.1.4.2. *Estimated* c*olonisation*

In line with their retention success the estimated colonisation success of tracers originating from aquatic zones was zero. For tracers originating from wet marginal zones estimated colonisation success was also very low at 0.0012% (Figure 4.5 & 4.6).

IV.4.1.5. In downstream backwaters - from backwaters

IV4.1.5.1. *Retention*

The retention of tracers in aquatic zones in downstream backwaters was very low (equivalent to 0.0002% of tracers produced in upstream backwaters) (Figure 4.5) and was caused by aquatic vegetation (100%). Mean dispersal distance before retention was 21.8 km (Table 4.1). The retention success of tracers in marginal zones equated to 0.015% of tracers produced in upstream backwaters and was caused mostly by woody debris (Figure 4.6 & Table 4.2). Mean dispersal distance before retention was 19.4 km. The probability to enter a backwater was unrelated to backwater flooding duration (r = 0.033; p-value = 0.932).

IV.4.1.5.2. *Estimated* c*olonisation*

Accordingly successful colonisation in downstream backwaters was also very low and represented 0.00013% of tracers in aquatic zones and 0.009% of tracers in marginal wet zones from production from upstream backwaters (Figure 4.5 & 4.6).

IV.4.2. Base flow simulation

IV.4.2.1. Flow characteristics

Tracers releases occurred on the 8th and 15th of June and 15th of July 2011. On these three occasions daily average water levels were stable and similar (respectively: 55 m^3/s; 38 m^3/s and 53 m^3/s).

IV.4.2.2. Within backwaters

IV.4.2.2.1. *Dispersion*

100% of tracers left in backwaters were moved, on average by 45 metres from their original release position (range: 0.5 m to 192 m) (Table 4.1). In total 43% of tracers were exported out of backwaters into the main channel (Figure 4.7 & 4.8). Export from backwaters varied from 6.2% to 63.5%. The export of material was not related significantly to water discharge in the main channel ($r = 0.98$; pvalue $= 0.106$).

IV.4.2.2.1. *Retention*

Successful retention of tracers in aquatic zones reached 56% within backwaters and 1.37% for in wet marginal zones (Figure 4.7 & 4.8). In aquatic zones tracers were mostly retained in backwaters by woody debris, rock substrate and existing aquatic vegetation (Table 4.3). In marginal zones tracers were principally retained on coarse substrate (100%).

IV.4.2.2.3. *Estimated* c*olonisation*

Estimated colonisation success of tracers in aquatic zones reached 33% but only 0.82% in wet marginal zones (Figure 4.7 & 4.8).

Table 4.3. Base flow model retention patterns percentages in the different habitats and considering the different origins of tracers. Grey shaded columns are results for strictly aquatic zones, white coloured columns are results for wet marginal zones. Results expressed in percentages.

					Downstream main channel		Downstream backwater			
	Within backwater		Within main channel		From backwater		From backwater		From main channel	
Woody debris (%)	43.6	-	50.2	0.2	16.6	-	-	-	22	-
Aquatic vegetation (%)	18.5	-	1.4	-	1.6	-	-	-	48	-
Riparian vegetation (%)	-	-	4.1	8.5	19.6	1	-	-	-	-
Riparian grasses (%)	-	-	-	-	-	-	-	-	-	-
Bare sediments (%)	-	100	1.3	-	1.6	-	-	-	-	-
Bare rock substrate (%)	37.9	-	43	91.3	60.6	99	100	-	30	100

IV.4.2.3. Within main channel

IV.4.2.3.1. *Dispersion*

100% of tracers originally left in the main channel were dispersed from their original position. On average these tracers dispersed for 1.7 km (range: 210 m to 4 km) (Table 4.1). Respectively 85% and 98% of tracers from main channel aquatic and marginal zones were never retrieved after dispersal and were considered moribund (Figure 4.7 & 4.8). However, 89% of tracers originating from aquatic zones (representing 39.5% of tracers of original backwater pool) and 95% of tracers originating from wet marginal (representing 40.8% of tracers exported from backwaters) were never retrieved and were assumed lost downstream. Tracers originating from backwaters and which were exported to the main channel dispersed on average for 1.4 km (range: 12 m to 4.1 km).

IV.4.2.3.2. *Retention*

Retention success of tracers originally left in the main channel was 14.5% in aquatic zones and 1.9% in wet marginal (Figure 4.7 & 4.8). Tracer retention in aquatic zones was mainly due to woody debris and rock substrate (Table 4.3). Tracer retention in marginal zones was mainly retained by rock substrate (Table 4.3). Once exported from backwaters, respectively 4.5% and 1.9% of tracers from aquatic and wet marginal zones backwater original propagule pool were retained into the main channel. Retention of exported tracers originating from aquatic zones was mainly by deposition on rock substrate, riparian vegetation and woody debris (Table 4.3). Retention in the wet marginal zone was principally the result of deposition on rock substrate (99%).

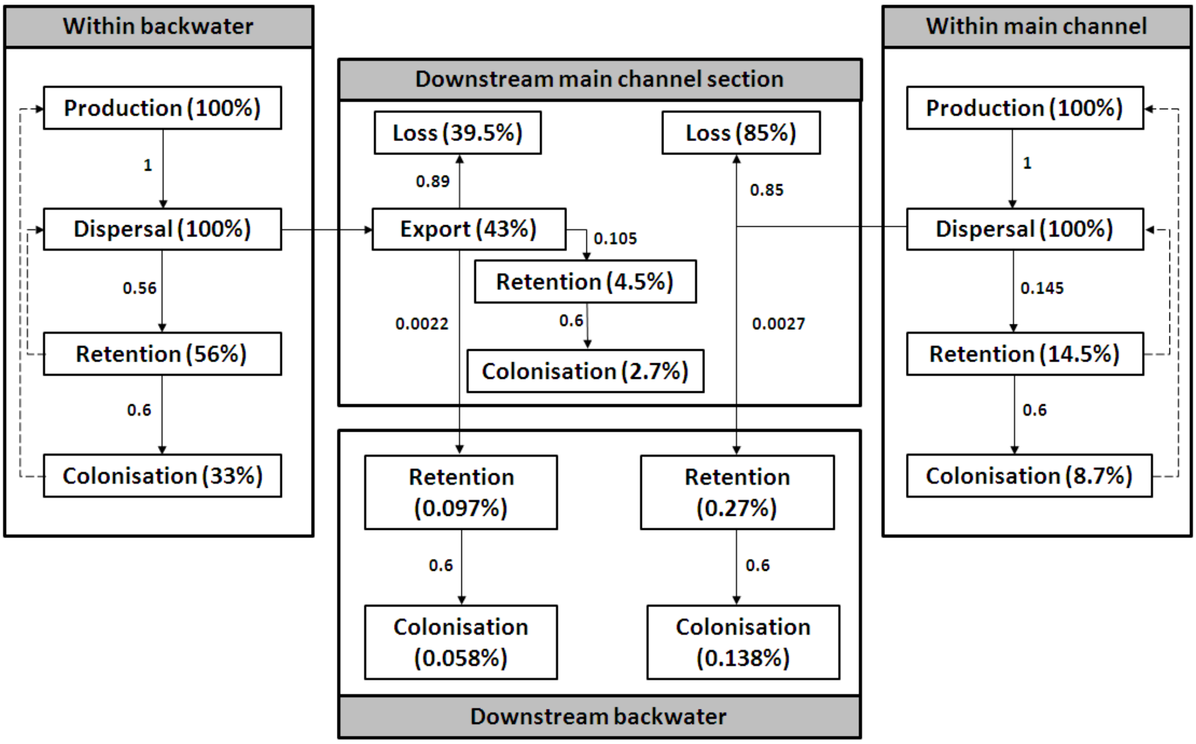


Figure 4.7. Base flow dispersal model from and to strictly aquatic zones within and between both backwaters and main channel. Numbers in the process boxes are the proportion of the initial release of tracers to successfully complete that process. Numbers between the process boxes are probabilities of successfully completing the process indicated. The retention process boxes only relate to retention within viable habitat for the tracers type concerned.

IV. 4.2.3.3. *Estimated colonisation*

Estimated colonisation success of tracers originally left in the main channel reached 8.7% in aquatic zones and 1.1% in wet marginal zones (Figure 4.7 & 4.8). For tracers left in backwaters and exported into the main channel colonisation success was 2.7% in aquatic zones and 1.14% in marginal zones. No loss of material to bank elevations above favourable zones for growth was observed since water levels were stable.

IV.4.2.4. In downstream backwaters - from main channel

IV.4.2.4.1. *Retention*

Tracer retention in downstream backwaters was higher in aquatic zones (0.27%) than in wet marginal zones (0.011%) (Figure 4.7 & 4.8). Mean dispersal distance before retention was 0.23 km in aquatic zones and 0.3 km in wet marginal zones (Table 4.1). Retention in aquatic zones was caused by aquatic vegetation, deposition on rock substrate and woody debris (Table 4.3). Retention was unrelated to discharge (pvalue = 0.845, r = 0.241).

IV.4.2.4.2. *Estimated* c*olonisation*

Having entered backwaters estimated colonisation success was 0.138% of the original release in aquatic zones and 0.0065% in wet marginal zones (Figure 4.7 & 4.8).

IV.4.2.5. In downstream backwaters - from backwaters

IV.4.2.5.1. *Retention*

Tracer retention success in downstream backwaters aquatic zones was very rare (equivalent to 0.097% from backwater pool) although retention in wet marginal zones was even less successful (0.0038% of the original pool) (Figure 4.7 & 4.8). Mean distance moved before retention was 0.65 km in aquatic zones and 1.1 km in wet marginal zones (Table 4.1). Tracer retention in aquatic zones was mainly caused by retention by aquatic vegetation and deposition on rock substrate for amphibious propagules (Table 4.3). Tracer retention in backwaters was unrelated to discharge in the main channel (p value = 0.01, R = - 1.0).

IV.4.2.5.2. *Estimated colonisation*

Accordingly, estimated colonisation success of tracers entering downstream backwaters aquatic zones from other backwaters was very low 0.058% but somewhat higher than that tracers deposited in the downstream backwater wet marginal zone (0.0023%) (Figure 4.7 & 4.8).

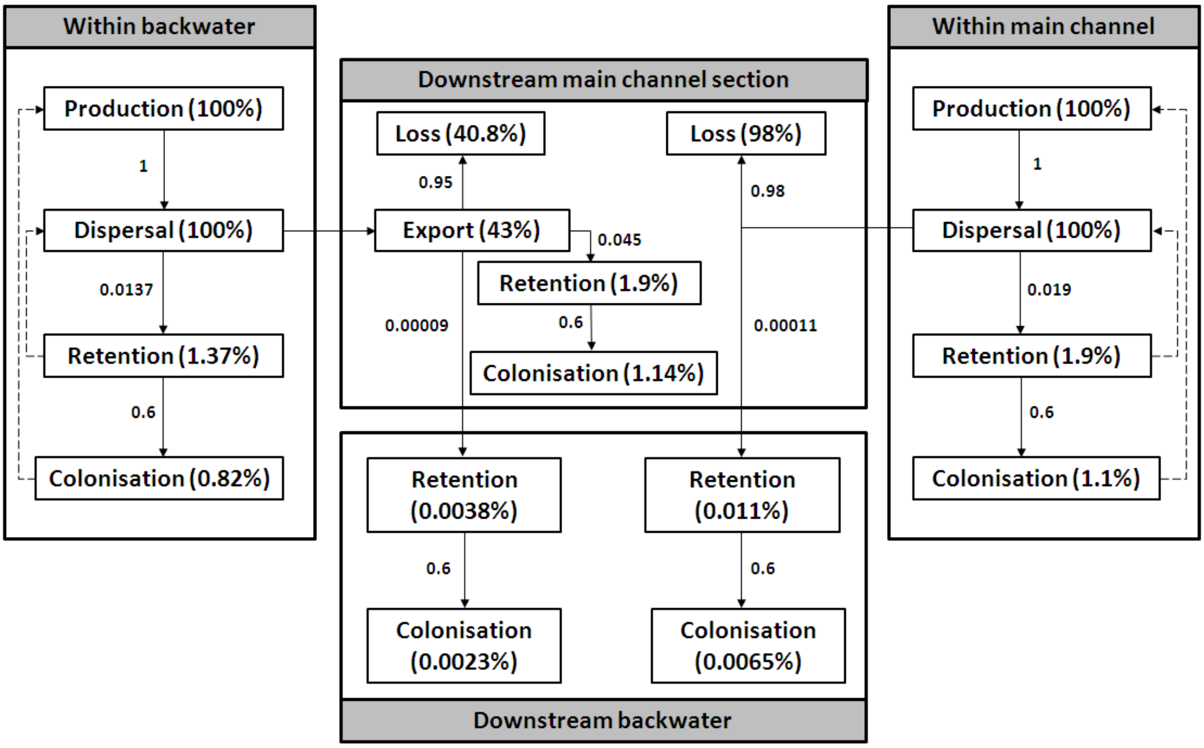


Figure 4.8. Base flow dispersal model from and to wet marginal zones within and between both backwaters and main channel. Numbers in the process boxes are the proportion of the initial release of tracers to successfully complete that process. Numbers between the process boxes are probabilities of successfully completing the process indicated. The retention process boxes only relate to retention within viable habitat for the tracers type concerned.

IV.5. DISCUSSION

Recent work on macrophyte communities in small river systems led Riis (2008) to hypothesise that macrophyte colonisation was not limited by propagule supply; rather that primary colonisation was the main constraint in successful establishment. In the present study we demonstrate that external diaspore supply and successful retention is the main bottleneck for macrophyte colonisation of riverine backwaters. Indeed, our backwaters had a high potential for inter-connection, since they all connected to the river both in flood and base flows, yet displayed low effective connection as the retention of propagules from external upstream sources was negligible.

We realise that modelling macrophyte dispersal using bamboo sticks is imperfect since it cannot precisely match natural buoyancy characteristics and drift processes or reflect the varied characteristics of a cocktail of dispersing propagules of different species and types. It potentially over-estimates dispersal distances as sticks are more robust and probably have higher buoyancy than most natural propagules which are then expected to disperse for shorter distances (Gurnell *et al.*, 2008; Kallstrom *et al.*, 2008). However, innovation is necessary and compromises are inevitable to meet the challenges of studying dispersal in riverine environments and our results are revealing in terms of potential pathways for dispersal under different flow regimes, associated features of retention and probabilities of successful colonisation. Nevertheless, previous works support our use of artificial wood propagule mimics in reproducing identical dispersal pattern of natural plants propagules (Nilsson & Grelsson, 1990; Andersson *et al.*, 2000).

The question of how colonisation success relates to propagule type (seeds or vegetative) and natural buoyancy and dispersal distances of propagules has existed for almost two decades (Barrat-Segretain, 1996) but remains of pure and applied relevance. Previous work has had opposing outcomes suggesting that either seeds drift for longer distances than shoots and rhizomes as seeds are normally more buoyant and have lower roughness (Alvarez *et al.*, 2005), or that seeds sink rapidly and have low dispersal potential as a result of low buoyancy (Barrat-Segretain, 1996). Non buoyant seeds were also shown to be transported over long distances (Marckwith & Leigh, 2008). Additionally Boedeltje *et al.* (2004) determined that seed release and dispersion occurs over short release and short dispersal periods whereas vegetative propagules are released and dispersed over longer time periods revealing their potential for long-distance dispersal. This adds a further dimension to the relative importance of buoyancy in sexual or asexual propagules in colonisation.

IV.5.1. Export and dispersal

Our results showed that tracers movement within the site of production, at both flood and base flow regimes (through wind action), could spatially re-organise plant communities at the site scale (Table 4.1). We also demonstrate that under both flow conditions backwaters are source habitats within the floodplain as a large net export of tracers to the main channel was recorded (Figure 4.5, 4.6, 4.7 & 4.8), in line with Cellot *et al.*, (1998). However, high energy flood flows have a higher potential for plant disruption (Henry *et al.*, 1996) and could therefore mobilise and export a larger number of tracers (in our case 83% of propagules placed in backwaters compared to 43% under base flow). As reported by Andersson *et al.* (2000) export within the site of production was positively correlated with flooding duration. At base flow the mobilisation of tracers could occur through plant breakage, along with foraging by animals or birds, wind-induced waves (Schutten *et al.*, 2005), re-suspension from sediments and natural detachment from parent plants. In both cases, exported tracers represented a major source of potential colonists of downstream habitats. Once exported from backwaters higher velocity flows and larger discharges caused tracers to disperse for larger distances within the river system than under base flow (Table 4.1) (Tockner *et al.*, 2000).

IV.5.2. Retention and connection

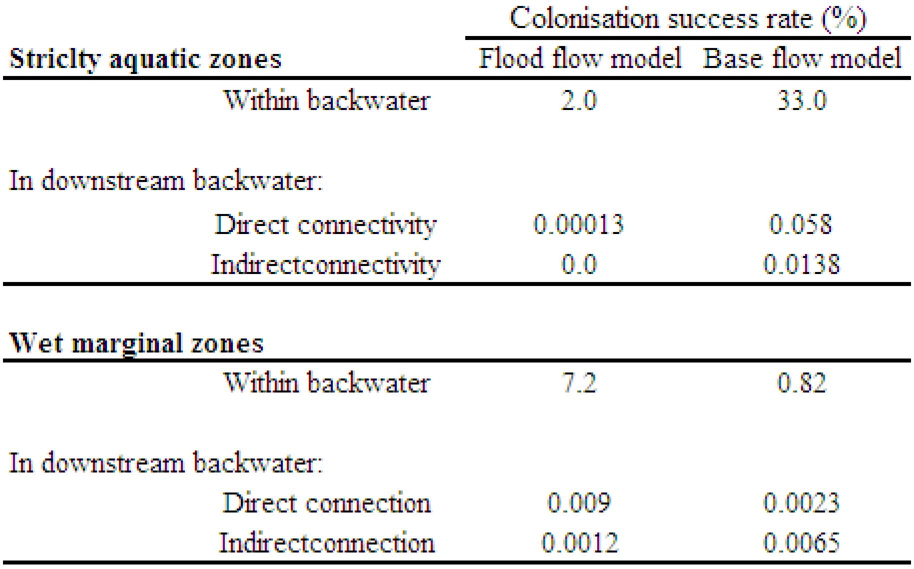
Cellot *et al.* (1998) have previously questioned the ultimate outcome of propagules exported from backwaters. In our study the largest proportion (95% in flood model and 92% in base flow model) of exported tracers were never recovered after dispersal and were therefore considered lost from the population (Figure 4.5, 4.6, 4.7 & 4.8). Moreover, the retention of tracers itself will lead to losses, since retention at high elevations on the river bank will prevent colonisation of suitable habitat. Such propagules (tracers) may therefore be considered moribund, while mortality of vegetative propagules will occur rapidly due to desiccation. This represented an important proportion of the drift for macrophytic vegetation but it may represent valuable colonists in terms of riparian species (Gurnell *et al.*, 2008). A lower proportion of tracers reached a suitable marginal wet habitat to colonise the main channel which is consistent with the very low abundance of macrophytes found in the main corridor of large rivers (Keruzoré *et al.*, in press). Finally, the percentage of initial tracers reaching a suitable backwater downstream from the site of release was extremely low (from 0% to 0.097%). Differences in the mechanism of connectivity were underlined with regards to flow conditions and to habitat. Under less turbulent flow conditions (base flows) tracers achieved higher success in reaching downstream aquatic backwaters zones and as an indirect dispersal process (originating from main channel). Conversely, tracers displayed higher success during flooding in terms of entering wet marginal backwater zones and as a result of a direct dispersal pathway (originating from a backwater and colonising a downstream backwater). Low dispersal success via indirect pathways under floods suggests that viable stranded tracers in the main channel will rarely experience successful dispersal in subsequent floods (Nilsson *et al.*, 2010). Both situations illustrate that a large range of hydraulic conditions in river floodplains contribute to the retention of propagules (tracers) (Merrit & Wohl, 2002; Stromberg *et al.*, 2007) and are important to many processes maintaining vegetation communities (Greet *et al.*, 2011). However, features such as woody debris and a well vegetated riparian zone are essential for this retention to take place (Horvath, 2004).

When backwater connection occurred, the distance drifted before entering a downstream backwater was much higher under flood flows (19 km on average) than at base flow (600 m on average). This implies that long range dispersal could occur at high flows but is then associated with a lower probability of successful colonisation, whereas at base flow shorter dispersal distances were observed, but with a higher probability of successful colonisation (Van Looy *et al.*, 2009). Therefore, colonisation of backwaters by macrophytes is arguably more likely to be the result of a ‘stepping stone’ type spreading process along the river channel. In systems with highly disconnected and isolated suitable habitat colonisation will therefore mostly rely on flooding (Moggridge *et al.*, 2009) but successful colonisation events will be rare. In this scenario dispersal by other mechanisms, such as zoochory (especially by wildfowl), may become proportionally more important (Figuerola & Green, 2002). The evidence for lack of propagule connectivity between isolated habitats may explain differences in their species diversity and composition. Our study suggests that the recovery of macrophyte populations in isolated backwaters after disturbance will mostly depend on their capacity for resistance or resilience and that colonisation via external sources will occur only very rarely.

IV.5.3. Estimated colonisation

In both flow regimes estimated colonisation was most likely to be successful when occurring within the site of propagule production and was therefore the best colonisation strategy (Table 4.4). In contrast, the percentage of tracers originating from a backwater and colonising a downstream backwater was very low (from 0% to 0.058%). From the initial point of formation of riverine backwaters our results suggest that their colonisation from external sources will be a slow and erratic process. Visual observations of apparently viable habitat on the Tay-Tummel system still bare after several years support this.

Table 4.4. Success rate of estimated colonisation in flood and baseflow models for tracers in strictly aquatic and wet marginal zones within backwater, in downstream backwater (both as in indirect and direct connectivity processes).



		Colonisation success rate (%)	
Striclty aquatic zones		Flood flow model	Base flow model
	Within backwater	2.0	33.0
In downstream backwater:			
	Direct connectivity	0.00013	0.058
	Indirectconnectivity	0.0	0.0138
Wet marginal zones			
	Within backwater	7.2	0.82
In downstream backwater:			
	Direct connection	0.009	0.0023
	Indirectconnection	0.0012	0.0065

Colonisation will strongly depend on the connection frequency of backwaters along a temporal gradient. It will also be driven by the number of individuals entering a site, the resources available, the level of disturbance and the abundance and composition of vegetation in the receiving habitat (Ward & Thornton 2000). However, the environmental stress that colonists experience to first establish and recruit is probably higher than that for primary colonisation. In 2002, Barsoum showed asexual propagules had a higher survival rate and that plant colonisation along rivers mainly relied on those. Once propagules do establish successfully they have the potential to generate up to several thousand viable sexual or asexual propagules within the same growing season of establishment (Casanova & Brock, 1999; Rogers & Breen, 1980). Thus, once establishment has occurred, extinction is comparatively unlikely.

In spite of this, one could argue that the abundance of propagules mobilised and dispersed in flood flows (Boedeltje *et al.,* 2004) may represent many millions of potential colonists which could quickly counterbalance the low probability for entry to backwaters in contrast to the lower number of propagules mobilised at base flow. The probability to receive inputs of externally-derived propagules in floods is, however, constrained by the narrow time window of connection (only a few hours to a few days per year for most backwaters) which is also most likely to occur at the least favourable time of the year for growth (Andersson & Nilsson 2002). Limited seed input during flood dispersal was also shown to be a possible scenario in the colonisation process of riverine habitats by van Eck *et al.,* (2005). By contrast, backwaters experience base flow at almost all times, especially in summer, when millions of propagules could also be dispersed (Riis, 2008) entering other backwaters via their permanent downstream connection. Moreover, the volume of water discharging in flood flows (i.e.: 903 m^3/s at flood peak on River Tay in this study) may dilute and thus lower propagule density and the probability of entering backwaters, unless there is a similar order of increase in propagule input during floods. In contrast the lower discharge at base flows (i.e.: 48 m^3/s on River Tay in this study) might concentrate propagule density and increase the probability of entry to backwaters.

IV.5.4. Perspectives

Techniques of genetic analysis applied to macrophyte populations in backwaters would complement the present study. While this would not illustrate the mechanistic processes of plant dispersal it would clarify effective pathways of dispersal from a genetic perspective. From our results little genetic differences should be expected within populations as there is limited external input to backwaters and asexual reproduction is likely to dominate (Kaplan & Štěpánek, 2003). Between-population differences might be higher as genetic drift may occur in isolated populations (Honnay *et al.*, 2010). Also molecular tools might be able to trace individual dispersion and would allow reconstruction of the dispersal history of individual populations. Survivorship of propagules of different types and species upon exposure to air would clarify the fate of dispersed propagules and their viability in cases of remobilisation by subsequent water level change (Barrat-Segretain & Cellot, 2007; Katja & Axel 2008; Silveira *et al.*, 2009). Finally reproductive strategies in macrophyte communities exposed to a gradient of flooding frequency, as found in backwaters, could also be determined to refine understanding of colonisation processes in large rivers (Keller, 2000; Pollux *et al.*, 2007).

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CHAPTER V.

Seed banks and established vegetation in riverine backwaters: the influence of connectivity and fluvial disturbance

Antoine A. Keruzoré[1], Nigel J. Willby[1]

[1]School of Natural Sciences, Biological and Environmental Sciences, University of Stirling, Scotland, UK

Contact: antoine.keruzore@stir.ac.uk

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V.1 ABSTRACT

In lentic aquatic ecosystems the seed bank appears to play an important role in storing macrophyte sexual propagule which may contribute to the established vegetation. In this study we aim to determine if connectivity and fluvial disturbance drive variation in the size and richness of the seed bank in riverine backwaters and its contribution to the established vegetation. The richness and abundance of viable diaspores stored in the sediment was measured with a seedling germination trial. Samples were collected in Scotland in two major catchments (river Tay and Spey) from 16 riverine backwaters experiencing different intensity of fluvial disturbance and frequency of connection to the main channel. T-Test was used to compare species richness between seed bank and established vegetation and GLMs were used to test the influence of disturbance and connectivity on species richness and seedling abundance. Compositional similarity between seed bank and established vegetation was measured using the Sørensen index and effects of connectivity and disturbance on composition were tested via CCA ordination. Our results showed that species richness was consistently lower in the seed bank than the established vegetation. Sørensen similarity index between seed bank and established vegetation was on average less than 50% and was unrelated to connectivity. Neither established vegetation nor seed bank richness and seedling abundance were related significantly to disturbance and connectivity regime. Species composition of the established vegetation was related to connectivity but not to disturbance. Seed bank composition was unrelated to either connectivity or disturbance. Therefore, we conclude that connectivity had a significant influence on the composition of established vegetation but not on properties of the seed bank. This suggests that, in low productivity systems, colonisation, maintenance and resilience of aquatic vegetation in riverine backwaters are supported mainly by in situ vegetative reproduction or external

vegetative waterborne inputs. The influence of connectivity on the linkage between seed bank and established vegetation is probably weakened through a trade-off between propagule supply and retention. Nevertheless a combination of external supply and internal generation may account for the higher seedling species pool observed in backwaters with intermediate connectivity.

V.2. INTRODUCTION

Rivers are linear components of floodplains and constitute major corridors for the flow of energy, matter and organisms through the landscape. River corridors are used by fish, drifting invertebrates and plants to achieve dispersal by water (Johansson *et al.*, 1996). The dispersal potential of running waters supports plant species-rich river corridors through the maintenance of a series of successional stages (Nilsson *et al.*, 2010). Indeed aquatic vegetation processes in riverine systems are usually driven by fluvial disturbance associated with the natural flow regime (Bornette & Amoros, 1996). However, population resilience is controlled by plant traits that increase persistence and survival during floods and droughts (Grime, 1979; Grillas & Battedou, 1998). Thus, riverine wetlands commonly hold extensive seed banks (Brock *et al.*, 2003). The production of dormant propagules offers the possibility to overcome unpredictable and potentially disturbing events. Research on aquatic vegetation has illustrated the important role of the seed bank in the resilience of plant assemblages in response to water level fluctuation and disturbance (Thompson, 1992; Henry *et al.*, 1996). Various ecological conditions may influence seed production and germination success in wetlands, such as nutrient concentration and light stress (Arthaud *et al.*, 2012). Across a spectrum of temporary to permanent backwaters Abernethy & Willby (1999) found that water depth was a major driver of species richness and seed density which were negatively correlated with increasing water depth and permanence. Similarly, Warwick & Brock (2003) showed that high fertility and plant biomass production had a positive impact on the number of reproductive units produced per plant. In temperate climates studies of seed bank ecology have considered various water-logged habitats including tidal saturated wetlands, ponds, lakes, navigation canals and floodplain wetlands (Bonis et *al.*, 1995; Westcott *et al.*, 1997; Dittmar & Neely, 1999; Boedeltje, 2003;

Hopfensperger *et al.*, 2009). Frequently disturbed riverine habitats, which encompass a range of different propagule sources, are more rarely considered (Abernethy & Willby, 1999; Capon & Brock, 2006) and less fertile fluvial systems are especially poorly understood. Consequently, the extent to which fertility moderates the regenerative strategy of aquatic vegetation in disturbed habitats is poorly understood.

In natural river floodplains the dynamics of the river channel lead to the formation of a variety of open waters, including oxbow lakes and palaeo-channels, which experience varying degrees of connectivity to the main river. These sites, collectively referred to here as ‘backwaters’, offer standing water-like conditions, and are thus usually well-vegetated, in contrast to the main channel of large rivers (Keruzoré *et al.*, in press). Connectivity controls two related but different processes: flow disturbance and linkage between waterbodies. Disturbances rejuvenate habitats by reducing or destroying biomass and creating empty patches (Ward, 1998) available for colonisation from internal or external sources. The connection between waterbodies that occurs during flooding events allows the input of waterborne propagules to aquatic habitats that normally are partially or totally disconnected (Bornette *et al.*, 1998), and hence for propagules to be potentially exchanged between backwaters. Connectivity and disturbance are positively related, especially in rivers with natural flow regimes (Ward & Stanford, 1995). However, the sinuosity of backwaters acts as a regulator of physical disturbance since it profoundly influences the energy of flood flows and the potential for retention of propagules within backwaters (Nilsson *et al.*, 2010). Whereas both connectivity and sinuosity may drive the diversity and dynamics of established vegetation (van Geest *et al.*, 2003) it remains unclear if these factors can also influence seed bank composition and its contribution to established aquatic vegetation. James *et* *al.* (2007) proposed that this contribution should vary with some degree of predictability with regards to hydrological influences.

In frequently disturbed habitats ruderal or flow-resistant species dominate the established vegetation and have developed reproductive strategies to face challenging or unpredictable conditions. For instance, ruderal species commonly produce large amounts of seed to enable rapid colonisation of disturbed habitat and which form a major component of dormant seed banks (Grime, 2001; Klimkowska *et al.*, 2009). Nevertheless, the seed bank species pool found in backwaters can also be supplemented with propagule inputs during flood connection. In recently formed and sparsely vegetated backwaters this is expected to be the main source of propagules (Abernethy & Willby, 1999). As backwaters age richness should increase through the progressive accumulation of external inputs (Hopfensperger, 2007) and the composition of such seed banks thus reflects the history of a site (LaDeau & Ellsion, 1999; Wetzel *et al.*, 2001). However, various processes may influence seed bank depletion (e.g. germination, mortality, granivory and flood scouring) and replenishment (e.g. internal seed production, external supply rates). In opposition to this trend the established community dynamic in ageing and rarely disturbed aquatic habitats should lead to lower diversity as a result of plant succession and exclusion through control of resources by the most competitive species and an associated shift to vegetative production.

The specific aims of this study are to (i) compare the diversity, composition and abundance of macrophyte propagule banks in backwaters along a gradient of connectivity; (ii) assess the influence of connectivity and disturbance on macrophyte seed bank species richness and composition; and (iii) determine if connectivity and disturbance affect macrophyte seed bank contribution to the macrophyte established vegetation. Our main hypothesis is that as connectivity and disturbance decrease the difference between established and seedbank vegetation will increase reflecting species accumulation along a successional gradient and the limited contribution of the seedbank to the maintenance of vegetation in stable environments.

V.3. MATERIALS AND METHODS

V.3.1. Study sites

The study was carried out during the 2011 growing season and used six riverine backwaters along the River Tay and its affluent River Tummel (Perthshire, Central Scotland) and 10 backwaters on the River Spey (Northeast part of the Scottish Highlands) (Figure 5.1). The River Tay and River Spey differ in catchment area (5200 and 3008 km^2 respectively, at the downstream points of sampling and mean discharge (170 m^3.s-1 and 64 $m^3.s^{-1}$respectively). Channel widths on the Tay/Tummel are typically 50-80 m compared to 30-50 m on the Spey. These are low fertility systems with soluble reactive phosphorus concentrations in the middle reaches of the Spey and its floodplain commonly close to the 1 ug/L detection limit during the growing season (Demars & Edwards, 2007) while equivalent concentrations in the Tay/Tummel system are typically 5-10 ug/L (Keruzoré *et al.*, in press). Both rivers are among the most dynamic and least impacted in the UK and, within the reaches studied, are characterised by a predominantly upland catchment, mobile gravel bed form, and present a high concentration of backwaters. They are therefore representative of the influence of natural hydrological conditions and ecological processes along large upland rivers.

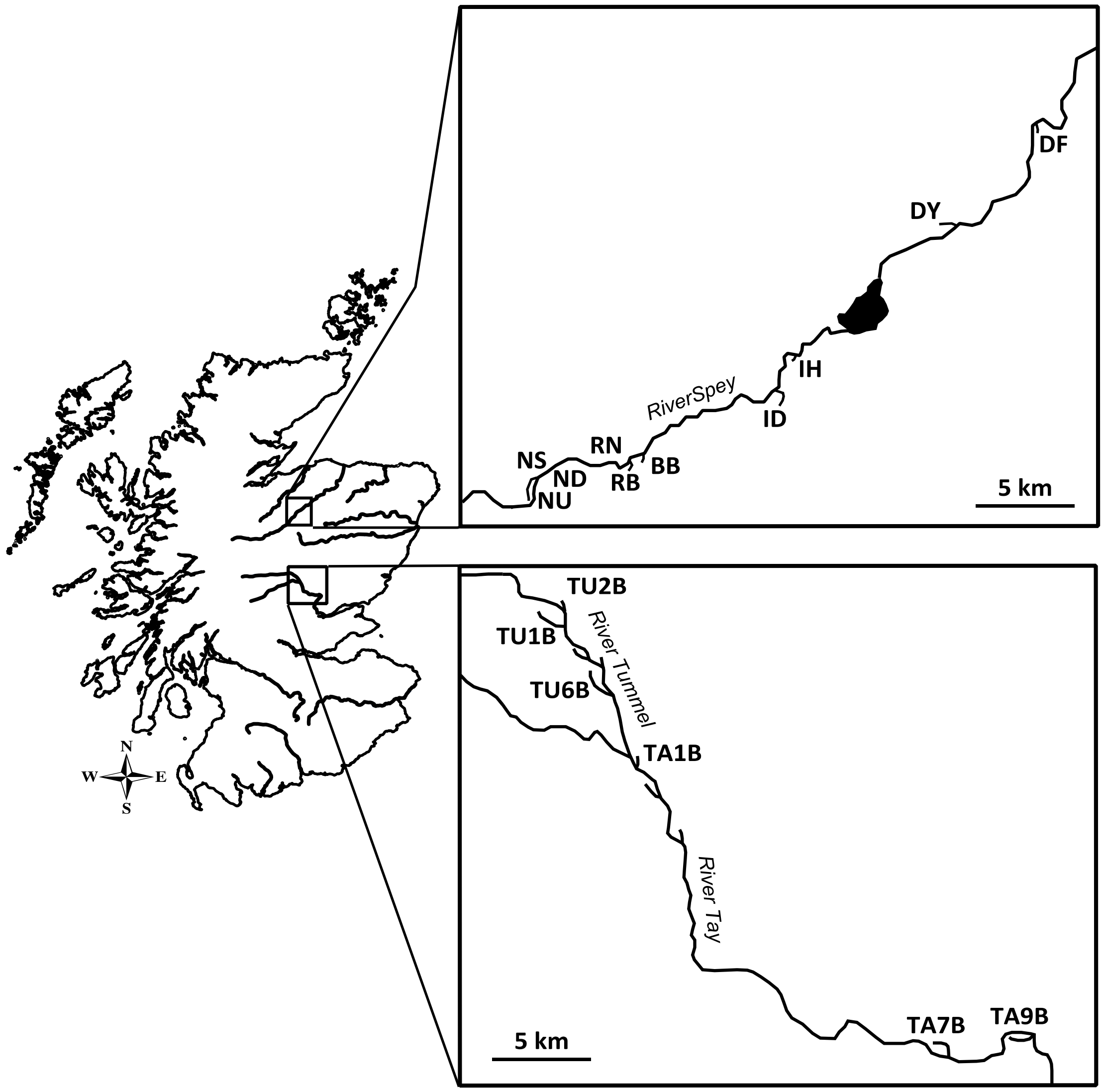

Figure 5.1. Map of Spey (top) and Tay (bottom) river floodplains showing the position of assessed riverine backwaters.

V.3.2. Measurement of connectivity and disturbance

All sampled sites experienced permanent and still water conditions for most of the year but were further inundated during flooding disturbances. Such inundation events affect backwaters via fluctuating water levels, increased water velocity and potential sediment scouring which vary in intensity with flooding and the frequency of connection between a backwater and its parent main channel. At each site connectivity frequency was determined via bathymetry transects between main channel and the water surface of backwaters at their upstream part to determine the water level rise needed to initiate connection. The number of connections was calculated for each backwater with hydrological data gathered from the Scottish Environment Protection Agency from 01/01/2000 to 31/12/2010 (station 15012 at Pitlochry (River Tummel, station 15006 at Ballathie (River Tay), station 1012 at Kinrara (River Spey)). In this study, connection frequency refers to the average number of connection events per year, as measured over the last 10 years, and ranged from 0.1 to 15 connections per year. Sinuosity of backwaters was used as an indicator of disturbance and flow energy experienced within backwaters during flood connectivity with the main channel. Sinuosity reflects channel slope which in turn regulates stream power and the ability to erode or transport sediment. Sinuosity of backwaters was measured as the ratio of channel length to the straight line distance between upstream and downstream points of connection to the main river channel.

V.3.3. Propagule bank sampling

Following winter stratification sediment cores were collected from each site. Five approximately equally spaced transects were located in each site. Five 0.1 m diameter cores were collected randomly along each transect to a depth of 0.05 m. To allow a comparison between the composition of the seed bank and the established vegetation, macrophyte surveys were conducted at each site covering an area 3 m either side of the sampled transects at the peak of the subsequent growing season and for which species richness and plant cover (%) were recorded.

Cores were stored at 4°C until the start of the germination trial to prevent premature germination. The five cores from the same transect were mixed by hand. Discernible roots, rhizomes, plant fragments, litter and large pieces of organic matter were carefully removed. Each sample was then sieved (0.2 mm mesh) to aid scarification and then subdivided into three equal parts and spread in a layer (~15 mm deep) overlying 20 mm of sand in a plastic tray (170 mm × 120 mm × 100 mm deep). Sediment flats were exposed to three different treatments: (i) *Permanent inundation*, the most common situation during the growing season, consisted of permanent flooding to 0.10 m depth; (ii) *Fluctuating water level*, comprised sediment moistened for a month, before flooding trays until the end of the trial, thus providing conditions of temporary exposure which some species require in order to germinate; (iii) *Moist sediment*, consisted of maintaining damp but not inundated sediment during the entire trial which represented exposed sediment found at the margin of backwaters. Each treatment was applied to the subsamples from each transect making 15 trays per site. Trays were placed in a randomised design and left to germinate for 5 months in the green house at about 20°C (5-6°C diurnal fluctuation) with natural light supplemented by 250 W lights for 16 hr per day. The present methodology should be adequate to detect the majority of species in the sediment bank in the early stages of succession (Abernethy & Willby, 1999).

Trays were examined every two days to ensure consistency of the watering treatment applied. The number of seedlings germinating was counted weekly to ensure that seedlings did not emerge and die between counts. Most germination occurred in the second and third month of the trial. Once plants could be identified they were removed from trays to prevent reseeding. Three control trays were prepared per treatment which confirmed the sterility of the sand and the absence of contamination by seed rain within the greenhouse. Species richness per sample was recorded as the total number of species that germinated across the three treatments and seed abundance was calculated by taking the maximum germination of each taxa across the three treatments, summing this and then converting to a density per m^2.

V.3.4. Data analysis

Data analysis was performed using the R statistical package. Species richness and abundance were first compared between seed bank and established species across all sites using a T-test. The similarity of species composition in seed bank and established vegetation was evaluated through calculation of the Sørensen's coefficient as in: $S = 2c / (a+b)$; where a stands for total number of species in the seed bank; b stands for the total number of species in the established vegetation; and c stands for the number of species common to both bank and established vegetation compartments (Sorensen, 1948). A coefficient value of 1 indicates high similarity between the two vegetation pools whilst a coefficient value of 0 indicates no species in common. Correlations were tested between values of Sørensen's coefficient and connectivity and disturbance.

Influence of connection and disturbance on richness and abundance were assessed using Generalised Linear Models followed by a chi-squared test of the deviance. In these analyses seedling abundance was square root transformed and richness was analysed using a Poisson distribution and a log link function. The influence of connectivity and disturbance on the species composition of the seed bank and established vegetation was tested using Canonical Correspondence Analysis (CCA).

Finally, a sample-based rarefaction was performed to estimate and compare species richness in samples collected from backwaters of different connectivity categories. Randomised resampling of transect data (50 runs) collected from a pooled group of samples was used to estimate the average increase in species richness with increasing number of samples. For the purpose of this analysis, backwaters were assigned to one of three categories of connectivity where low = 0 to 3 connections/year - (six sites); intermediate 3.1 to 10 connections/year - (six sites); and high = 10.1 to 15 connections/year - (four sites).

V.4. RESULTS

V.4.1. General patterns across rivers

An initial exploration of differences between the two studied river systems (data not presented here) revealed no significant effects and the results presented are therefore based on the combined dataset.

V.4.1.1. *Species richness*

Across the two rivers a total of 73 species was recorded in the established vegetation. Established vegetation richness averaged 20 species per site (range 14-30). The seed bank germination trial revealed a total of 47 species across the 16 backwaters. Seed bank richness averaged 12 species per site (range 5-17). Established vegetation and seed bank species richness in backwaters were positively correlated ($r = 0.548$; $p = 0.028$). Species richness was always higher in the established vegetation than in the seed bank compartment (T-test; $p = 6.1^{e-06}$) (Figure 5.2). The species recorded are listed in Appendix 5.1 and 5.2.

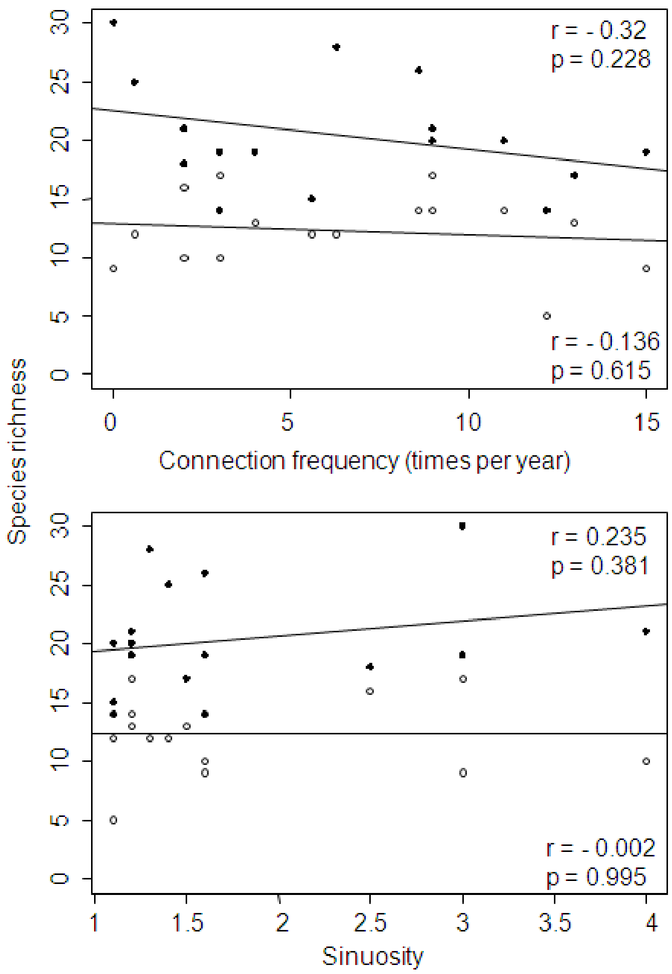

Figure 5.2. Species richness in established vegetation (●) and seed bank (○) macrophyte species along a gradient of connectivity and sinuosity across sampled backwaters of River Tay and Spey.

V.4.1.2 *Seed abundance*

Over the duration of the germination trial, a total of 2939 seedlings germinated from the seed bank samples collected from backwaters. Across the backwaters studied density averaged 4898 seedlings per m^2, (range 381-11 265 seeds per m^2). Seedling density was uncorrelated with connectivity (r = - 0.226; p = 0.4) and sinuosity (r = 0.07; p = 0.797) (Figure 5.3). Abundance of seedlings and species diversity were not correlated (r = 0.12, p = 0.66).

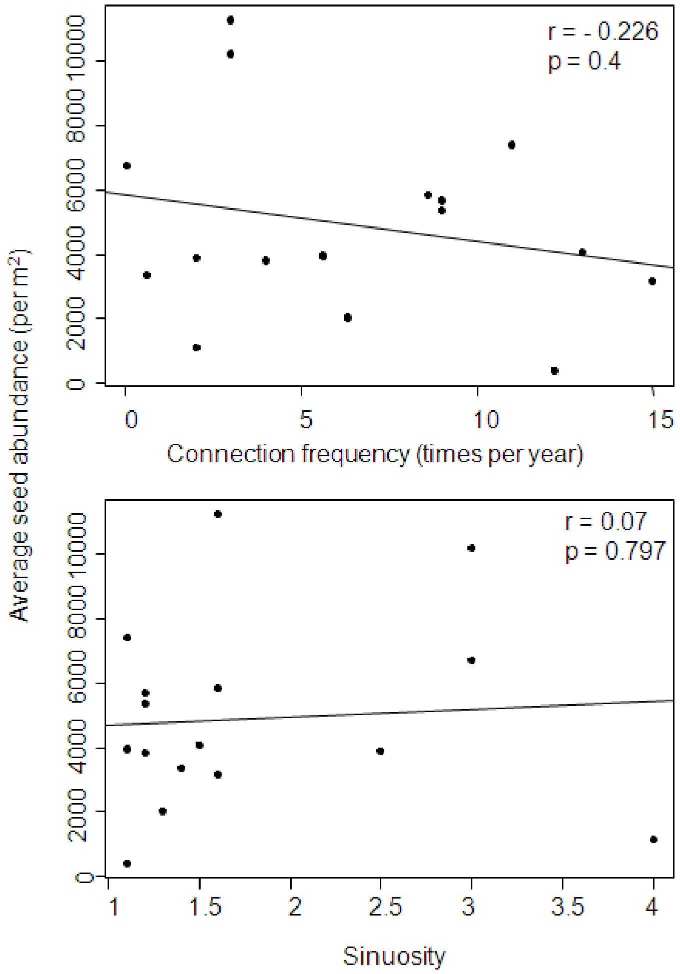

Figure 5.3. Average seedling abundance (per m/^{2}) in the seed bank of backwaters distributed along a gradient of connection frequency and sinuosity across sampled backwaters of River Tay and Spey.

V.4.1.3. *Similarity between seed bank and established vegetation*

The Sørensen similarity index between established vegetation and seed bank averaged 0.47 and ranged from 0.11 to 0.68. Values were independent of both connectivity (r = 0.019; p = 0.944) and sinuosity (r = - 0.18; p = 0.506) (Figure 5.4). The status of these relationships was not changed by the removal of one outlying site on the River Tay (Figure 5.1 – site KE) with a very low similarity value (0.11). There was no evidence that relationships differed between river systems although the similarity between seed bank and established vegetation was generally higher in sites from the River Spey.

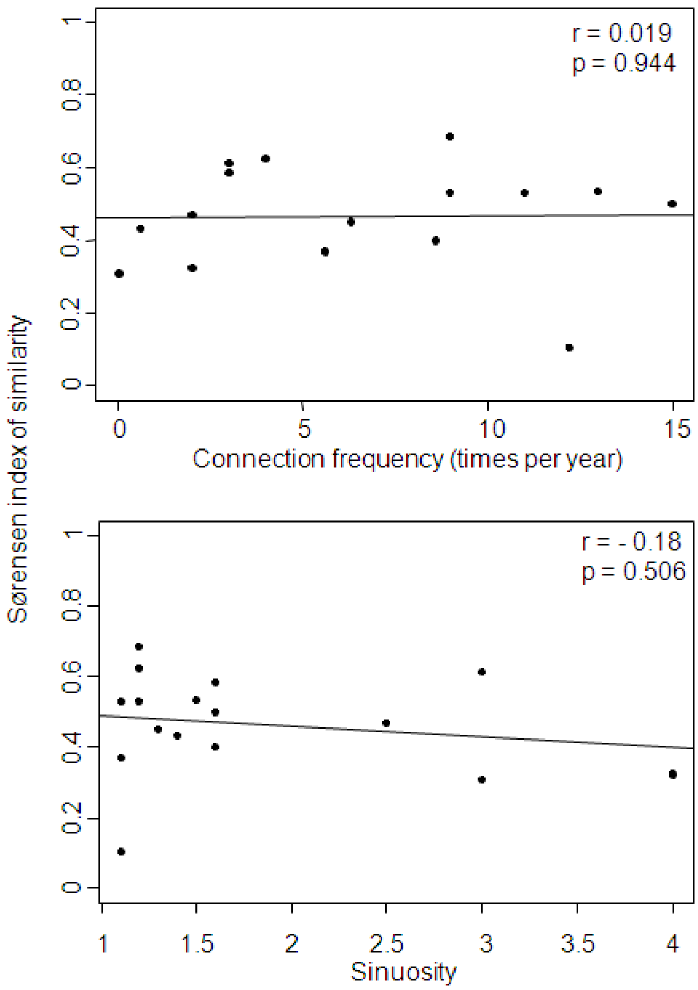

Figure 5.4. Sørensen similarity index between seed bank samples and established vegetation along a gradient of connection frequency and sinuosity across sampled backwaters of River Tay and Spey.

V.4.2. Influence of connectivity

V.4.2.1. *Species richness*

The analysis of species richness in relation to connection frequency revealed no significant effect on either seedling richness or the richness of the established vegetation (Table 5.1). Nevertheless sample-based rarefaction indicated a larger overall species pool in the seed bank of backwaters of intermediate connectivity compared to those with low or high connectivity (Figure 5.5). For a sample size of n = 20, 95% confidence interval of the estimated richness was ±2.6 whereas differences in species richness between categories were higher than 5.6 species. On this basis one can assume that there are statistically significant differences in the size of the species pool between categories of connectivity.

V.4.2.2. *Seed abundance and established plant cover*

Connection frequency of backwaters did not influence seed bank size (expressed as seedling density) but a significant influence on established plant cover with lower plant cover at high connectivity (Table 5.1).

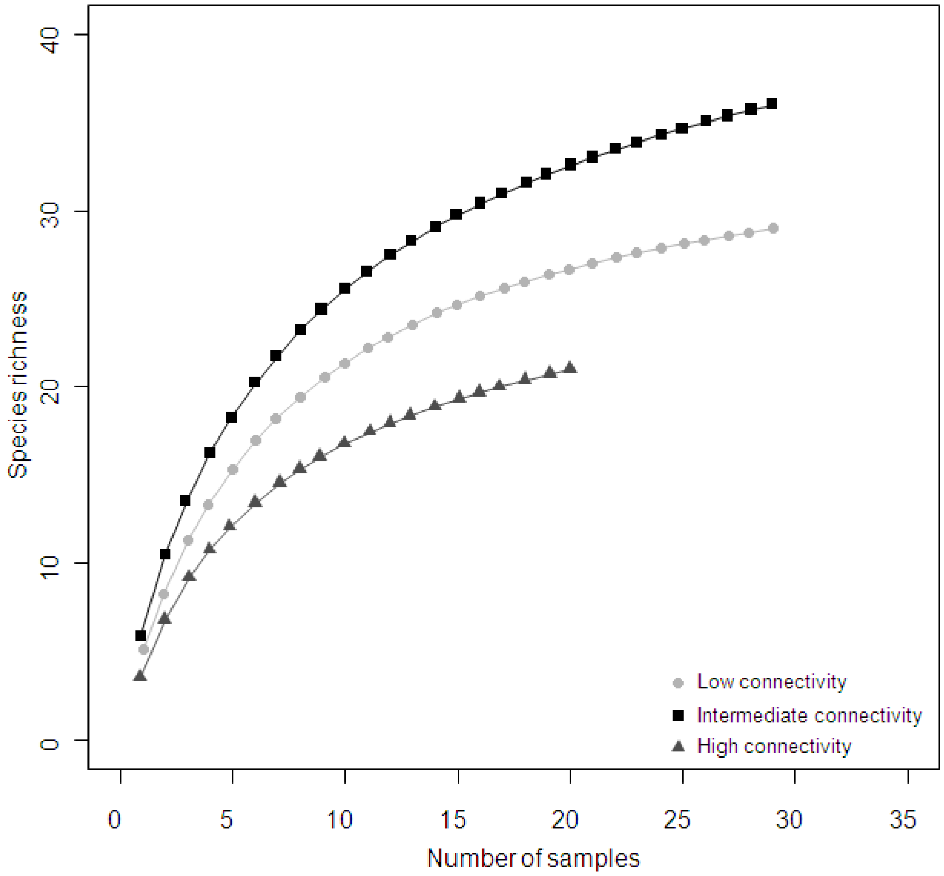

Figure 5.5. Sample-based species accumulation curve for seed bank samples collected from backwaters in the river Spey and Tay floodplains. Symbols refer to category of backwater connection frequency with ● = low connectivity, ■ = intermediate connectivity, ▲ = high connectivity.

V.4.2.3. *Species composition*

The spatial ordination of backwaters in the CCA analysis revealed no significant influence of connectivity on seed bank species composition (presence-absence data) in backwaters (F = 1.01; p > 0.05) whereas the influence of connectivity on the composition of the established vegetation (presence-absence data) was close to significance (F = 1.56; p = 0.06) (Figure 5.6). Also, the CCA analysis revealed no significant influence of connectivity on seed bank composition in backwaters when weighted by the numbers of individuals of different species (F = 0.97; p > 0.05) whereas the equivalent analysis for established vegetation weighted by cover showed a marginal significance (F = 0.31; p = 0.09) (Figure 5.7).

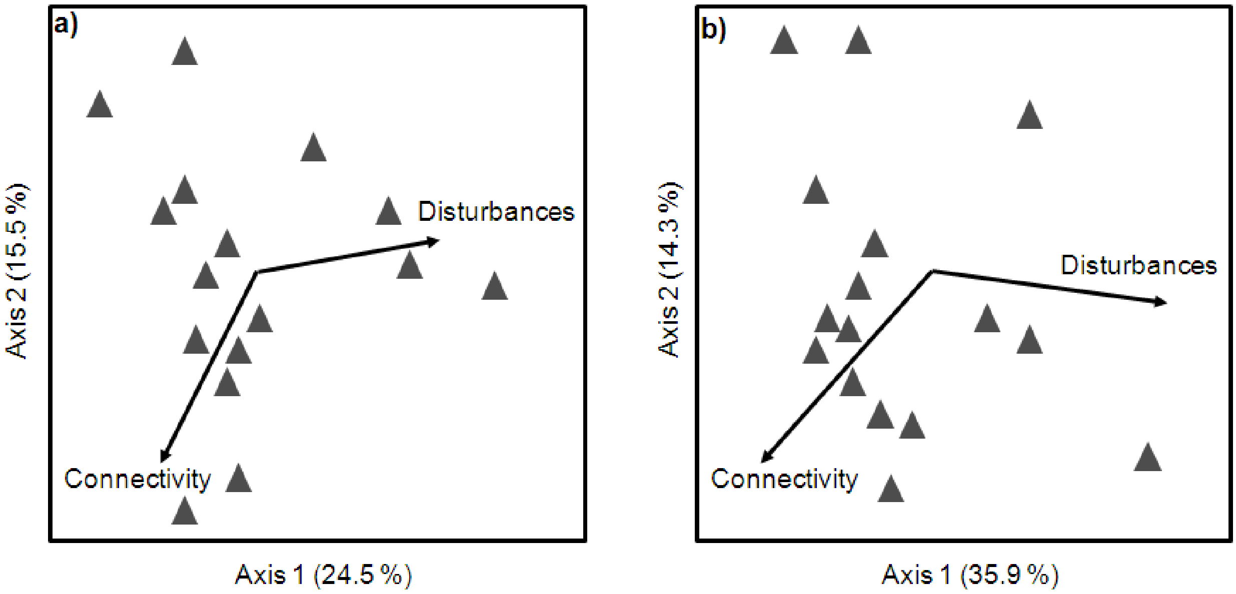

Figure 5.6. Canonical Correspondence Analysis ordination of sites by presence-absence species composition: a) seed bank; and b) established vegetation.

V.4.3. Influence of disturbances

V.4.3.1. *Species richness*

Species richness of both the seed bank and the established vegetation was unrelated to sinuosity (Table 5.1).

V.4.3.2. *Seed abundance and established plant cover*

Disturbance, as inferred from sinuosity, did not affect the total abundance of seedlings and established plant cover in backwaters (Table 5.1).

V.4.3.3. *Species Composition*

The spatial ordination of backwaters in the CCA analysis revealed no significant influence of disturbance on seed bank species composition in backwaters (F = 1.31; p > 0.05) but a significant influence on established vegetation composition (F = 1.87; p = 0.01) (Figure 5.6). Similarly, the CCA analysis indicated that flood related disturbance did not have a significant influence on numerical composition of the seed bank (F = 1.34; p > 0.05). The equivalent analysis showed no significant influence of disturbance on established vegetation weighted by cover (F = 0.34; p > 0.05) (Figure 5.7).

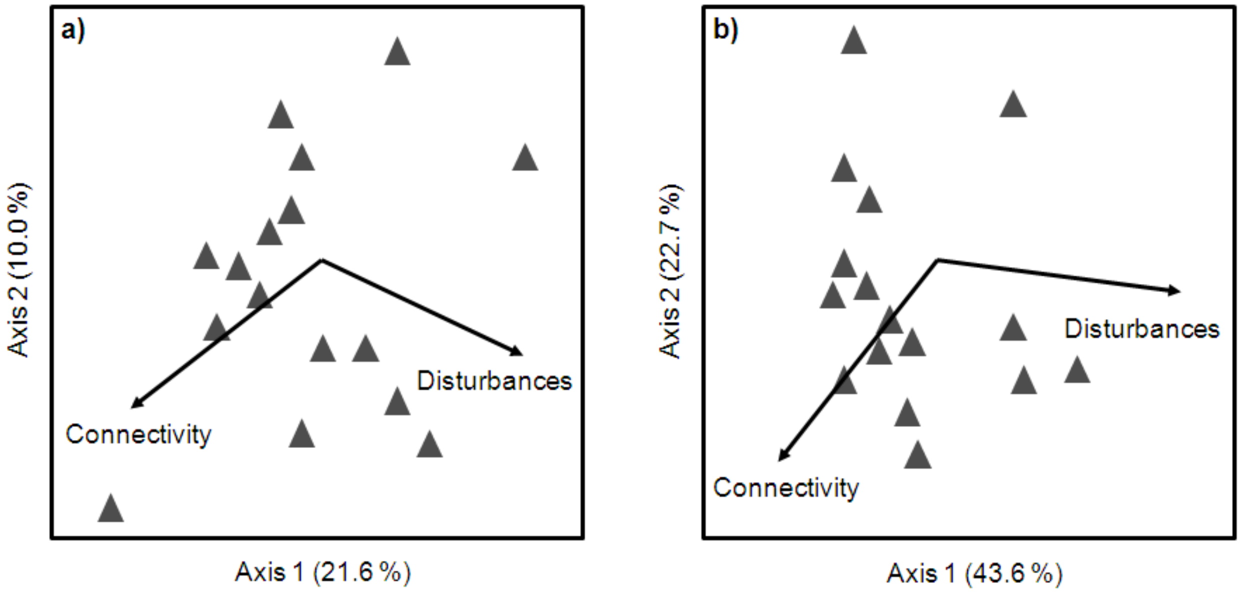

Figure 5.7. Canonical Correspondence Analysis ordination of sites by abundance species composition: a) seedling abundance; b) established plant cover.

V.4.4. Influence of coupled connectivity and disturbance

There were no significant interactive effects of connectivity and disturbance on any of the vegetation parameters assessed in both seed bank and the established vegetation (Table 5.1).

Table 5.1. Generalised linear model results for seed bank and established species richness, Sørensen similarity index and abundance of seedlings and established vegetation cover recorded in 16 backwaters along the River Tay/Tummel and Spey.

	d.f.	F	P
Species richness - seed bank			
Connectivity	1	0.321	0.581
Disturbance	1	0.102	0.754
Connectivity x Disturbance	1	1.586	0.231
Species richness - established vegetation			
Connectivity	1	1.382	0.262
Disturbance	1	0.066	0.800
Connectivity x Disturbance	1	0.087	0.772
Sørensen similarity index			
Connectivity	1	0.005	0.940
Disturbance	1	0.670	0.428
Connectivity x Disturbance	1	3.645	0.080
Abundance of seedlings			
Connectivity	1	0.746	0.404
Disturbance	1	0.062	0.806
Connectivity x Disturbance	1	0.264	0.616
Established vegetation cover			
Connectivity	1	5.724	0.033*
Disturbance	1	0.284	0.603
Connectivity x Disturbance	1	0.0002	0.989

V.5. DISCUSSION

V.5.1. Influence of connectivity

At the floodplain scale, backwater species richness was shown to be principally driven by habitat heterogeneity or dispersal limitation, partially determined by connectivity (Bornette *et al.*, 1998; Amoros & Bornette, 2002). Indeed in river systems hydrochory is recognized as the major mechanism in plant propagule dispersal (Boedeltje, 2003), remobilisation (Pettit & Froend, 2001) and in the structuring of riparian plant communities (Andersson *et al.*, 2000). Our results, in contrast to Leyer (2006), showed no significant influence of connectivity on seed bank and established species richness (Table 5.1). Nonetheless, sampled-based species accumulation curves revealed that the largest seed bank species pool was found in backwaters of intermediate connectivity (Figure 5.1) which might reflect the greater diversity of propagule sources (external inputs + internal generation) then contributing to the seed bank compared to when connectivity is either high or low. At a local scale, freshwater habitats are heterogeneous and tend to be widespread regionally and thus create, at a wider scale, a largely uniform aquatic environment. This uniformity is claimed to facilitate colonisation and the large scale distribution of aquatic plants (Santamaria, 2002). In addition, aquatic plants display high phenotypic and reproductive plasticity which contributes to their widespread distribution and enables rapid colonisation and a high capacity for local adaptation (Barrat-Segretain, 1996; Pilon & Santamaria, 2002). Finally, the similarity in species richness across backwaters could also be a consequence of successful dispersal by wind or animals to isolated sites. For instance bird migration is recognised to be a major vector for aquatic plant dispersal between distant habitats (Green *et al.*, 2002) and disconnected backwaters tend to be well vegetated and therefore more frequently visited by water birds (pers.obs).

However, CCA analysis showed that species composition differed across a gradient of connectivity in established vegetation only (Figure 5.6 and 5.7). Therefore we suggest that connectivity somehow acts as a filter on species colonisation and recruitment in backwaters. Nevertheless, the lack of influence of connectivity on seed bank composition may be a general reflection of low seed production and seed rain at any level of connectivity. A small propagule bank, such as we observed, is considered typical of permanent open water habitats (Collins & Wein, 1995). Seed density in this study (average of 4898 per m^2) was lower than density recorded in waterbodies along the Elbe river (average of 8906 seeds m^{-2}) (Leyer, 2006) and considerably lower than in more fertile freshwater systems as in Amiaud & Touzard (2004) with seed density exceeding 23 000 seed m^{-2}). Also, our results showed that seedling abundance in backwater sediments was independent of connectivity (Figure 5.3) in contrast to Leyer (2006) or Wetzel *et al.* (2001). This result raises various hypotheses that remain to be explored: (i) colonisation from external sources is very constrained; (ii) the major contributor to the seed bank in riverine backwaters is internal production; (iii) hydrochory is not the dominant method of downstream colonisation.

The similarity between seed bank and established vegetation was found to be average and not to vary in relation to a gradient of connectivity (Figure 5.4). This could imply that population maintenance is primarily dependent on vegetative reproduction regardless of connectivity and species composition.

V.5.2. Influence of disturbances

Whereas flood disturbances are regularly considered to drive species richness (Ward *et al.*, 2002) our results appear to partially contradict this view as species richness was not influenced by sinuosity, a surrogate for flood related disturbances in backwaters (Table 5.1). Neither seed bank nor established vegetation richness varied significantly between backwaters along a gradient of disturbance. In frequently disturbed sites the addition of seeds dispersed by flood waters could contribute to higher seed bank abundance and richness but depletion by flood scouring may equally have the opposite effect (Combroux & Bornette, 2004). In rarely disturbed sites, gross external inputs become fewer as a direct effect of a decrease in connectivity but retention may be correspondingly higher. Aside from considerations of flood-borne inputs or outputs in backwaters (Cellot *et al.*, 1998), similarity between seed bank and established vegetation along a disturbance gradient might reflect a reproductive strategy that is increasingly founded on vegetative production by rhizomes or turions (Combroux & Bornette, 2004) or short lived sexual propagules (Amiaud & Touzard, 2004) as connectivity decreases. Differences between sites with similar connectivity may also reflect limitations on dispersal caused by differences in the potential for propagules to enter a site (Hopfensperger *et al.*, 2009) and specific reproductive strategies (Combroux *et al.*, 2001).

The influence of disturbance on species composition reflects the pattern of vegetation succession in backwaters whereby pioneer species (e.g. *Lythrum portula*, *Callitriche hamulata*) firstly colonise frequently disturbed sites, followed, with backwater ageing, by more generalist species (e.g. *Potamogeton natans*). In less frequently disturbed backwaters, the most competitive species, such as nymphaeids, will control habitat and resource use. Therefore at the floodplain scale a range of backwaters presenting a broad spectrum of connectivity are then required to support higher diversity of macrophyte propagules stored in the sediments of backwaters (Figure 5.5). These in turn contribute to resilience at the floodplain scale (Abernethy & Willby, 1999).

However, the abundance of viable seed in sediments of backwaters was unrelated to fluvial disturbance (Table 5.1), in contrast to Grelsson & Nilsson (1991) who found that wave action favoured seed deposition and germination. There are various possible hypotheses for our results; backwaters that favour storage of seeds in the sediment may be poorly scoured as well as being prone to significant seed rain during floods. Also, vegetative reproduction for rapid colonisation, or seed bank depletion through germination, mortality or flood export (with lower retention occurring in backwaters of high connectivity) could explain the absence of any significant pattern in abundance of seeds of different species.

V.5.3. Contribution of seed bank to vegetation dynamics

Unlike recent studies (Capers, 2003; Amiaud & Touzard, 2004) our study revealed consistently higher species richness in the established vegetation and an average similarity between seed bank and established vegetation in backwaters that was unrelated to connectivity or disturbance (Figure 5.2 & 5.4). A poor match between seed bank and established vegetation has already been reported along large rivers and in a freshwater tidal marsh (Kimber *et al.*, 1995). Assuming that plant succession controls the vertical stratification of seeds in the sediment this may suggest that even though backwaters experienced flooding, sediments where seeds are deposited may not be significantly physically eroded or mixed during disturbances and will therefore rarely contribute to the establishment of individuals of new species, unless these originate from recently deposited seed (van Eck *et al.*, 2005). However, it is also probable that most previous studies have concerned more productive systems in which seed rain and inputs to the propagule bank are higher than in the low-moderate productivity systems considered in the present study. Indeed, the Tay and Spey are representative of rivers of northern temperate latitudes with cool, nutrient-poor and slightly humic waters and a naturally dynamic and unpredictable flow regime. Comparisons with other river systems should therefore be undertaken with caution.

A high Sørensen similarity index between seed bank and established vegetation composition could reveal evidence of local influences (Hopfensperger *et al.*, 2009). Conversely, a low Sørensen similarity index could be symptomatic of either the influence of the regional species pool via dispersal and connection or of internal plant succession through vegetative development. Jansson *et al.* (2005) showed that increasing flooding frequency is most likely to increase homogeneity through mechanical disturbances suggesting that frequent flooding acts by filtering from the seed bank those species with regenerative or morphological attributes that favour colonisation and long term survival (Klimkowska *et al.*, 2009). In frequently connected sites, even though hydrochory ensures the replenishment of seed bank from upstream sources (Nilsson *et al.*, 1991), the lack of stable conditions might lead to low propagule retention and could potentially interrupt replacement of the seed bank by recently colonising individuals. In rarely connected backwaters infrequent flood-related inputs could decrease the size of the seed bank along with increased mortality of existing seeds in later successional stages (Capon & Brock, 2006). Moreover, in stable and well vegetated habitats seeds were shown to recruit less rapidly than vegetative fragments (Barrat-Segretain, 1996). Nonetheless, the match between seed bank and established species should be interpreted with caution: presence in both compartments is not conclusive proof that one contributes to the other, and the regenerative strategies of plants may change as populations age. Indeed environmental factors (e.g. water depth) and vegetative reproduction and colonisation (in situ or via external inputs) could lead to incorrect inference of the role of the seed bank in the establishment of aquatic vegetation (Barsoum, 2002; Combroux & Bornette, 2004; Gurnell *et al.*, 2006).

V.6. CONCLUSION

Our seedling germination trial revealed consistently lower species richness in the seed bank of riverine backwaters than in the established vegetation. This trend reverses that seen in many other seed bank studies and may be particular to less productive systems. Disturbance regime or connectivity did not significantly influence species richness or abundance of either seed bank or established species. Inferred seed bank contribution to the established vegetation was also independent of connectivity and disturbance. Also, seed bank species composition was not related to connectivity or disturbance in contrast to established vegetation composition. We conclude that species composition in backwaters is driven by recruitment from both regional and local sources but with locally-derived propagules dominating the seed bank in later successional stages. Our results also suggest that vegetative reproduction is more important in the colonisation, regeneration, persistence and resilience of aquatic species in riverine backwaters.

Our conclusions do not diminish the potential role of the seed bank in the population dynamics of large numbers of species and in the resilience of aquatic vegetation to disturbance (Combroux *et al.*, 2001), as well as the role of connectivity in driving species diversity (Bornette *et al*., 1998) at larger spatial scales and in maintaining the diverse propagule bank necessary for floodplain resilience and colonisation of new sites. However, our results may be representative of infertile rivers with unpredictable flows. In such an environment seed bank processes in riverine backwaters seem to be supported mainly from internal sources and vegetative reproduction and therefore similarity between seed bank and established vegetation does not change predictably with connectivity. There is no evidence that higher connectivity increases the size or diversity of propagule inputs, suggesting that high propagule input at high connectivity may be offset by poor retention, or that high in situ propagule production at low connectivity can compensate for reduced external supply. Nonetheless, connectance is critical for primary colonisation, and fluvial disturbance aligned with connectivity appears to be an important filter on which propagules successfully colonise to form the established vegetation. Evidently those backwaters that experience an intermediate frequency of connection have a greater overall seedling species pool than other sites, perhaps because they are strongly served by both internal generation and external supply. Additional detailed mechanistic research on how propagule sources change with connectivity may offer greater understanding of seed bank dynamics in such habitats.

ACKNOWLEDGMENTS

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Appendix 5.1. Seed bank and established vegetation submerged species recorded in riverine backwaters on River Tay/Tummel and Spey.

	Seed bank species		Established species	
	Spey	Tay	Spey	Tay
Apium inundatum		√		√
Callitiche sp.				√
Callitriche hamulata	√	√	√	√
Callitriche platycarpa				√
Callitriche stagnalis		√		√
Chara virgata				√
Crassula helmsii		√		√
Eleocharis acicularis				√
Eleogiton fluitans	√		√	
Elodea canadensis	√		√	√
Elodea nuttallii				√
Juncus bulbosus	√	√	√	√
Lemna minor		√		√
Littorella uniflora			√	
Lythrum portula		√		√
Myriophyllum alterniflorum	√	√	√	√
Nitella flexilis	√		√	√
Nitella transluscens			√	
Nuphar lutea		√		√
Nymphaea alba	√		√	
Persicaria amphibia				√
Potamogeton alpinus			√	
Potamogeton berchtoldii	√	√	√	√
Potamogeton crispus				√
Potamogeton natans	√	√	√	√
Potamogeton obtusifolius	√		√	√
Potamogeton polygonifolius	√		√	
Sparganium angustifolium	√		√	√
Sparganium emersum				√
Sparganium natans		√		√
Subularia aquatica				√
Utricularia vulgaris			√	

Appendix 5.2. Seed bank and established vegetation emergent species recorded in riverine backwaters on River Tay/Tummel and Spey.

	Seed bank species		Established species	
	Spey	Tay	Spey	Tay
Agrostis canina	√		√	
Agrostis stolonifera	√	√	√	√
Alisma plantago-aquatica		√		√
Alopecurus geniculatus			√	
Caltha palustris	√		√	√
Cardamine pratensis		√	√	
Carex aquatilis	√		√	
Carex lepidocarpa			√	
Carex nigra	√			√
Carex rostrata	√	√	√	√
Carex vesicaria	√		√	√
Carex virgata			√	
Carex sp.		√		
Cicuta virosa			√	
Deschampsia cespitosa	√			
Eleocharis palustris	√		√	√
Equisetum fluviatile			√	√
Galium palustris	√		√	√
Glyceria fluitans	√		√	√
Hippuris vulgaris		√	√	√
Iris pseudacorus				√
Juncus acutiflorus				√
Juncus articulatus	√	√	√	√
Juncus bufonius	√	√	√	√
Juncus effusus	√	√	√	√
Lycopus europaeus				√
Mentha aquatica	√		√	√
Menyanthes trifoliata			√	√
Mimulus guttatus				√
Montia fontana			√	
Myosotis scorpioides	√		√	√
Phalaris arundinacea	√		√	√
Potentilla palustris	√		√	
Ranunculus flammula	√		√	√
Ranunculus lingua				√
Ranunculus repens	√	√	√	√
Rorippa nasturtium aquaticum				√
Sagina procumbens	√			
Scirpus sylvatica		√		√
Scutellaria gallericulata				√
Sparganium erectum	√		√	√

Typha latifolia		√
Veronica beccabunga		√
Veronica scutellaria	√	√

CHAPTER VI.

GENERAL DISCUSSION

Over the last decade there has been a growing interest in trying to define and describe good ecological status of waterbodies to inform restoration of impacted habitats by reaching relevant objectives (Ward, 1998; Buijse *et al.*, 2002; Boon & Lee, 2005). The need to understand and describe the ecology and functionality of water bodies in natural systems, as a reference marker for measuring ecosystem ‘naturalness, has been encouraged by the EU Water Framework Directive. Therefore setting environmental quality objectives involves assessment of the present ecological status of water bodies but most importantly it requires data that is representative of natural and semi natural water body features (Collier, 2011; Willby, 2011). At present in Europe, most river floodplains have been greatly reduced or degraded by human activities (Tockner *et al.*, 2002). In this context the collection of ecological data from minimally impacted and degraded sites is therefore rare but essential. Even more, large rivers system present complex hydrological and geomorphological conditions, with channel dimensions, water depth and velocity, which present significant challenges in achieving relevant assessments of such ecosystems.

The present research is based on the assessment of a 33 km reach of three semi natural rivers in central Scotland, the River Tummel, Tay and Spey. In particular, this work focused on backwaters, which are a product of the lateral dynamic in natural river floodplains (Ward *et al.*, 2002). This presented work was designed to understand the role of natural mechanisms, such as lateral dynamic and connectivity, in driving and maintaining natural ecological processes. This framework particularly focused on riverine backwaters along large rivers and the fluvial aquatic plant community in order to assess the role and potential importance of such habitats and their contribution to floodplain-river system ecology. Surveyed backwaters presented a gradient of connectivity and disturbance to the river dynamic, from the frequently connected and fluvially disturbed to the almost isolated and rarely disturbed. In addition than in backwaters, species presence and productivity was also quantified in the adjacent main channel sections. Sampling was carried out at three different times during the growing season and under different flow conditions. The interface between main channel and backwaters (upstream and downstream ends) were particularly examined in order to assess the connectivity of backwaters with the main channel at low and high flows.

Chapter 2 aimed to explore the role, importance of the products of lateral dynamics in river floodplains in driving the distribution, diversity and production of macrophytes in large rivers. Where hydrology of flows remains natural and unregulated, lateral instability is created in the river floodplain and is responsible for the formation of a variety of lateral aquatic habitats such as backwaters (Ward *et al.*, 2002; Yager *et al.*, 2011; De Jager & Rohweder, 2012). By contrast, impacted river floodplains would mainly consist of a single and uniform river corridor lacking aquatic habitats on a lateral gradient (Hohensinner *et al.*, 2004). The macrophyte survey of backwaters, as products of lateral dynamics, revealed the outstanding value of backwaters in maintaining macrophyte diversity and productivity in large river ecosystems. While comparing both diversity and productivity with the river corridor only, 65% of species were confined to backwaters and 89% of the biomass was produced in backwaters despite the fact that they only represented 5% of the total area of aquatic habitat in the

33 km reach. Meanwhile, the main channel only uniquely supported 5% of species found across the floodplain and was responsible for 11% of floodplain aquatic productivity. Such pattern was independent from seasonality across the growing season, with backwaters being always more species rich and more productive. However, species richness varied between backwaters themselves and was mainly influenced by contrasting hydrology, as in connection frequency of backwaters, with the river dynamic in flood flows (Flinn *et al.*, 2008). Species richness was typically highest at low connection frequency, as already reported by Bornette *et al.* (1998). Production was not influenced by connection frequency, even though high productivity was found at medium frequency of connection to the river. As in the flood pulse concept (Junk *et al.*, 1989) these results stress the significance of river hydrodynamics and flood pulses in creating lateral habitats, since backwaters played a key role in maintaining macrophyte community diversity along large rivers systems (Thorp *et al.*, 2006). Backwaters provide ideal conditions and shelter for plant colonisation and recruitment. In large rivers they therefore represent hotspots of diversity and productivity along an unfavourable and barely vegetated main river channel. Also, differences in the response to backwater connectivity to the river dynamic emphasises the importance of hydrological interactions and processes between the different components of a floodplain, and its role in contributing to ecological heterogeneity and diversity of floodplains (Amoros & Bornette, 2002). From a conservation and management perspective, the consequences of the complete loss of backwater habitat from large rivers are therefore likely to be considerable, both in terms of biodiversity and ecosystem functioning (Heiler *et al.*, 1995; Willby & Eaton, 1996; Bartosova *et al.*, 2001; Hohensinner *et al.*, 2004; Ollero, 2010).

However, plant richness and biomass observed in backwaters was stable between years (as in Strauz & Janauer, 2007) even though connectance, through major flood disturbances, occurred on multiple occasions over the survey period of this study. Therefore a finer scale of investigation is requisite to identify the mechanisms of connectivity that are driving species richness and productivity. Further studies could focus on processes, separately or as a set of interactions, such as physical flow disturbance, mediation of dispersal and other ecological processes and on a longer timescale than the one observed here (Franklin *et al.*, 2008).

Even though backwaters are the natural result of river floodplain dynamics they are commonly omitted from river assessments or considered as separate components from the river system (Thorp *et al.*, 2006). The main reason to explain this perception of backwaters is that they only partially and intermittently connect with the main channel. Also backwaters represent standing water habitat in a system where running water habitat is the norm (Wiens, 2002). A more holistic approach is required to the assessment of large river systems by focusing on the entire riverscape (floodplain and main channel) (Bornette *et al.*, 1998b). Furthermore such results well demonstrate the potential role of backwaters as source habitats in supplying propagules and organic matter to downstream reaches.

Chapter 3 intended to investigate the role of flood-related disturbance in driving species diversity in riverine backwaters. Flooding is commonly expected to induce mechanical disturbances in plant communities and is assumed to be the main agent of disturbance in river systems (Bornette & Amoros, 1996; Ward *et al.*, 1999). Ecological theory (in the form of the Intermediate Disturbance Hypothesis), suggests that disturbance frequency is responsible for driving species diversity and composition (Huston, 1979; White & Pickett, 1985) by removing biomass and creating gaps, thus allowing the recruitment of new species and increased coexistence (Roxburgh *et al.*, 2004). We showed that macrophytic vegetation growing in backwaters and exposed to frequent flooding could resist flood disturbances. Indeed plants appeared to bend and be flattened on the sediment with flow as the backwater connected to the river and biomass was thus able to avoid the flow disturbance. This contradicts disturbance theory and suggests that in the studied riverine ecosystem the mechanisms driving species diversity do not operate through the destruction of biomass. Instead we propose that connectivity and disturbances, as in flooding flows, are two different mechanisms. Whereas connectivity refers to a permanent and episodic links between the main river corridor and floodplain waterbodies, disturbance refers to discrete events disrupting an ecosystem, community, or population structure and changes physical features of a habitat and its resources (White & Pickett, 1985). In our context we suggest that little or no biomass is removed with flooding, and that species accumulate and diversity increases in response of a temporal and connection gradient (Figure 6.1). In both hypotheses species diversity decreases as a habitat is ageing and disconnecting from river dynamic as competitive species, such as nymphaeids, exclude the least competitive ones (Arts, 2002). Therefore, in backwaters, the role of disturbance per se in driving species diversity and coexistence does not seem to be significant. Moreover, and unlike Cellot *et al.* (1998), our study seems to suggest that mechanical disturbances, as associated with flood flows, do not generate large amounts of propagules through the breakage of fragments from established plants, and potential colonists to be dispersed.

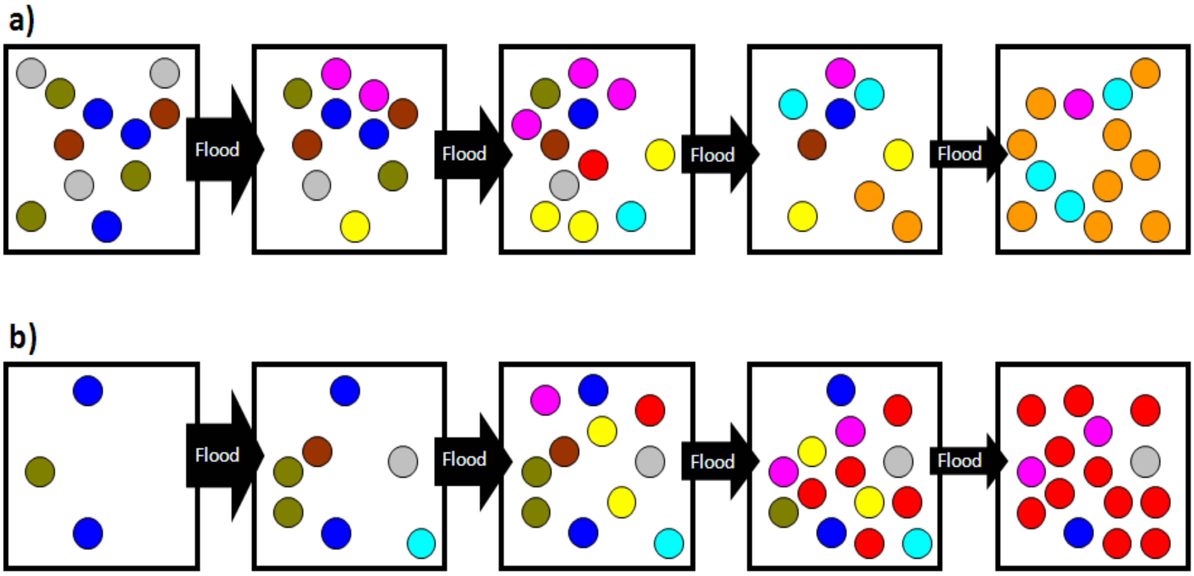

Figure 6.1. Model of evolution of species diversity along a temporal and connection gradient with a) Intermediate Disturbance Hypothesis, where biomass is removed with flooding allowing the emergence of new species until competitive exclusion occurs and decreases diversity; b) suggested model, where biomass is not removed with flooding, but species accumulate along a temporal gradient until competitive exclusion occurs and decreases diversity.

However, the effect of nutrient concentration, in sediments or in the water column, on aquatic vegetation response to flooding would need more investigation. Plants in low fertility systems may have evolved mechanisms to resist disturbance whereas in high fertility systems, where most work is carried out, resilience may be more critical (Brock *et al.*, 1987). Also a detailed examination of flooded backwater hydrology could detail the understanding of macrophyte plants response to flood flows. For instance, the accumulation of sediment and woody debris at the upstream part of backwaters may play a significant role in protecting macrophytes from destructive flows (e.g. height and the effect of sediment accumulation in stratifying water velocity in the water column in backwaters, or increased roughness). Indeed the height of sediment accumulation coupled with the amplitude of the flood will control connection duration and flow disturbance intensity in backwaters. Finally, a scenario where plants show resistance to flooding could suggest that their occurrence in backwaters is a direct reflection of their capacity for colonisation of flow-stressed environments; many of the commonest plants that occur in backwaters are characteristic components of the flora of moderate to fast flowing smaller upland river systems. The hypothesis of propagule inputs and accumulation could be tested by quantifying the colonisation of a newly created site over time, although evidence from the Tay and Spey, where sedimentation rates are naturally very low, suggests that the observed chronosequence may extend over several hundred years.

Chapter 4 sought to examine the potential role of connectivity in driving dispersal through the input of waterborne propagules. In river floodplains, the dispersal of seeds or vegetative fragments of aquatic plants is largely driven by water flow (Nilsson *et al.*, 2010) and more especially by high flows, as in flood disturbance events (Sculthorpe, 1967; Okada *et al.*, 2009). High flows have the potential to produce plant fragments by breaking aquatic vegetation, mobilising seeds from sediments (Boedeltje *et al.*, 2004) and allowing connection of isolated habitats and the input of potential colonists (Moggridge *et al.*, 2009). However, at base flow conditions, backwaters remain partially connected (through downstream end) and potentially interact via the river channel. In our context of study, since macrophyte diversity and productivity are almost exclusively concentrated in backwaters, especially for submerged species (see chapter 2), the study of dispersal required looking at both within-backwater dispersal, through re-organisation of established plant propagules, and the potential dispersal and connection from backwaters in exchanging plant material in flood flows (when upstream and downstream ends are connected to the river) and at base flow (when only the downstream end is connected) to downstream backwaters (Andersson *et al.*, 2000). As in Cellot *et al.* (1998) our results showed that a large amount of propagule mimics were potentially exported from backwaters and enriched the main channel propagule drift and confirm that backwaters are a net source of propagules at the river floodplain scale (export of propagules was higher in flood flows). Once exported, tracers (propagules mimics) drifted for larger distances in flooding flows than at base flow (Groves *et al.*, 2009). Tracers exported out of backwaters had a very high chance (> 92% in a flood and > 95% at base flow) to never be retained along the river corridor and thus represent a major loss (although the contribution of particulate organic matter to downstream reaches may be important). In fact, under both flow regimes the highest chance for tracers to successfully disperse and reach available habitat was to be retained within the site of production. When exported, and even though backwaters interconnected via the main corridor, the chance to receive tracers from upstream sources in both flow regimes was extremely low (Figure 6.2).

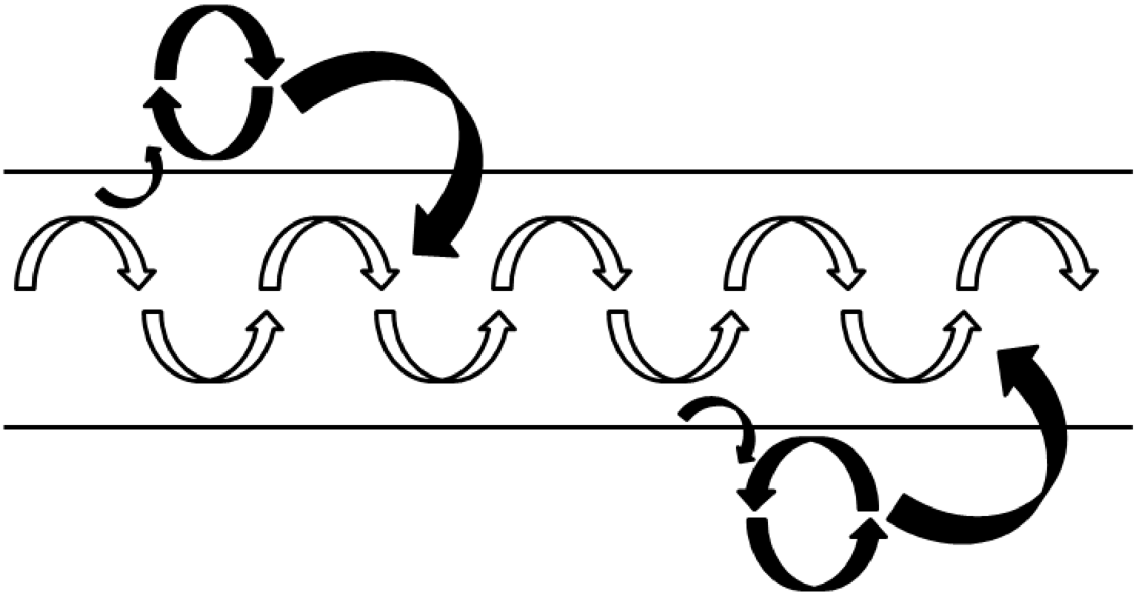

Figure 6.2. Import and export model of backwaters along the river corridor (modified from Ward, 1989; Nilsson & Svedmarck, 2002). Model shows a medium retention of propagules within backwaters. Export of tracers (large black arrows) is high whereas the import from waterborne tracers into backwaters is proportionally smaller (small black arrows). White arrows model dispersal in the main channel.

This suggests that backwaters are not sink habitats and that reaching a suitable habitat (i.e. another backwater) was the main bottleneck for macrophytes species dispersing from backwaters (Figure 6.2). Differences in successful connection between backwaters were revealed to vary in accordance with flow regime. Over all, whereas connection with the river corridor at low flow was only partial (through backflow current at the downstream end), connectivity appeared to be higher than in a flood where complete connection occurred. Also, the benefits of each flow regime for dispersal varied with species ecology (aquatic vs. amphibious species). Flood flows exported most tracers (propagules mimics) out of water (Schneider & Sharitz, 1988) favouring mostly emergent species colonisation in backwaters. Conversely, at low flow most propagules mimics stayed in water favouring colonisation of backwaters by submerged species whereas emergent species would mostly likely not be able to recruitment in such conditions. Our results revealed that fluvial dispersal and riverine backwater connectivity is not only dependent upon flooding, as is commonly presented in river ecology (Amoros & Bornette, 2002; Boedeltje *et al.*, 2004; Gurnell *et al.*, 2008), but that a range of hydraulic conditions will favour higher dispersal (Merrit & Wohl, 2002; Stromberg *et al.*, 2007). Also, it suggests colonisation success in backwaters from external sources will be a rare and slow process, whereas colonisation is more likely to be mainly supported by local sources via internal spatial re-organisation. The low connectivity between backwaters, as in low inputs from external sources, also highlights the relative isolation of backwater in river floodplains (Figure 6.2).

However, the timing of release and the number of natural propagules exported in the main river corridor in flood and base flows may balance our conclusions about colonisation of backwaters (Boedeltje *et al.*, 2004). Buoyancy of propagules may also influence our results. Less buoyant propagules will drift short distances and may follow a different pattern of deposition and are presumably more likely to end up in water, whereas propagules with high buoyancy, such as seeds, might drift on larger distances (Barrat-Segretain, 1996). Long range dispersal may allow seeds to escape competition from the parent plant that will decrease recruitment success but seeds seem to be deposited near the point of release (Riis & Sand-Jensen, 2006; Groves *et al.*, 2009). Also, we showed that long distance dispersal success was very low, and therefore these seeds would need to be produced in high numbers to offset such limitations. Even so, Barsoum (2002) showed that even though riparian sexual propagules are produced in higher numbers than asexual propagules, successful colonisation was mainly supported by vegetative colonists. Also, seeds are more likely to be released under flood flow since there is no advantage in releasing buoyant propagules under baseflow when they may only travel small distances from the parent. Likewise, there is a disadvantage in releasing vegetative propagules at high flow as there is an increased chance of physical damage and a high probability of being left trapped above low water level. The ability of macrophytes, and especially submerged plants, to resist desiccation upon exposure when exported out of water could provide an indication of the regeneration potential of such propagules if subsequently brought back into water through a later water level change (Barrat-Segretain & Cellot, 2007; Michelan *et al.*, 2010).

Chapter 5 enquired about the influence of connectivity and fluvial disturbances in driving the size and richness of the seed bank in riverine backwaters and its contribution to the established vegetation. Whereas the seed bank previously appeared to play a major role in supporting established vegetation (Thompson, 1992; Henry *et al.*, 1996), in our study the seed bank species appeared to have a low or average contribution to the established vegetation as seed bank richness was always poorer than established species richness. This result suggests that in aquatic vegetation in backwaters vegetative reproduction is prioritised as previously showed (Boedeltje, 2003; Capers, 2003; Combroux & Bornette, 2004; Okada *et al.*, 2009). Also, surprisingly and in contrast to Leyer (2006), no significant influence could be demonstrated between the connectivity or disturbances regime and observed seed bank or established species richness, or SØrensen index of similarity and seed abundance (unlike Capon & Brock, 2006). However, our results might be representative of oligotrophic systems and differ from previous studies looking at more fertile river floodplains. Connectivity and disturbances were only influential on species composition of established vegetation. The lack of influence of hydrological disturbance on aquatic vegetation seems to imply, as in chapter 3, a resistance and persistence of macrophyte to potential flood-related disturbance. Nevertheless, species composition was related to connectivity or disturbance and suggests that species composition in backwaters is driven by recruitment from both regional and local sources but with locally-derived propagules dominating the seed bank in later successional stages. Also the absence of difference in seed abundance found in backwater sediments along a gradient of connectivity suggest that colonisation from external sources is very constrained (as in chapter 4) and that backwaters are rather biologically isolated from the river corridor, as well as seed production in riverine backwaters may be mostly supported by internal production.

According to chapter 4 & 5 the relative abundance and colonisation success of sexual and vegetative propagules of macrophytes in these backwaters would benefit from further investigation (as in Barsoum, 2002). Aquatic plant spread was showed previously to be supported mainly through clonal propagules (Pilon & Santamaria, 2002). However, it seems unclear if local consolidation of populations in riverine backwaters along a temporal and disturbances gradient, and especially in young backwaters, is supported by clonal reproduction or high seed production to rapidly colonise empty habitat patches.

To summarise, this research work offers a mechanistic understanding of river floodplain and associated aquatic habitats (e.g. backwaters) and their ecology and functioning (Figure 6.3). This research revealed that lateral dynamic and backwaters play a crucial role in the vegetation dynamic in large river ecosystems. We established that lateral backwaters concentrated macrophyte species and productivity and were the key habitats for macrophyte dynamics. The main stem of the river system was comparatively unvegetated. Whereas aquatic vegetation sheltered in backwaters appeared to resist flow disturbances; these plant communities also proved to be a potential source of colonists to disperse downstream from the point of release. Nevertheless, it also revealed that even though the backwaters have great potential for connectance they are relatively isolated habitats in the riverscape. Connectance was predominantly from internal sources whereas connectance from externally-derived plant diaspores was extremely rare despite the great potential of backwaters for interconnectance. The vast majority of potential colonists were lost in downstream drift and never reached suitable habitat. Finally, colonisation, maintenance and resilience of aquatic vegetation are mainly supported by in situ vegetative reproduction or external vegetative waterborne inputs. Neither connectivity nor disturbances influenced seed bank dynamics in floodplain riverine backwaters.

In conclusion, this research exposed the deterministic role of backwaters in sustaining macrophyte dynamics along the studied rivers. Whereas the main channel is mostly used as a dispersal pathway in the system, backwaters appeared to concentrate the rest of the key aquatic vegetation processes (Figure 6.3). Therefore, river dynamic and lateral instability is crucial for the formation of lateral habitats such as backwaters. However, once these are formed, ecological interactions with the river dynamic appear to be restricted with the exception of the dispersal process, although dispersing propagules are mostly unable to reach suitable habitats. Therefore, vegetation processes in the studied riverine environment rely on the natural dynamic of river at a landscape scale, but appear to be more independent at a habitat scale.

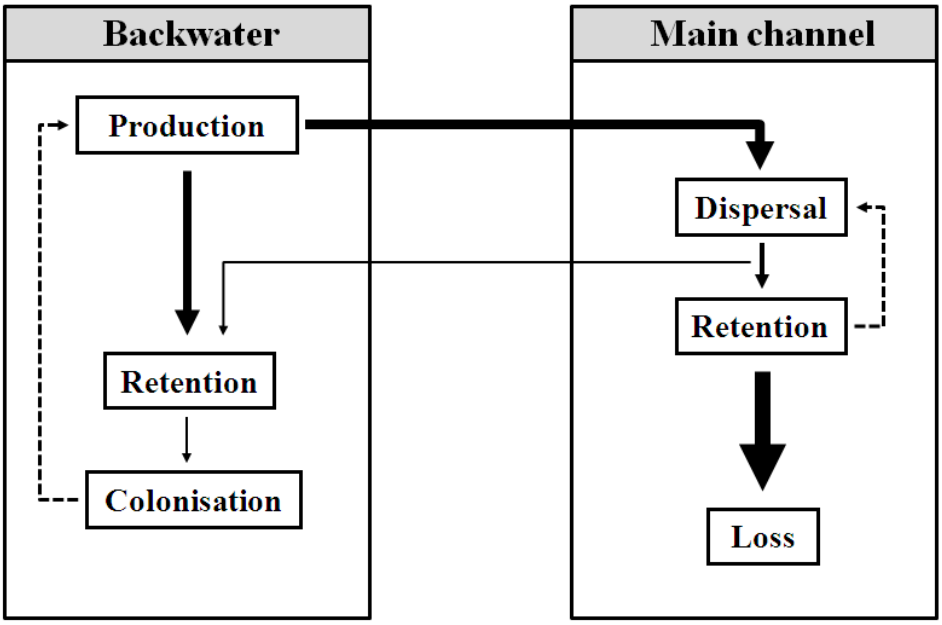

Figure 6.3 Model of aquatic vegetation dynamic in the studied riverine ecosystem (River Tummel and Tay, central Scotland, Perthshire). The size of the arrows is representative of the intensity of the process. The model highlights the central role of backwaters in the establishment of aquatic plant population and as a source of diaspores. This model also emphasises the role of the main river channel acting as a dispersal pathway for plant diaspores where most propagules are lost in drifting downstream from their point of release. Connectivity between backwaters and main channel (and indirectly between backwaters) is shown to be very restricted. Backwaters in the model are therefore isolated aquatic habitats even though they have a great connectance potential during floods.

Large rivers assessments are rare and potentially flawed due to the complexity of modelling large scale ecological interactions and the technical difficulties encountered in doing so. The research presented demonstrates the importance of such study in order to understand river floodplain ecology at both landscape and local scale. It has demonstrated the central and driving role and importance of lateral dynamics and connectivity for aquatic vegetation processes in natural river floodplain system. In Europe, whereas most of the large floodplain rivers have experienced intense reduction and deterioration, we offer here a synopsis of natural large river system ecology and functionality. Such studies are particularly revealing in defining and setting ecological quality objectives as aspired to by the EU Water Framework Directive. This work could also be used as the basis for defining undisturbed reference conditions for comparable large rivers elsewhere in Europe.

Figure 6.4. Photograph of River Tay at Kindallachan in February 2011 (© Antoine Keruzoré).

Figure 6.5. Photograph of River Tay at Kindallachan in June 2011 (© Antoine Keruzoré).

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APPENDICES

Conference talks

Keruzoré A., Willby N., Gilvear D., (2011), *The importance of lateral dynamics to aquatic vegetation in large rivers*, 87th Scottish Freshwater Group meeting, Stirling, Scotland.

Keruzoré A., Willby N., Gilvear D., (2011), *Macrophyte diversity in riverine backwaters; do floods really matter?*, 2nd Symposium of the International Society for River Science – ISRS, Berlin, Germany.

Keruzoré A., Willby N., Gilvear D., (2011), *The role of disturbance in the maintenance of macrophytes diversity in large river floodplains*, 54th Symposium of the International Association for Vegetation Science – IAVS, Lyon, France.

Keruzoré A., Willby N., Gilvear D., (2010), *Hydrological connectivity and the maintenance of aquatic plant diversity in riverine backwaters*, 85th Scottish Freshwater group meeting, Stirling, Scotland.

Conference poster presentation

Keruzoré A., Willby N., Gilvear D., (2011), *The role of backwaters in the maintenance of macrophyte diversity in large rivers*, 2nd Symposium of the International Society for River Science – ISRS, Berlin, Germany.

Keruzoré A., Willby N., Gilvear D., (2010), *Effects of flooding magnitude on aquatic plant biomass in backwaters,* 85th Scottish Freshwater group meeting, Stirling, Scotland.

Keruzoré A., Willby N., Gilvear D., (2009), *The influence of connectivity and fertility on aquatic plant communities of riverine backwaters*, 12th EWRS International Symposium on Aquatic Weeds, Jyväskylä, Finland.