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A review of hydrochory (seed dispersal by water) with implications for riparian rehabilitation

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Abstract

Working alongside natural regeneration processes is an important part of an ecosystem approach to long-term, self-sustaining, riparian rehabilitation. Hydrochory (seed dispersal by water) is a key influence on such rehabilitation and has received limited attention. This review of hydrochory suggests it is the relationships between hydrology, fluvial geomorphology and seed biology which determine seed deposition and germination. In-stream geomorphic and hydraulic diversity are important for both seed transport and seed retention in fluvial systems. Woody debris and flotsam are important for long-distance seed dispersal, especially for seeds without specialised floating phenology. Lateral connectivity between the channel and floodplains, as well as timing of seed release, for example with receding flood flows, influence whether seeds are transported to sites with favourable germination conditions. Not all hydrochory is desirable, such as the spread of invasive plant species in New Zealand. It is clear that much more attention should be given to hydrochory to better align riparian management with natural ecosystem processes and improve the long-term outcomes of riparian rehabilitation.

Keywords

hydrochory; seed dispersal; fluvial processes; ecosystem approach; riparian rehabilitation

The role of hydrochory in an ecosystem-based approach to riparian rehabilitation

Substantial time, energy and money have been invested in riparian re-vegetation and weed eradication in the past thirty years (Palmer *et al.*, 2005). Given these investments and the importance of riparian vegetation both as an amenity and for river health (Smaill *et al.*, 2011), there is inherent pressure for rehabilitation projects to be successful (Palmer *et al.*, 2005; Palmer and Allan, 2006). Palmer *et al.* (2005) argued that most riparian schemes are nowhere near as successful in the long-term as they should be, due to plant dieback and weed invasions; and there are a number of challenges in ensuring effective implementation and successful results (Brierley *et al.*, 2006; Fryirs and Brierley, 2009). Groves *et al.* (2007) demonstrated that a key reason for reduced planting success is a limited understanding of long-term riparian sustainability, particularly for areas that are located in isolated pockets and are susceptible to weed infestation. It is clear that rivers and streams continue to degrade, despite an increase in rehabilitation efforts (Palmer and Allan, 2006).

The advent of ecological perspectives prompted a paradigm shift in river conservation through the 1970s and 1980s. During this period papers stressed the adversity of human impacts on river systems, and promoted research and investment in riparian and river rehabilitation (e.g., Behnke, 1978; Kauffman and Krueger, 1984; Glade, 2003; Brierley *et al.*, 2005). A move to more ecosystem-based management is evident in approaches in which systems are viewed as continuously changing entities, influenced by a complex array of controls, including social processes (Glade, 2003; Brierley *et al.*, 2005). Nevertheless, in practice, many riparian revegetation projects follow traditional horticultural approaches to riparian planting (e.g., personal communication with Chris Ferkins Project Twin Streams Waitakere City Council, 2010). The approach stems from a 'command and control' ideology, which emphasises human control over nature and involves a high level of human investment in rehabilitation. Each seedling is selected and placed in a given site and a typical measure of success is survival rate. This approach has many disadvantages, including high monetary costs and human effort and may not lead to a naturally functioning ecosystem.

Differing approaches to riparian vegetation have caused debate over how to manage riparian planting. With growing awareness of the critical relationship between vegetation dynamics and river forms and processes emerging from the 1980s onward, researchers have questioned how interdisciplinary research, in terms of a whole-of-system approach, might be used to enhance the results of river and riparian rehabilitation (e.g. Allen *et al.*, 2011).

A number of researchers have suggested that natural seed dispersal and deposition would be useful to incorporate into riparian rehabilitation (e.g. Groves *et al.*, 2007; Gurnell *et al.*, 2008; Goodson et al., 2003). Seeds can be dispersed across the landscape in a variety of ways, including birds and other animals, gravity, wind and water. Hydrochory – seed dispersal by water – is an important mechanism, particularly in riparian environments and may influence seed bank structuring and riparian composition (Nilsson *et al.*, 1991; Johansson *et al.*, 1996; Andersson *et al.*, 2000; Goodson *et al.* 2002). Fenner and Thompson (2005) state that all riparian species are likely to be dispersed by water to some extent. Seeds are released into water where they can be dispersed downstream at great distances from parent trees or onto higher elevations during flooding, depending on flow magnitude (Naiman *et al.*, 1988). Skoglund (1990) found an average of 35,000 seeds m^{-2} in a 10-cm layer of drift material that had been deposited onto floodplains along the lower Dalalven River, Sweden. Hydrochory may also remobilise species already dispersed by other mechanisms (Bennett and Simon, 2004).

Although water is an obvious dispersal vector in riparian environments, it has received limited attention in literature compared to the other dispersal mechanisms. Riparian rehabilitation that is mindful of the role of hydrochory in seed dispersal will ultimately achieve better long-term rehabilitation results. Clearly the key processes that drive water dispersal must be understood. As a step towards incorporating hydrochory in successful riparian rehabilitation, this paper reviews the current knowledge of seed dispersal by water and its associated processes, focusing on links between hydrology, seed biology and fluvial geomorphology. Discussion is provided on ways that knowledge of these processes and their interactions might be applied.

A review of research on hydrochory

Botanists have recognised hydrochory as an important mechanism of seed dispersal since Darwin (Goodson *et al.*, 2002), although relatively few studies dealing specifically with water dispersal were documented until the latter half of the 20th century. Willson *et al.* (1990) examined the spectrum of seed dispersal mechanisms, but specific seed adaptations to water dispersal were deemed too rare to warrant more than a mention. Research has grown rapidly in the past decade or so. Nilsson *et al.* (2010) reported an almost exponential increase in research reports from 1984-1999 to 2000-2010, and more recently hydrochory has been shown to be a very effective mechanism for moving seeds.

Hydrochory research has implications for flow regulation, restoration, climate change and the spread of native and invasive species. Studies have shown that water dispersal is important for transporting and depositing freshly produced seeds (Cellot *et al.*, 1998; Thebauld and Debussche, 1991; Merritt and Wohl, 2002; Boedeltje *et al.*, 2003; Goodson *et al.*, 2003; Tabacchi et al., 2005), remobilising seeds (Goodson et al. 2003; Pettit & Froend 2001), structuring riparian plant communities (Andersson *et al.*, 2000; Johansson *et al.*, 1996; Nilsson et al., 1991; Goodson *et al.*, 2002; Tabacchi *et al.*, 2005; Groves *et al.*, 2009) and maintaining high riparian diversity (Nilsson *et al.*, 1994; Johansson *et al.*, 1996; Andersson *et al.*, 2000). Of course, hydrochory can disperse native species through a river course and spread invasive weed species, e.g., *Salix* spp. commonly known as Willow, and *Usnea* spp. or Old Man's Beard, which are both weeds in New Zealand (Groves *et al.*, 2009). Hydrochory can thus be both beneficial and detrimental to efforts to manage riparian plants.

The influence of water dispersal on riparian vegetation composition is debated in literature. Some studies have measured seed quantity and vegetation composition and found organic flotsam along rivers to be richer in species than the wind-dispersed seed rain, which suggests that flotsam in streams and rivers is an important mechanism for dispersing seeds (Merrit and Wohl, 2002). Hughes and Cass (1997) ascertained that water dispersal has an important influence on vegetation structure by comparing propagule species with standing vegetation species. In their study of a floodplain forest, newly deposited seeds transported in flotsam during flooding were found to contribute new species to the deposition site (40 seeds were deposited by flood waters, of which only 14 were present in the standing vegetation). This difference in species type supports the idea that river transport plays a role in structuring patterns of vegetation.

Research by Andersson *et al.* (2000) supported the conclusion that hydrochory is important for riparian species richness. Wooden cubes were used as a proxy for seeds and released in the free-flowing Vindel River, Sweden. The number of cubes deposited was found to correlate with high above-ground species richness. Additionally, it was found that seed floating ability was not important for vegetation composition because flotsam could transport seeds during regular spring floods. Most recently, Nilsson *et al.* (2010) suggested that although water has the potential to colonise sites that other dispersal vectors may not reach, this depends on the interplay between other factors, such as the timing of dispersal and the environmental conditions of a deposition site necessary for successful establishment.

Parolin (2005) categorised hydrochory into three forms: (1) dispersal by water currents on the surface, (2) dispersal by water currents on the bottom of a channel, and (3) dispersal by rain falling on a plant. These dispersal types (particularly the first two) play a role in long-distance dispersal, which is important for landscape connectivity and for maintaining and extending species populations at the landscape scale (Merrit and Wohl, 2006). Nilsson *et al.* (2010) suggested that water can disperse seeds to greater distances than other dispersal mechanisms.

Clearly, increased knowledge of long-distance dispersion through river corridors can improve understanding of how landscapes are colonised by plants.

A number of processes influence hydrochorous seed dispersal and deposition patterns, but many of the process relationships and seed responses remain unclear. Merrit and Wohl (2002) identified three processes: '(1) the hydrological regime during seed release and transport, which is determined by the timing and magnitude of peak flow and the rate and direction of change in discharge, (2) channel morphology and (3) the phenology of seed release as it relates to the hydrologic regime'. Researchers tend to agree that once seeds enter the fluvial system, the local hydrological regime is the most important in terms of determining dispersal distance and deposition location (e.g., Schneider and Sharitz, 1986; Edwards *et al.*, 1994; Walker *et al.*, 1995; Danvind and Nilsson, 1997; Poff *et al.*, 1997; Middleton, 2000; Andersson *et al.*, 2000; Pettit *et al.*, 2001; Merritt and Wohl, 2002; Nilsson *et al.*, 2002; Boedeltje *et al.*, 2003; Hampe, 2004; Edwards *et al.*, 1994; Riis and Sand-Jensen, 2006; Richter *et al.*, 1997). However, the way that the hydrology interacts with fluvial geomorphology, stream hydraulics, and seed biology together determine the final location of water-dispersed seeds. These controls are dynamically adjusted, meaning that a change in one will often produce a change in the others (Brierley and Fryirs, 2000; Gurnell *et al.*, 2002; Montgomery *et al.*, 2003). Francis (2006) has suggested that more advanced approaches in riparian management are limited by the absence of research that considers interrelationships between hydrology, geomorphology and ecology.

The influence of flow regime on seed dispersal

Walker *et al.* (1995) described the flow regime as 'the maestro that orchestrates pattern and process'. Ecologically significant aspects of flow regime include flow magnitude, flow variability, rate of flow change, magnitude and frequency of flow conditions, and flow predictability (Richter *et al.*, 1996).

Flow velocity, in particular surface flow velocity, plays a key role in determining seed entrainment and dispersal distance. Merrit and Wohl (2002) found significant differences in seed deposition between units with low surface flow (e.g., pools, slack waters) and units with high surface flow (e.g., straight reaches, cut banks, riffle-run sequences, cascades, rapids, waterfalls). Groves *et al.* (2009) found variation of flow velocity between reaches to be the major driver underlying differences in seed suspension and deposition. Chambert and James (2009) found that different flow velocities along the dispersal pathway led to preferential sorting of seed species type. Johansson and Nilsson (1993) and Andersson *et al.* (2000) suggested that small increases in flow velocity result in an almost exponential increase in the dispersal distance of seed mimics. Fischer *et al.* (1979) described the relationships between particle dispersal and velocity. An increase in velocity results in an increase in shear stress. This in turn reduces surface flow dead zones along the bank, which limits the ability of the bank to trap seeds, and leads to extended seed dispersal. As a result of differences in shear stress, seeds move faster through the central streamline than along channel banks (Fischer *et al.*, 1979).

Studies on sediment dispersal processes have proved useful to understand seed dispersal. The relationship between sediment and seed deposition was first observed by Nilsson *et al.* (1993) in their study on northern European rivers. Goodson *et al.* (2003) found a positive relationship between hydrochorous seed deposition and sediment deposition at different elevations along the Dover River, England, and Cerdà and Garcia-Fayos (2002) reported in laboratory experiments that seeds (<50mg) were suspended at the same flow threshold as similar-sized sediment particles.

Groves *et al.* (2007) described similarities in seed and sediment movement. Seeds that float are generally transported with washload sediments (e.g., fine clays), which move with similar velocities and directions to surface flow, although seeds can settle out of the washload as they become waterlogged. Surface flow velocity varies laterally and longitudinally through the river channel in relation to channel roughness, which is controlled by riparian vegetation cover, large woody debris and channel sinuosity (Groves *et al.*, 2007). The location and concentration of washload sediments and floating seeds also vary throughout the river channel. Washload sediments and floating seeds move most quickly through the channel thalweg and settle out in areas with still surface flow, such as pools and slack water and on bar surfaces, alongside channel banks and floodplains. As a result of this geomorphic and hydraulic diversity, floating particles are challenging to model at small reach and geomorphic unit scales (Meade *et al.*, 1990).

Floating seeds can become waterlogged and sink over time. Dispersal pathways for sinking seeds are analogous to those for suspended or bedload material (Groves *et al.*, 2007). These materials are entrained into suspension when the stream power threshold is met, usually at higher than normal flow stage, and can be deposited onto areas that are infrequently inundated and disturbed providing opportunity to germinate.

A large number of sediment dispersal models have been developed; they vary in complexity, including their input variables/processes, the scale to which they are applied, and their inherent assumptions. A comprehensive review of sediment transport models, including detailed descriptions of several common models, is provided by Merrit *et al.* (2003), who concluded that although there are clear advantages in the use of sediment dispersal models, more work is needed to generate simple, physically realistic models that will be of most practical use to river managers. The accuracy of spatial modelling required in sediment dispersal models remains an issue, as do a lack of datasets for calibration (Merrit *et al.*, 2003), which are similar issues facing seed dispersal models.

As flow regime is very important for seed dispersal patterns, a number of studies have focused on seed dispersal in regulated rivers (e.g., Andersson *et al.*, 2000; Jansson *et al.*, 2000; Jansson *et al.*, 2005, Merrit and Wohl, 2006). The majority of studies in regulated rivers have noted the positive contributions that hydrochory can make to riparian biodiversity but, as we know, hydrochory can also disperse invasive weeds.

Regulated flow regimes have been found to constrain seed dispersal. Jansson *et al.* (2000) found riparian composition to vary between adjacent impoundments in a regulated river, as a result of a forced uneven distribution of floating propagules. Merrit and Wohl (2006) found higher species richness in reaches downstream of reservoirs compared to upstream, suggesting that seeds from an upstream catchment area are combined with seeds from local sources along free-flowing river reaches, whereas seeds along regulated reaches are predominantly from local sources. Andersson *et al.* (2000) found dam impoundments to have much weaker currents than free-flowing rivers, limiting dispersal distances.

As dispersal distances can be limited by regulated flows, the probability of seeds reaching suitable sites for germination is also reduced (Francis, 2006). Studies have demonstrated the role of flooding in connecting otherwise disjunct populations (e.g., Vogt *et al.* 2004; Schneider and Sharitz, 1986). Overall, seed deposition patterns during floods remain poorly understood. Of course, seeds need to be available for floods to disperse the seeds.

Implications of the connections between flow regime and hydrochory for riparian rehabilitation

Flow velocity is particularly important for determining seed entrainment, transport and deposition. It also leads to preferential sorting of seeds along the river margin. Seeds are likely to be deposited in low-flow surface units, such as pools and slack water, while units with higher surface flow, such as straight reaches, cut banks and riffle-run sequences, can increase dispersal distance. It is important to maintain a diversity of low and high surface flows, which is a function of hydrology and channel roughness, so that seeds can be dispersed to downstream rehabilitation sites but can also be retained in the system for remobilisation in flood flows. Environmental flows in regulated rivers may increase seed dispersal distances and the likelihood of seeds reaching sites suitable for germination.

Biological influences on hydrochory – traits of seed phenology and life history

The timing of seed releases determines when seeds will enter the fluvial system. Relationships between the timing of seed releases and flow regimes are clearly important for establishing dispersal distances, pathways, and suitable sites for germination. Kubitzki and Ziburski (1994) demonstrated that the synchronisation of fruiting with predictable floods is the most important adaptation to hydrochory. For water to be an effective means of transport, seed fall needs to coincide with favourable flow conditions, such as receding floodwaters when soil is exposed (White, 1979).

Merrit and Wohl (2002) found a significant relationship between flow regime and timing of seed release, which resulted in distinctive deposition patterns along channel margins. Pettit and Froend (2001) studied four dominant species found along the Blackwood and Ord Rivers, Australia, and found seed fall to coincide with the end of the rainy season. Seeds were thus released during high flows and high flow recessions and were therefore deposited onto sediments ideal for germination (bare and moist). This adaptation by seed phenology is found with *Populus* and *Salix* species in the central USA (Bradley and Smith, 1986) and in the south-eastern USA (Schneider and Sharitz, 1988), and was reported by Estabrook *et al.* (1982) to be fairly common among some species.

The anatomical characteristics of seeds, such as their size and shape, might make them prone to particular dispersal vectors. A study by Andersson *et al.* (2000) found that *Helianthus annuus* (sunflower) seeds were deposited in very similar ways to wooden cubes (22mm in size) and suggested that depositional patterns across a range of seed sizes may be consistent. Particular seed morphologies or life history traits aid dispersal by water (Howe and Smallwood, 1982; Johansson and Nilsson, 1993; Malanson, 1993). A general question which remains largely unanswered is whether different seed floating abilities influence riparian distribution patterns.

A number of studies have looked at the effects of seed buoyancy traits on transport pathways, with varying results. van den Broek *et al.* (2005) linked increasing seed buoyancy of vegetation zones with increasing inundation rates along wetland ecosystems in The Netherlands and Germany. The study illustrated that seed buoyancy is important for determining the distribution of a range of species in wetland systems, which are inundated for a long period of time each year.

In contrast, a study by Danvind and Nilsson (1997) hypothesised that seed floating ability would correlate with long-distance dispersal, yet found that species distribution was not significantly correlated with variation in seed buoyancy and that high floating ability is not necessary for effective dispersal. One obvious explanation is that woody debris and flotsam can trap seeds and increase seed dispersal distances from the parent plant, regardless of floating ability (Johansson and Nilsson, 1993). This was illustrated in a dispersal study by Nilsson *et al.* (2002) in which wooden cubes, used as seed mimics, were mostly stranded on riverborne litter deposits. Nilsson *et al.* (1994) suggested that spring floods can transport seeds a long way in a short period of time (the spring flood peak moves along a 230 km stretch in 2.5-0.64 days in the free-flowing Vindel River, Sweden). This allows seeds even with brief floating abilities to be dispersed over long distances. Therefore, seed buoyancy may not be as important in rivers with high flotsam loadings and in free-flowing rivers with unregulated high (spring) flood peaks.

Nilsson *et al.* (2002) found that seed buoyancy may influence vegetation composition at the reach scale; linking to hydraulic variability between reaches. Species with long-floating propagules were found more along river lakeshores and tranquil reaches and short-floating species found more along turbulent reaches. Overall, the importance of seed buoyancy in structuring vegetation communities seems to depend on river type, reach-scale variability, and associated flow paths.

Fenner and Thompson (2005) argued that it is difficult to be certain of any particular dispersal mechanism based on phenological attributes alone. Although many species possess buoyancy characteristics, seeds without these traits can still float or become suspended in the water. Danvind and Nilsson (1997) suggested that the influence of buoyancy is complicated by multiple mechanisms of dispersal.

Dispersal distance is an important factor in determining which native (or invasive) stands upstream contribute to downstream plant rehabilitation. Seeds have higher potential of retaining viability if they are deposited in drift materials along channel margins; otherwise they may become waterlogged, sink to the channel bed and lose viability (Hughes and Cass, 1997; Andersson *et al.*, 2000). Andersson *et al.* (2000) found that river banks which received the most drift material, including seeds, were the most species rich.

Implications of the connections between plant biology and hydrochory for riparian rehabilitation

The connections between timing of seed fall, flood flows and geomorphic availability are important for hydrochorous seed transport, deposition and germination. The best time for seeds to enter a stream or river is during receding floodwaters so that seeds can be transported long distances and deposited onto elevated floodplain surfaces. Floodplains are often left coated with moist and fertile sediments following flood flows, which are particularly favourable conditions for germination. They are also infrequently inundated or disturbed, providing an opportunity for plants to establish. Flood flows are clearly important for riparian rehabilitation to be self-sustaining, as is high lateral connectivity between a river and its floodplains. Furthermore, the fact that organic flotsam and woody debris aid seed transportation means that seeds do not require specialised floating ability to be dispersed by water.

Fluvial geomorphology and hydrochory

The *quantity* of seeds and the *quality* of the dispersal of each seed combine to determine 'disperser effectiveness', which was defined by Schupp (1993) as 'the contribution a dispersal makes to the future reproduction of a plant'. This is largely dependent on the biotic and abiotic conditions that characterise the sites on which seeds become deposited (Schupp, 1993; Dennis *et al.*, 2007). Fluvial geomorphology (including substrate characteristics, channel shape and size, geomorphic unit assemblages, floodplain attributes) provides the physical template upon which seeds may become deposited, germinated, buried, reworked, or remobilised.

Species tolerance to particular hydrogeomorphic conditions, along with competition by other species, are key factors driving successful species germination (Bendix and Hupp, 2000). Geomorphology of the deposition surface plays a key role in plant growth and riparian species composition.

Different geomorphic unit types have characteristic micro-environmental conditions. There are dynamic relationships between hydrology and fluvial geomorphology, involving substrate destruction and creation, which work together to influence patterns and directions of seed dispersal, and create groupings of geomorphic units (Bendix and Hupp, 2000). Analysis of units can be used to interpret the fluvial processes that formed them, which is a function of the available energy and sediment characteristics (Brierley and Fryirs, 2005).

Individual geomorphic units have inherent hydrological characteristics, for example, bars and benches are inundated under bankfull flow stage, whilst floodplains are inundated in overbank flow stage. Geomorphic units and groupings are easily identified in the field and can be used in management to select appropriate plant species for the site. Seeds may also be stored on river beds, thus channel bed geometry is important for preferential seed storage (Gurnell *et al.*, 2007).

A benchmark study by Merrit and Wohl (2002) used an experimental flume study to explore whether seed dispersal and deposition along river margins could be predicted on the basis of hydrological regime, geomorphic features, and timing of release. More seeds were found deposited in areas of reduced velocities, which related to geomorphic and hydraulic units including eddies, flow expansions, point bars, pool margins, and slack water. Conversely, fewer seeds were found deposited on units relating to high flow velocities such as cut banks, flow constrictions, islands and straight margins. This demonstrates the importance of relationships between flow regime and geomorphic unit type and the potential to use geomorphic units as a proxy for predicting species deposition. The study suggests that low surface-flow velocities are important for retaining seeds in the river system, where they can be remobilised in flood flows and deposited onto sites more suited to plant germination.

Geomorphic groupings vary longitudinally, laterally, and vertically as a result of catchment position and related controls. Vegetation patches form in relation to different geomorphic groupings at varying scales, which include: '(1) the landscape scale (contrasts in physical environmental characteristics between reaches), (2) the reach scale (contrasts between within-reach landforms such as bars and floodplain surfaces) and (3) the bar scale (contrasts between patches of varying sedimentary or topographical characteristics within the same bar)' (Francis, 2006).

Depending on the particular scale of enquiry, different geomorphic controls, processes and features will relevant. Vogt *et al.* (2004) recommended that high-resolution sampling measures (reach or geomorphic unit which link to hydraulics) are required for meaningful results when studying hydrochorous seed transport. Geomorphic assemblages clearly differ according to river type.

Most riparian species require bare soils to become established, as they tend to be pioneer species that do not compete well with later succession species (Francis, 2006). However, site suitability for germination is variable, as geomorphic forms and their spatial arrangements continuously adjust (Schupp, 1993). Even so, the presence or absence of particular geomorphic characteristics within a reach, at a given time, is clearly significant for determining patterns of seed dispersal. Connectivity is also important, particularly between rivers and their floodplains, so that seeds can be transported to suitable sites for germination (Bornette *et al.*, 1998; Tockner and Ward, 1999).

Vegetation, sediment and litter transported by rivers can collect on preferential geomorphic units (Goodson *et al.*, 2001). Changxing *et al.* (1999) found organic matter containing numerous seeds accumulated on concave benches and bars along the regulated lower Dee River, UK. Following the scouring of these surfaces in post-flood events, the newly bare sites provided ideal surfaces for seed germination. Deposited seeds may also form part of the seed bank (Goodson *et al.*, 2001).

Andersson *et al.* (2000) correlated the stranding patterns of an artificial diaspore (wooden cubes) with environmental variables in the free-flowing Vindel River, northern Sweden, and found some conflicting results. Rapids was the only predictive variable correlating to number of stranded cubes at a site. Correlations were not significant between riverbank height, width, or vegetation cover. This could be explained by the spring flows, which vary in elevation and duration between years. Additionally, weather conditions influence different wind patterns and currents, which affect dispersal patterns.

Despite the importance of these connections, the role of fluvial geomorphology in seed dispersal has been largely overlooked in hydrochory literature. Much more could be made of the potential for fluvial geomorphic insight to assist in riparian rehabilitation, particularly at the unit scale.

The geomorphic substrate provides the surface upon which seeds can be deposited, remobilised and/or germinate. Geomorphic units and groupings of units involve substrate destruction and creation due to hydrology and substrate type. Diversity of geomorphic units is important to provide a range of surfaces for plants with different hydro-geomorphic tolerances to germinate. It is likely that seeds will deposit on low-flow units, which is important for seed retention in the river system. These surfaces are frequently reworked and seeds may become remobilised in flood flows and transported to sites more suitable for germination.

Geomorphic units and their groupings can be used to estimate inundation frequency where flood data does not exist. This could be useful in selecting plants most suited to the given site. For example, the New Zealand natives *Cortaderia richardii* (toe-toe), *Phormium tenax* (harakeke, New Zealand flax) and *Carex secta* (purei) tolerate water inundation and could grow on geomorphic surfaces that flood periodically (Ledgard and Henley, 2009).

Incorporating hydrochory into ecosystem-based riparian rehabilitation

Current understandings of the key processes involved in structuring riparian communities, including seed supply, dispersal, deposition and germination are not being fully utilised in riparian rehabilitation (e.g., Holmes *et al.*, 2005). Hydrochory is an important seed dispersal mechanism in riparian environments (Groves *et al.*, 2007; Gurnell *et al.*, 2008; Nilsson and Svedmark, 2002) however there is very little guidance in scientific literature on how knowledge of hydrochory might be incorporated into riparian rehabilitation plans. This paper suggests that an understanding of the key processes that drive hydrochory, including hydrology, fluvial geomorphology and seed biology, can be used in riparian rehabilitation to aid natural regeneration processes.

Petts and Amaros (1996) listed three principles for any ecosystems approach to river management. Firstly is the need for a catchment-scale approach. This is a reoccurring message in rehabilitation literature (e.g., Brierley and Fryirs, 2000; Allan *et al.*, 2011). Rehabilitation strategies should reflect upstream catchment conditions, e.g., consideration of native vegetation sources in the upstream catchment, catchment modifications and how these have affected river flows. Longitudinal connectivity is clearly important. Management at an individual site or reach might provide short-term benefits, but catchment scale planning will be required for long-term success (Petts and Amaros, 1996).

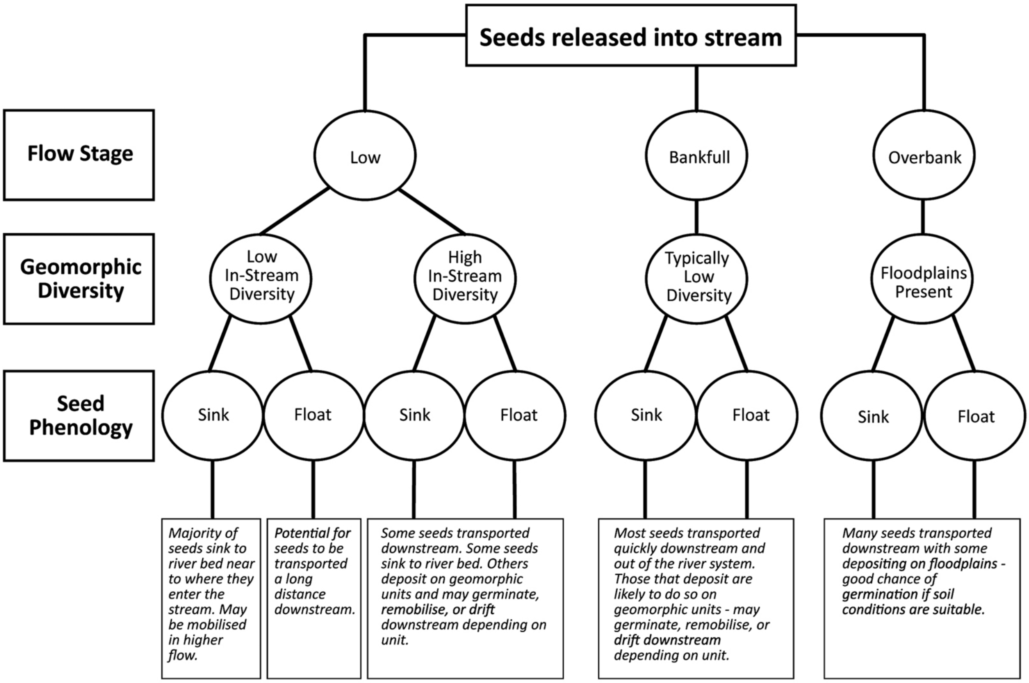
Secondly, lateral exchanges at the land-water interface are important for sustaining long-term functionality of river systems. Thirdly, there is a need to view the natural range of variability of rivers systems, involving hydrological, geomorphological and ecological interactions. It makes sense that riparian and river rehabilitation plans need to be adapted depending on river type and catchment modifications.

Implicit in this message is the need to 'know your catchment', so that river and riparian rehabilitation strategies can be adapted to work with the natural conditions and characteristics of a particular site. This might involve several strands of work: historical review of the river catchment to determine if and where the river has been modified; ascertaining channel-floodplain connectivity (frequency of bankfull flow stage/overbank flow stage); mapping geomorphic features; and mapping riparian plants to locate native /invasive plants in the catchment (i.e., what seeds are likely to be dispersed to the rehabilitation site).

A conceptual model (Fig.1) illustrates how interactions between flow stage, geomorphic diversity (meaning the range of geomorphic units such as bars, benches, floodplains) and seed phenology influence hydrochorous seed dispersal and deposition in riparian ecosystems. The value of understanding these process interactions can be demonstrated by considering their influence on seed deposition and implications for rehabilitation in two conceptual scenarios – intact and modified catchments.

In intact catchments with lots of native riparian vegetation and high in-stream geomorphic diversity, seeds that enter the stream during low flow stage may be retained in units with slow surface flow such as pools and slack water, and on geomorphic units such as bars and benches. Seeds retained in these slow-flow units may be remobilised in high flood events and transported onto floodplains, which can provide favourable conditions for seed germination. An input of woody debris and plant flotsam materials into the stream from intact riparian zones in the catchment will aid seed transport and increase seed dispersal distances. A rehabilitation strategy might consider protecting native seed sources in the catchment particularly those up-stream. Minimal active planting should be required. The New Zealand focus might involve weeding and site monitoring.

In a modified catchment with low in-stream geomorphic and hydraulic diversity and little input of woody debris and plant flotsam, seeds that enter the stream or river during low flow stage have less chance of being retained and/or deposited and are more likely to be transported through the fluvial system. If flood flows are restricted (e.g., stop



Majority of seeds sink to river bed near to where they enter the stream. May be mobilised in higher flow.

Potential for seeds to be transported a long distance downstream.

Some seeds transported downstream. Some seeds sink to river bed. Others deposit on geomorphic units and may germinate, remobilise, or drift downstream depending on unit.

Most seeds transported quickly downstream and out of the river system. Those that deposit are likely to do so on geomorphic units - may germinate, remobilise, or drift downstream depending on unit.

Many seeds transported downstream with some depositing on floodplains - good chance of germination if soil conditions are suitable.

Figure 1 – Interactions between flow stage, geomorphic diversity and seed phenology and their influence on hydrochorous seed dispersal and deposition.

banks, river channeling, river bed scouring), this reduces the lateral connectivity between the channel and floodplains, with less opportunity for hydrochorous seeds to reach floodplains and germinate. A key strategy in working towards a more functioning and natural system may be to reconnect riparian zones that have been isolated from the river (system?) (Nilsson and Svedmark, 2002). Native seed sources could be protected and native riparian vegetation in the upstream catchment could be promoted. Propagule dispersal (local soil seed banks or intact patches of vegetation in the catchment) have been found to be critical for natural recovery (Holmes *et al.*, 2005).

In highly modified catchments, native propagule dispersal is likely to be low. In these cases planting may be required both in the upstream catchment and at key rehabilitation sites. Critically, the planting should take into account fluvial geomorphology, substrate conditions and likely inundation frequency. Some rehabilitation sites may lack environments that are suitable for seed germination and might require new strategies designed to work within a new environmental setting.

In highly modified rivers, floodplain-channel lateral connectivity and high flow events may need to be re-established. In-stream geomorphic diversity could also be re-established to generate hydraulic variability in the channel and create sites for seed deposition. Nilsson and Svedmark (2002) described passive management strategies as those which ‘let the river do the work’, such as reconstructing natural geometry by reconnecting floodplains to river flows, for example by lowering embankments and weirs. In the lower Missouri River vegetation responded quickly to the reconnection with its floodplain, with the recovery of perennial and invasive plants following flood scouring (Nilsson and Svedmark, 2002).

With any rehabilitation efforts, the complex relationship between processes means that there will always be uncertainty about where seeds will be deposited. However, knowledge of how key processes interact can be used to plan rehabilitation strategies and link the ideas of seeds entrainment and deposition with fluvial geomorphology and hydrology for more desirable outcomes.

Conclusions

A review of hydrochory suggests the subject has been largely ignored until recently when research has grown rapidly. Hydrochory has been shown to be important for transporting, depositing and remobilising seeds, structuring plant communities and maintaining riparian diversity. Improved understanding and utilisation of hydrochory and the processes that drive it (importantly hydrology, seed biology and fluvial geomorphology) may lead to more self-sustaining riparian rehabilitation practices.

There are complex interactions between hydrology, seed biology and fluvial geomorphology. Surface flow is an important transport vector as many seeds float and those without floating abilities can be transported in rivers or streams in woody debris or flotsam. Seeds will collect in areas of slow flow, such as pools and slack water and will be transported downstream in fast flowing zones, such as riffle-run sequences. Hydraulic diversity is clearly important for both seed transport and seed retention in a river system.

The timing of seed release interacts with flow regime to influence dispersal pathways and distance. Floodwaters are especially important, as seeds can be transported and deposited onto floodplain surfaces, which may be left bare and moist following inundation. This provides favourable germination conditions. In modified river catchments, flood flows have been re-instated to enable long-distance seed dispersal and improve channel-floodplain connectivity.

Fluvial geomorphology provides the physical template, upon which seeds can be deposited, buried, reworked, remobilised, or germinate. There are clear hydrology and fluvial geomorphology process relationships that involve substrate creation and destruction. Geomorphic diversity (e.g., bars, benches, banks, floodplains) is important for seed deposition and germination, as different plants have different hydro-geomorphic tolerances. Vegetation patches are known to form in relation to these different geomorphic groupings and at varying spatial scales. Riparian rehabilitation must take into account the interaction between native and invasive plant species. Geomorphic landforms, particularly substrate conditions and inundation frequency, should be considered in the selection of suitable protection and planting sites (if planting is necessary). A hydrologic and geomorphic appraisal should be part of any riparian management efforts. Integrated approach to riparian rehabilitation that consider process-based interactions across river contexts and at different scales is needed to improve the implementation of hydrochory and the long-term success of riparian rehabilitation.

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