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**Characterization of the long-distance dispersal of Johnsongrass (*Sorghum halepense*) in  
a vegetated irrigation channel**

**Short title : Hydrochorous dispersal of Johnsongrass in a vegetated channel**

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## ABSTRACT :

Hydrochorous dispersal may play a major role in the propagation of weeds such as *Sorghum halepense* (Johnsongrass). However, the long-distance dispersal of this weed via agricultural intermittent channel networks, such as irrigation channels, has been poorly studied. In this study we focused on a seed dispersal kernel obtained after an irrigation event in a vegetated channel. The main objectives of the study were to highlight the specificities of irrigation channels in relation to seed transport, and investigate hydraulic factors and microscale channel features associated with the deposition of seeds along the channel. Our results showed that despite very different flow and morphological conditions compared to natural waterways, seeds of Johnsongrass were able to travel hundred meters at the scale of one irrigation event. This is likely due to the floating ability of more than 50% of the Johnsongrass seeds. A Regression Tree algorithm, which explained 72% of seed deposition variability, showed the importance of the channel features such as the width of the section and the hydraulic structures, sluice gates and culvert, to explain the patterns of seed deposition. A complex role of the emergent vegetation was highlighted. The results suggest a threshold of vegetation density should be reached to enhance seed deposition. The results indicate that the spread of existing Johnsongrass populations could be limited by preserving existing hydraulic structures, or maintaining areas where the density of terrestrial vegetation is sufficient to enhance seed retention downstream.

**Keywords:** Seed dispersal ; Hydrochory ; Weed ; Agricultural networks ; ditch ; CART

# 1. INTRODUCTION

Diaspore dispersal is a major mechanism in plant distribution and propagation (Bolker and Pacala, 1999 ; Bullock et al., 2006, Nilsson et al., 2010). For many species living next to open channels, such as irrigation channels or surface drainage ditches, water is a major vector of transport (Favre-Bac et al., 2014 ; Soomers et al., 2010 ; Van Dijk et al., 2014). Channels have been shown to be important corridors in agricultural landscapes (Van Dijk et al., 2014). Rainfall or irrigation events are episodic events that can be crucial for dispersal (Cain et al., 2000) in open channels.

For weeds, dispersal determines the dynamics of invasion. *Sorghum halepense*, also called Johnsongrass, is one of the most widespread weeds in the world (Holm et al., 1977). This herbicide-resistant perennial grass is mostly found in Mediterranean and tropical areas (McWhorter, 1989). Warm temperatures and good moisture conditions have been reported to enhance its development (Andújar et al., 2013), which explains why it is commonly found next to irrigation channels (Holm et al., 1977). Johnsongrass has been reported in maize fields (Andújar et al., 2011 ; Ghersa et al., 1993), tomato fields (Andújar et al., 2013), and poplar fields (San-Martín et al., 2016). Its presence causes yield losses due to high competition with crops and consequently lower incomes for farmers. Warwick and Black (1983) showed that Johnsongrass can spread by both rhizomes and seeds. However, the long-distance dispersal of Johnsongrass, mainly associated with seeds, has been poorly studied.

Attempts have been made to characterize long-distance dispersal kernels for seeds despite the inherent difficulty of this process (Cain et al., 2000). Long-distance dispersal can be defined as a dispersal distance that is more than 100 m, or the distance of dispersal of the seeds that are in the upper 1% of the total seed dispersal distances (Cain et al., 2000 ; Turchin, 1998). Long-distance dispersal, or, more simply, the tail of the dispersal kernel, is very important because its estimation affects the results of models of population spread at large spatial scales (Bullock et al., 2006) but has been little studied in streams (Nilsson et al., 2010) and, to the best of our knowledge, never in irrigation channels. Some formulas for characterizing dispersal kernels have been proposed over time, that were mainly functions of the distance from the seed release location (Bullock et al., 2006 ; Greene and Calogeropoulos, 2002 ; Nathan et al., 2011). Over the years, some authors have highlighted the fact that these models did not effectively take into account the heterogeneity of the environment crossed by the seeds (Bullock et al., 2006).

There is a large literature focusing on hydrochory in natural waterways, i.e. rivers and upland streams (Boedeltje et al., 2003, 2004; Riis, 2008; Jansson et al., 2005; Greet et al., 2011; 2012, 2013). By comparing seedlots trapped with net and their nearest stands, authors have estimated distance events of several kilometres (Boedeltje et al., 2003). They have also highlighted effects of seasonal flow variation on composition of riverine seed banks dispersing by hydrochory (Greet et al., 2011, 2012, 2013). Compared to natural waterways, irrigation channels have specificities that justify a study on their influence on seed dispersal. Indeed, these channels sometimes contain hydraulic structures for irrigation purposes such as culverts or sluice gates that could impact hydrochory. Due to their restricted hydraulic capacities and operation rules, flow patterns in irrigation channels present less variations than those encountered in natural streams, and do not experience extreme flow (flood pulse) conditions resulting in erosion of sediments and seeds as can happen in rivers (Riis et al.,

118 2008; Boedeltje et al., 2003, 2004). This could limit long-distance hydrochorous dispersal.  
119 Also, while main channels can be perennial, lower level channels conveying water to fields  
120 are intermittent. Such channels, covering by far the largest cumulated length of irrigation  
121 channels, experience long periods without water that allow non-aquatic species to develop  
122 inside the channel bed, the latter being submerged during water inflow events of limited  
123 duration compared to natural waterways. They also have a smaller width than rivers, which  
124 could limit the long distance dispersal of seeds by hydrochory due to increased retention  
125 probability on banks (Nilsson et al., 2010).

126 Regardless, irrigation channels convey important flows in networks of many kilometres, and  
127 the factors that can affect the transport of seeds during an irrigation event are numerous. We  
128 differentiate intrinsic factors that correspond to the traits of the seeds from extrinsic factors  
129 such as the morphology of the channel (Nilsson et al., 2010).

130 Amongst the intrinsic factors shaping seed dispersal kernel figures its buoyancy or its ability  
131 in spending time in water (Boedeltje et al., 2003). For example, some authors indicated that  
132 dispersal distance of seeds is enhanced by high seed buoyancy (Boedeltje et al., 2004; Riis,  
133 2008; van den Broek et al., 2009). When considering the extrinsic factors affecting seed  
134 dispersal, we know that flow hydraulics is the first determinant of the pattern of the kernel  
135 (Merritt and Wohl, 2002 ; Nilsson et al., 2003), as it has been determined for riverine  
136 landscapes. Hydrodynamic phenomena that develop both at the free surface and in the water  
137 column are crucial for seed deposition but are very difficult to estimate in real channels  
138 because they depend on several factors. Seeds also interact with channel microscale features,  
139 such as the density of the living or dead vegetation (Chambert and James, 2009 ; Defina and  
140 Peruzzo 2010 ; O'Donnell et al., 2015), the channel morphology (Merritt and Wohl, 2002 ;  
141 Soomers et al., 2010), and the presence of hydraulic structures (Merritt and Wohl, 2006). Due

to the high number of interacting factors, their variability along channels (Groves et al., 2009), and the inherent difficulties in assessing some of them for an entire channel, the models for predicting water-dispersed kernels lack accuracy.

To calibrate these models, continuous dispersal kernels are needed (Portnoy and Willson, 1993). Three main methods have been used to determine dispersal kernels in the field: tracking (Lagrangian method), trapping (Eulerian method) and ‘re-locating’, i.e., the relocation of diaspores after the dispersal event (Eulerian method). Tracking is a very time-consuming method, and the small number of seeds tracked does not generally allow an accurate shape of the kernel to be obtained. Trapping is more efficient, but the choice of the trap locations can largely affect the results. Re-locating is therefore potentially the best method for water ecosystems but also raises the problem of the rate of seed relocation. For small seeds, such as those of Johnsongrass, relocation is a real challenge (Bullock et al., 2006).

This study focused on the dispersal kernel of seeds of Johnsongrass obtained at the event scale (a single irrigation event of around one hour) in an irrigation channel. We worked on the tail of the dispersal kernel because we focused on the factors affecting the long-distance dispersal. The objectives of the study were to (i) highlight the specific intrinsic and extrinsic factors affecting the long-distance dispersal of Johnsongrass, (ii) implement an efficient method to reconstitute and characterize a seed dispersal kernel in intermittent channels. Our main hypothesis was that the tail of the dispersal kernel is largely affected by channel microscale features (especially bank and in-channel vegetation).

## 2. MATERIAL AND METHODS



The method employed in this paper followed three main steps: (i) a relocation experiment in a vegetated irrigation channel, (ii) the interpolation of the seed dispersal data using kriging in order to reconstitute the full dispersal kernel, (iii) the study of the factors affecting the tail of the dispersal kernel.

## 2.1. Study site

The Crau plain is a 600 km<sup>2</sup> flat area in southern France. The first channel networks were built between the 12<sup>th</sup> and 15<sup>th</sup> century to divert water from the Durance River for different land uses, such as mill functioning and irrigation. Currently, the channel network is still operational and supplies some 14 000 hectares of irrigation command area.

The Crau climate is Mediterranean with mean annual rainfall of approximately 560 mm with high interannual variability and high potential evapotranspiration (1060 mm/year) (data issued from the INRA CLIMATIK platform, [https://intranet.inra.fr/climatik\\_v2](https://intranet.inra.fr/climatik_v2)). Crau agriculture is mainly high-quality hay produced in permanent grasslands. Border irrigation is a widespread practice in the area. Water is conveyed from primary channels to secondary or tertiary channels that border the grassland plots. Water is then ponded by closed sluice gates and overflows from the channels to irrigate sections of the plots called ‘calans’. The high hydrological connectivity in the system is thought to favour weed diaspore transport into the grasslands.

The ‘Domaine du Merle’ is an experimental and educational station (Montpellier SupAgro) in the Crau region. The channel chosen for the experiment (Fig. 1) is straight and flows from north to south (43.644478 N-5,007125 E to 43,640391 N-5,005966 E). The channel depth varies from 0.34 to 0.74 m with a mean upper width of 2.11 m. It is a tertiary channel that irrigates a 4.2 ha plot divided into 6 “calans” (irrigated surface unit). The mean slope is 0.31%, and the length is approximately 450 m. The channel has an upstream valve controlling

the flow of water, and five other hydraulic structures (four sluice gates and one pipe culvert) (Fig. 1) located on the studied section serve to irrigate each calan in the plot. The channel is heterogeneously vegetated with terrestrial vegetation species that were found at different densities according to the location in the channel such as *Conyza Canadensis*, *Paspalum Dilatatum*, *Plantago spp.*, *Picris spp.*, *Cyperus spp.*

## **2.2. Channel experiment: Release of seeds during an irrigation event**

Seeds from Johnsongrass (Fig. 2) were collected at the end of summer 2016 and their main characteristics are presented in Table 1. The seeds were shaken within sieves of different diameters to separate the seeds from larger and smaller fractions of the plant. We estimated the length and width of the seeds using calipers. The longest axis (length) and the diameter of the seed (width) were measured in millimetres with calipers and averaged over 10 seeds. We estimated the mean weight of the seed by weighting 10 samples of 100 seeds each using a high-precision balance (Precisa XB 160M, precision: 0.001 g and accuracy: 0.01g).

As buoyancy could be an important factor affecting seed dispersal (Boedeltje et al., 2003, 2004; Carthey et al., 2016), we estimated the potential duration of buoyancy following the protocol from Boedeltje et al. (2003). According to this protocol, we placed ten samples of 50 seeds in polyethylene cylindrical pots filled with tap water. The pots were then shaken for 5 s and the number of floating seeds counted immediately, then every 4 min during the first hour, every 30 min during the four following hours, and daily for two weeks. We determined the  $t_{50}$ ,  $t_{90}$ , and  $t_{\max}$  periods after which 50%, 90%, and all of the seeds had sunk, respectively (Table 1). The complete dataset of seed buoyancy is described in Appendix S1.

Tekiela and Barney (2013) proposed the use of fluorescent powders (which does not affect the floating behaviour of the seeds) to efficiently detect the seeds after a dispersal event using UV

lights. We adapted the method developed in Tekiela and Barney (2013) for a one-dimensional channel. The Johnsongrass seeds were then placed in plastic pots and shaken with an UV powder in order to spread the powder uniformly onto all the seeds and entirely coat them. The powder we used was the Ultraviolet Ultrabright Red Fluorescing Powder (UVXPBR), distributed by LDP-LLC, Carlstadt, USA, as proposed in Tekiela and Barney (2013). The test on the effect of the powder on seed buoyancy is described in Appendix S2, following the protocol described in Tekiela and Barney (2013).

The release experiment in the channel occurred in October 2016. Using a high precision balance, we measured 30.47 g of seeds to get a sample of approximately 7000 +/- 250 seeds, according to the mean weight of the seed. The sample was then marked with UVXPBR powder. Thirty minutes before the experiment, the seeds were shaken in a bottle of water to remove any possible additional powder. The irrigation water was released in the channel using the upstream valve with a flow of around  $0.07 \text{ m}^3 \cdot \text{s}^{-1}$ . The five sluice gates located downstream in the channel remained open for the duration of the experiment. No overflow into the grassland plot occurred because the purpose of the study was to understand the dispersal of seeds inside the channel. After the valve was opened, the canal gradually filled, and the flow became steady after approximately 20 minutes. After the steady regime had been established, we released the seeds directly into the flow by submerging a pot containing the seeds in the release area (Fig. 1). The upstream valve was closed 50 minutes after the valve opened.

After stopping the inflow (by closing the upstream valve), a drainage time of 3 hours was allowed to empty the channel by infiltration. Under dark conditions (at night), we walked along the entirety of the channel with a 50 W UV high-powered rechargeable light (LDP-LLC reference XniteFlashBFLUV) to identify the seeds marked with the fluorescent powder. A

236 series of photos was taken along the channel according to distance intervals described below  
237 using a Nikon D3200 camera with an AF DX Fisheye-Nikkor objective set to infinity. A  
238 fluorescent wooden frame (80×155 cm) was used to delimit a surface for photographing the  
239 deposited seeds. The camera was fixed onto the frame. Considering the dark conditions, the  
240 exposure of the camera was set to 10 seconds, and the entire surface of the wooden frame was  
241 scanned with a UV light. From the seed release area to the first sluice gate (the first 25 m), the  
242 channel was photographed exhaustively, but from the first sluice gate, photographs were  
243 taken every 5 m because the density of deposited seeds exponentially decreased.

244 All image analyses were run in batch mode using the software ImageJ (Schneider et al.,  
245 2012). Every photo in RGB colour mode was cropped to remove the wooden frame. The  
246 photos were resized considering the known length and width of the wooden frame. Then, the  
247 background was corrected using a rolling ball algorithm to delete the illuminated areas of  
248 vegetation or ground. The red channel (because UVXPBR powder is red) was separated into  
249 black and white images using a threshold filter. Seed contours were counted on each image  
250 using a particle segmentation algorithm to obtain number of seeds per image.

251 During the steady-state flow, the water-surface elevation was measured using an electronic  
252 tacheometer every 5 m. In dry conditions, the channel topography, i.e. the Digital Terrain  
253 Model (DTM) and Digital Surface Model (DSM), was characterized. The DTM was created  
254 from elevation cross-sectional profiles every 10 m from the tacheometer. The DSM, i.e. the  
255 channel topography including the vegetation cover, was continuously characterized by a  
256 multi-view stereo approach. We obtained approximately 4000 images with a Nikon D3200  
257 camera with a fixed 28 mm AF Nikkor objective along the channel and we reconstructed the  
258 DSM using digital image matching with Photoscan Pro<sup>®</sup> (Gillanet al., 2014) (Fig. 1). The

DSM was aligned to the DTM using ground control points distributed every 5 meters along the channel.

### **2.3. Interpolation of the dispersal data via a kriging method**

The seed deposition dataset along the channel came from each photo location as described above and was thus irregularly sampled along the channel. To characterize the local spatial structure of seed dispersal and perform appropriate interpolation, the spatial variation in seed deposition was first studied using a 1D variogram. First, a log-normal transformation was performed on the data. Then, using an automatic procedure in geoR (Ribeiro and Diggle, 2001), we fitted the variogram model assuming a stationary isotropic covariance model, and we determined the nugget, sill and range. The interpolation and extrapolation of the whole dispersal data was conducted using ordinary kriging. The step for the interpolation was 0.8 m because this length corresponded to the width of the wood frame we used to take the photos of the seeds. The kriging was performed using the R RandomFields package (Schlather et al., 2015).

### **2.4. Factors affecting the tail of the dispersal kernel**

We worked on the reconstituted dispersal data from a set distance (15 m) from the seed release area. Although this was not strictly considered to be the tail of the dispersal kernel according to the definitions given by Cain et al. (2000), we considered this distance to be outside the influence of the first peak of the dispersal kernel. The distance was determined observing the shape of the dispersal kernel.

The explanatory factors we chose could be differentiated between “hydraulic” factors and factors linked to channel microscale features. The hydraulic factors were: the hydraulic radius ( $Hr$ ), the mean velocity ( $V$ ) and the width of the section at the water-surface (*WidthSection*).

Factors linked with channel microscale features were the downstream influence of hydraulic structures (*Down\_Struct*), the percentage of vegetation cover above the level of the water (*Pem*) and below the level of the water (*Pim*).

*Hr* and *WidthSection* could be directly derived from the DTM and DSM, and from the water-surface elevation data measured during the channel experiment at steady flow. The mean velocity *V* was estimated based on simulation results from SIC software (Baume et al., 2005) that solves the full one-dimensional flow equations in open-channel networks. *Down\_Struct* was calculated as the square-root of the downstream distance to the hydraulic structure, the length of eddies caused by the flow expansion after a hydraulic structure provided threshold values (Abbott and Kline, 1962 ; Nashta and Garde, 1987). From the water-surface elevation and DSM and DTM, we could also extract the percentage of wetted area covered by vegetation below (*Pim*) and above (*Pem*) the water level. Note that all these variables were determined at the step of 0.8 m. Any multi-collinearity issues between variables was assessed using Pearson product-moment correlation tests, all correlation coefficients were lower or equal to 0.6.

The selected approach for exploring the factors affecting the tail of the dispersal kernel relied on the Classification and Regression Trees algorithm (CART) (Breiman et al., 1984). The response variable used by the CART algorithm was this ratio :

$$\frac{\text{Number of deposited seeds by channel section}}{\text{Total number of non-deposited seeds having reached the considered section}} \quad \text{Eq.1}$$

The CART algorithm was implemented in the R rpart package (Therneau and Atkinson, 2014). We chose the CART algorithm because the zero-inflated distribution of the explained data prevented us from using classic regression analyses, either linear or generalized. We also chose CART for its robustness, low overfitting (when used with its default pruning process),

its measure of explanatory variables importance and its simplicity of interpretation. This analysis was conducted on nearly the whole channel (240 m from 15 m after the seed release area), as well as on three subsets of the channel, in order to compare the influential factors according to the location within the channel. We did not use the CART algorithm to analyse the pattern of seed deposition after 240 m because the hydraulic conditions were altered by the presence of pools.

### 3. RESULTS

The kriging estimation of the dispersal data for which the obtained covariance is presented in Fig.3 resulted from a fitted variogram with a range of 2 m and a sill of 9.25 m<sup>2</sup>. The deposited seeds extended from the release area to the end of the channel (300 m further). They had a typical negative exponential power shape of hydrochorous dispersal kernels with a very sharp peak in the first 15 meters from the seed release area and a fat tail after 15 meters. We took the value of 15 m to consider the long distance dispersal factors.

We estimated according to the kriging procedure at 4284 and 2650 the number of seeds before and after the limit of 15 meters separating the peak from the tail of the dispersal kernel, respectively. Note that the total number of released seeds in the channel was estimated to be approximately 7000, and that the mean number of released seeds in the interpolated dispersal data was 6934 seeds, which suggests that despite interpolation, the spatial sampling of seed deposition was consistent with the studied process.

The number of seeds in the tail of the interpolated dispersal data was therefore not a source of bias for the following analysis of influential variables. The variation in the explanatory

variables along the channel is presented in Fig. 4. The relative importance of variables calculated by the CART algorithm on the different sections is presented in Table 2. Considering the whole studied section (0–240 m), the CART algorithm highlighted the importance of the variables *WidthSection* and *Pem* (Table 2). In the first subset (0–80 m), *Pim* was classified as the most influential factor (but all the other factors except *Down\_Struct* were nearly equally important), whereas in the second subset (80–160 m), *Pem* was clearly the most influential factor, and in the third subset (160–240 m), *Down\_Struct* was the most influential. The CART algorithm predicted with a fairly good accuracy the pattern of seed deposition ( $R^2$  of 0.72) over the whole studied section (0–240 m) (Fig. 5). The regression trees obtained for the whole section and the three subsets are presented in Appendix S3.

## 4. DISCUSSION

### 4.1. Dispersal traits of Johnsongrass

Our study demonstrates that Johnsongrass seeds can be transported considerable distances from their sources (hundreds of meters), at the time-scale of a single irrigation event. Dispersal distances of this range have been observed for other hydrochorous seeds in agricultural networks (Soomers et al., 2010), but with very different hydraulic conditions (lower mean velocities) and higher transfer times. This ability to be transported considerable distances from the source has to be analyzed jointly with the ability of effective germination and establishment to make conclusions on the potential spread of this weed via channels (Riis, 2008). Note that Johnsongrass seeds have been reported to keep a strong ability to germinate at least two and a half years after soil burial (Warwick and Black, 1983).

Amongst species traits, buoyancy could be considered a key factor determining species dispersal abilities (Boedeltje et al., 2004). Johnsongrass seedlots belong to semi-aquatic and



terrestrial bank species with relatively low buoyancy (see Appendix S1 in Boedeltje et al. (2003)), because a significant part of the Johnsongrass seedlots sunk immediately after soaking (35%) and had a  $t_{50}$  lower than the day. This trait is in accordance with the result found by Boedeltje et al. (2004) for species hydrochory on floodplains, namely that  $t_{50}$  of Johnsongrass lasted the same duration as the irrigation event.

The shape of the dispersal kernel suggested that the peak was principally due to non-floating seeds that were trapped by the morphology of the channel bottom, the tail being primarily composed of floating seeds. This assumption of short range dispersal of non-buoyant seeds is in contradiction with Markwith and Leigh (2008) that estimated a potential subaqueous hydrochory over several kilometres for large seeds of *Hymenocallis coronaria* in rivers during flood events. Long dispersal distances were not observed in this study. On the one hand, the bottom shear stresses and the mean velocities were lower in the studied channels than in rivers during floods. On the other hand, we think that non buoyant seeds are likely to be trapped quickly after release due to vegetation and its role on benthic velocity and filtering effect. In all cases, as buoyancy is a dynamical process, it could be useful to test this assumption using a mechanistic model (for an example of a wind/water dispersal model, see Soomers et al. (2012)).

## **4.2. Structural effects of channel on the tail of the dispersal kernel**

The results of this study also support the assumption that the deposition of seeds along a channel is both associated with channel microscale features (Levine and Murrell, 2003; Soomers et al., 2010), and hydraulic characteristics (Merritt and Wohl, 2002). Width of the section was an important factor for seed deposition in our study. Based on the results of the

373 regression trees, higher values of section widths were linked with important deposition rates.  
374 This result could be related to area of low velocities and probably recirculating zones  
375 favouring the seed deposition. It was noted that the major rises in channel widths were located  
376 after the hydraulic structures where most seeds deposited. The increase of the channel width  
377 at the water-surface can also be linked with the increase of the roughness of the channel (the  
378 latter causing an increase of the water level, the channel cross-section being trapezoidal). This  
379 would cause a decrease of local mean velocity and consequently enhanced deposition of  
380 seeds.

381 The effect of the mean flow velocity was poor compared to other variables. Based on the  
382 results of the regression tree 0–80 m, a higher velocity was associated with a higher  
383 deposition rate. It appears that the local acceleration of mean velocity in the channel was  
384 linked to the presence of the hydraulic structures because they create local narrowing of the  
385 channel. Merritt and Wohl (2002) also reported that in such high-energy areas, seed  
386 deposition could be enhanced due to macroturbulent waves that could deposit seeds a little  
387 above the water level.

388 As in other studies, hydraulic structures, such as the culverts studied in Beltman et al. (2005)  
389 and Soomers et al. (2010) and their hydraulic impacts, such as backwater effects (Merritt and  
390 Wohl, 2002; Nilsson et al., 1991), were linked with a high rate of deposition, especially for the  
391 third section of the channel where a culvert was located. In our study, the expansion after the  
392 hydraulic structures created large eddies, and their presence was positively linked with seed  
393 deposition. In line with our results, Merritt and Wohl (2002) reported that the recirculation  
394 index defined in their study was associated with a high rate of deposition, and Cunnings  
395 (2013) linked the importance of storage areas with the magnitude of eddies. In our study, it  
396 appears that the culvert had more influence on seed deposition than the sluice gates, but no

study comparing the hydraulic effects of sluice gates with those of culverts could confirm this result (the calculation of the length of eddies we made for the calculation of downstream influence of hydraulic structures was based on a rectangular section for all the hydraulic structures: sluice gates and culvert). However, the indirect effects caused by the presence of hydraulic structures can both be linked with a change of the morphology of the channel over time, and modify local hydraulic conditions, creating favourable conditions for the deposition of seeds. This is a specificity of highly managed networks: the presence of hydraulic structures (even in open position) creates discontinuities that partly shape the pattern of seed deposition and the community composition in the long-term (Favre-Bac et al., 2017).

#### **4.3. Effects of vegetation on the tail of the dispersal kernel**

Emergent obstacles, such as vegetation, have been reported to enhance the deposition of seeds (Soomers et al., 2010; Schneider and Sharitz, 1988). In this study, the role of emergent vegetation was complex to interpret, because vegetation above water level could have a positive or negative influence on deposition. Non-linear effects could explain this apparent contradiction. Indeed, Gambi et al. (1990) found that the turbulent kinetic energy initially increased with stem density, then decreased as stem density increased further. According to Defina and Peruzzo (2010), another expected effect of emergent vegetation on floating seed trapping in such hydraulic conditions would be the net-trapping effect, i.e. when plant leaves form a netlike structure at the water surface that intercepts the floating seeds. In our study, when the cover of emergent vegetation was sparse (between 0 and 20% of surface according to the regression tree over the whole channel, see Appendix S3), the increase of stem-scale turbulences may explain why emergent vegetation has a negative effect on seed retention. When emergent vegetation cover increases (more than 50% of the surface according to the regression tree on the whole channel, see Appendix S3), the cumulative effect of the decrease

of turbulences and increase of net-trapping effect can explain a positive effect on seed retention. Obviously, the thresholds associated with these different behaviours may vary both with plant architectures and specific spatial organizations in the channel, and with the flow regime. These preliminary results should be confirmed in controlled conditions using flume experiments to disentangle the influence of plant architecture, spatial organisation, density, and flow regime.

Moreover, these effects caused by emergent vegetation can interact with the effect of submerged vegetation. In this study, the main effect of vegetation below water level is that it decreases the deposition of seeds. Indeed, by increasing the roughness, vegetation below water level decreases the depth-averaged velocity, but also can create local acceleration of flow velocity or large-scale turbulence (Nepf, 2012a) in the upper layer of the water, explaining this particular effect on the deposition of floating seeds. However, these effects of vegetation are difficult to disentangle and assess simultaneously (Peruzzo et al., 2012), especially at the reach scale.

#### **4.4. Potential of the relocating method for intermittent channels**

The method used in our experiment represents a significant improvement compared to other approaches because it relies on a relocating method that makes a snapshot of the seed deposition at several specific locations to characterize the whole dispersal kernel of the seeds. Generally, methods attempting to characterize seed dispersal by hydrochory in natural waterways use nets to quantify the diaspores at one specific location, the protocol being difficult to reproduce multiple times across the length of the stream (Boedeltje et al. 2003, 2004, Greet et al., 2012). Combined with a kriging procedure to fill the non-observed locations, our method provides a complete overview of one-species dispersal kernel regardless of their buoyancy over hundreds of meters distances.

The method is reproducible for characterizing the dispersal kernel of other small diaspores and could be used for other linear water ecosystems. Note that the method requires intermittent flows because the relocating method is hampered when water is still present in the channel. The method also illustrated the possibility of describing microscale variability linked with channel morphology and vegetation along an irrigation channel. We also estimated that the method could be replicated within drainage channels that display similar characteristics to irrigation channels, with similar shapes and operation rules, but different hydraulic structures and greater slopes (Dollinger et al., 2015). This is a significant improvement for the development of future mechanistic transport models, because as underlined in Groves et al. (2009), these data are often lacking for field conditions and therefore are rarely considered in modelling studies.

## 5. CONCLUSION

This study presents an experiment aimed at characterizing the dispersal kernel of Johnsongrass seeds in a vegetated irrigation channel. Johnsongrass seeds can travel long-distances (hundreds of meters) during a single irrigation event. Our results validate the hypothesis that channel microscale features influence the tail of the dispersal kernel and demonstrated the importance of the characteristics of open channels in comparison to natural waterways in explaining seed deposition, such as channel width, emergent vegetation and hydraulic structures. Compared to natural waterways, the vegetation found in open channels is emergent and terrestrial and sometimes covers the whole section. The results suggest a threshold of vegetation density has to be reached to enhance seed trapping. The hydraulic structures, sluice gates and culvert, largely affect hydrochory by presenting physical barriers

to dispersal. Based on these results, we recommend adjusting maintenance strategies of the irrigation channels according to presence of Johnsongrass population gone to seed. Existing hydraulic structures could have a beneficial role in limiting seed dispersal. High densities of terrestrial vegetation should be locally maintained when no hydraulic structure is present on the channel.

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**Table 1 :** Characteristics of the Johnsongrass seeds. Weights were measured using a high-precision balance. Lengths and widths were measured using calipers.  $t_{50}$ ,  $t_{90}$ , and  $t_{\max}$  correspond to the time after which 50, 90, or all the seeds had sunk, respectively. All means and standard errors are estimated on the basis of 10 replicates.

Parameter	Mean	Standard error
Weight (mg)	4.36	0.15
Length (mm)	4.52	0.45
Width (mm)	1.87	0.24
Instant buoyancy after soaking (%)	65	6
$t_{50}$ buoyancy (min)	100	-
$t_{90}$ buoyancy (days)	6.8	-
$t_{\max}$ buoyancy (days)	11	-

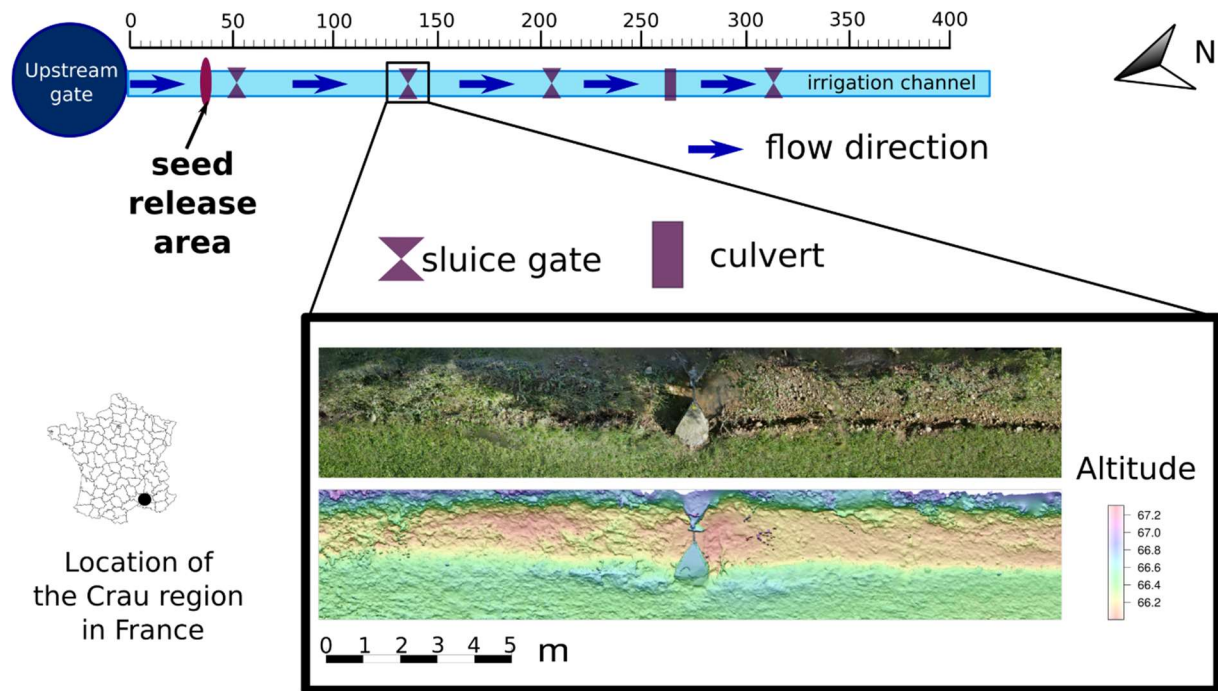




675 **Table 2 :** Relative importance of the factors calculated from the CART algorithm relating the proportion of  
676 trapped seeds to the downstream influence of hydraulic structures (*Down\_Struct*), the hydraulic radius (*Hr*), the  
677 percentage of emerged (*Pem*) and submerged (*Pim*) vegetation, the mean velocity (*V*) and the width of the  
678 section at the water-surface (*WidthSection*). Factor importance was calculated on 3 subsets of the channel (0 – 80  
679 m ; 80 – 160 m ; 160 – 240 m) and on the whole studied section (0–240 m). The  $R^2$  corresponded to the  
680 coefficient of determination of the CART model.

Importance (%) of the variables classified by CART							R <sup>2</sup>
	<i>Down_Struct</i>	<i>Hr</i>	<i>Pem</i>	<i>Pim</i>	<i>V</i>	<i>WidthSection</i>	
Subsets of the channel							
0–80 m	7	19	17	24	15	18	0.51
80–160 m	3	17	54	13	3	10	0.56
160–240 m	44	11	0	9	14	22	0.59
Total section of the channel							
0–240 m	3	11	33	4	9	40	0.72

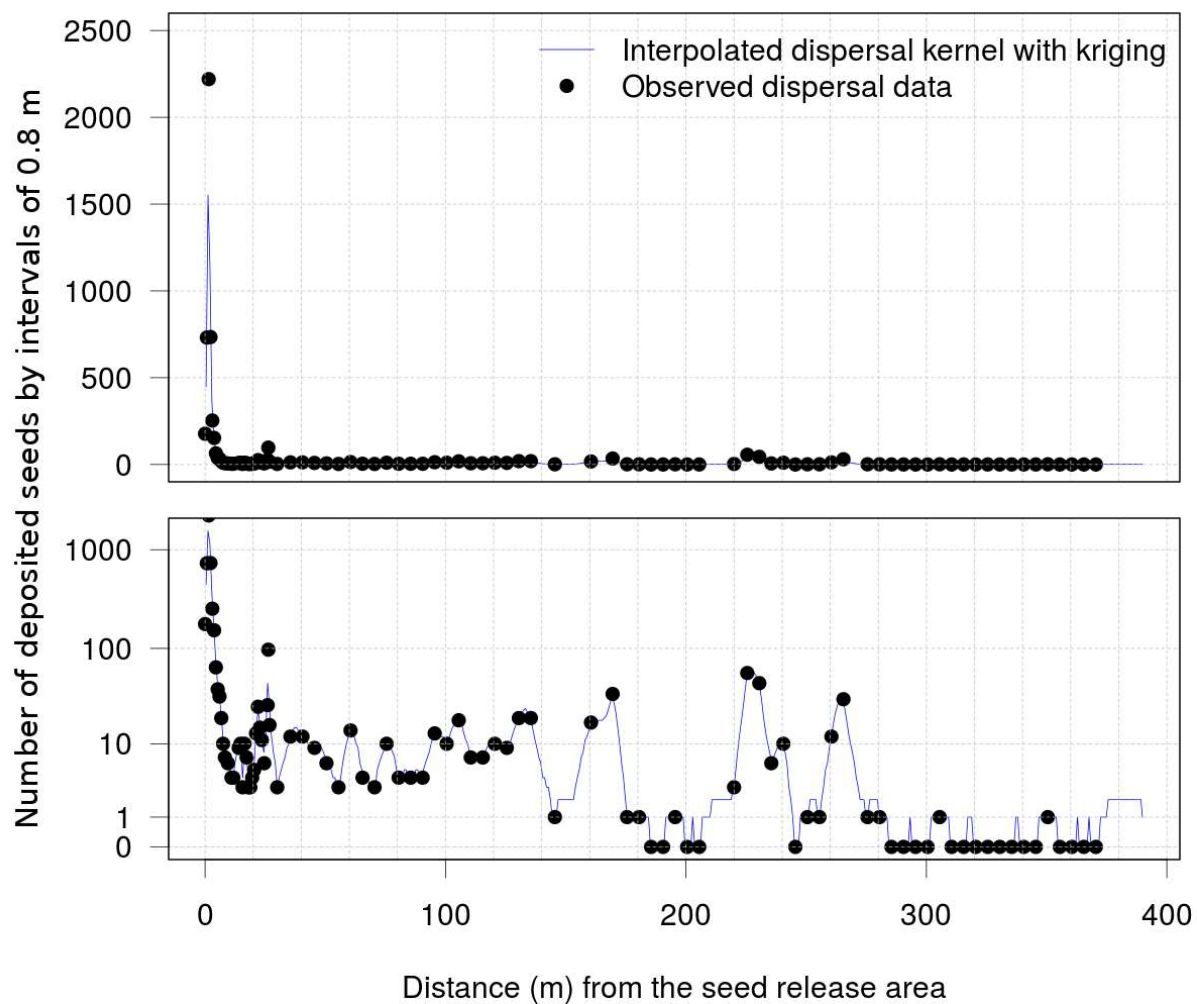
**Figure 1.** Location and main characteristics of the studied irrigation channel. A diagram of the channel figures in the upper part of the Figure (Please note that hydraulic structures and width of the channel are over estimated in the diagram). The seeds were released 37 m downstream the gate. A zoomed box indicates a modelled view using a multi-view stereo approach of a 20 m section of the channel including a sluice gate. A RGB orthoimage and a DSM model at 1 cm resolution is represented top-down in the box.



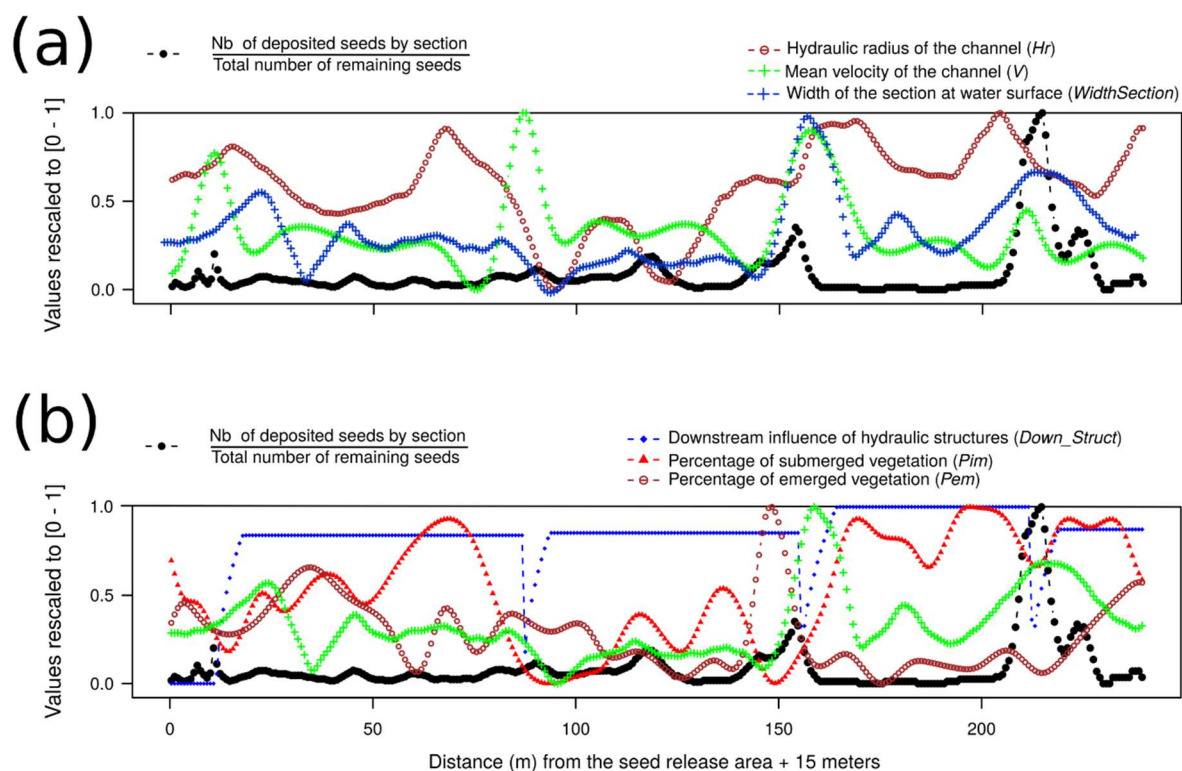
**Figure 2.** Picture of a seed of Johnsongrass using a macro lens.



**Figure 3.** Observed dispersal data of Johnsongrass (black points) and their interpolated values (blue lines) along the channel obtained by ordinary kriging using a 0.8 m window, presented normally (top part) and log-transformed (bottom part).



**Figure 4.** Variation of the explanatory factors explaining seed deposition of Johnsongrass along the channel. The lines represent the ratio of deposited seeds by section on total number of remaining seeds (in black) compared to (a) the hydraulic factors and (b) the effects of other elements (hydraulics structures and vegetation) (in colors). The origin of x-axis corresponds to the beginning of the fat tail of the dispersal kernel considered for the estimation of the explanatory factors.



**Figure 5.** Observation versus prediction of the seed deposition of Johnsongrass along the channel using the CART algorithm. The origin of x-axis corresponds to the beginning of the fat tail of the dispersal kernel considered for the estimation of the explanatory factors.

