



# MMCP Collaboration Final Report 2019

## Vegetation Dispersal

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**Prepared by:** Daryl Nielsen and Rebecca Durant

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# **The MMCP Collaboration Final Report 2019 – Vegetation Dispersal**

Final Report prepared for the Murray–Darling Basin Authority.

Murray–Darling Basin Authority  
Level 6, 33 Allara Street | GPO Box 1801  
Canberra City ACT 2601

Ph: (02) 6279 0100; Fax: (02) 6248 8053

For further information contact:

**Daryl Nielsen**

PO Box 821  
Wodonga VIC 3689  
Ph: (02) 6024 9650

Email: daryl.nielsen@csiro.au  
Enquiries: cfe@latrobe.edu.au

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**Author affiliation(s):** <sup>1</sup>CSIRO Land and Water, Wodonga

<sup>2</sup>La Trobe University, Wodonga

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## Overview

This project seeks to understand how the delivery of water through infrastructure modifies the movement of seeds between different components of the riverine-floodplain landscape. We test the hypothesis that while seeds of many species will occur in the drift, in the source water (e.g. river channel) only a small proportion of these species will be moved through infrastructure (e.g. pumps or regulators) into the receiving wetland or creek channel.

## Objectives

The objectives of this project are to:

- Determine the physical characteristics of seeds that facilitate dispersal.
  - The physical characteristics of seeds will determine the distance that they drift in the water column and whether they drift on the surface or lower in the water column. Knowledge of seed morphology will enable predictions on which seeds are likely to persist in the drift and how infrastructure will influence drift.
- Understand how the operation of water delivery infrastructure (pumps, channels, regulators) may affect seed dispersal.

In meeting these objectives, we anticipate the following management outcomes:

- *Protect and restore water-dependant ecosystems.* This work will improve our understanding of how the operation of infrastructure (pumps, regulators, channels) to restore lateral connectivity could lead to changes in aquatic and riparian vegetation communities.
- *Ensure that water-dependant ecosystems are resilient to climate change and other risks and threats.* By better understanding the impacts of using infrastructure to maintain lateral connectivity, managers will be able to manage connectivity to protect water-dependant ecosystems as the demand for water resources increases under climate change scenarios.

## Background

Dispersal plays a central role in a wide range of ecological processes, including community assembly, the maintenance of biodiversity, species coexistence, biological invasions, and ecosystem function (Myers & Harms 2009). Despite widespread interest in the role of dispersal in community assembly, we still lack a synthetic empirical understanding of how species pools and ecological filters interact to structure local biodiversity. To date, experimental tests of the role of propagule supply in natural communities have largely focused on terrestrial plants. In general, these experiments have indicated evidence for seed dispersal to be limited (Clark *et al.* 2007; Eriksson & Ehrlén 1992).

The movement of plant propagules within the landscape is an important factor in both the replenishment of dormant propagule banks and in the diversity of extant aquatic communities (Nilsson *et al.* 2010). However, very little is known regarding the extent and frequency of dispersal for most species, especially within river-floodplain habitats such as wetlands, creeks and the main channel. Therefore, an understanding of how biota disperse is fundamental to how wetlands and creek systems are managed for the conservation of biota in fragmented aquatic habitats. The extent and frequency of dispersal can have important implications for population dynamics, population genetics, biogeography, and macro-evolution.

The distribution and abundance of aquatic and riparian plants is strongly influenced by hydrology and the availability of water (Kehr *et al.* 2014; Merritt & Wohl 2002). Changes in flow regimes or

hydrological connectivity, are therefore likely to significantly impact the distribution of aquatic and riparian plants (Merritt *et al.* 2010). Changed connectivity may occur through the disconnection of components of the landscape caused by changes in flow regime, construction of barriers that physically impede dispersal, or through the artificial movement of water between rivers and wetlands. However, interrogation of long-term wetland and riparian data sets collected as part of Murray–Darling Basin Authority’s, ‘The Living Murray’ program has indicated a high degree of uniqueness of plant species between locations and at individual sites within locations during periods of both low and increased hydrological connectivity (Campbell & Nielsen 2014a). However that’s not to say that dispersal is not occurring. Dispersal may be occurring but local factors may restrict germination and establishment (Bornette & Puijalon 2011; Lacoul & Freedman 2006); or alterations in the arrangement of habitats spatially and temporally may prevent communities from being expressed (Amoros & Bornette 2002; Bornette *et al.* 1998b). It does appear that many wetland and riparian plant communities are very heterogeneous, with many species only being recorded from single locations (Alexander *et al.* 2008; Bornette *et al.* 1998a; Campbell *et al.* 2014).

The dispersal of propagules longitudinally and laterally along river channels is predominantly influenced by flow regime factors such as seasonality, magnitude and duration. River regulation has altered hydrological connectivity and flow regime characteristics throughout the Murray–Darling Basin (MDB). Water control measures are increasingly being used to manipulate flow within the system to meet ecological needs (Rampano 2009); however, the use of infrastructure may lead to a loss of ecological integrity by reducing the movement of biota and other associated material (Jones & Stuart 2008). These alterations are likely to have affected the dispersal patterns for many plant species. In theory, increased connectivity and movements between sites should lead to the homogenisation of aquatic and floodplain plant assemblages by facilitating the dispersal of propagules. However, increased spatial heterogeneity coupled with habitat requirements of individual species may also increase species diversity between sites and locations. Equally, it has been suggested that decreased connectivity may homogenise assemblages by reducing the spatial and temporal diversity of habitats (Campbell & Nielsen 2014a).

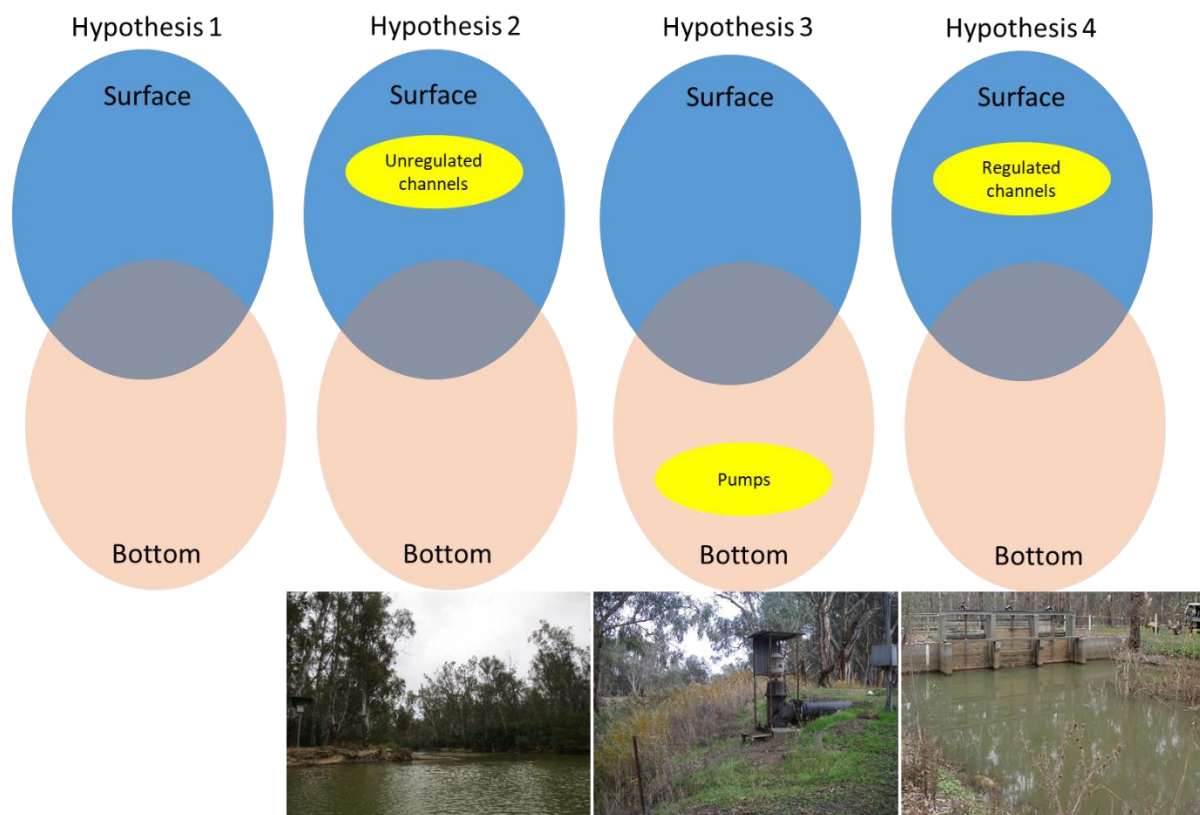
One of the major dispersal paths for wetland and riparian plants is believed to occur via drift in waters. The timing of seed release for many plants is likely to be linked to variations in the natural flow regimes (Riis & Biggs 2003). It is possible that managed flows occur at times that are sub-optimal for the effective dispersal and establishment of some plant species. Combined with this is the use of regulators and pumps to move water into creeks and wetlands. These delivery methods may favour the dispersal of some groups of plants over others (Jansson *et al.* 2000). For example, plants that have floating seeds may be less likely to move through pumps that are sourcing water from lower in the water column. There is however, limited information on the dispersal of seeds and propagules by water in Australian landscapes (Capon *et al.* 2009; Groves *et al.* 2009).

This project seeks to improve our understanding of the movement of seeds through pumps and regulators. In this study, we test four hypotheses (Figure 1). We hypothesise that:

1. The seed communities drifting on the river surface differ to those drifting along the bottom of the river. This is important as the manner in which water is moved into wetlands has the potential to select either for seeds drifting on the surface or seeds drifting sub-surface.
2. Seeds moving into wetlands un-impeded by any structures will reflect seed communities drifting on the surface of the river channel.
3. The seed community that passes through pumps will reflect the seed community drifting sub-surface in the river channel.



4. Seeds moving into wetlands through regulators will reflect seed communities drifting on the surface of the river channel.



**Figure 1. Diagrammatic representation of the hypotheses tested.**

## Methods

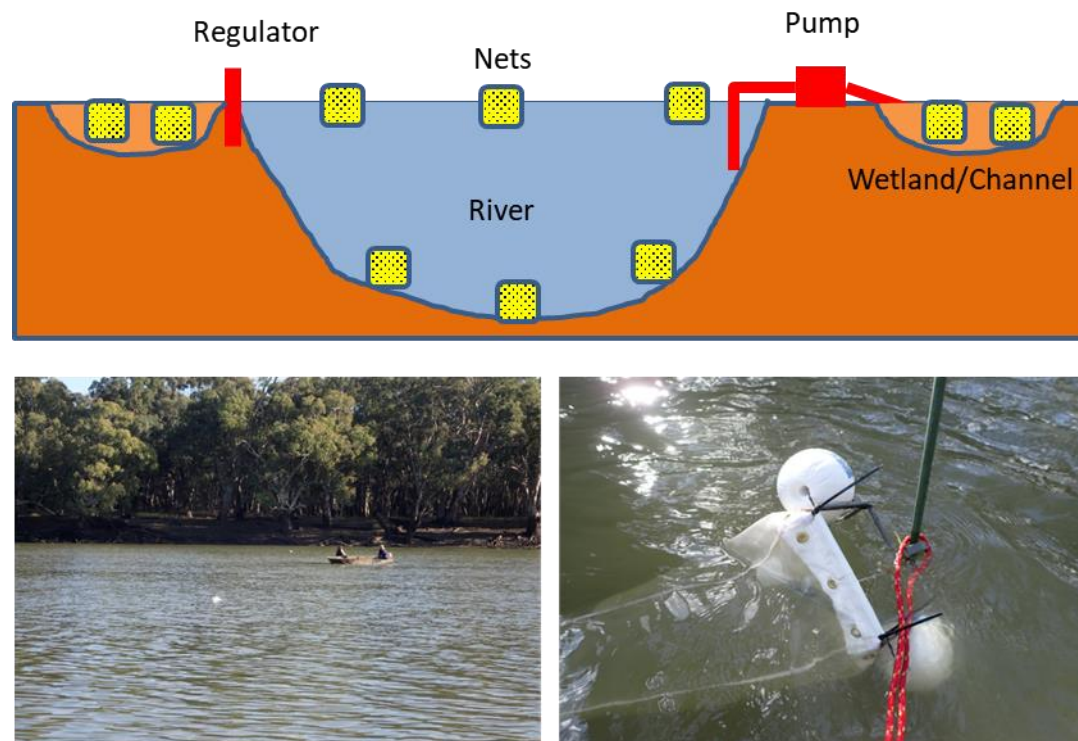
### Drift samples

Field sampling has been undertaken of water moving through unregulated creeks, regulated creeks and pumps (Table 1). At Thegoa Lagoon, water is moved in through a siphon as opposed to a pump, but as the siphon is drawing water from sub-surface, the lagoon has been treated as a pump site. The capacity of the pumps sampled was 36 ML.day<sup>-1</sup> at Speewa Creek and Thegoa Lagoon, and 70 ML.day<sup>-1</sup> at Wee Wee Creek. In comparison, pumps used at Hattah Lakes have the capacity to move 1000 ML.day<sup>-1</sup> (Murray-Darling Basin Authority 2012). Water flow through the regulators was via undershot structures, which release water underneath steel gates as opposed to over a fixed crest where water flows over the top of the regulator. These regulators were only partially opened to approximately 30 cm or less, as it was envisioned that a fully opened regulator would essentially represent an unregulated system.

**Table 1. Types and locations of infrastructure sampled.**

Infrastructure	Creek name	Date sampled
Unregulated creeks	Black Engine Creek	October 2017
	War Creek	October 2017
	Little Budgie Creek	September 2017
Regulated creeks	Big Woodcutter Regulator	August 2018
	Island Creek Regulator	August 2018
	Sapling Creek Regulator	September 2018
Pump	Wee Wee Creek	June 2016
	Speewa Creek	June 2016
	Thegoa Lagoon	June 2016

At each site, six nets were set in the main river channel. Three of these nets were floating on the surface either near the right or left banks or in the centre of the channel. The other three nets were set on the bottom of the channel in a similar configuration. Two nets were set in the receiving creek. As the water in the receiving creek was turbulent and well mixed, these were floating on the surface (Figure 2). Within the mouth of each net, a flowmeter (General Oceanics model 2030R) was positioned to record the amount of water being filtered by the nets. Nets were placed in the water for 60 minutes and this was repeated three times to give three replicate samples at each site in the river and the receiving water.



**Figure 2. Schematic representation and photographs of nets set in the main river channel and receiving wetland.**

## **Laboratory sampling**

As there is limited information relating seed morphology to species, all identifications were to morphotype based on a reference collection compiled by the Centre for Freshwater Ecosystems (CFE) over a number of previous projects. Seeds were counted and identified to morphotype using a Leica M8 microscope.

## **Analysis**

As previous studies have indicated that the relationship between the numbers of propagules occurring in the drift and the volume of water that passes through nets is not linear, standardising the numbers of seeds by volume sampled may obscure any underlying patterns that maybe occurring (Brooks *et al.* 2017; Downes 2010). Consequently, we standardised the number of seeds collected in each sample (net) as relative abundance. Taxon richness was reported as the total number of morphotypes per sample. PERMANOVA+ for PRIMER 6 (PRIMER-E, Plymouth, U.K.) was used to investigate differences in the relative abundance and richness (morphotypes) and community composition of seeds between the source channel and receiving creek. For the community analysis, data was not transformed prior to analysis. Analysis was then derived from Bray-Curtis similarity matrices (Anderson *et al.* 2008). Two-way PERMANOVA (Anderson *et al.* 2008) was used to explore differences between sites and the source of seeds using the model 'Location + Source + Wetland x Source' to determine whether significant differences could be detected in the seed community, where 'Location' = name of structure and 'Source' = placement of nets (i.e. either river channel (surface or bottom) or in the channel on the wetland side of the structure).

Non-metric multidimensional scaling (nMDS) using boot-strap averages was used to visualise patterns of community composition and differences between the sources of seeds at each type of structure (Clarke *et al.* 2014).

## **Seed traits and flotation experiments**

### **Seed collection**

Seeds were opportunistically collected from mature plants. They were air-dried for five days, and then stored in zip lock bags in darkness at about 4 °C, until the trials were commenced. One-hundred-and-fifty seeds were randomly selected and set aside for trait analysis and 250 randomly selected seeds were set aside for the buoyancy trials.

### **Seed traits**

#### **Seed size**

The length (L), width (W) and height (H) of 50 randomly selected seeds per species were measured in millimetres using a microscope and the measuring software "Zen" (v2.3. Carl Zeiss Microscopy). From these measurements, we approximated seed surface (S) area using  $S = L \times W$ ; and seed volume (V) using  $V = L \times W \times H$ . Average seed mass (M) in milligrams was also determined by weighing five lots of 10 seeds and obtaining the average. The approximate density (D) of the seed was then calculated using  $D = M/V$ .

#### **Seed form**

The seed form of each species was determined using the methods described by Hintze *et al.* (2013). Seeds were classified as either:

- spherical ( $L/W < 3$ ,  $W/H < 3$  and  $L/W + W/H < 4.5$ )
- flat ( $W/H \geq 3$  and  $L/W < 3$ )
- elongated ( $L/W \geq 3$  and  $W/H < 3$ )
- elongated and flat ( $L/W \geq 3$  and  $W/H \geq 3$ ).

### Seed shape

The seed shape was calculated by measuring seed length, width and height and dividing all values by length before calculating the variance between the three values by dividing the summed squared deviation from the mean:

$$\sigma = \frac{\sum(x - \bar{x})^2}{(n - 1)}$$

Where  $\sigma$  = variance,  $x$  = length, width or height,  $\bar{x}$  = mean (length + width + height) and  $n = 3$ . The equation quantifies the deviance of the seed from a sphere and can vary from 0 (describing a perfectly spherical seed) to 3 (describing an elongated and flattened seed). In this way, the shape becomes dimensionless and allows for a numerical determination of the seed form in such a way that shape becomes independent of size (Bekker *et al.* 1998; Ruprecht *et al.* 2015).

### Buoyancy trial

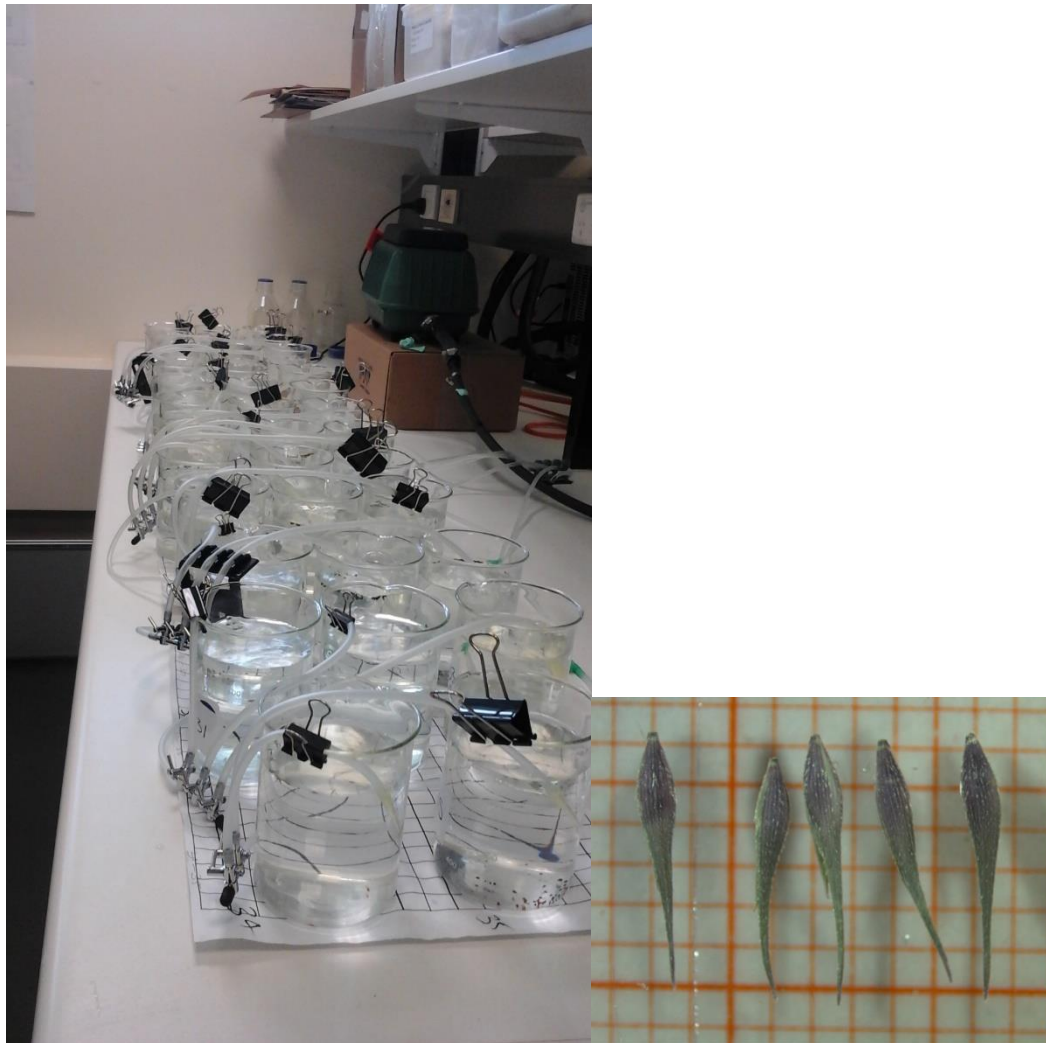
For each species, five replicates of 50 seeds were placed into 600 ml glass beakers filled with tap water (Figure 3). Each beaker was gently aerated with the use of an air-pump to simulate moving water and the water level was maintained at the 500 ml marker (Figure 3). The number of sunken seeds was recorded after 0, 1, 3, 24, 48 and 72 hours and then weekly for four weeks, resulting in a total of 10 different sampling occasions.

Floating fraction (seed buoyancy) was determined by the calculation of floating fractions per species per replication, based on methods outlined in Cross *et al.* (2015) using the equation:

$$B = \sum((\frac{F_t}{F_{total}})/n)$$

Where 'B' is buoyancy, ' $F_n$ ' is the number of floating seeds after n time, ' $F_{total}$ ' is the total number of seeds and 'n' is the number of sampling times. Values of buoyancy range from 0 (all seeds sink immediately) to 1 (all seeds remain floating). Seed species were then grouped according to their buoyancy and each group compared against the morphological characteristics of its seeds.

For most species, it was the seed that was used in the flotation experiment. However, for some species, the fruiting body was the primary unit of dispersal (i.e. *Pseudoraphis spinescens*), and it was this fruiting body that was used in the flotation experiments. The seeds of some species were sourced from existing reference collections; as a consequence these were 'dry' seeds that may have behaved differently from 'fresh' seeds (Figure 3).



**Figure 3. Experimental setup for floatation experiments and an example of seed capsules used in the experiment.**

### **Analysis**

Seed buoyancy was expressed as the number of seeds of each species floating at each time interval. We expressed seed buoyancy as the number of days after which a percentage of seeds were still floating and termed this floating percentage (FP). The following steps were distinguished: FP>90 (91-100), FP90 (76-90), FP75 (51-75), FP50 (26-50) and FP25 (11-25) FP10 (0-10); where FP>90 indicated that the majority of seeds were floating and FP10 indicated that the majority of seeds had sunk (van den Broek *et al.* 2005).

## **Results**

### **Seed drift**

From all sampling events that were undertaken, a total of 168 seed types were identified. Sixty five of these seeds were identified to either the taxonomic level of genus or species. The rest were identified as morphotypes and allocated a unique number.

### ***Unregulated channels***

Ordination of the seed communities at the locations where water passed through unregulated channels indicated that differences were occurring between seed communities (Figure 4).

PERMANOVA analysis of the community of seeds sampled from each source confirmed that there were differences in the community of seeds ( $P = 0.005$ , Table 2). Pairwise comparisons of each of the sources of seeds indicated that the seed communities differed between the river surface and river bottom ( $P = 0.016$ ), and between the river bottom and the seeds entering the wetland ( $P = 0.006$ ). However, there were no differences between the seed communities on the surface of the river and those entering the wetlands via the channels ( $P=0.304$ ). This indicated that seeds drifting into a wetland through an unregulated channel are similar to those in the drift on the surface of the river (Figure 4). Importantly there was no significant interaction between Location and Source of seeds ( $P = 0.345$ , Table 2). This indicated that a similar pattern in drifting seed communities was occurring at all sites.

**Table 2. PERMANOVA results for seed communities sampled passing through ‘unregulated channels’.**

Structure	Term	df	SS	MS	Pseudo-F	P
Unregulated channels	Location	2	15786	7892	2.81	<0.001
	Source	2	9821	4910	1.75	0.005
	Location x Source	4	12018	3005	1.07	0.345
	Residual	39	109660	2812		
	Total	47	147500			

### ***Pumps***

Ordination of the seed communities at the locations where water passed through pumps indicated that differences were occurring between seed communities (Figure 4). These differences were confirmed by PERMANOVA analysis ( $P < 0.001$ , Table 3). Pairwise comparisons between each of the source of seeds indicated that the seed communities differed between the river surface and river bottom ( $P = 0.023$ ). In contrast to what was occurring in the unregulated channels, there were differences between the seed community drifting on the surface of the river channel and the seed community passing through the pumps ( $P < 0.001$ ), but there was no difference in the community of seeds drifting sub-surface in the river channel and the community that passed through the pumps ( $P = 0.107$ ). As with the samples taken at the unregulated sites, there was no significant interaction between Location and Source of seeds ( $P = 0.345$ , Table 3). This indicated that a similar pattern in the drifting seed communities occurring in the drift was again occurring at all sites.

**Table 3. PERMANOVA results for seed communities sampled passing through ‘pumps’.**

Structure	Term	df	SS	MS	Pseudo-F	P
Pumps	Location	2	10618	5309	2.35	0.002
	Source	2	11278	569	2.49	<0.001
	Location x Source	4	11306	2827	1.25	0.137
	Residual	35	79195	2263		
	Total	43	112710			

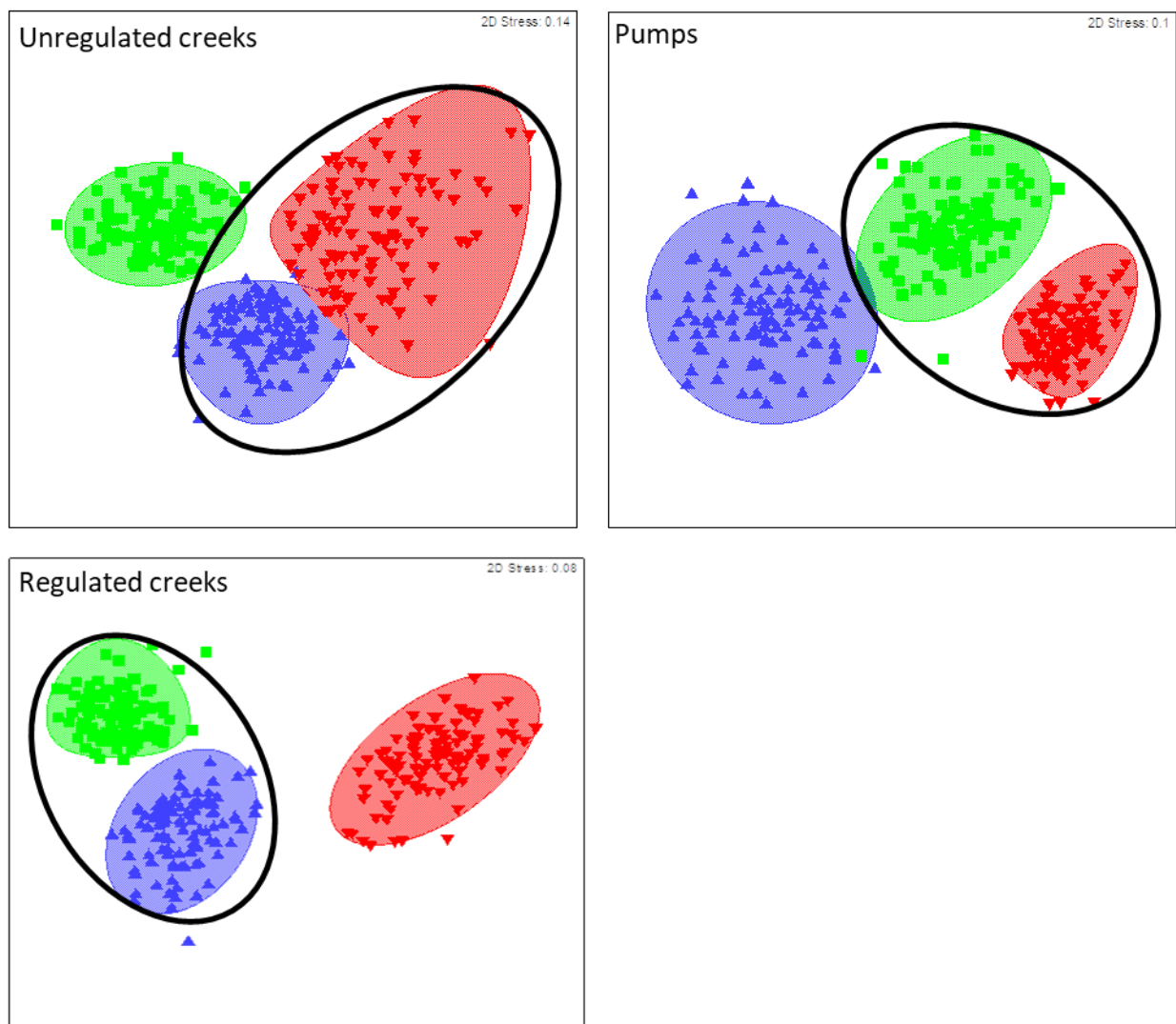
***Regulated channels***

Ordination of the seed communities at the locations where water passed through regulators also indicated that differences were occurring between seed communities (Figure 4), and these differences were confirmed by PERMANOVA ( $P < 0.001$ , Table 4). Pairwise comparisons, however, indicated that the seed communities on the surface of the river channel and at the bottom of the river channel were similar ( $P = 0.054$ ), and that the seed community passing under the regulator differed from both the seed community on the surface of the river ( $P = 0.002$ ) and the seed community drifting on the bottom of the river ( $P < 0.001$ ). As with the samples taken at the unregulated sites, there was no significant interaction between Location and Source of seeds (Table 4Table ). This indicated that a similar pattern in drifting seed communities was occurring at all sites.

**Table 4. PERMANOVA results for seed communities sampled passing through ‘regulated channels’.**

Structure	Term	df	SS	MS	Pseudo-F	P
Regulators	Location	2	14160	7080	2.57	<0.001
	Source	2	17739	8869	3.22	<0.001
	Location x Source	4	12730	3183	1.16	0.189
	Residual	39	107320	2752		
	Total	47	151200			





**Figure 4.** nMDS scaling of the community of seeds at each location. Blue – seeds in the drift in the river channel on the surface. Green – seeds drifting along the bottom of the river channel. Red – seeds passing into the wetland. The presence of a black oval indicates seed communities that are similar to each other.

## Seed flotation

The floating abilities of the seeds of the 59 species of aquatic and terrestrial plants were assessed to determine the capacity of each species' seeds to disperse by drifting either on the surface or sub-surface, and whether there was a link to physical characteristics (Appendix 1).

Results from the flotation trials indicate that a substantial proportion of seeds begin to sink within one hour of being placed in water, with only 68% of species still floating at this time (FP>90). After 24 hours, 50% of all species examined in this study had begun to sink and would be drifting sub-surface; and after 4 weeks less than 10% of seeds were floating on the surface (Table 5, Figure 5).

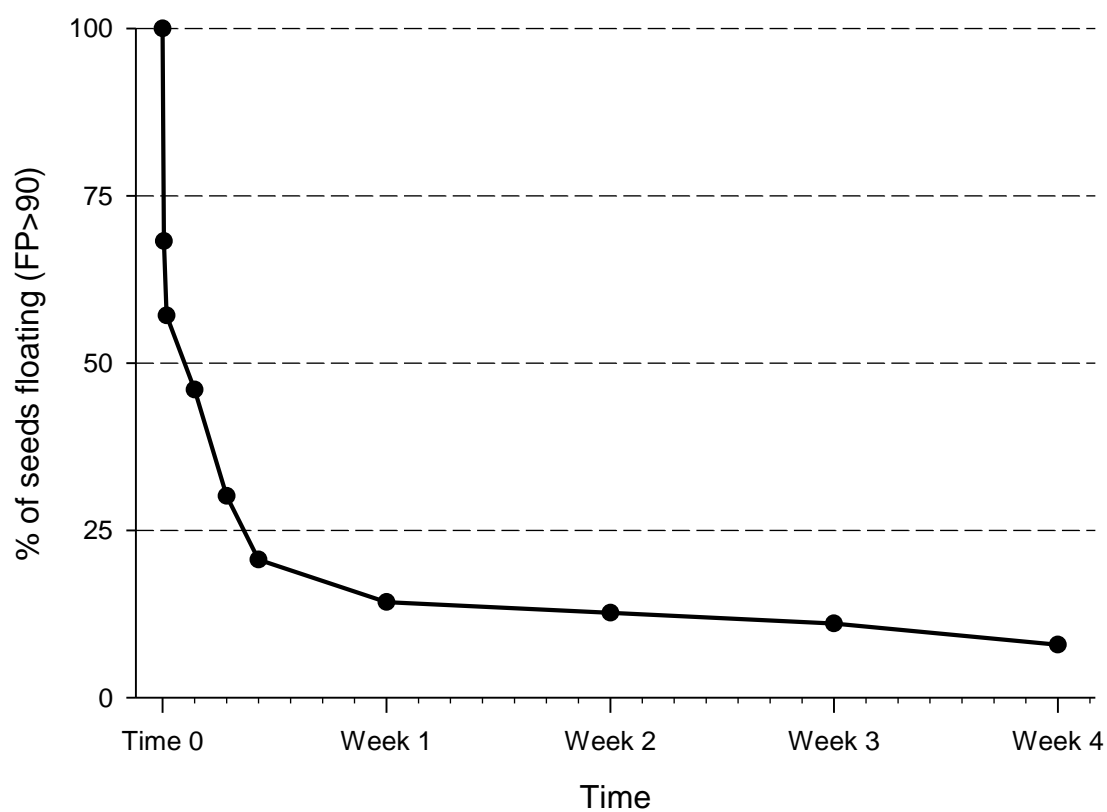
There was no pattern of floating ability with respect to the different functional groups (Aquatic, Emergent, and Terrestrial) (Appendix 2). A few species in each functional group were able to float for extended periods; however, the majority of species tended to sink. For example, in the Aquatic functional group, *Pseudoraphis spinescens* floated for the duration of the experiment. In contrast, *Cotula coronopifolia* did not float at all (Appendix 2). Surprisingly, species adapted for wind dispersal, such as *Typha orientalis*, did not float on the water surface for extended periods of time.



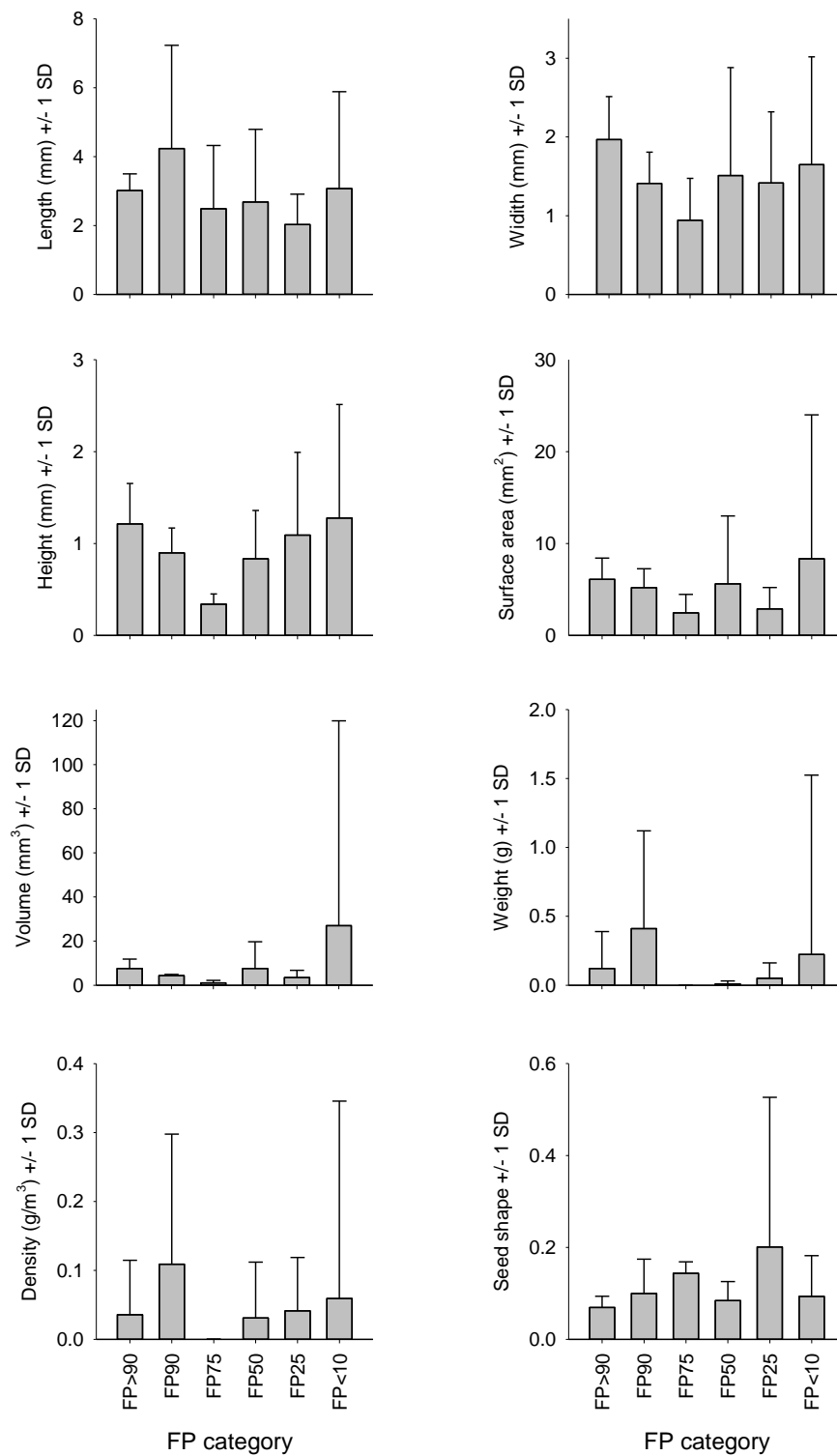
Of the physical features of each species of seeds measured, no single attribute could be linked to the floating percentage categories at the end of four weeks, with all measured parameters varying within each category (Figure 6).

**Table 5. Percentage of species in each floating percentage category at each sampling interval (n =63).**

	Time									
	Time 0	1 hour	3 hours	24 hours	48 hours	72 hours	168 (1 week)	336 (2 week)	504 (3 week)	672 (4 week)
FP>90	100	68	57	46	30	21	14	13	11	8
FP90	0	17	16	8	13	17	5	3	3	5
FP75	0	10	16	19	16	10	16	3	5	5
FP50	0	2	8	17	22	21	11	14	10	11
FP25	0	3	3	6	10	13	17	13	11	11
FP<10	0	0	0	3	10	19	37	54	60	60



**Figure 5. Percentage of seeds in the FP>90 category at each sampling time.**



**Figure 6. Physical attributes of seeds in each of the floating percentages categories (mean  $\pm$  SD). FP<90 n = 5; FP90 n = 3; FP75 n = 3; FP50 n = 7; FP 25 n = 7; FP<10 n = 38.**

### ***Flotation of native and exotics***

Of the 59 species tested for their ability to float, eight species were introduced. None of these introduced species floated, with all species beginning to sink within a day (Appendix 2).

## **Discussion**

In this study, 168 seeds were identified which represents approximately 20% of the known species of riparian and wetland plants associated with the Murray River channel (Campbell & Nielsen 2014b). Due to a lack of information in the taxonomy of many aquatic or semi-aquatic plants, only 65 types of seeds were able to be identified to the taxonomic level of either genus or species. The remaining species were identified to unique morphotypes that may encompass multiple species.

Seed dispersal by water can be categorised into two types: (1) dispersal by floating on the surface, and (2) dispersal of seeds that sink and are dispersed along the bottom of a channel (Parolin 2006). These dispersal types have a role in the dispersal of seeds, for maintaining and extending species populations at the landscape scale (Merritt & Wohl 2006). This study indicates that seeds from plants associated with wetlands and floodplains do not drift on or near the water surface for extensive periods of time. Indeed more than 50% of seeds had sunk within 24 hours. This suggests that many seeds are more likely to be moved along the bottom of a river where they are more likely to be entrapped and remain within the river channel. This finding was in concordance with other studies that have also indicated that not only do seeds sink over time, but that they are likely to be washed out of the drift and entrapped along the margins of rivers within relatively short distances. Such studies have also shown that the distance seeds drift is likely to be dependent in part on the physical characteristics of the river channel (i.e. sinuosity, width) and flow regime (Hyslop & Trowsdale 2012), with published estimates of dispersal distances ranging from tens of meters to kilometres (Groves *et al.* 2009).

These findings partially support hypothesis 1: 'The seed communities drifting on the river surface differ to those drifting along the bottom of the river'. In this study, we found that on two of the sampling events seed communities differed among sources on these occasions. On the third sampling event (at regulated locations), they were marginally not significantly different ( $P = 0.054$ ). Within a species, some seeds are likely to float for longer periods than others (Danvind & Nilsson 1997). This implies that at any given time, it is likely that there will be a gradient of seeds sinking. The degree of separation of the two communities will vary depending on the environmental conditions related to turbulence created by flow and wind, and the ability of a seed to float (van den Broek *et al.* 2005).

Water is considered to be a major vector for seed dispersal, although few studies have linked the physical characteristics of seeds to a species' ability to float. This study indicates that the floating ability of a seed is not related to its morphological characteristics, and that for a seed to successfully disperse by water it is not necessary to have morphological adaptations to float (Johansson *et al.* 1996). It is likely that seeds that are dispersed by water will have the ability to use one or more vectors (Danvind & Nilsson 1997). The perception that a seed needs to have a high floating potential to increase a species' chances of long distance dispersal is potentially misleading, and it is likely that seeds that sink may also be dispersed. Seeds may also be entrapped in waterborne debris and may be moved over considerable distances during multiple flow events (Nilsson & Grelsson 1990).

The differences between surface- and bottom-drifting seed communities imply that different types of infrastructure used in the Murray–Darling Basin are likely to influence the seed communities that

are transported into wetlands. This study clearly supports hypothesis 2: *'Seeds moving into wetlands unimpeded by any structures will reflect seed communities drifting on the surface of the river'*. Our results clearly indicate the seed communities drifting on the surface in the river channel were being transported laterally into wetlands and those drifting sub-surface were not.

Results from this study also support hypothesis 3: *'The seed community that passes through pumps will reflect the seed community drifting sub-surface in the river channel'*. Our results clearly indicate that the seed community drifting on the surface of the river channel was not represented in the seed community passing through the pumps. In contrast to what was occurring at the unregulated channels, pumps were selecting for those seed communities drifting sub-surface.

Our results did not support hypothesis 4: *'Seeds moving into wetlands through regulators will reflect seed communities drifting on the surface of the river channel'*. The data suggests that, at the time of sampling, there was no difference between the seed communities drifting on the surface and sub-surface of the river channel. The reason for this remains unclear, but may reflect the gradient of seed communities that occurs as seeds sink through the water column. The data also indicates that the community being transported into the wetland was not representative of either of the communities in the river channel. The undershot regulators used in this study were only open 30 cm from the bottom and debris was observed to build up in front of the regulator, so this may also have been entrapping seeds and preventing them from passing through (Figure 7).








**Figure 7. Debris build up in front of Big Woodcutter regulator.**

These findings suggest that infrastructure will influence the seed communities being transported into wetlands, which may impact on the recovery after disturbances such as extended drought. There are four main types of infrastructure used within the MDB: undershot and overshot regulators, pumps and lay-flat gates. Typically, these structures are put in place to manage water quality, improve fish movement or restore wetting regimes to wetlands. Other ecological effects are rarely considered. Nevertheless, each of these structures pose potential risks to the movement of seeds and other vegetative propagules (Table 6). These results suggest that different water delivery mechanisms may be implicated in determining the diversity of plants found within wetlands.

Differences in the seed communities arise due to the different modes of transport by propagules and seeds within the river. Propagules, seeds, fragments and even whole plants are delivered to the river by physical processes, but for seeds, the morphological characteristics of seeds and the timing of seed release also influence seed delivery. The dispersal of seeds is then controlled by flow, seed morphology and seed buoyancy and it's analogous to the movement of sediment within river systems (Andersson *et al.* 2000; Gurnell 2007; Merritt & Wohl 2002).

**Table 6. Potential risks to seed dispersal from key infrastructure in the MDB.**

Structure	Considerations	Best likely outcome (rank)
<p><u>Unregulated channel</u></p> <ul style="list-style-type: none"> <li>• Connection between river and wetland unimpeded by any structure.</li> </ul>	 <p><u>Impact</u></p> <ul style="list-style-type: none"> <li>• Nil.</li> </ul>	<p><u>1 (best)</u></p>
<p><u>Pumps</u></p> <ul style="list-style-type: none"> <li>• Connection between river and wetland maintained by pumping water.</li> <li>• Water pumped sub-surface.</li> </ul>	 <p><u>Impact</u></p> <ul style="list-style-type: none"> <li>• Selects for seeds floating sub-surface.</li> <li>• Potential for seeds to be damaged.</li> </ul> <p><u>Mitigation</u></p> <ul style="list-style-type: none"> <li>• Adjust height of float valve to modify depth from which water is pumped.</li> </ul>	<p><u>5</u></p>
<p><u>Undershot (sluice) regulators</u></p> <ul style="list-style-type: none"> <li>• Flows modified by raising sluice and allowing water to flow underneath.</li> <li>• Used to prevent water moving either into or out of a wetland.</li> </ul>	 <p><u>Impact</u></p> <ul style="list-style-type: none"> <li>• Entrapment of seed and other debris drifting on the surface.</li> </ul> <p><u>Mitigation</u></p> <ul style="list-style-type: none"> <li>• Complete opening of sluice.</li> </ul>	<p><u>4</u></p>

Structure		Considerations	Best likely outcome (rank)
<p><u>Overshot (drop-board) regulators</u></p> <ul style="list-style-type: none"><li>• Flows modified by removing or adding boards.</li><li>• Used to prevent water moving either into or out of a wetland.</li></ul>		<p><u>Impact</u></p> <ul style="list-style-type: none"><li>• May reduce the potential for seed dispersal due to reduced flows and potential entrapment of seeds.</li></ul> <p><u>Mitigation</u></p> <ul style="list-style-type: none"><li>• Removal of all boards to allow maximal water movement into wetlands.</li></ul>	<p><u>3</u></p>
<p><u>Tilting (Lay) flat gates</u></p> <ul style="list-style-type: none"><li>• Flows modified by tilting weir on its bottom horizontal axis.</li><li>• Used to prevent water moving either into or out of a wetland.</li></ul>	 <p>(www.awmawatercontrol.com.au)</p>	<p><u>Impact</u></p> <ul style="list-style-type: none"><li>• Minimal.</li><li>• Titling of gates should allow seeds to be washed into wetlands.</li></ul> <p><u>Mitigation</u></p> <ul style="list-style-type: none"><li>• Full tilt of weir(s) for maximum water movement into wetlands.</li></ul>	<p><u>2</u></p>

None of the physical characteristics measured as part of this study had a strong relationship with seed floating ability (Danvind & Nilsson 1997; Fenner & Thompson 2005). Nor was there any indication that introduced species were more likely to disperse by floating compared to native species. This suggests seeds that float are not likely to undergo long distance dispersal (Higgins *et al.* 2003). Potentially this may be due to the multiple pathways that many seeds can be dispersed by. For example, plumes that provide the potential to disperse by wind will both increase the potential to float and disperse by wind (e.g. *Typha* spp.). This suggests that dispersal is complex and will vary with the type and number of vectors that can be utilised, which will, in turn, depend on seed morphology (Levin *et al.* 2003).

That is not to say that a seed's ability to float is not important to dispersal. This study indicates that while seeds remain floating, they may be laterally dispersed from the river into floodplains, provided that their movement is not impeded by the imposition of physical structures such as pumps. To maximise the potential for lateral dispersal to occur, structures such as regulators should be fully opened at times that are linked to maximum seed release. Studies have also indicated that floating seeds are moved down the river, and are moved to the shoreline where they are likely to be entrapped. Seeds that sink are more likely to undergo long distance dispersal when multiple flow events provide opportunities for seeds to be moved further downstream. The way that the hydrology interacts with fluvial geomorphology, stream hydraulics and seed biology together, determines 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 (Gurnell & Petts 2002; Hyslop & Trowsdale 2012).

## Summary

Concern about the loss of plant diversity in the Murray–Darling Basin has resulted in management efforts aimed at delivering water into wetlands, with the aim of restoring wetland plant communities. However, often these restoration attempts have not always been successful with respect to the re-establishment of target plant communities, even if the abiotic conditions required were met (Lockwood & Pimm 1999), suggesting that a lack of propagules could be a major constraint. Therefore, dispersal of seeds or other vegetative propagules into restored and newly created habitats lacking a viable seed bank may be considered a key process for the establishment of species (Bakker *et al.* 1996). How many and which species are able to be transported into these habitats will depend on the type of connection and life history traits of the available species pool (Nathan & Muller-Landau 2000).

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**Appendix 1. Physical characteristics of seeds, floating fraction and floating groups (Seed form: F = flat, E = elongated. S = spherical). (c = seed capsule, d = dry seed) \* = introduced species.**

Species	Length (mm)	Width (mm)	Height (mm)	Surface (mm <sup>2</sup> )	Volume (mm <sup>3</sup> )	Weight (g)	Density (g/mm <sup>3</sup> )	Shape variance	Seed form
<b>Aquatic</b>									
<i>Amphibromus fluitans</i>	6.02	1.37	1.09	8.34	9.34	0.00026	0.000028	0.14	E
<i>Amphibromus nervosus</i>	7.31	1.64	0.89	12.03	10.73	0.00302	0.000282	0.15	E
<i>Callitriche stagnalis</i> *	1.26	0.68	0.32	0.86	0.28	0.06000	0.215001	0.09	S
<i>Centipeda minima</i>	0.84	0.34	0.22	0.28	0.06	0.00001	0.000225	0.10	S
<i>Cotula coronopifolia</i> *	1.15	0.52	0.22	0.60	0.13	0.00004	0.000290	0.12	E & F
<i>Cycnogeton procerum</i>	7.35	3.19	1.73	23.44	40.74	8.03000	0.197087	0.11	S
<i>Damasonium minus</i>	2.51	1.24	1.24	3.14	3.98	0.00024	0.000059	0.06	S
<i>Elatine gratioloides</i>	0.56	0.31	0.14	0.18	0.02	0.00002	0.000912	0.10	S
<i>Ludwigia peploides</i>	1.90	1.66	1.19	3.16	3.76	1.23000	0.326820	0.03	S
<i>Myriophyllum caput-medusae</i>	1.17	0.48	0.39	0.57	0.22	0.00013	0.000583	0.09	S
<i>Myriophyllum verrucosum</i>	1.08	0.58	0.53	0.63	0.33	0.09000	0.271283	0.06	S
<i>Potamogeton sulcatus</i>	4.23	3.46	3.46	14.82	52.91	0.00094	0.000018	0.01	S
<i>Pseudoraphis spinescens</i>	7.61	0.95	0.66	7.27	4.85	0.00038	0.000079	0.18	E & F
<b>Emergent</b>									
<i>Bolboschoenus caldwellii</i>	3.17	2.34	0.98	7.44	7.31	0.00329	0.000450	0.08	S
<i>Bolboschoenus caldwellii</i>	3.23	2.53	0.92	8.13	7.52	0.00322	0.000429	0.09	S
<i>Bolboschoenus medianus</i>	3.25	2.52	1.01	8.22	8.31	0.00337	0.000406	0.08	S
<i>Carex appressa</i>	3.19	1.62	0.85	5.20	4.47	0.00106	0.000236	0.09	S
<i>Carex fascicularis</i>	5.59	1.60	1.52	8.94	13.59	0.00154	0.000114	0.12	E

Species	Length (mm)	Width (mm)	Height (mm)	Surface (mm <sup>2</sup> )	Volume (mm <sup>3</sup> )	Weight (g)	Density (g/mm <sup>3</sup> )	Shape variance	Seed form
<i>Carex tereticaulis</i>	2.73	1.45	0.85	3.97	3.39	0.60000	0.177098	0.08	S
<i>Cyperus difformis</i>	0.98	0.54	0.40	0.54	0.22	0.00007	0.000311	0.06	S
<i>Cyperus eragrostis</i> *	1.17	0.64	0.61	0.75	0.46	0.00010	0.000222	0.05	S
<i>Eleocharis acuta</i>	2.16	1.09	0.81	2.35	1.93	0.03000	0.015550	0.07	S
<i>Eleocharis plana</i>	1.40	0.93	0.45	1.30	0.60	0.00024	0.000397	0.08	S
<i>Eleocharis pusilla</i>	2.01	1.06	0.70	2.12	1.49	0.30000	0.201386	0.08	S
<i>Ficinia nodosa</i>	1.25	0.68	0.46	0.86	0.39	0.00088	0.002254	0.07	S
<i>Juncus ingens</i>	0.44	0.21	0.14	0.09	0.01	0.00002	0.001756	0.09	S
<i>Persicaria decipiens</i>	2.36	1.56	1.39	3.82	5.76	0.00152	0.000264	0.03	S
<i>Persicaria hydropiper</i>	1.94	1.32	0.97	2.57	2.52	0.00074	0.000295	0.05	S
<i>Persicaria lapathifolia</i>	2.26	1.36	0.89	3.09	2.75	0.00086	0.000315	0.06	S
<i>Persicaria prostrata</i>	3.64	1.58	0.96	5.86	6.05	0.00027	0.000044	0.10	S
<i>Phragmites australis</i>	4.60	0.97	0.46	4.53	2.33	0.00043	0.000186	0.17	E
<i>Rumex crispus</i>	2.33	1.42	1.37	3.32	4.57	0.00111	0.000244	0.04	S
<i>Rumex crispus</i>	3.92	3.49	3.12	13.87	44.75	0.00210	0.000047	0.01	S
<i>Schoenoplectus validus</i>	2.36	1.58	0.78	3.74	2.92	0.00127	0.000435	0.08	S
<i>Typha orientalis</i>	2.67	0.55	0.40	1.47	0.58	0.05000	0.085859	0.15	E
<b>Terrestrial</b>									
<i>Alternanthera denticulata</i>	1.58	1.46	0.32	2.32	0.76	0.00028	0.000405	0.13	F
<i>Alternanthera</i> sp. A	4.71	4.39	1.61	20.90	33.85	0.00030	0.000010	0.09	F
<i>Atriplex leptocarpa</i>	4.95	1.25	1.08	6.22	6.77	0.00139	0.000206	0.13	E
<i>Atriplex nummularia</i>	5.53	3.56	2.05	19.96	41.21	0.00319	0.000077	0.07	S

Species	Length (mm)	Width (mm)	Height (mm)	Surface (mm <sup>2</sup> )	Volume (mm <sup>3</sup> )	Weight (g)	Density (g/mm <sup>3</sup> )	Shape variance	Seed form
<i>Centipeda cunninghamii</i>	1.14	0.33	0.15	0.37	0.06	0.00045	0.007813	0.14	E
<i>Centipeda cunninghamii</i>	1.29	0.39	0.24	0.51	0.12	0.00004	0.000359	0.13	E
<i>Chenopodium album</i> *	0.71	0.59	0.40	0.43	0.17	0.00014	0.000798	0.03	S
<i>Conyza bonariensis</i> *	1.15	2.00	3.09	2.31	7.13	0.00002	0.000003	0.51	S
<i>Duma florulenta</i>	7.22	4.45	3.45	31.13	102.54	0.00169	0.000017	0.35	S
<i>Dysphania pumilio</i>	1.60	1.62	1.23	2.63	3.32	0.00015	0.000046	0.02	S
<i>Echinochloa crus-galli</i>	3.63	1.86	1.26	6.80	8.61	0.00228	0.000264	0.08	S
<i>Eucalyptus camaldulensis</i>	1.18	0.69	0.47	0.82	0.40	0.00017	0.000430	0.07	S
<i>Eucalyptus largiflorens</i>	0.84	0.35	0.18	0.30	0.05	0.00002	0.000285	0.11	S
<i>Euphorbia drummondii</i>	2.40	1.33	1.33	3.19	4.24	0.00011	0.000026	0.04	S
<i>Glycyrrhiza acanthocarpa</i>	5.46	3.92	2.03	21.61	44.59	0.01355	0.000304	0.07	S
<i>Heliotropium europaeum</i> *	3.26	2.39	1.92	7.81	15.04	0.00060	0.000040	0.03	S
<i>Juncus usitatus</i>	0.38	0.23	0.19	0.09	0.02	0.00002	0.000893	0.05	S
<i>Paspalidium jubiflorum</i>	5.53	2.43	1.85	13.47	25.03	0.00066	0.000027	0.09	S
<i>Paspalum dilatatum</i>	3.47	2.19	0.76	7.61	5.75	0.00204	0.000355	0.10	S
<i>Polygonum plebeium</i>	3.47	2.10	1.49	7.31	10.89	0.00029	0.000026	0.06	S
<i>Pseudognaphalium luteoalbum</i>	0.51	0.19	0.12	0.10	0.01	0.02000	1.747473	0.11	S
<i>Rumex brownii</i>	1.53	1.11	1.05	1.70	1.80	0.00059	0.000331	0.02	S
<i>Rumex conglomeratus</i> *	1.69	1.25	1.04	2.11	2.20	0.00142	0.000646	0.03	S
<i>Rumex tenax</i> *	1.74	1.02	1.02	1.79	1.87	0.00093	0.000500	0.04	S
<i>Rumex tenax</i> *	3.55	1.91	1.91	6.86	14.30	0.00093	0.000065	0.05	S
<i>Sphaeromorphaea australis</i>	0.99	2.97	2.97	2.94	8.84	0.00005	0.000005	0.93	S

Species	Length (mm)	Width (mm)	Height (mm)	Surface (mm <sup>2</sup> )	Volume (mm <sup>3</sup> )	Weight (g)	Density (g/mm <sup>3</sup> )	Shape variance	Seed form
<i>Verbena bonariensis</i> *	1.22	0.49	0.39	0.60	0.23	0.00017	0.000707	0.09	S
<i>Xanthium occidentale</i> *	14.62	6.14	6.14	90.48	570.04	0.26578	0.000466	0.08	S

**Appendix 2. Floating percentages (FP) in days for each species (c = seed capsule, d = dry seed). \* = introduced species.**

	FP>90	FP90	FP75	FP50	FP25	FP<10		FP>90	FP90	FP75	FP50	FP25	FP10
<b>Aquatic</b>							<b>Terrestrial</b>						
<i>Damasonium minus</i>	1	3	3	3	7	14	<i>Alternanthera denticulata</i>	1	3	28	<28	<28	<28
<i>Amphibromus fluitans</i> (c)	3	3	7	14	28	>28	<i>Alternanthera sp. A</i> (c)	3	3	7	28	>28	>28
<i>Amphibromus nervosus</i> (c)	<1	<1	<1	1	1	28	<i>Atriplex leptocarpa</i> (c)	<1	<1	1	2	2	14
<i>Callitriche stagnalis</i> *	<1	<1	<1	<1	1	14	<i>Atriplex nummularia</i> (c)	2	3	3	3	7	28
<i>Centipeda minima</i>	>28	>28	>28	>28	>28	>28	<i>Centipeda cunninghamii</i>	14	28	>28	>28	>28	>28
<i>Cotula coronopifolia</i> * (d)	<1	<1	<1	<1	<1	28	<i>Centipeda cunninghamii</i> (d)	<1	<1	1	7	7	29
<i>Cycnogeton procerum</i> (c)	2	2	6	6	7	14	<i>Chenopodium album</i> *	<1	<1	<1	2	2	3
<i>Elatine gratioloides</i>	<1	<1	<1	<1	<1	1	<i>Conyza bonariensis</i> *	<1	<1	<1	2	3	7
<i>Ludwigia peploides</i>	1	28	>28	>28	>28	>28	<i>Duma florulenta</i> (c)	2	3	7	7	7	28
<i>Myriophyllum caput-medusae</i>	<1	<1	<1	3	14	28	<i>Dysphania pumilio</i> (c)	<1	1	3	28	>28	>28
<i>Myriophyllum verrucosum</i>	<1	1	3	7	21	28	<i>Echinochloa crus-galli</i> (c)	1	1	2	3	3	28
<i>Potamogeton sulcatus</i> (c)	<1	<1	1	2	3	28	<i>Eucalyptus camaldulensis</i>	<1	<1	1	3	7	14
<i>Pseudoraphis spinescens</i> (c)	21	28	>28	>28	>28	>28	<i>Eucalyptus largiflorens</i>	<1	<1	2	2	3	28
<b>Emergent</b>							<i>Euphorbia drummondii</i>	<1	<1	1	7	7	21
<i>Bolboschoenus medianus</i>	2	7	7	28	>28	>28	<i>Glycyrrhiza acanthocarpa</i> (c)	1	2	3	3	3	7
<i>Bolboschoenus caldwellii</i>	7	14	28	>28	>28	>28	<i>Heliotropium europaeum</i> *	<1	<1	<1	<1	1	2
<i>Bolboschoenus caldwellii</i> (d)	3	7	21	28	>28	>28	<i>Juncus usitatus</i>	<1	<1	1	7	7	14
<i>Carex appressa</i>	>28	>28	>28	>28	>28	>28	<i>Paspalidium jubiflorum</i>	<1	1	2	2	3	28
<i>Carex fascicularis</i>	>28	>28	>28	>28	>28	>28	<i>Paspalum dilatatum</i> (c)	2	2	7	14	21	>28
<i>Carex tereticaulis</i>	1	3	7	28	>28	>28	<i>Polygonum plebeium</i> (c)	1	1	3	3	14	28
<i>Cyperus difformis</i>	<1	<1	<1	1	2	28	<i>Pseudognaphalium luteoalbum</i>	<1	<1	<1	1	1	21
<i>Cyperus eragrostis</i> *	<1	<1	<1	<1	2	7	<i>Rumex brownii</i>	<1	<1	<1	3	3	28
<i>Eleocharis acuta</i>	<1	<1	2	3	14	28	<i>Rumex conglomeratus</i> *	<1	<1	<1	1	3	21
<i>Eleocharis plana</i>	<1	<1	1	2	3	21	<i>Rumex tenax</i>	<1	1	2	3	7	28
<i>Eleocharis pusilla</i>	1	2	7	7	28	>28	<i>Rumex tenax</i> (c)	>28	>28	>28	>28	>28	>28
							<i>Sphaeromorphaea australis</i>	<1	<1	<1	1	7	28

	FP>90	FP90	FP75	FP50	FP25	FP<10		FP>90	FP90	FP75	FP50	FP25	FP10
<i>Ficinia nodosa</i> (d)	>1	>1	>1	2	2	21	<i>Verbena bonariensis</i>	0	0	2	1	2	4
<i>Juncus ingens</i>	<1	<1	<1	<1	3	7	<i>Xanthium occidentale</i> * (c)	<1	<1	<1	1	7	7
<i>Persicaria decipiens</i> (c)	2	3	7	14	21	28							
<i>Persicaria hydropiper</i> (c)	1	3	3	3	7	28							
<i>Persicaria lapathifolia</i> (c)	1	2	3	3	7	28							
<i>Persicaria prostrata</i> (c)	2	3	7	28	<28	<28							
<i>Phragmites australis</i> (d/c)	14	14	28	>28	>28	>28							
<i>Rumex crispus</i>	<1	1	2	7	7	28							
<i>Rumex crispus</i> (c)	>28	>28	>28	>28	>28	>28							
<i>Schoenoplectus validus</i>	<1	<1	1	3	3	7							
<i>Typha orientalis</i> (c)	<1	<1	2	14	21	28							