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Weed Seed Fate During Summer Fallow: The Importance of Seed Predation and Seed Burial

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Maximizing weed seed exposure to seed predators by delaying tillage after harvest has been suggested as a way to increase weed seed losses to predation in arable fields. However, in some areas of northeastern Spain, fields are still tilled promptly after cereal harvest. Tillage usually places seeds in a safer environment compared to the soil surface but it can also increase seed mortality through seed decay and fatal germination. By burying the seeds, tillage also prevents weed seed predation. Weed seed fate in a tilled *vs*. a no-till environment was investigated during the summer fallow months in three cereal fields in semi-arid northeastern Spain. Rigid ryegrass and catchweed bedstraw seeds were used. Predation rates were measured in a no-till area within each field in 48-hour periods every 3 weeks and long-term predation rates were estimated. Fate of buried seeds was measured by burying twenty nylon bags with 30 seeds of each weed species from July to

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September 6 cm deep in a tilled area contiguous to the no-till area. Predation rates over the entire summer were 62 and 49% for rigid ryegrass and catchweed bedstraw, respectively. High availability of crop seeds (preferred by ants) on the soil surface may have decreased predation of weed seeds early in the season. Seed losses due to burial were 54 and 33% for rigid ryegrass and catchweed bedstraw, respectively. Unusual above-average precipitation probably prompted higher than normal weed germination rates (fatal germination) in some fields, and thus led to higher seed mortality rates compared to an average year. These results suggest that leaving the fields untilled after harvest maybe the optimum strategy to reduce inputs to the weed seed bank during the summer fallow period in semi-arid systems.

Nomenclature: Rigid ryegrass, *Lolium rigidum*; catchweed bedstraw, *Galium aparine*.

Keywords: harvester ants, background seed density, crop seeds, seed preference, semi-arid, tillage

Post-dispersal weed seed predation is an important ecosystem service that can help reduce the number of weed seeds entering the seed bank after being dispersed from the mother plant (Westerman et al. 2006, 2012). In order to maximize seed losses due to predation, some studies have suggested increasing exposure time of weed seeds to predators by allowing them to remain on the soil surface after being shed (Westerman et al., 2006, 2009). In annual arable crops such as winter cereals this can be achieved by delaying some management practices like harvest or soil disturbance, mainly tillage after harvest. Opportunities for delaying tillage can be difficult to find within a cropping system since there may be other reasons for soil tillage that may offset seed predation termination. However, in other circumstances, tillage could be delayed without many drawbacks. In semi-arid regions such as the rain-fed areas of northeastern Spain, low rainfall allows just one crop per year, mainly winter cereals, which grow from late October – early November to late June – early July. After crop harvest, fields are left fallow until the next sowing season in autumn. Despite widespread adoption of no-till practices in certain semi-arid areas, some farmers still chisel-plow the fields after cereal harvest. Reasons for tillage include burying the crop stubble, preventing soil compaction in autumn, managing summer weeds, and burying winter weed seeds.

Stubble tillage may have contrasting effects on weed populations. Usually, tillage places seeds in a “safer” environment, the soil matrix, compared to the soil surface (Mohler 1993 and references therein). In this sense, tillage can contribute to the buildup of the weed seed bank (Buhler et al. 1997). However, tillage can also be used as a weed management strategy if seeds are buried to a depth from where they cannot successfully emerge (fatal germination) (Chauhan et al. 2006; Cousens and Moss 1990; du Croix Sissons et al. 2000) or if they are attacked by soil microorganisms (seed decay) (Davis et al. 2006; Gomez et al. 2013). In semi-arid systems, conservation tillage and no-till seem to enhance soil microbial biomass carbon and soil enzymes, which are indicators of microbial activity, compared to conventional fully tilled systems (Alvaro-Fuentes et al. 2013). However, there is still very little information about the effects of those organisms on weed seeds, especially during the summer.

In rain-fed cereal fields in NE Spain, *Messor barbarus* L. harvester ant populations are large, especially in no-till and minimum tilled fields (Baraibar et al. 2009, 2011). Ants are active from spring to late autumn and their activity coincides with the period of seed shed and seed availability on the soil surface of most of the important weeds in these systems. Seed removal by *M. barbarus* ants was estimated to be around 72% of the weed seeds produced annually before crop harvest (Westerman et al. 2012). So, seed predation in these systems seems to be an effective strategy to decrease weed seed incorporation into the soil bank. Because it buries seeds, tillage stops weed seed predation since ants and most seed predators do not dig for buried seeds.

Though pre-harvest seed predation has been studied, post-harvest predation has seldom been addressed (but see Baraibar et al. 2009, Spafford Jacob et al. 2006) and many questions still remain regarding weed seed fate in this period. For example, seeds could be buried under the straw after cereal harvest and become less visible for ants, thus decreasing seed encounter rates by predators and consequently removal rates (Baraibar et al. 2011, Westerman et al. 2006, 2009). Similarly, the density of different seed species on the soil surface, including crop seeds, after crop harvest (seed environment or background seed density) may influence predation rates of different weed species since it can change ants' seed preference (Detrain et al. 2000, Lopez et al. 1993; Reyes-Lopez and Fernandez-Haeger 2002; Risch and Carroll 1986). Seed environment on the soil surface can also change ants' spatial exploration range (Detrain et al. 2000, Lopez et al. 1993). If resources are scarce, ants may explore a wider area of the field, whereas if seeds are available in high densities close to the nest, the area explored may be smaller and some seeds placed away from the nest may remain undiscovered and eventually enter the seed bank. Understanding seed predation magnitude after crop harvest and factors influencing it can help design management practices to try to maximize it.

In this study, we followed weed seed fate in a tilled *versus* a no-till area in three cereal fields during the summer fallow period. In the no-till areas, we measured seed predation rates of two weed species (presented in Petri dishes) and assessed the effects of straw on seed encounter and seed predation rates. We also measured seed background density to understand if the seed environment predators were experiencing during the summer influenced predation rates of our experimentally added seeds or ants' exploration behavior. In the tilled areas, we followed the fate of a known number of seeds after being buried. Our objective was to compare mortality rates of exposed *vs*. buried weed seeds during the summer fallow to inform our recommendations to farmers about weed seed management strategies during this period.

Materials and methods

Site. Experiments took place in the rain-fed cereal region of northeastern Spain. Mean annual temperature is 15°C and average rainfall is 342 mm (Agencia Estatal de Meteorología, 1983-2010) concentrated mainly in spring and autumn. Summers are hot and dry (average max. 31ºC) and winters are mild (average min. 2°C). Accumulated rainfall at the end of the summer of the experiment (2014) was between 31 and 118% higher than the average (120 to 214 mm more than average depending on the location). Three winter cereal fields were chosen, one in Algerri (41º 49' 13" N 0º 35' 34" E), one in Balaguer (41º 48’ 3”N 0º 45’ 45” E) and one in Vilanova de Bellpuig (41º 35’ 28” N 0º 58’ 44” E). The field in Algerri was organically certified and followed a three-year rotation of wheat (*Triticum aestivum* L.), spelt (*Triticum spelta* L.), and a mixture of oats and vetch (*Secale cereale* L. – *Vicia sativa* L.) for forage. The other two fields were farmed conventionally (not organically) and grew barley (*Hordeum vulgare* L.) as a monoculture. Algerri was the northernmost field, 100 m in altitude higher than the other two locations, and received considerably more rainfall than the other two. Based on climatology and the farmer’s schedule, cropping operations such as planting or tillage in Algerri occurred two weeks later than in the other two fields. The three fields were chisel plowed at a depth of 15-20 cm two times a year, once after crop harvest in June/July and again before crop sowing in October.

Experimental Design. Per field, two 50 x 50 meter areas were flagged. The two areas were separated by a 10 - 20 m strip. Two or three days after harvest, while the straw was still on the fields, seed predation was measured for 48 hours in one of the areas (called “no-till area”, see below for seed predation experiment details). After this first seed predation assessment took place, straw was removed and the entire field was chisel-plowed, except for the “no-till area” and the contiguous strip which was left untilled throughout the summer.

Weed Seed Fate in the No-till Area. Weed seed Predation. The no-till area was used to measure seed predation during summer. Two weed species were used, rigid ryegrass (*Lolium rigidum* Gaudin, 1.8 g per 1000 seeds) and catchweed bedstraw (*Galium aparine* L., 6.8 g per 1000 seeds). These species were chosen because they differ in weight, size, shape and preference by predators. If offered together, rigid ryegrass is highly preferred by harvester ants over catchweed bedstraw (Westerman et al. 2012). Rigid ryegrass seeds collected from areas close to the experiments were used for the first seed predation measurement date and seeds from Herbiseed (Reading, UK) were used for later dates. All catchweed bedstraw seeds were collected from local populations close to the fields.

To measure weed seed predation, 25 Petri dishes (9 cm diameter) per species were installed in the field (50 Petri dishes total). Each dish had two 15 mm-wide openings in the sides to facilitate predator access. Seeds of the two species were not mixed but each had their own Petri dish. Petri dishes from the same species were arranged 10 meters apart on two regular grids of 5 rows and 5 columns. Petri dish grids from the two species were five meters apart from each other (Fig.1). Seed removal was measured throughout the summer every 3 weeks from harvest in June until September (Table 1). Seed removal in Algerri was measured four times during summer while in the other two fields seed removal was measured five times.

On the first measuring date, 2 grams of each species were left on each of the dishes to resemble high weed seed densities immediately after harvest. Seeds were left in the field for 48 hours and then retrieved and weighed in the lab. Seeds returning from the field were dried before being weighed to ensure similar moisture contents before and after field exposure. The difference between the initial and the recovered weight was considered removed by predators. On this first date, right after cereal harvest, fields still had the straw arranged in lines every 10-15 m approximately, covering around 20% of the field area. Accordingly, 20% of the Petri dishes (10 random dishes per species) were placed under the straw lines, trying to keep the distance between dishes constant as much as possible. Straw layer was approximately 15 cm thick. Straw was removed by farmers two days after the first measuring date. In the subsequent measuring dates, 1 g of each species was used. Field days were chosen to avoid extreme weather conditions such as strong wind and heavy rain so seed weight removed could be attributed to seed predators and not to climatic conditions.

Seed Background Measurements. The same day that dishes were placed for the predation assessment, background seed density was measured in five random 1 m^2 quadrats using an insect suction sampler (Vortis insect suction sampler, Burkard Manufacturing Co. Limited, England). Sampled areas were noted in order to avoid double sampling the same area on later dates. Samples were taken to the lab and seeds were separated from dirt and straw using a set of sieves. Seeds were identified to species and counted. Seed background measurements were correlated to predation and dish encounter rates.

Harvester Ant Nest Density. In August, all *M. barbarus* ant nests in the no-till area were counted to get an estimate of predator density in each field. Once a nest had been counted, the area next to the entrance was sprayed with colored paint to prevent double counting. Nest density per hectare was calculated.

Ant Searching Activity. Ant searching activity was approximated by calculating the proportion of Petri dishes found by ants in each sampling date. Dishes were considered found if proportion of seeds removed was higher than 20% of the initial seed weight following Baraibar et al. (2011).

Weed Seed Fate in the Tilled Area. In the tilled area, 20 nylon bags per species (10 x 12 cm and 0.08 cm mesh size) were buried 6 cm deep. This depth was chosen because it is the depth where most of the seeds are buried after chisel cultivation (Mohler et al.

2006). Each bag contained 30 seeds of one of the species together with 200 cm^3 of soil. The goal of soil incorporation was to decrease the possibility of a fungal contamination from seed to seed (Van Mourik et al. 2005) and mimic real burial conditions, where seeds are usually mixed up with soil particles. Burial location was random within the 50 x 50 meter area. Bags were left buried throughout summer and were retrieved at the end of September or beginning of October (Table 1) based on the farmers’ intentions to till the fields. Bags were taken to the lab and frozen until they could be processed. Bag contents were washed using an elutriator (Wiles et al., 1996) and seeds were recovered using sieves and visual inspection. Recovered seeds were classified as either dead or alive. Dead seeds included those that had germinated (if we could still see the hypocotyl or the radicle), those that were decomposed and those non-viable (no visible signs of germination, dead embryo). Decomposed seeds could have decomposed after germination but we could not assess the causes of mortality for this group (10% of the seeds). Non-viable and alive seeds were separated by incubating them in a 1% triphenyl-tetrazolium chloride for 48 hours. Initial seed viability used to correct the results of viable seeds was 100% for rigid ryegrass and 96% for catchweed bedstraw.

Statistical Analyses.

Weed Seed Fate in the No-till area. Weed seed Predation. A Bayesian analysis framework with Markov Chain Monte Carlo (MCMC) techniques was adopted to estimate the proportion of seeds lost to predators. Bayesian inference is a method of statistical inference in which Bayes' theorem is used to update the initial probability for a hypothesis (prior) as more evidence or information becomes available. Because the dependent variable was a ratio, Bayesian methods seemed an appropriate approach to analyze the data. First, data exploration was applied following the protocol described in Zuur et al.

(2010) to investigate outliers, homogeneity, normality, zero trouble, collinearity, relationships, interactions and independence. Then, a beta distribution was used to model the ratio of predated weight and initial weight. This distribution is appropriate if the response variable is a continuous variable ranging from x_1 to x_2, with a logistic link function (Zuur et al. 2016). To account for the repeated measurements on the same Petri dish, a random intercept "station" term was added. Hence the following GLMM was used:

$$\text{Ratio}_{ij} \sim \text{beta}(\text{theta} * \text{Pi}_{ij}, \text{theta} * (1 - \text{Pi}_{ij}))$$

$$\text{Expected}(\text{Ratio}_{ij}) = \text{Pi}_{ij}$$

$$\text{Logit}(\text{Pi\_ij}) = \text{Date}_{ij} * \text{Weed}_{ij} + \text{Background}_{ij} + \text{Field}_{ij} + \text{Station}_i \quad \text{(equation 1)}$$

where Ratio_{ij} is the j^{th} observation at station i, and Station_i is a random intercept which is normally distributed with mean 0 and variance σ^2. Date, weed species and field were fitted as categorical variables. Field was treated as a fixed effect because of too few levels of the factor (Bayesian statistics require at least five levels to be able to consider an effect to be random, Zuur A. personal communication). Markov Chain Monte Carlo (MCMC) techniques were then applied to estimate the parameters in the model. Analyses were done with a program for Bayesian hierarchical models called JAGS (Plumer et al. 2016) via the package R2jags in R (R Core Team 2014). Diffuse normal priors were used. A prior is the probability distribution of the initial hypothesis. Because of no previous knowledge about the prior distribution, a normal distribution with large variance (diffuse) was used. A half-Cauchy (5) distribution was used for σ, and a half-Cauchy (25) for theta. Sigma and theta are shape parameters of the beta distribution. Three chains were used, each with a burn-in of 25,000 iterations (burn-in refers to the practice of discarding an initial portion of a Markov chain sample so that the effect of initial values on the posterior inference is minimized). The thinning rate was 10 (*i.e.* every 10th draw from the algorithm is actually used to compute credible sets and medians of the posterior distribution) and. 15,000 iterations were used for the posterior distribution of each parameter. Once the model was fitted, a model validation was applied to ensure normality and homoscedasticity of residuals. Estimated proportions of seed losses were later used to estimate long-term losses due to predation.

Long-term losses due to predation. Long-term losses due to predation were calculated in two separate ways. Both methods followed the models by Westerman et al (2003) and Davis et al (2011) but they differed on the seed availability used to base the calculations. Models were developed to estimate the annual proportion of newly produced weed seeds consumed by granivores ($\overline{Mp}$) before crop harvest. In these models,

$$\overline{Mp} = 1 - \overline{Sp} \qquad \text{(equation 2)}$$

with $\overline{Sp}$ the annual proportion of newly produced seeds that survive predation:

$$\overline{Sp} = \frac{\sum_{i=1}^{n}(Yi \prod_{i=j}^{k} Sj)}{\sum_{i=1}^{n} Yi} \qquad \text{(equation 3)}$$

These equations are used to estimate weed seed losses during weed seed rain. Consequently, annual seed production, Y, is divided into multiple pulses (Y_i) occurring within n periods of a specified length. Seeds from each pulse survive at the episodic rate S_j, where the k is the duration of the seed exposure. In our experiment, there was not any seed rain. Weed seed rain stopped with cereal harvest, so the only seeds available to predators were the ones present on the soil surface on the first sampling date (first measurement of background seed density). However, densities of seeds on the soil surface were so unexpectedly low that the model estimated losses to predation to be 100% four days after the start of the experiment, which was not supported by our background measurements, which showed rigid ryegrass seeds even on the last sampling date. So, we calculated long-term losses following equations 2 and 3 assuming that seeds offered in

Petri dishes (g) plus the background seed weight of rigid ryegrass and catchweed bedstraw on each sampling date constituted the seeds available in each date.

Straw Effect on Number of Dishes Encountered and Seeds Removed. The effects of the straw on the number of dishes found and the weight of seeds removed were analyzed using a GLMM with a binomial error distribution and a linear mixed model respectively. Fields and Petri dishes were treated as random effects and weed species and the presence/absence of straw as fixed effects. Seed weight was log (x+1) transformed before running the analysis. All analyses were performed using the lme package in R (R Core Team 2014).

Weed Seed Fate in the Tilled Area. The number of alive *vs*. dead seeds was analyzed using a GLMM with a binomial distribution of the error using R (R Core Team 2014). Weed species and field were entered as fixed effects while bag number was entered as a random effect. Here, field was considered a fixed effect to be able to compare mortality rates due to burial to mortality caused by predation for each field.

Results and Discussion

Weed Seed Fate in the No-Till Area. Data exploration did not indicate outliers or the presence of co-linearity. Mixing of the chains (a diagnostic tool to measure convergence of the model in Bayesian statistics) was good for all parameters, except for sigma (values were small indicating that the station effect was rather weak). Model validation did not indicate any model violations. The MCM output for equation 1 is shown in Table 2 following Zuur and Ieno (2016). The posterior mean of the fitted values and 95% credible intervals per field and weed combination for all dates are presented. Posterior means are the predicted values for seed predation rates, which are conditional on the observed data. There are no p-values in Bayesian statistics and significance of the factors cannot be determined from the table. However, since we were not comparing different treatments, the significances of each factor are not as important as the overall trend of removal rates. Table 2 provides the numerical output to estimate weed seed predation rates for each combination of weed, field, and date. Interpreting this numerical output can be challenging (Zuur and Ieno, 2016), so the fitted values are sketched in Figure 2 (minor random jittering was applied along the x-axis to ensure that points are not plotted on top of each other). The proportion of seed losses due to predation ranged from 20 to 80% per two days (Fig. 2). Main seed predators were probably *M. barbarus* harvester ants, which were present in high densities in those fields (340, 335 and 360 nests.ha^{-1} in Vilanova de Bellpuig, Balaguer, and Algerri, respectively). Granivorous mice are very scarce in the area and leave clear signs when they visit Petri dishes that were not seen in this experiment (i.e. droppings, seed chaff; Baraibar et al. 2009). Thus, rodents likely did not contribute to seed removal. We cannot exclude the possibility that birds were removing some seeds in our experiment. However, the few studies that have investigated seed losses due to bird predation show that they tend to be low during the summer (Holmes and Froud-Williams, 2005).

Predation rates were low in June and tended to increase after the beginning of July. Weed seed predation rates observed were in accordance with other studies in the region for the same time period (Baraibar et al. 2009), thus suggesting that seed removal patterns by harvester ants in this region are consistent over time. Low removal rates immediately following crop harvest had been already documented by Baraibar et al (2009). One of the possible causes for these low rates is background seed densities. Table 3 shows the density of crop and weed seeds recorded on each sampling date. Weed seed density was extremely low and most of the seeds present on the soil surface were crop seeds (barley or spelt grains). A significant negative relationship between background density and seed predation of our experimentally added seeds was observed in Algerri and Balaguer (R^2=0.54 and 0.6, p= 0.02 and 0.015, respectively). This relationship suggests that when crop seeds were abundant (*i.e.* right after harvest), harvester ants consumed them preferentially over weed seeds, and specially avoided less preferred seeds like catchweed bedstraw. Then, as crop seed density decreased, ants consumed more of the experimentally added weed seeds. Similarly, in these two fields we observed a negative correlation between background seed density and the proportion of dishes found although it was only significant in Balaguer (R^2=0.27 and 0.70, p=0.18 and 0.002, respectively), suggesting that ants foraged closer to the nest when resources were high (*i.e.* right after harvest) and shifted to search a wider area as resources became scarcer. This fact is in agreement with other studies that showed that *M. barbarus* foraging trails are shorter and more branched when seed availability is high (Lopez et al., 1993). In the third field (Vilanova de Bellpuig), which had the highest background seed density (Table 3), weed seed removal was not significantly correlated to background seed density or to the proportion of dishes found. The lack of correlation was mainly driven by what happened in the first sampling date, when seed availability on the soil surface was highest. Differently to the other fields, during harvest, the small chaff portion of the straw (together with weed and crop seeds) was dumped from the combine and left in several piles across this field. An average of up to 217 crop seeds and 25 rigid ryegrass seeds were counted in a 10 cm^3 volume taken from these mounds (data not shown). Those high-density areas did not occur in the two other localities and may have caused a change in ant’s foraging behavior (Detrain et al. 2000; Lopez et al. 1993). Ant trails consistently ended in the high-density piles, probably because this foraging strategy maximized resource acquisition (Detrain et al. 2000). The proportion of dishes encountered in this date and field was close to 100%, thus confirming that a larger area was explored but removal of weed seeds from the dishes was low, especially for the less preferred catchweed bedstraw seeds. These results suggest that crop seeds were ‘distracting’ ants from eating weed seeds, thus, weed seed predation rates may have been higher if the density of crop seeds on the soil surface had been lower. Avoiding cleaning out harvesting machinery in the field or careful adjustment of combines to prevent crop seed losses at the time of harvest may be two strategies to reduce the density of crop seeds on the soil surface and increase weed seed removal. Similarly, the use of machinery designed to grind weed seeds as they come out of the combine (*e.g.* Harrington seed destructor, Jacobs and Kingwell, 2016) could also decrease the amount of weed and crop seed returning to the soil surface after harvest and prompt ants to search a wide area of the field and be less selective on the weed seeds they harvest.

Contrary to our expectations, straw did not seem to be an obstacle for ants to locate or exploit weed seeds located underneath the straw on the first sampling date. Straw did not seem to be a barrier to ant movement and it did not prevent foraging or dish encountering. This result is encouraging because it means that seed losses to predation right after crop harvest are not being limited by straw and, thus, straw management by farmers does not require any changes (Spafford-Jacob et al. 2006).

Long-term seed removal rates. Long-term seed losses to predators calculated following equations 2 and 3 were 60, 65 and 62% for rigid ryegrass and 47, 55 and 44% for catchweed bedstraw in Vilanova de Bellpuig, Balaguer, and Algerri, respectively.

Westerman et al (2012) reported that 25 – 40% of rigid ryegrass seeds are shed at the time of harvest, thus, predation rates during the fallow period such as those reported here are likely to have a large impact on populations of this species. Losses may be even higher if combined with predation rates before harvest (0.67 for rigid ryegrass; Westerman et al. 2012). There is fewer information about seed shed timing of catchweed bedstraw in semi-arid systems. A close relative, false cleavers (*Galium spurium* L.), shed most of its seeds before harvest and had high levels of predation before the summer fallow (Westerman et al. 2012). Removal rates during the summer months could help decrease even further the amount of seeds of this species entering the seed bank.

Seed Fate in the Tilled Area. The interaction of the effects of weed species and field on seed mortality in the soil was significant. Proportions of dead seeds are shown per field and weed species separately in Figure 3. Seed mortality due to burial was highly variable across the fields and ranged from 52 to 58% for rigid ryegrass and from 24 to 50% for catchweed bedstraw. Rigid ryegrass seed mortality was significantly greater than for catchweed bedstraw seeds except in Vilanova de Bellpuig. Rigid ryegrass seed losses caused by burial were significantly higher in Vilanova de Bellpuig and Algerri compared to Balaguer, whereas catchweed bedstraw mortality was significantly higher in Vilanova de Bellpuig compared to the other two fields. Main causes of mortality also differed across fields. Whereas in Vilanova de Bellpuig germination was the most important cause of weed seed loss, in the other fields, and especially in Balaguer, seed decay was the main cause of mortality. Differences in causes of mortality were unexpected and remain unexplained as we lack information about soil properties and microbial activity in those fields. Future research should explore seed mortality due to decay during summer and main factors driving it, since it can largely contribute to weed seed mortality.

Seed mortality due to burial (germination plus decay) was unexpectedly high considering the relatively short period of time the seeds were buried (Boyd & Van Acker 2003, Chauhan et al. 2006). However, both species used are considered to have transient weed seed banks and a relatively low persistence in the field, which may partially explain the high losses observed (Barralis et al. 1988, Goggin et al. 2012; Jensen et al. 2009). High precipitation rates during this particular summer in all locations may have also prompted exceptionally high germination rates; this probably would not have occurred in a normal dry year. High moisture levels are also known to favor microbial activity and prompt seed decay (Wagner and Mitschunas, 2008), which could have further contributed to the high seed losses reported here. Survival rates in the soil of other important weed species in cereal systems with more persistent weed seed banks such as corn poppy (*Papaver rhoeas* L.) or common lambsquarters (*Chenopodium album* L.) should be expected to be higher than those reported for rigid ryegrass and catchweed betstraw and thus, extending seed exposure to predators may be even more important to decrease those species' seed banks.

Overall, the results of this experiment showed that long-term seed losses due to predation were higher than those caused by seed burial. This suggests that tilling the field immediately after crop harvest would have resulted in higher weed seed survival rates compared to leaving seeds on the soil surface exposed to predators. Both for transient and for more persistent weed seeds, leaving the fields untilled throughout the summer and maximizing seed exposure to predators seems to be the optimum weed management strategy during the fallow period in these systems. Decreasing the density of crop seeds on the soil surface by carefully adjusting the harvesting equipment has the potential to increase weed seed mortality to predation even further.

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Table 1. Harvest date; bag burial and recovery dates (number in parentheses indicates the number of days seeds were buried); and date when weed seeds were placed on each field to estimate predation rates (seeds were left 48h and retrieved).

Field	Harvest date	Bag burial and recovery* dates	Seed placement dates to estimate predation
Vilanova de Bellpuig	5/06/2014	22/07/2014	6/06/2014
			8/7/2014
			29/07/2014
			25/08/2014
		* 29/09/2014 (68 days)	18/09/2014
Balaguer	7/06/2014	4/07/2014	11/06/2014
			8/07/2014
			29/07/2014
			25/08/2014
		*6/10/2014 (93 days)	18/09/2014
Algerri	21/06/2014	28/07/2014	8/07/2014
			29/07/2014
			25/08/2014
		* 19/09/2014 (54 days)	18/09/2014

Table 2. Posterior mean values, standard errors and 95% credible intervals for the posterior mean values per field, date, and weed species and the interaction between date and weed species (*). Sigma and theta are shape parameters of the beta distribution.

	Estimated mean	*se*	*Credible intervals*	
			2.5%	*97.50%*
(Intercept)	-0.39	0.23	-0.84	0.05
Date 2	-0.67	0.25	-1.16	-0.18
Date 3	0.10	0.26	-0.40	0.62
Date 4	0.59	0.25	0.10	1.09
Date 5	1.61	0.26	1.09	2.13
L. rigidum	0.16	0.27	-0.37	0.70
Field Balaguer	0.28	0.13	0.04	0.53
Field Vilanova	-0.11	0.13	-0.36	0.15
Background	0.20	0.06	0.08	0.31
Date 2 * *L. rigidum*	0.88	0.35	0.19	1.56
Date 3 * *L. rigidum*	0.67	0.35	-0.02	1.37
Date 4 * *L. rigidum*	0.39	0.35	-0.30	1.07
Date 5 * *L. rigidum*	-0.12	0.34	-0.79	0.55
sigma.st	0.06	0.05	0.01	0.17
theta	0.43	0.02	0.40	0.47

Table 3. Background seed density. Crop, rigid ryegrass, and total seed density (seeds m^{-2}) in each field and sampling date.

Field name	**Date**	**Crop seeds/m^2**	**Rigid ryegrass seeds/m^2**	**Total seeds/m^2**
Vilanova de Bellpuig	06/06/2014	77.8	18.4	96.2
	08/07/2014	6.8	0	6.8
	31/07/2014	45.8	3.6	49.4
	25/08/2014	4	0	4
	18/09/2014	13.4	13.2	26.6
Balaguer	11/06/2014	17.6	0	17.6
	08/07/2014	20.6	0	20.6
	29/07/2014	3.2	0	3.2
	25/08/2014	9	1.4	10.4
	18/09/2014	0	0	0
Algerri	08/07/2014	69.6	2.8	72.4
	29/07/2014	18.8	2.6	21.4
	25/08/2014	3	1.6	4.6
	18/09/2014	0.4	5.2	5.6

Figure 1. Schematic drawing of the location of the Petri dishes in the no-till area. Black dots represent Petri dishes filled with rigid ryegrass seeds and white dots represent dishes with catchweed bedstraw seeds.

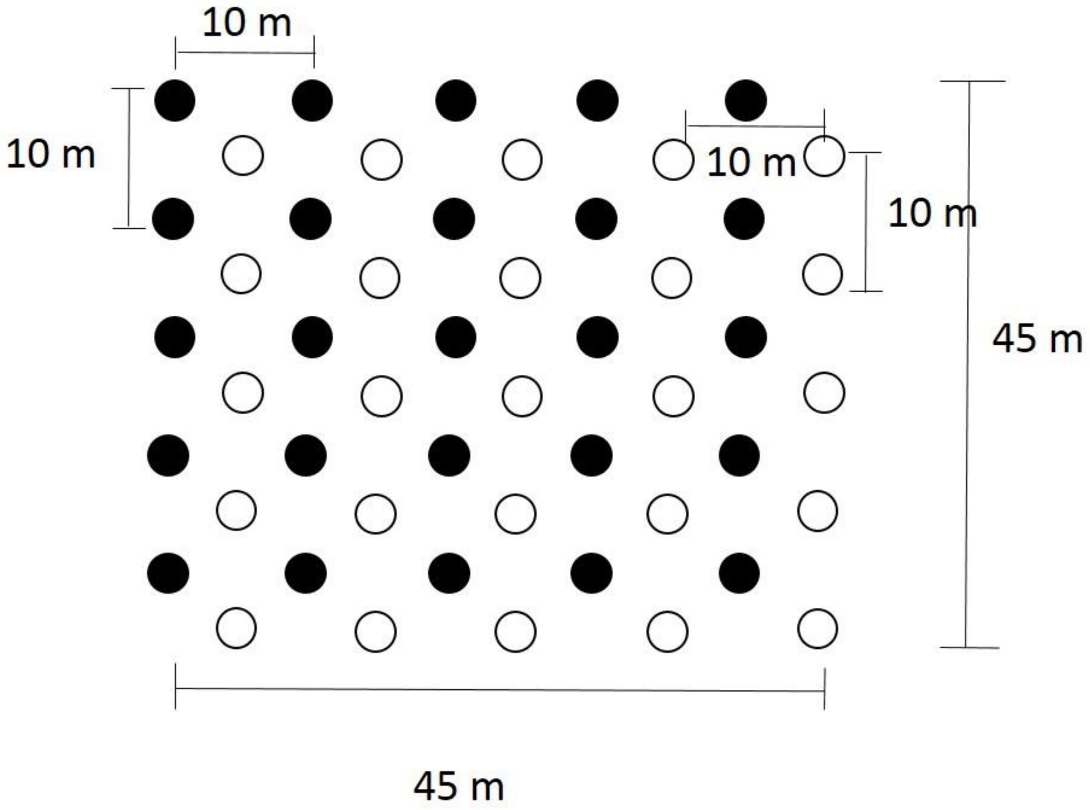

Figure 2. Estimated proportion of seeds removed for each species (rigid ryegrass and catchweed bedstraw) during 48-hour intervals in each field (Vilanova de Bellpuig, Balaguer and Algerri). Dashed lines represent the 95% credible intervals for the posterior mean values.

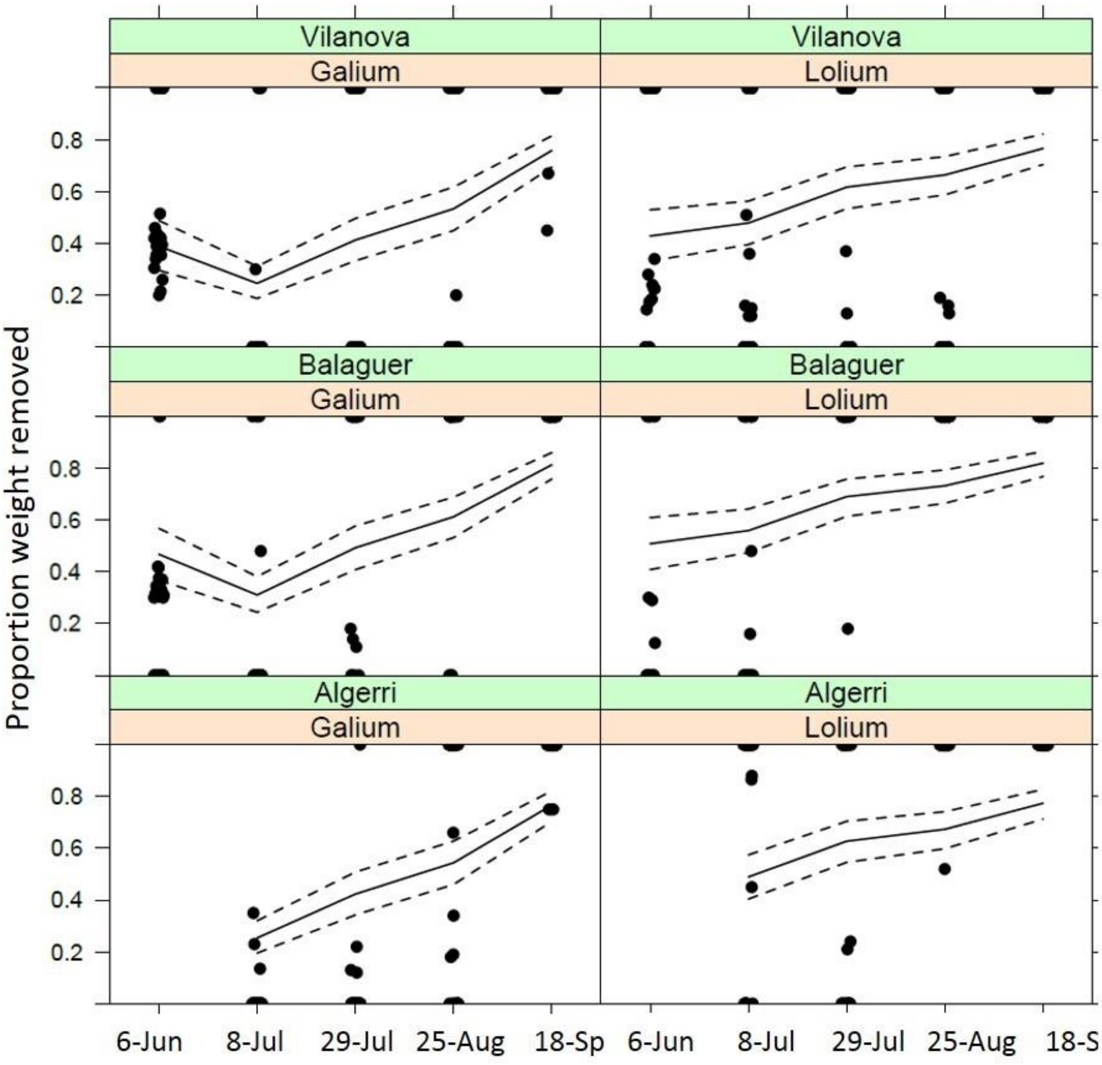

Figure 3. Seed losses due to germination (black), decay (dark gray) and to unknown causes (light gray) for every field and weed species. Bars represent standard errors. Bars with different letters are significantly different with P<0.05.