Vegetation cover at the water surface best explains seed retention in open channels

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ABSTRACT

Hydrochorous dispersal through agricultural channels plays a role in structuring plant communities across agricultural landscapes. To date, research on seed retention in vegetated areas has mainly focused on vegetation types with simple architecture (often cylinders), which consequently do not represent real vegetation features. Here, we test the hypothesis that vegetation cover estimated at the water surface best explains floating seed retention in open channels. We therefore proposed an experiment to measure seed retention in a controlled environment across a large range of hydraulic conditions and vegetation architecture types. We used three types of artificial plants with contrasting morphotypes, and real seeds of *Rumex crispus*. Vegetation metrics were calculated on the basis of 3D plant models. We also tested the additivity of seed retention as a function of the length of vegetated area crossed by the seeds. We developed a semi-empirical formula for predicting seed retention. The main results of the experiment show that (i) the seed retention rate reacts differently to changes in density according to species (ii) vegetation cover at the free water surface, potentially in contact with seeds, is a generic predictor of floating seed retention whatever the nature of the vegetated cover (iii) 95% of seed retention was reached for a large range of surface vegetation ratios and length of vegetation cover. The proposed formula could be used by

stakeholders (farmers and ecologists) to estimate the amount of vegetation needed in a channel to limit or enhance seed dispersal.

Keywords (max 8): Vegetated channel; Agricultural drainage networks; Propagule dispersal; Vegetation porosity; Vegetation metrics; Hydrochory; *Rumex crispus*; 3D plant model

1. INTRODUCTION

Hydrochorous dispersal plays a major role in structuring vegetation communities (Gurnell et al., 2006; Nilsson et al., 1991, 2010; Ridley, 1930). In agricultural areas, some plant species are able to travel hundreds of metres via semi-natural waterways, such as ditches or irrigation channels (Rudi et al., 2018; Soomers et al., 2010; van Dijk et al., 2014). Plant dispersal can therefore be favoured by a network-like organization of waterways, and propagules can readily travel through the agricultural landscape, either causing economic losses for farmers when the propagules compete with their crops (Petit et al., 2011), or contributing to the maintenance of community species richness and increasing genetic diversity in populations (Nilsson et al., 2010). Plant richness in agricultural channels provides numerous microhabitat types and contributes to the connection of populations of mobile organisms, including amphibians, mammals and insects, which would otherwise be isolated in intensively cropped areas (Dollinger et al., 2015).

The interplay between propagule features, hydrodynamic characteristics and waterway properties drives propagule dispersal (Greet et al., 2011, 2012; Hyslop and Trowsdale, 2012). The propagules' features, especially those determining the duration of buoyancy (Boedeltje et al., 2003; Carthey et al., 2016; Riis and Sand Jensen, 2006), are important factors for explaining the distance of transportation by water in natural ecosystems. The ability to float is mostly linked with the features of the propagules, such as density, size and shape. For floating propagules, the mean flow velocity (Defina and Peruzzo, 2010) and turbulent diffusion (White and Nepf, 2003) as well as hydrodynamic conditions at the water surface, can be related to the rates of deposition in the channels (Merritt and Wohl, 2002). Other retention factors include the presence and abundance of vegetation (Chambert and James, 2009; Cornacchia et al 2019, Defina and Peruzzo, 2010; Liu et al 2019; Peruzzo et al. 2012, 2016), and vegetation type (Jager et al., 2019), especially in narrow agricultural waterways, such as channels and ditches (Rudi et al., 2018; Rudi et al., 2020; Soomers et al., 2010).

At the local scale, Defina and Peruzzo (2010) describe two mechanisms for temporary trapping of propagules in emergent vegetation: (i) wake trapping, in which the propagules are retained in the recirculation zone behind a plant (White and Nepf, 2003), and (ii) inertial impaction, in which the inertia of a propagule allows it to escape from the streamline and meet a stem (Palmer et al., 2004); and two possible mechanisms of permanent trapping: (i) net trapping, in which a bunch of stems or leaves forms a net-like structure, and (ii) the "Cheerios effect" (Vella and Mahadeven, 2005), which is explained by the deformation of the water surface linked with surface tension. For permanent propagule retention, note that the Cheerios effect is significant when the spacing between stems is greater than the propagule size and in slow-flowing conditions (Chambert and James, 2009). Some semi-empirical models have been developed to characterize propagule retention distances in vegetated media relying on channel experiments (Defina and Peruzzo, 2010; Liu et al 2019; Peruzzo et al., 2012, 2016). These models have been mainly developed for slow flowing water and low to medium vegetation densities and focused mainly on the Cheerios effect. They described the probability of interaction and capture of propagules in vegetation. As described by Defina and Peruzzo (2012), the probability that a propagule reaches a specific distance depends on the propagule mean path length before permanent capture, the probability of interaction, the probability of permanent capture, and the mean centre-to-centre spacing between stems. In these experiments, the vegetation has usually been represented with rigid arrays, except in Defina and Peruzzo (2010, 2012), who used flexible plastic plants. The vegetation metrics used in the developed models are the mean centre-to-centre distance between stems, the mean spacing between adjacent cylinders (taking into account the stem diameter), and the density of plants (Defina and Peruzzo, 2010, 2012; Liu et al. 2019, Peruzzo et al. 2012, 2016).

However, in field conditions, complex vegetation patterns are frequently observed. Vegetation exhibits a vertical variability, and consequently, the area of vegetation at the water surface that can potentially interact with propagules varies with the fluctuations in the water level. There is currently a lack of vegetation metrics and semi-empirical generic formulas able to predict the rates of propagule retention in the large range of hydrodynamic conditions observed in the field. Some attempts have been made to measure the percentage of plant cover at the water surface (Rudi et al., 2018) or the plant cover "porosity" (Vinatier et al., 2018) for real plant covers to characterize patterns of propagule deposition along agricultural channels. In these experiments, the tallest layers of vegetation hid the vegetation at the water surface and made it difficult to reconstruct the patterns of vegetation cover at the water surface. Moreover, as pointed out by Green (2005), the vertical heterogeneity of the vegetation profile needs to be taken into account in studies focusing on interactions between vegetation and fluxes of matter. Testing the importance of the specific vegetation surface permeability to propagules against other traditional metrics describing the vegetation cover seems necessary for a better comprehension of hydrochory.

The study was motivated by questions on the retention ability of terrestrial and semi-aquatic vegetation growing in agricultural channels and ditches in Mediterranean areas. One of the specificities of these patches is that they generally cover the total width of the channels, and form a relatively homogeneous cover. As will be detailed below, the experimental set-up therefore reflects the conditions commonly observed in these systems.

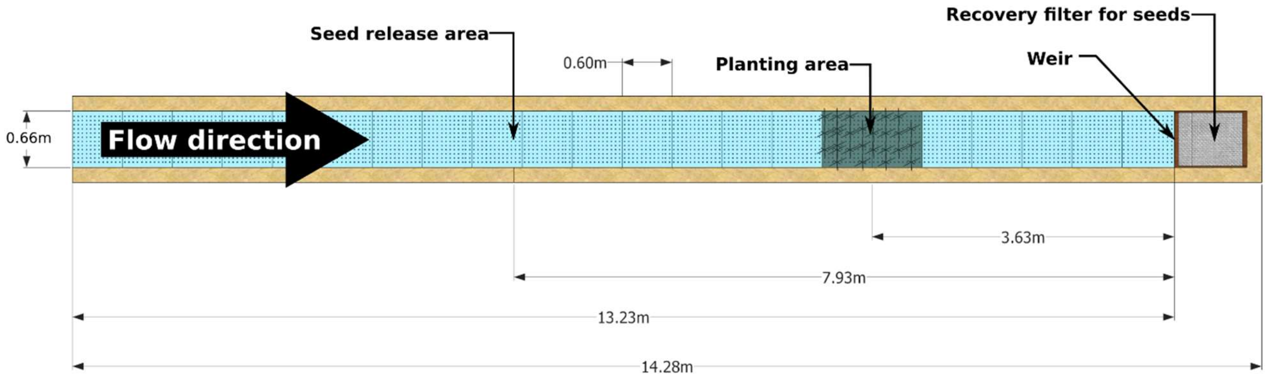
In this study, floating seed retention in vegetated channels is investigated, focusing on a large range of plant densities for three different types of emergent vegetation with complex architectures, representative of the types of vegetation that can be found in agricultural drainage or irrigation channels with medium velocity flow conditions. We hypothesized that vegetation cover estimated for the fine layer constituting the water flow surface is the best predictor of seed retention compared to other vegetation metrics. The specific purpose of the study was (i) to investigate seed retention rates in various artificial plant covers that closely reproduce the plant covers observed in the field, (ii) to test the hypothesis of additivity of seed retention according to the length of the vegetated area, and (iii) to establish a semi-empirical retention function based on two components depending on plant metrics and hydrodynamic conditions to test the relevance of the vegetation cover at the surface to explain seed retention.

2. MATERIALS AND METHODS

2.1. Experimental channel design

The experiments were conducted in controlled hydraulic conditions in an experimental cement channel located at the Institut Agro – Montpellier SupAgro (Montpellier, France). The channel is rectangular (9 m long and 0.66 m wide) (**Figure 1**). The slope is 0.0013 m/m. This channel was chosen because its dimensions were consistent with those of the channels and ditches found in southern France and with the morphologies of those channels, in which flows are generally subcritical and turbulent. Commonly observed Froude and Reynolds numbers of these systems could be reproduced in the channel. The water inflow was regulated thanks to a control structure (constant level gate followed by baffle module weirs) ensuring a constant discharge (±5%). Then, a flow tranquilizer followed by a 5-metre reach ensured the formation of a well-established flow upstream of the channel. The downstream water level was controlled by a rectangular weir with a sill of 10 cm. At the end of the channel, a net was placed to collect seeds. The water was then filtered and recycled through the closed system.

Figure 1: Schematic representation of the experimental channel.

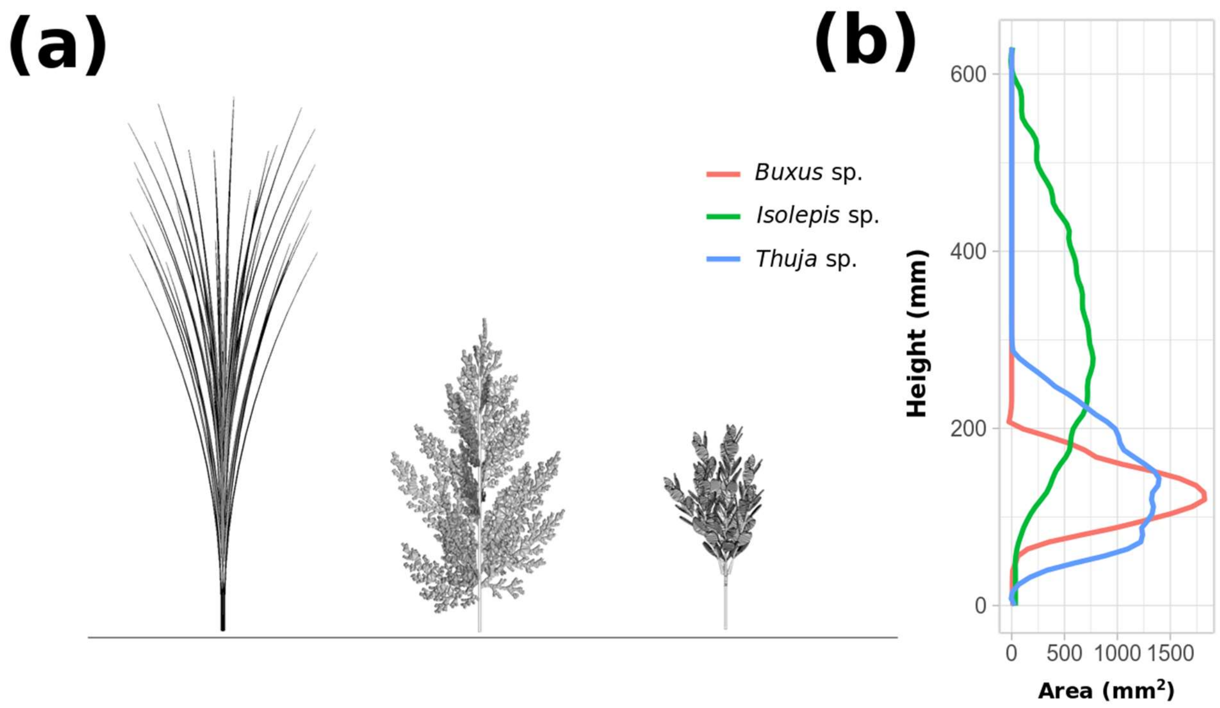


The selected steady-state flow rates varied from 10 $L.s^{-1}$ to 40 $L.s^{-1}$, determined with an accuracy of +-5% (Vinatier et al., 2017). The range of variation in the discharges is based on the heights of the plants, in such a way that plants are never submerged.

2.2 Plant material and its spatial arrangement

Three types of plastic plants of different architectures were chosen for the experiment: a Cyperaceae (*Isolepis* sp.), a Cupressaceae (*Thuja* sp.) and a Buxaceae (*Buxus* sp.) (https://www.artificielles.com) (**Figure 2**). We chose these types of plants because they represented a diversity of architectural topologies characteristic of the plant diversity found in intermittent agricultural channels. The Cyperaceae morphotype represented by *Isolepis* sp. (thin and elongated) is similar to the grasses frequently encountered in channel banks, colonizing an intermediate ecological niche between terrestrial and wetland environments. The Cupressaceae morphotype (*Thuja* sp.) is characteristic of shrubby vegetation encountered in less well-managed channels. The Buxaceae morphotype (*Buxus* sp.) is similar to that of some Asteraceae found in the bottoms of channels, with a specific architecture consisting of a long stem surmounted by a vegetative spike. **Table 1** presents the diversity of morphological characteristics of the studied artificial plants.

Figure 2: (a) 2D representations of the three plants (*Isolepis* sp., *Thuja* sp. and *Buxus* sp., from left to right) used for the experiment and (b) the vertical profile of their surface area according to a horizontal plane.



The plants were fixed on concrete panels (0.66*0.60 m) drilled with 144 holes, i.e., approximately 362 holes/m^2, filled with screw anchors to fix the plants. Fourteen densities were established in a staggered pattern, representing the variability in natural plant densities found in ditches (Rudi, pers. com). A picture of the vegetated area with a medium density (36 plants per concrete panel) from above the channel for two panels is presented in **Figure 3**. The arrangement of plants in the channel for all the density configurations is provided in **Appendix A.** Note that for all the density configurations, the vegetation filled the channel width and was homogeneously distributed in the channel.

Figure 3: Picture of the vegetated area (*Isolepis* sp.) in the experimental channel (36 plants per concrete panel on two panels).

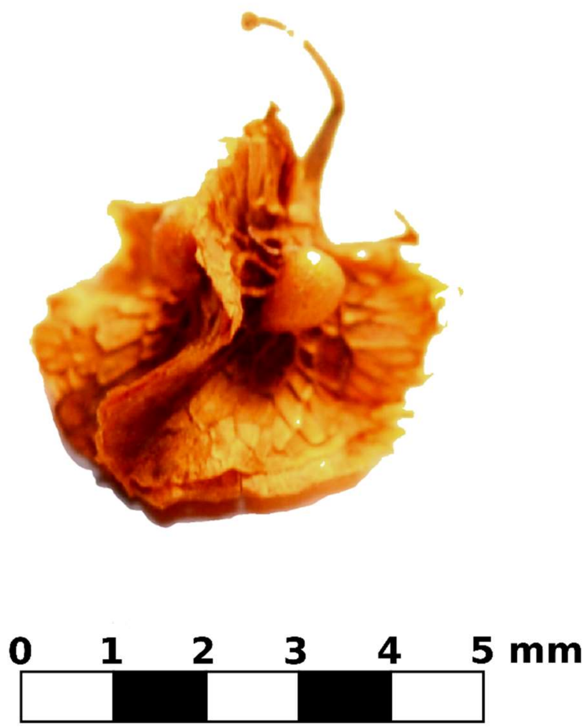
2.3. Overview of the experiments

Two seed release experiments were conducted in the experimental channel. The first experiment aimed to characterize the retention rate of seeds in patches of vegetation with constant lengths (over the length of two concrete panels, i.e., 1.2 m, with different plant density configurations, see **Table 2**) to assess the interactive effects of density per panel (D), species (SP) and discharge (Q) on seed retention. In the second experiment, the same plant density was planted on one to eight panels (i.e., 0.6 to 4.8 metres) to characterize the effect of the length of the patch (where NB is the number of panels) on the seed retention and test the hypothesis of additivity of seed retention (**Table 2**). It is important to note that for the second experiment, discharge and density were chosen to explore the largest range of retention rates from one panel to 8 panels and differed for each species. A trial without plants was conducted for each discharge tested in the experiment. Moreover, the results from these two experiments were used to calibrate the developed model of seed retention based on new vegetation metrics.

2.4 Seed release and counting

Seeds from curly dock (*Rumex crispus)* (**Figure 4**) were collected in Lattes (Hérault, France) in October 2018. This weed was chosen because it is common in rural areas, and its seeds have the potential to disperse via flow because they are contained in the calyx of the flower which has good buoyancy (Uva et al., 1997). The buoyancy of the collected seeds was assessed by immerging 200 seeds in 10 pots of water (20 seeds per pot) for 5 days. This experiment showed that 100% of the seeds were buoyant during the first 10 h of immersion (details of the experiment are provided in **Appendix B**). This was consistent with the results of Cavers and Harper (1964) and Favre-Bac et al. (2017), who classified *R. crispus* seeds as having long-term buoyancy compared to other species. The weight of the seeds (5.35 mg (+/- 0.68 mg)) was estimated from the measurement of 10 lots of 10 seeds with a high-precision scale (Precisa XB 160M; precision: 0.001 g; accuracy: 0.01 g). The seed diameter was measured as the average of 50 seeds (4.96 mm (+/- 0.76), including the calyx) with a calliper.

Figure 4: Picture of a curly dock (*Rumex crispus*) seed



During the experiment, following the Eulerian framework described in Defina and Peruzzo (2010), lots of 50 seeds were released at the head of the channel in the seed release area using a 60 cm-long piece of metal. The lots were distributed homogeneously using this piece of metal, which covered the width of the channel. For each release, we counted the seeds that travelled to the end of the channel after a defined amount of time, depending on the length of the patch and the water discharge. The retention rate of seeds was calculated according to the following formula:

$$R_r(x) = \frac{N_{release} - N_{out}}{N_{release}} \quad \textbf{Equation 1}$$

where $R_r(x)$ is the retention rate over a vegetated distance of x metres, $N_{release}$ is the number of seeds in each release (50 for this experiment) and N_{out} is the number of seeds reaching the tail end of the experimental channel. Each release was repeated three times for one set of Q, SP and D.

Following Defina and Peruzzo (2010), we estimated that seeds were permanently trapped after a period equal to one order of magnitude above the mean travel time of a seed for the whole test section. For the first experiment (with two vegetated panels), this period was set at 2 min and 1 min 30 s for discharges equal to 10 L.s-1 and above 10 L.s-1, respectively, which is in accordance with the period of 2 min set in Cornacchia et al. (2019), and with preliminary tests showing that there was no seed release once these time limits were exceeded. For the second experiment, we adapted the period to the number of vegetated panels, by multiplying the length of the period according to the total number of vegetated panels, based on the periods chosen for two vegetated panels. For each release, when the time elapsed, we collected all the seeds trapped in the patch of vegetation before the next release. In total, 264 releases of 50 seeds were made in the first experiment and 111 in the second experiment, representing 18750 released seeds in total.

2.5. Characterization of the seed retention rates relative to the experimental variables

The effects of the experimental variables and their interactions on the R_r were analysed using a binomial generalized linear model with logit link function (analysis of deviance with binomial error). The experimental variables were Q, D, SP, and NB. The significance of each variable was assessed via the change in deviance between the models with and without the variable. Overdispersion was accounted for using quasi-binomial instead of binomial models.

For each combination of SP x Q for the first experiment (2 panels, corresponding to a distance of 1.20 metres), a sigmoid curve with the form

$$R_r(1.2) = \frac{1}{1+e^{\left(-slop\ \times(D-D_{50})\right)}} \qquad \textbf{Equation 2}$$

is fitted using the nonlinear least squares method to obtain D_{50} (the density needed to reach 50% seed retention) and the slope of the linear relation between D and R_r.

2.6. Characterization of the vegetation metrics

Among the different metrics describing the influence of vegetation on ecohydrological processes are the proportion of surface area containing vegetation (Green, 2005), the percentage of submerged or emergent vegetation (Rudi et al., 2018), and the porosity of the vertical section of a channel induced by vegetation (Vinatier et al., 2018); we reviewed all of these metrics to test the hypothesis that vegetation at the water surface is the best predictor of seed retention.

Because of the complexity of the architecture of individual plants, there are no simple measurements of the vegetation cover metrics, especially for the vegetation area in the thin slice corresponding to the water surface that can potentially interact with the floating seeds. Consequently, we constructed a three-dimensional model of each of the three artificial plants. This was made possible because of the homogeneity of the artificial plants and their repetitive elements.

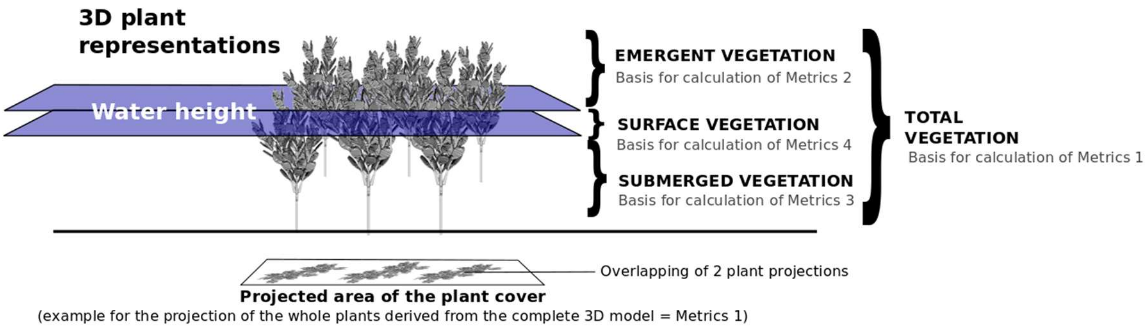
A 3D model of each plant was realized by first establishing a master of all plant attributes. Each leaf of the artificial plant has been cut, numbered and scanned using a professional scanner (600 dpi resolution). Leaf thickness, stem diameters and spacing between the different stem portions were measured using a calliper. Orientations of leaves and stems were measured using a protractor. Then, meshes of all plant attributes were assembled using CloudCompare software (Girardeau-Montaut 2014) to produce a continuous mesh for each plant.

After this step, different vegetation metrics were derived from the projection of the 3D plants on the horizontal plane of the channel (**Figure 5**):

- the projection of the whole plants on a horizontal plane, derived from the complete 3D model (basis for calculation of Metrics 1),
- the projected areas of the emergent and submerged vegetation (emergent and submerged vegetation on **Figure 5**) on a horizontal plane, derived from the model cropped by a plane at the level of the water surface (basis for calculation of Metrics 2 and 3), and

- the area of the plant at the free surface of the water derived from the model sliced by two planes at 1 mm above and below the water level (basis for calculation of Metrics 4) (surface vegetation on **Figure 5**).

Figure 5: Illustration of the different types of vegetation metrics for a group representing the plant arrangement for a given density.



The different areas were calculated from (i) the product of each individual projected area by plant density for each experiment ("product" method) and (ii) a scene representing the 3D models arranged according to the spatial patterns found for each density ("scene" method). By construction, the overlapping surfaces of the high-density projections were summed in the "product" method and were merged in the "scene" method.

Then, we calculated the ratio of occupation of each vegetated area by dividing the area occupied by vegetation by the total planting area of the channel (on a horizontal plane) to obtain the four vegetation metrics, called $Metrics_{veg}$.

2.7. Characterization of hydrodynamics

The literature survey suggests that the hydrodynamic conditions at the water surface, and especially the velocity at the water surface, largely influence the retention rates. More specifically, seeds are transported with the current, and we expect their probability to pass the vegetation filter to increase with turbulence. Therefore, we introduced the non-dimensional Reynolds number, $\mathfrak{R}$, to characterize the nature of the flow patterns:

$$\Re = U \times H/v \qquad \textbf{Equation 3}$$

where U corresponds to the average velocity over a section in m.s^{-1} ($U=Q/(B*H)$), H is the water height in m (corresponding to the characteristic length), B the width of the experimental channel in m, and v is the kinematic viscosity in m^2.s^{-1}. Weakly turbulent flows (low Reynolds number) should result in high retention rates ($R_r \rightarrow 1$) (in this case, surface tension will facilitate the capture by vegetation stems), while highly turbulent flows (large $\Re$) should result in low seed retention ($R_r \rightarrow 0$). The range of the Reynolds numbers in our experiments was assessed between 15000 and 60000.

2.8. The additivity effect

Based on a constant probability of capture on each panel, we tested the additivity of our model based on the following formula:

$$R_r(x) = 1 - \left(1 - \widehat{\mathrm{R_r}}(1.2)\right)^{\left(\frac{x}{l}\right)} \qquad \textbf{Equation 4}$$

where x is the vegetated distance travelled by the seeds (in metres), $\widehat{R_r}(1.2)$ is the mean experimental retention value for two vegetated panels, and l is the length of the two vegetated panels, i.e., 1.2 metres.

2.9. The generic formula for seed retention

The relation linking R_r to $Metrics_{veg}$ and $\Re$ could be approximated by an exponential model of the form:

$$R_r(1.2) = 1 - e^{\left(\frac{-Metrics_{veg}}{a \times \Re \times 10^{-5}}\right)} \qquad \textbf{Equation 5}$$

where a is a dimensionless parameter to estimate. The mathematical form respects the expected trends between R_r and $\Re$.

Combining **Equation 4** and **Equation 5**, we obtained the generic formula for seed retention:

$$R_r(x) = 1 - e^{\left(\frac{-Metrics_{veg} \times x}{a \times \Re \times 10^{-5} \times l}\right)} \qquad \textbf{Equation 6}$$

Based on **Equation 6**, we tested what vegetation metrics best explained the seed retention rate (R_r) from the two experiments on the basis of the R^2 and the RMSE between the estimated and observed $\widehat{R_r}(1.2)$.

2.10. Softwares

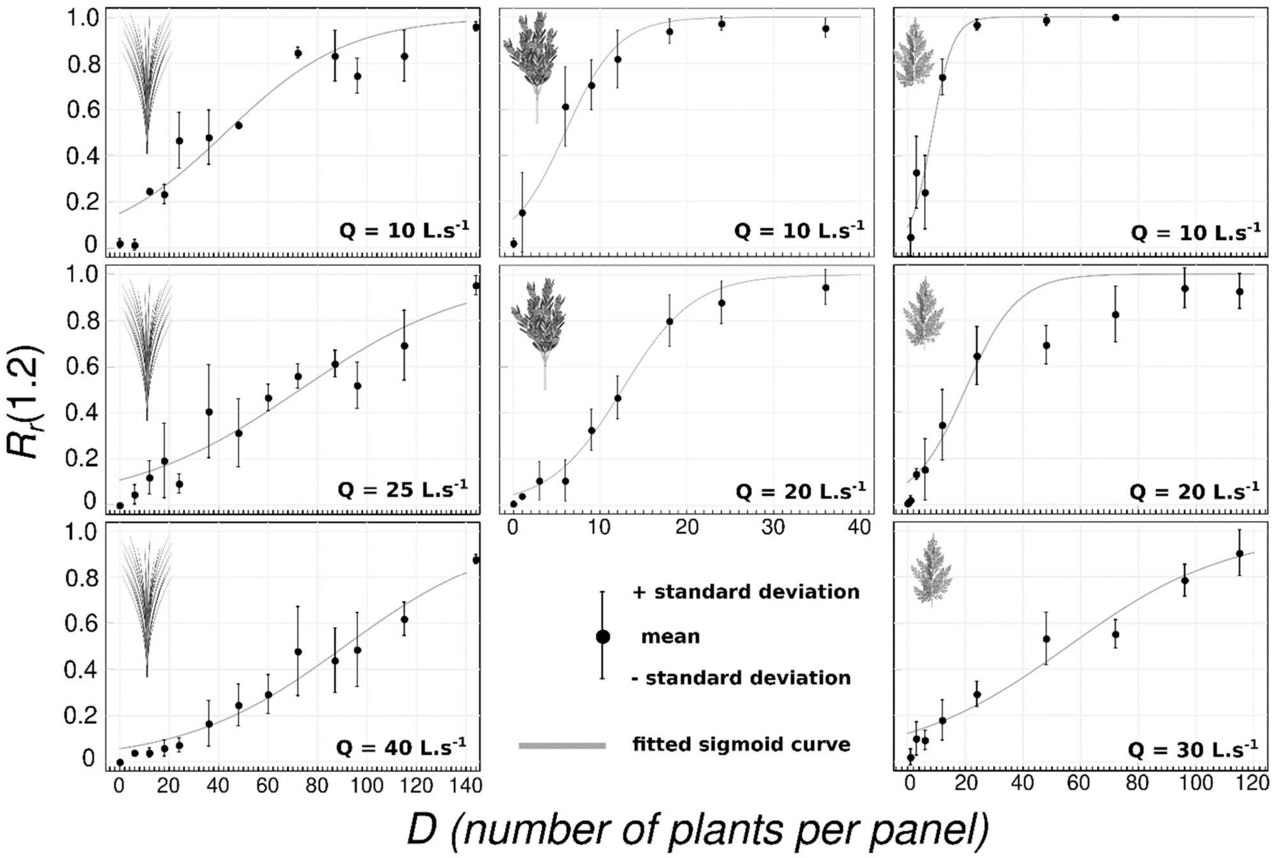
All the statistical analyses were performed using R software (R Core Team, 2017). The processing of the 3D models was performed using dedicated R packages (Rvcg, Morpho and data.table).

3. RESULTS

3.1 Effect of density, discharge and type of species on seed capture

The results of the statistical analysis (**Table 3**) show that the discharge, density or type of species significantly affects the rate of seed retention. The significant interaction between density and species means that the seed capture rate react differently to changes in density according to species. The results for the retention curves, as functions of plant density for each type of studied plant, are presented in **Figure 6**. Fitted parameters are presented in **Table 4**.

Figure 6: Seed capture rates R_r as a function of plant density D (number of plants by panel) for *Isolepis* sp. (first column), *Buxus* sp. (second column), and *Thuja* sp. (third column). The solid line represents a sigmoid curve fitted using the nonlinear least squares method for each combination of SP and Q. Fitted parameters are given in **Table 4**.



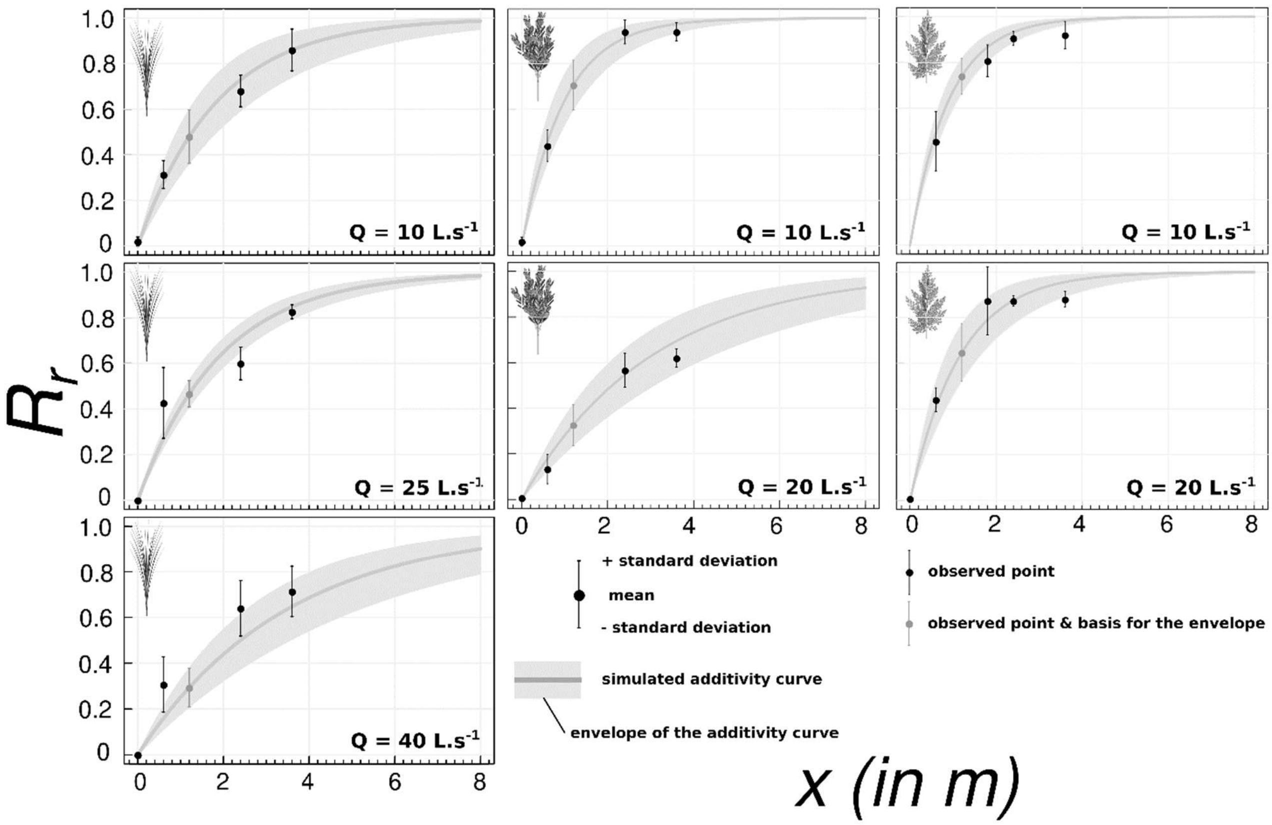
3.2. Additivity of the seed capture rate as a function of vegetation patch length

We first tested the significance of the influence of the number of vegetated panels on water height. We found that in the conditions of the study, the number of panels had a non-significant influence on water height (p-value = 0.123). This could be explained by the low density values tested for additivity (therefore, the vegetation did not significantly affect the hydraulic resistance). Consequently, we could neglect this effect in our experimental conditions.

The envelope of the additivity curve, extrapolated from the standard error of the $\widehat{R_r}(1.2)$, generally encompasses the observed points for 1, 4, 6 and 8 panels (**Figure 7**). The global R^2 of the proposed model is 0.77 (+-0.16).

Figure 7: Comparison between the observed seed capture rates and predicted capture rates based on the additivity formula for the three plants (*Isolepis* sp. (first column), *Buxus* sp. (second column), and *Thuja* sp. (third column)). The mean and standard deviation (black points and arrays) values were calculated on the 3 repetitions of seed release experiment. The grey point

and array is the mean and standard deviation for two vegetated panels, which served as a base for the calculation of the envelope (light grey).



3.3. A generic formula for floating seed capture in differentiated plant covers

The calculated surface vegetation ratio was between approximately two-fold and ten-fold lower than the whole, submerged and emergent vegetation ratios. The Pearson cross product correlation test was significant between vegetation metrics ($p < 0.001$). However, the correlation is low ($0.2<cor<0.6$) between surface vegetation and the other metrics, and higher ($cor>0.6$) when comparing the metrics calculated by summing individual areas with the metrics calculated from a scene (**Figure 5**). The metrics calculated from the "product" method exceeded the total area of the channel, especially for the whole and emergent vegetation of *Isolepis* sp., due to the high degree of overlap observed for this species.

As shown in **Table 5,** the use of the surface vegetation ratio (Metrics 4) led to the best results (R^2=0.90 and RMSE=0.083 for the "scene" method, and R^2=0.58 and RMSE=0.178 for the "product" method), regardless of how it was calculated. Considering a scene representing real spatial arrangements instead of the product of each individual plant area by density increased the performance of the models. The metrics calculated for the total vegetation (Metrics 1) and the emergent vegetation (Metrics 2) led to the worst results (R^2<0.30 and RMSE>0.25).

Regarding the seed retention rate in the best model corresponding to the scene method and use of "Surface vegetation ratio" metrics (Metrics 4) (R^2=0.90 and RMSE=0.083), **Figure 8** shows a homogeneous dispersion of the whole dataset across the fitted model. The data from the second experiment (additivity) were also included in the model, although they cover a lower range of vegetation metrics and hydraulic conditions. In **Table 6**, we observed that every studied plant was well fitted by the model.

Figure 8: (a) Seed capture rate (R_r) as a function of the best combination of vegetation metrics and $\Re$. The solid line corresponds to the fit of the nonlinear model to the data. (b) Comparison between the observed and estimated R_r according to the model. The dashed line indicates a perfect fit between the observation and estimation.

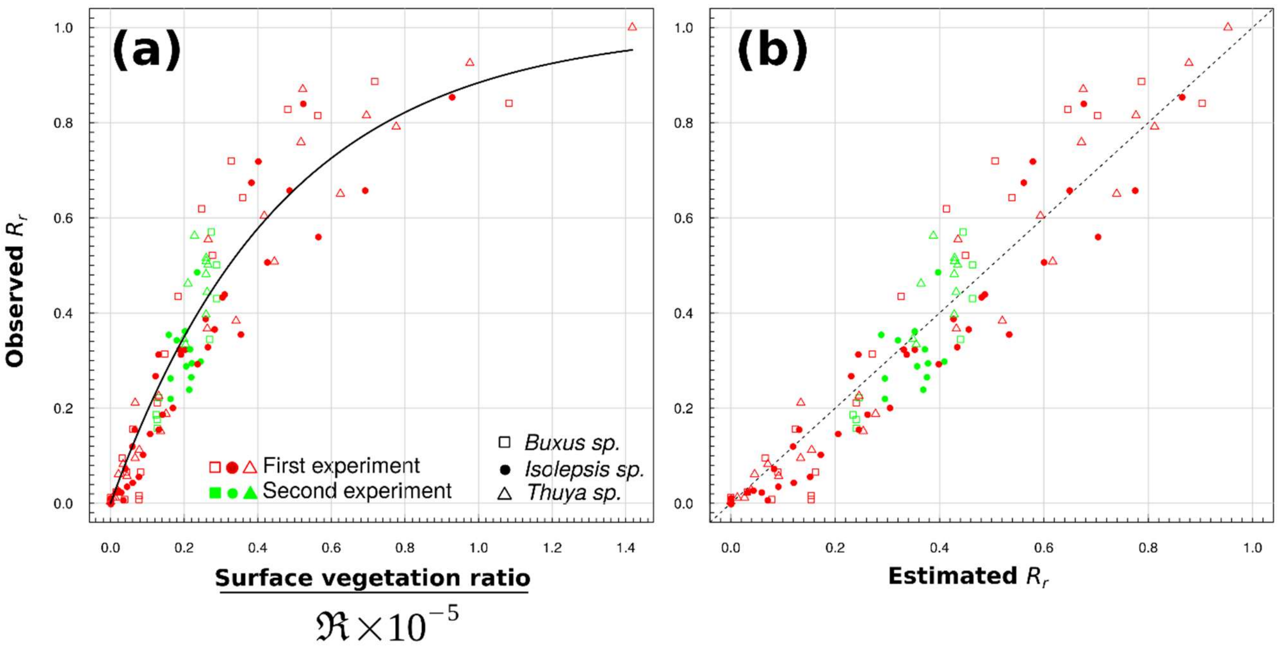
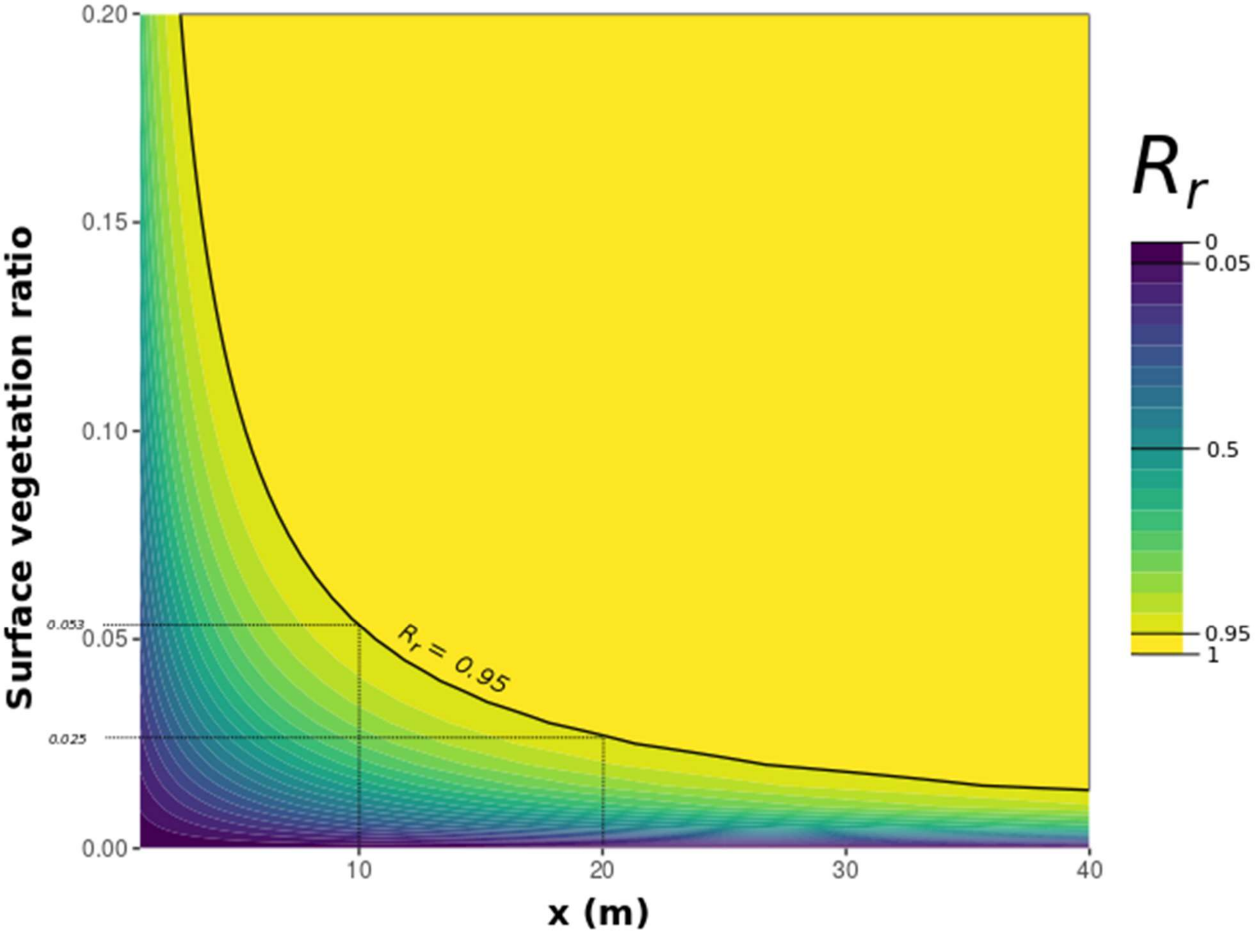


Figure 9 indicates that 95% seed retention was reached for a large range of surface vegetation ratios and channel lengths (in hydrodynamic conditions allowing a Reynolds $\Re$ of 32000). Basically, with an R_r isoline equal to 0.95, channels of 10 metres and 20 metres retained 95% of the seeds if the surface vegetation covered 5.3% and 2.5% of the water surface area, respectively.

Figure 9: Lattice plot based on the generic formula (Equation 6) and calibrated on the experimental data for a surface vegetation ratio between 0 and 20% and a channel length between 0 and 40 metres, with the $\Re$ value being fixed in the formula at 32 000 (which can correspond, for example, to a water height of 15 cm and an average velocity of 0.21 m.s^{-1})



4. DISCUSSION

4.1. The area occupied by vegetation at the water surface is a relevant metric for seed retention prediction in a vegetated cover

This experiment showed the relevance of using the area occupied by vegetation at the water surface instead of the area calculated from the total, emergent or submerged vegetation as a predictor of the seed capture rate in a vegetated channel. The use of the area occupied by vegetation at the water surface is interesting when focusing on plant covers with varied morphologies, because this metric is generic and works for the three types of vegetation covers tested.

In the experiment, the variations of discharge affected more the retention rates for *Thuja sp.* and *Buxus sp.* than for *Isolepis sp.* This is due to the fact that discharge affects directly water height in the channel, and the first two species display a greater variability of surface area according to water height than *Isolepis sp* (see Figure 2b).

The additivity of the formula has been demonstrated on distances under 10 m with low vegetation densities. Higher vegetation densities would exert a significant influence on hydraulic conditions, especially height and velocity (Nepf, 2012), and the Reynolds number should be corrected as a consequence.

Our results reinforce the idea that representing vegetation cover as a porous media is an efficient approach for understanding water transport and particle transport in vegetated areas, as was highlighted in recent works focused on interaction between water transport and vegetation (see Rubol et al., 2018 and Vinatier et al., 2017 for example). However, in this experiment, the spatial distribution of plants in the channel is relatively homogeneous. In configurations in which the vegetation is heterogeneously distributed, preferential transfers are observed (Cornacchia et al., 2019; Erktan et al., 2013; Nepf et al., 2012). Indeed, the phenomena of flow divergence at the patch scale explain these preferential transfers, which could be susceptible to modifications in the relationship between the area occupied by vegetation and seed capture.

4.2. 3D representation of vegetation is an original and efficient method for characterizing plant cover at the water surface

The 3D representation of vegetation is an efficient approach, especially in contexts of high plant density or when plants are largely above the water level; in the latter case, techniques using photographs to reconstruct the area covered by vegetation from above have poor accuracy (because of the effect of sheltering), as revealed by our results. In situations in which we possess 3D models for each type of plant encountered in agricultural channels, we could represent any vegetated cover and calculate the area at the water surface. Moreover, in the future, 3D plant models could help to calculate more evolved vegetation metrics commonly used in landscape ecology, such as core area or patch cohesion formed by the vegetation at the water surface.

However, the use of 3D plant models has limits. First, the production of 3D models is time consuming for real plants, and it would be even more time consuming if we wanted to create models for plants at different phenological stages. Moreover, in this study, the hydrodynamic conditions did not significantly modify the plant structure. However, plant reconfiguration has been observed under some hydrodynamic conditions (Vogel, 1996), and the degree of bending is usually a function of water velocity (Chapman et al., 2015; Luhar and Nepf, 2011) and height. The 3D models that we developed would be improved by being able to bend under flow drag forces. The integration of computational fluid dynamic tools, such as OpenFOAM (www.openfoam.com) or Fluent (www.ansys.com), could allow the creation of this type of bowed plant model, but the amplitude of reconfiguration, the flex points and the representation of the streamlining of leaves as a function of water velocity still need to be characterized by further studies.

It will be necessary to test the effect of seed characteristics in the context of the main processes controlling vegetation and seed interactions. It has been shown that seed traits such as weight, size, density and shape influence interactions with vegetation when the Cheerios effect is the major mechanism of seed retention (Chambert and James, 2009; Liu et al., 2019; Peruzzo et al., 2016), i.e., when the water velocity is slow and the spacing between the stems of the vegetation is greater than the particle diameter (Chambert and James, 2009; Liu et al., 2019; Peruzzo et al., 2016). In our hydrodynamic conditions, with net trapping being the major mechanism of seed capture, it is possible that seed features also influenced the rate of seed retention in our experiment. For example, de Jager et al. (2019) showed that large seeds were less affected by net-trapping than smaller ones. The number of seeds released in the channel should also be considered. In our experiments, we observed that seeds sometimes formed clusters (due to the Cheerios effect) more susceptible to being captured by vegetation, especially when vegetation presented indented patterns, as for *Buxus* sp. and *Thuja* sp.

4.3. Implications for the agroecological management of agricultural channels

It has been shown that agricultural channels could be significant dispersal vectors for weeds because they allow seeds to travel hundreds of metres in a few hours (Rudi et al., 2018; Soomers et al., 2010). From a practical point of view, the developed formula provided an indication of the surface vegetation cover needed for a given channel length to reach a specified objective of retained seed rate. For portions of ditches of 10 metres, it would be necessary to have a surface vegetation ratio of 5.3% to retain 95% of seeds (with a Reynolds of 32 000, see Figure 9). Considering that the surface vegetation ratio is between twice and ten times lower than the total vegetation ratio (see §3.3), vegetation coverage of 53% in the channel (5.3% * 10) should be sufficient to retain 95% of the seeds transported by the channel. Previous studies of vegetation cover dynamics in agricultural channels (Dollinger et al., 2017; Levavasseur et al., 2014) have revealed that management practices were a lever to control vegetation cover in space and time, and we should then be able to control hydrochorous seed dispersal through these management practices.

This work also confirms that water height variations, even moderate, play a role in the dispersal and subsequent establishment of plants in agricultural waterways, as observed by Engström et al. (2009) and Cornacchia et al. (2019) in other aquatic ecosystems. Consequently, in agricultural channels, conserving a part of the vegetation that exceeds the maximal depth of the channel can guarantee retention and limitation of dispersal. In this sense, tall plants (i.e., taller than 50 cm) can play a preponderant role, because maximal depths in drainage channels and secondary/tertiary irrigation channels are generally approximately 50 cm in the studied ecosystems.

The developed prediction formula for seed retention is rather easy to use and can serve to assess the services of weed spreading limitation in agricultural landscapes or natural revegetation. Therefore, it is well adapted to be integrated in studies assessing benches of ecosystem services provided by vegetation of hydro-agricultural waterways such as ditches and channels (water transport regulation, weed spreading limitation or enhancement, erosion limitation). Indeed, one of the drawbacks of multifunctional studies is the need to choose between indicator-based approaches (such as biomass, as a distant proxy for estimating the propagule retention capacity of vegetated channels), and physical approaches (e.g., using advection-dispersion equations, which need parameterization and substantial computing capacity and cannot be deployed when studying services on extended networks of channels) (Rudi, 2019; Rudi et al., 2020). Therefore, the developed formula in this research proposes a semi-empirical approach of medium complexity, process-based, to assess seed retention in agricultural channels.

5. CONCLUSION

Seed dispersal by hydrochory through agricultural channels greatly influences weed spatio-temporal distributions at the landscape scale. Natural vegetation growing in these channels plays a major role in the retention rates of weed propagules, and these retention rates are greatly influenced by both vegetation features and hydrodynamic conditions. This research focused on the characterization of *R. crispus* seed capture rates in three different artificial vegetation covers (*Isolepis* sp., *Thuja* sp., and *Buxus* sp.) in an experimental channel. We compared the relevance of different vegetation metrics and showed that the cover of vegetation at the water surface, calculated from 3D plants, was the best predictor of seed capture. We proposed a generic and semi-empirical formula to predict the seed capture rate in vegetated channels as a function of vegetation cover at the water surface and hydrodynamic conditions. This research supports the idea that the use of 3D plant models is an efficient way to understand water-plant-particle interactions in open channels. Our results have practical implications for the agroecological management of agricultural channels because they can inform on the relevant maintenance practices to manage vegetation according to the intended objectives of weed spreading limitation or natural revegetation through agricultural networks. Indeed, the choice between different options for vegetation management involves different vegetation dynamics along the year in terms of density or height of the cover (Dollinger et al., 2017; Levavasseur et al., 2014). The proposed formula could be used as a basis for a wide variety of vegetation covers and extended to other types of floating seeds.

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CONFLICT OF INTEREST

No conflict of interest was declared.

DATA AVAILABILITY STATEMENT

The data that support the findings of the study will be available online (Rudi et al. 2020 - https://doi.org/10.5281/zenodo.3947814) from the date of publication.

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TABLES

Table 1: Characteristics of the studied artificial plants. The ramification number was based on the methodology detailed in Godin and Caraglio (1998).

Variable	***Isolepsis* sp.**	***Thuja* sp.**	***Buxus* sp.**
Standing length (cm)	63	30	20
Ramification number	0	1	2
Number of branching stems	0	30	11
Volume (cm^3)	241	230	147
Collar diameter (mm)	6	3	3
Leaf number	8	30	15
Projected surface area on horizontal plane (cm^2)	162	40	52
Cumulative leaf surface area (cm^2)	465	276	197

Table 2: Summary of the experimental design. SP represents the species, Q the discharge, D the density of plants by panels of 0.66*0.6 m and NB is the number of concrete panels filled with vegetation.

SP	Q (in $L.s^{-1}$)	D	Density per m^2	NB
First experiment				
Isolepis sp.	10-25-40	0-144	0-361.9	2
Buxus sp.	10-20	0-36	0-90.5	2
Thuja sp.	10-20-30	0-96	0-241.3	2
Second experiment				
Isolepis sp.	10	36	90.5	1, 2, 4, 6, 8
	25	60	150.8	1, 2, 4, 6, 8
	40	60	150.8	1, 2, 4, 6, 8
Buxus sp.	10	9	22.6	1, 2, 4, 6, 8
	20	9	22.6	1, 2, 4, 6, 8
Thuja sp.	10	12	30.2	1, 2, 3, 4, 6, 8
	20	24	60.3	1, 2, 3, 4, 6, 8

Table 3: Effect of discharge (Q), density (D), species (SP), and interactions between density (D) and species (SP) on the rates of seed capture in a generalized linear model (glm) with a binomial error distribution. Density and discharge were used as the continuous variables, and species was used as the categorical variable. The P value indicates the significance of the model.

	d.f.	Deviance (Chi^2-value)	Residual d.f.	Residual deviance	P value
Q	1	654.4	253	7047.3	< 0.001
D	1	3708.3	252	3339.0	< 0.001
SP	2	718.16	250	2620.8	< 0.001
D x SP	2	440.5	248	2180.3	< 0.001

Table 4: Parameters fitted to the sigmoid curves from Equation 2. ***Q*** is the discharge, D_{50} the density needed to reach 50% seed retention, and ***Slope*** the slope of the linear relation between the density (***D***) and the seed retention rate (R_r).

Studied plant	Q (in $L.s^{-1}$)	D_{50}	Slope	R^2
Isolepis sp.	10	43***	0.04***	0.86
	25	73***	0.03***	0.82
	40	91***	0.03***	0.88
Buxus sp.	10	6***	0.33***	0.90
	20	12***	0.24***	0.95
Thuja sp.	10	8***	0.28***	0.92
	20	20***	0.11***	0.85
	30	55***	0.04***	0.91

Significance codes of each parameter of the sigmoid curve fitted using non-least squares:
'***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 5: Presentation of the results of the fitted generic formula across various $Metrics_{veg}$ and $\Re$ values.

$Metrics_{veg}$	$\Re \times 10^{-5}$		
	R^2	**RMSE**	**a**
Scene representing real plant arrangements ("scene" method)			
Total vegetation ratio (Metrics 1)	0.24	0.255	3.678
Emergent vegetation ratio (Metrics 2)	0.18	0.279	3.669
Submerged vegetation ratio (Metrics 3)	0.77	0.126	0.961
Surface vegetation ratio (Metrics 4)	0.90	0.083	0.464
Product of the projected area of individual plants by plant densities ("product" method)			
Total vegetation ratio (Metrics 1)	0.12	0.321	11.55
Emergent vegetation ratio (Metrics 2)	0.08	0.339	14.95
Submerged vegetation ratio (Metrics 3)	0.49	0.205	1.448
Surface vegetation ratio (Metrics 4)	0.58	0.178	0.654

Table 6: Estimation of the R^2 and RMSE of the best fitted generic formula for the three studied plants.

SP	Whole dataset	
	R^2	RMSE
Buxus sp.	0.83	0.26
Isolepis sp.	0.90	0.22
Thuja sp.	0.91	0.21