

Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators

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Summary

1. Agricultural intensification can cause a huge increase in productivity. However, associated costs in terms of reduced, self-regulation and increased reliance on external inputs for the control of pests, diseases and weeds are seldom taken into account or acknowledged. A pro-active approach in which ecosystems services are documented and potential effects of changes in agricultural practices evaluated may lead to more informed decisions prior to implementation.

2. We investigated the effects of management of cereal production in a semi-arid region on weed seed mortality caused by predators. Seed losses have a greater impact on weed population size than any other life cycle process and should therefore be of significance for natural weed control. We hypothesized that the conversion from rain-fed to irrigated production should lead to reduced and the adoption of no-till techniques to increased seed predation.

3. Seed removal and seed predator populations were monitored in irrigated ($N = 3$) and rain-fed cereal fields ($N = 6$) and field margins. Of the dryland fields half was conventionally tilled and the other half no-till. Seed removal ($\text{g g}^{-1} 2\text{-days}^{-1}$) was followed from April 2007 until June 2008, using Petri-dishes and enclosure cages. Populations of harvester ants were estimated by direct nest counts; rodent populations by Sherman live traps.

4. Seed removal in dryland cereals, mainly by harvester ants *Messor barbarus* was high from mid April to mid October, and should cause a strong weed suppressive effect. Seed removal in irrigated cereals, mainly by granivorous rodents *Mus spretus*, was low.

5. Seed removal was higher in no-till than in conventional fields and corresponded to differences in harvester ant nest densities.

6. *Synthesis and applications.* Our results show that tillage and irrigation in a semi-arid cereal production system results in a reduction and total annihilation of granivorous harvester ants, respectively. The concurrent decline in weed seed mortality could lead to increased herbicide use and dependency. In particular, in areas where economic margins are small or the environmental costs of tillage and irrigation high, the increased costs of chemical weed control may exceed the benefits. Here, preserving biodiversity to enhance natural weed control is a viable alternative to agricultural intensification.

Key-words: weed seed predation, soil management, irrigation, harvester ants, granivorous rodents, habitat management, functional diversity

Introduction

Seventy to 99% of the weed seeds produced in arable fields do not emerge as seedlings nor can they be recovered from the soil bank the next season (Cardina & Norquay 1997; Gerowitt

& Bodendörfer 1998). Seed predation seems to be responsible for the larger part of these losses (Westerman *et al.* 2003a) and therefore contributes substantially to weed control. When combined with other (non-chemical) control tactics, seed predation may foster reductions in herbicide use (Westerman *et al.* 2005) and thus cut environmental and monetary costs.

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Much of the above-mentioned research was done in temperate climates. Little is known about weed seed losses due to predation in the semi-arid regions, or how these losses are influenced by factors related to cropping system or production intensity. Crop management practices in semi-arid cereal production in north-eastern Spain are changing in two important ways. First, the area that is irrigated will soon double due to an expansion of the irrigation channel network. Secondly, there is an increasing rate of adoption of minimum- and no-till in the remaining rain-fed dryland. Both changes may affect natural weed control by seed predators. The primary goal of this study was to estimate seed removal by predators in cereals and to evaluate the potential consequences of changes in crop management on natural weed control. Seed removal by predators was followed over time in irrigated and dryland cereals, of which half was conventionally tilled and the other half was managed without tillage (no-till).

The two main groups of seed predators in Spain, namely harvester ants *Messor* spp. and granivorous rodents, *Mus spretus* Lataste and *Apodemus sylvaticus* L. (Díaz 1992a,b), differ considerably in habitat requirements and in activity patterns, and it is therefore likely that they will respond differently to the pending changes in cereal crop management. Irrigation, in particular inundation, will affect survival chances of both harvester ants and rodents as nests, burrow systems and underground storage chambers are periodically flooded. In dryland areas, however, water shortage during summer may limit rodent numbers and activity. Tillage, in particular mouldboard ploughing, can damage the nests of harvester ants (Díaz 1991) and the burrow systems of rodents (Loman 1991), and redistribute weed seeds stored in superficial chambers. Harvester ant activity is limited to the April–November period due to temperature constraints (Cerdá & Retana 1994); peak activity is in May to mid-June, which coincides with the period of weed seed shed. Rodents are active all year round, but peak activity in cereals occurs in spring (Watson *et al.* 2003; Westerman *et al.* 2003a). A second objective was to determine if and how tillage and irrigation influence the activity of the predators by determining the relative importance of vertebrates and invertebrate in seed removal using appropriate enclosures.

During disturbances, such as tillage, irrigation or harvest, non-crop areas can provide refuges to seed predators. Seed predation by rodents is closely related to canopy cover (Díaz 1992a; Heggenstaller *et al.* 2006). Rodents resort to vegetated field margins to avoid disturbances and bare soil (Tattersall *et al.* 2001) or use field margins as a permanent habitat while foraging in crop fields. Seed removal will thus vary within fields and is expected to be higher near vegetated field margins than farther away. Similarly, harvester ant densities and their seed harvesting activities have been reported to be higher outside crop fields (Díaz 1991, 1992b). However, harvester ants prefer open and dry habitats (Azcarate & Peco 2003), which are more abundant in the field than outside the field. It is therefore unclear if and how much harvester ants will benefit from refuges in field margins. The third and final objective of this study was to evaluate the importance of field

margin vegetation as refuges for seed predators by analysing the spatial variability in seed removal and by comparing predator densities between field margin and interior.

Methods

Trials were conducted in commercial barley *Hordeum vulgare* L. and wheat *Triticum aestivum* L. fields in Vilanova de Bellpuig (Lleida), in the Ebro-Segre valley in north-eastern Spain. Average annual temperature is 14.7 °C (1971–2000; Agencia Española de Meteorología 2008), and average annual rainfall is 369 mm, concentrated in spring and autumn. Summers are hot (average max. 33 °C) and winters mild (average min. 0 °C). The year 2007 was average regarding temperatures and rainfall, but 2008 was not; it was characterized by an extremely dry winter (20–50 mm; December 2007–February 2008), compared to the 29-year average (1961–1990) of 60–80 mm, followed by unusually high rainfall in spring, (200–250 mm; March–May 2008), compared to the 29-year average of 100–140 mm (Servei Meteorològic de Catalunya 2008). This resulted in poor crop establishment, little or no tillage, stunted crop growth and abundant summer weed growth.

An irrigation channel runs through the area, providing irrigation to fields to the west of the channel. In the eastern dryland area, the average field sizes are 20 ha and the main crops are barley, olive *Olea europaea* L. and almond *Prunus amygdalus* L. The irrigated fields are about 4.5 ha and the main crops are alfalfa *Medicago sativa* L., maize *Zea mays* L., and orchards [peaches *Prunus persica* (L.) Batsch, apples *Pyrus communis* L. and pears *Malus domestica* Borkh.]. Three irrigated and six rain-fed barley or wheat fields were used in both 2007 and 2008 (Supporting Information, Table S1). Different fields were used in the 2 years, except for one pair of dryland fields (nos 1A and 1B), which was used in both years. In 2007, barley in the irrigated area was followed by a late sunflower *Helianthus annuus* L. crop, sown between 1 and 11 July 2007 and harvested in late October. Between June and October, dryland fields were left fallow.

In the dryland area, three pairs of adjacent fields were chosen such that one was no-till (A) and the other conventionally tilled (B) (2007, 1A and B, 2A and B, 3A and B; 2008, 1A and B, 7A and B, 8A and B; Supporting Information, Table S1). Conventional tillage included one tillage operation soon after harvest (cultivator, 15–20 cm working depth) and another either in late summer or in October–November just before sowing. All fields were planted to barley in both years, using direct drilling. The most abundant weed species in May 2007 were *Papaver rhoeas* L., *Lolium rigidum* Gaudin and *Filago pyramidata* L. (5, 4 and 1 plants m⁻², respectively) in the conventional fields, and *Herniaria hirsuta* L., *L. rigidum* and *P. rhoeas* (15, 9 and 7 plants m⁻², respectively) in the no-till fields.

In 2007, all fields in the irrigated area (field nos 4, 5 and 6) were planted to barley. No irrigation was required, but the sunflower crop received between 120 and 180 L m⁻², depending on the field, on two or three irrigation dates (15 July, 15 August and 6 September 2007). In 2008, fields were planted to wheat (field nos 9 and 10) or barley (field no. 11). All fields received 120 L m⁻² divided over two irrigation dates (field no. 9, 3 April, 10 May; field no. 10, 3 April, 6 May; field no. 11, 27 March, 7 May). The most abundant weed species were *Cynodon dactylon* (L.) Pers., *Capsella bursa-pastoris* (L.) Medic. and *Poa annua* L. (60, 44 and 9 plants m⁻², respectively). The survey was based on field nos 4 and 6 conducted in May 2007.

Herbicides were used in all fields, except field nos 2A and 3A (Supporting Information, Table S1). In sunflower, herbicides [in grams of active ingredients (a.i.) per hectare] were applied in July

(1500 g a.i. ha⁻¹ glyphosate + 400 g a.i. ha⁻¹ MCPA) and August (1200 g a.i. ha⁻¹ Aclonifen).

EXPERIMENTAL DESIGN

Seed predation was measured as the percentage seed removal from Petri dishes in 24–25 locations (stations) per field over a 2-day period. Stations were arranged 10 m apart, on a regular grid of 3 rows × 8 columns (field nos 3, 4, 5, 8), 4 rows × 6 columns (field nos 6, 9 and 11), or 5 rows × 5 columns (field nos 1, 2, 7 and 10), depending on the dimensions of the field, such that stations were at least 10 m from the field edge. Where the grid was located close to vegetated field margins (10 m) additional stations were placed in the margins parallel to the grid. In the dryland area, pairs of no-till and conventional fields shared a common field margin, except field nos 2A and 2B, which were separated by a road. In the irrigated area, additional stations were placed along two field margins in field nos 5 and 6, and along a single field margin in the other fields (nos 4, 9, 10, and 11). In the dryland fields, margins consisted typically a 50-cm strip or a small stony fence with a sparse vegetation (*L. rigidum*, *Avena sterilis* L., *P. rhoeas*, *Fumaria officinalis* L.) and an occasional olive or almond tree. In the irrigated fields, margins were typically wider (±1 m), elevated and had a lush and more diverse vegetation frequently with trees (*Juglans regia* L.), shrubs (*Rubus ulmifolius* Schott) or reed [*Phragmites communis* (Cav.) Trin ex Steudel]. Species common to all fields were; *Galium aparine* L., *Elytrigia repens* (L.) Desv., *Convolvulus arvensis* L. and *Equisetum ramosissimum* Desf.

Each station harboured two 9-cm diameter Petri dishes, containing the seeds, designed to estimate either vertebrate or invertebrate seed removal (treatment), modified after Díaz (1992a,b). The vertebrates dish was placed in a 14 cm diameter dish on top of a 20 cm high plastic tube, which was coated with fluon (Polytetrafluoroethylene, BioQuip Products Inc., Rancho Dominguez, CA, USA) to prevent insects from climbing up. The bottom of the tube was pushed into the soil. The invertebrate dish had four 1.5 cm wide openings in the sides to facilitate insect entrance, and was covered with a 1 cm mesh plastic or metal cage (10 × 11 × 3 cm) and nailed to the soil. During each exposure, dishes started with 2 g of non-treated *Lolium multiflorum* Lam. (3.95 ± 0.033 mg seed⁻¹) and 2 g of *Vicia villosa* Roth seeds (31.3 ± 0.239 mg seed⁻¹) (Semillas Battle, Bell-lloc, Spain). We intended to use seeds of one prevalent monocotyledon and dicotyledon weed species, but given the quantities needed (> 20 kg), our choice was limited to commercially available seeds. *L. multiflorum* was chosen as a substitute to *L. rigidum* (2.09 ± 0.02 mg seed⁻¹), although seed weight was half that of *L. multiflorum*. *V. villosa* was thought representative of round-seeded dicotyledon weed species, such as *V. peregrine* L., *V. sepium* L., *Galium aparine* L., or *Convolvulus arvensis* L. After exposure, the remaining seeds were retrieved and weighed. In cases where seeds became wet due to rainfall or dew, they were dried for at least 4 h at 40 °C. Estimates based on seed weight were expected to yield similar results as estimates based on seed number, because (i) harvester ants remove entire seeds; (ii) rodents usually only leave chaff and seed coats behind; and (iii) partial seed consumption caused by carabids and other invertebrates was negligible, because invertebrates other than ants were rare or their role in predation was marginal (see Results). Sampling occurred once per month between April 2007 and June 2008, but was interrupted from October–December 2007 to facilitate winter cereal planting (seed bed preparation, sowing and herbicide application) and in May 2008, when excessive rainfall prevented meaningful observations. Dishes were removed and re-installed within a 3- to 4-week period to

accommodate harvest, tillage, herbicide applications and irrigation. Because sunflower crop establishment in field no. 6 was very poor and results no longer comparable to the other fields, this field was abandoned prematurely (16 August 2007).

We assumed that seeds that were removed from the dishes were actually consumed, or stored and consumed later; once inside harvester ant nests, seeds have a low survival probability (Levey & Byrne 1993). Vertebrate dishes frequently contained damaged seeds, piles of husks, and rodent faeces, characteristic of consumption by small rodents. Trials conducted during heavy rain or strong wind were discarded and repeated under more favourable weather conditions. Control dishes, to assess the amount of seeds lost due to wind, rain, or handling, would require the exclusion of ants, which is possible only by using an extremely fine mesh exclusion cage. However, fine mesh cages would obstruct rain and wind, leading to a potential underestimation of background seed losses. Controls were therefore deemed useless and not included.

SEED PREDATOR IDENTITY

Rodents were sampled using Sherman live traps, and invertebrates were sampled using pitfall traps. However, insect catches were not processed. In the dryland fields, carabid beetle numbers were negligible and harvester ants were the main invertebrate seed predator. Pitfall traps are unsuitable to estimate harvester ant densities, because these ants forage in columns, which may or may not cross a pitfall trap, resulting in either extremely high numbers or zero animals per trap. We therefore changed the sampling strategy to counting harvester ant nests complemented by a qualitative estimation of nest size (see below). In the irrigated fields, carabid beetles, mainly *Harpalus* (syn: *Pseudoophonus*) *rufipes* (Degeer), were the most abundant granivorous invertebrates. However, seed removal by invertebrates was negligible (see Results). No further reference will be made to the pitfall traps.

Sherman traps were set up in fields (and field margins) at each of the stations used for seed removal (minimum of 24 traps per field). Traps were baited with dough (wheat flour, oats, peanut butter, water and oil). Synthetic cotton-wool was added as nesting material. Trapping was done around new moon when the movement of rodents was least impaired by moonlight (Díaz 1992a; Plesner Jensen & Honess 1995). Three to 4-day trapping sessions were conducted in 2007 in the periods 27 May–1 June and 5–11 August (dryland fields) and 11–14 June and 5–11 August (irrigated fields). Cereal crops had not been harvested at the time of the June trapping session, but had been harvested at the time of the August session. Sunflower was present during the August session in the irrigated fields. The percentage of rodent recaptures always exceeded 50% after 3–4 nights. Rodents were identified, weighed, sexed, ear-tagged, and released. Rodent captures were standardized to number of captures per trap-night.

Harvester ant densities were approximated by counting nests of *Messor* spp. in each 10 × 10-m square within the sampling grid on 4 October 2007 during the release of the reproductives (MacMahon, Mull & Crist 2000). Squares between field edge and the first row of stations (0–10 m) were designated 'field edge'. Densities were standardized to nests per hectare. Nest size was estimated as the surface area occupied by openings created by workers to facilitate release of the reproductives (queens and males). This measure was based on the assumption that the larger the colony, the more reproductive adults would be produced and the more openings would be required for their release. Four size categories were distinguished: 1 (< 0.4 m²), 2 (0.4–1 m²), 3 (1–2 m²) and 4 (> 2 m²).

STATISTICAL ANALYSIS

Effect of predator, irrigation and tillage on seed removal

Only results from stations in the field interior were used. A linear mixed regression model was used to describe weight loss of total exposed seeds (4 g) as a function of (i) area (dryland, irrigated), (ii) predator type (invertebrate, vertebrate), and (iii) sampling date (April–October). A preliminary analysis had indicated a highly significant interaction between area and the other factors ($P < 0.01$), and therefore, analyses were conducted for irrigated and dryland fields separately. Soil management (conventional tillage, no-till) was added as an explanatory variable in the analysis of the dryland fields.

Effect of location on seed removal

The results obtained from field margins were included. A linear mixed regression model was used to describe seed loss as a function of (i) location (field margin, field interior), (ii) predator type, and (iii) sampling date. Analyses were done separately for the irrigated and dryland areas. Results from the conventional and no-till fields within a dryland pair were pooled and compared to seed removal in the shared field margin. Field nos 2A and 2B had no common field margin and were excluded. A further spatial analysis comparing removal rates at different distances from the field margin indicated that removal was uniform within the crop fields (not shown).

In both regression models, a logit-link and a binomial variance function that allows for overdispersion were used. Random effects were fields, stations, treatments, and time. The random effect caused by repeated measurements on the same location was included in the lowest stratum. The models were fitted to the data using Iteratively Reweighted Restricted Maximum Likelihood (IRREML; Keen & Engel 2005) in GENSTAT (version 10). Because different fields had been used in 2007 and 2008, analyses were conducted for the 2 years separately.

Results

SEED PREDATOR IDENTITY

In the dryland fields, harvester ant *Messor barbarus* L. nests density was higher in no-till than in conventional fields (Table 1), but differed between pairs (contingency table; $\chi^2 = 125$; d.f. = 2; $P < 0.01$). This difference was unrelated to the number of years of no-till, namely 15 years for field no. 1B, and 3 years for field nos 2B and 3B. Size distribution was the same for conventionally tilled and no-till fields ($\chi^2 = 3.20$; d.f. = 3; $P = 0.361$); 55%, category 1; 30%, category 2; 13%, category 3; and 3%, category 4. On average, nest density was higher in the field interior (417 ha⁻¹) than in the field margin

Table 1. Numbers of *Messor barbarus* nests per hectare in dryland fields as affected by soil management

Conventionally tilled		No-till	
Field no.	Nests ha ⁻¹	Field no.	Nests ha ⁻¹
1A	313	1B	444
2A	181	2B	619
3A	200	3B	643

(0–10 m; 362 ha⁻¹), suggesting that harvester ants avoided field edges.

Mus spretus was the main vertebrate predator in dryland fields. Birds, mainly pigeons, did not enter the fields until after crop harvest and can thus not be responsible for the observed vertebrate seed removal in May and June (see below). However, we cannot exclude the possibility that birds were removing some seeds in our trials. On both trapping sessions, rodents were more frequently captured in the margin than in the field interior; June 2007, 0.26 and 0.05 animals trap-night⁻¹, respectively; August 2007, 0.17 and 0.0 animals trap-night⁻¹, respectively. We noticed large numbers of burrow entrances in the field margins.

In irrigated fields, the main vertebrate predator was *M. spretus*; only two *A. sylvaticus* (field nos 4 and 6) were caught, and therefore, rodent captures were pooled (0.68 animals trap-night⁻¹). Equal numbers of rodents were caught in the margin and field interior in June (0.35 and 0.32 animals trap-night⁻¹, respectively), but more animals were trapped in the field margin than in the interior in August (0.69 and 0.09 animals trap-night⁻¹).

SEED REMOVAL IN DRYLAND FIELDS

Predator type and effect of tillage

Seed removal in dryland cereal fields was significantly higher in no-till than in conventional fields in 2007, but not in 2008 (Fig. 1; Table 2A). Seed removal was higher for invertebrates than vertebrates (2007, 58% and 5%; 2008, 13% and 3%, respectively). Seed removal rates by invertebrates were high in spring, variable in summer, with peaks in June and August and troughs in July and September, and low in winter (Fig. 1A). The trough in July may have been caused by harvest in June, which affected seed removal in conventional fields more than in no-till fields. The lower seed removal rates in September may have been caused by the fact that harvester ant colonies enter the reproductive phase, which requires most of the colony's resources and time (Díaz 1992b). After release of the reproductives in early October, invertebrate removal rates resumed normal levels. Invertebrates removed significantly more seeds from no-till than from conventional fields in April, May, July and August 2007, and in April 2008, while seed removal was higher in conventional than in no-till fields in June 2008 only (Fig. 1A).

Seed removal rates by vertebrates were high in April 2007 and low during the remainder of the period (1–7%), except for a small peak in June 2007 (20%) (Fig. 1B). There were no differences in vertebrate seed removal rates between no-till and conventionally tilled fields. Vertebrate seed removal during April–June in 2007 was higher than during the same period in 2008, and may have been caused by poor crop development in 2008.

Effect of location

In dryland cereals, similar amounts of seeds were removed from the field interior and margin, except in April 2007 when

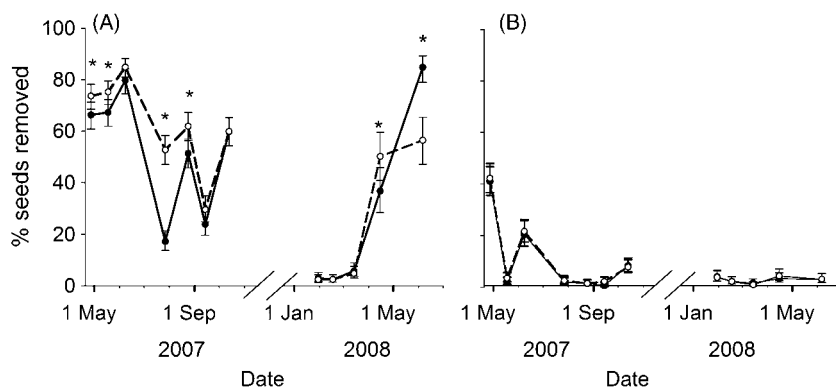


Fig. 1. Percentage of seeds removed by invertebrates (A) and vertebrates (B) in no-till (---) and conventionally tilled fields (—) in dryland. Asterisks indicate significant differences in seed removal between tillage systems. Bars represent 95% confidence intervals around the mean.

Table 2. The effects of tillage (conventional or no-till), predator type (invertebrate or vertebrate) and sampling time (month) on the amount of seeds removed from (A) dryland cereal fields and (B) irrigated cereal fields (generalized linear mixed model, IRREML; Wald statistics and *P* value)

Fixed term	2007				2008			
	Wald	d.f.	Wald/d.f.	<i>P</i>	Wald	d.f.	Wald/d.f.	<i>P</i>
(A)								
Tillage	61.37	1	61.37	< 0.001	1.09	1	1.09	0.295
Predator	1194.24	1	1194.24	< 0.001	551.45	1	551.45	< 0.001
Month	1353.32	6	225.55	< 0.001	756.06	4	189.01	< 0.001
Tillage × predator	5.21	1	5.21	0.023	0.51	1	0.51	0.475
Tillage × month	34.91	6	5.82	< 0.001	61.71	4	15.43	< 0.001
Predator × month	328.91	6	54.82	< 0.001	272.43	4	68.11	< 0.001
Tillage × predator × month	32.87	6	5.48	< 0.001	11.41	4	2.85	0.022
(B)								
Predator	107.35	1	107.35	< 0.001	4.83	1	4.83	0.028
Month	481.05	6	80.18	< 0.001	110.65	4	27.66	< 0.001
Predator × month	152.74	6	25.46	< 0.001	21.77	4	5.44	< 0.001

Table 3. The effects of location (field margin or field interior), predator type (invertebrate or vertebrate) and sampling time (month) on the amount of seeds removed from (A) dryland fields and (B) irrigated fields (generalised linear mixed model, IRREML; Wald statistics and *P* value)

Fixed term	2007				2008			
	Wald	d.f.	Wald/d.f.	<i>P</i>	Wald	d.f.	Wald/d.f.	<i>P</i>
(A)								
Location	4.14	1	4.14	0.042	0.87	1	0.87	0.352
Predator	820.64	1	820.64	< 0.001	713.83	1	713.83	< 0.001
Month	717.55	6	119.59	< 0.001	822.9	4	205.72	< 0.001
Location × predator	0.01	1	0.01	0.918	2.46	1	2.46	0.117
Location × month	15.34	6	2.56	0.018	22.08	4	5.52	< 0.001
Predator × month	223.74	6	37.29	< 0.001	286.72	4	71.68	< 0.001
Location × predator × month	5.54	6	0.92	0.477	9.28	4	2.32	0.054
(B)								
Location	34.1	1	34.1	< 0.001	298.56	1	298.56	< 0.001
Predator	48.74	1	48.74	< 0.001	12.6	1	12.6	< 0.001
Month	477.18	6	79.53	< 0.001	13.67	4	3.42	0.008
Location × predator	19.51	1	19.51	< 0.001	20.81	1	20.81	< 0.001
Location × month	41.23	6	6.87	< 0.001	85.21	4	21.3	< 0.001
Predator × month	200.67	6	33.44	< 0.001	38.43	4	9.61	< 0.001
Location × predator × month	18.15	6	3.02	0.006	132.52	4	33.13	< 0.001

more seeds were removed from the field interior than from the margin (invertebrates, 76% and 41%, respectively) (Table 3A; Fig. 3A), and in March and April 2008 when more seeds were removed from the field margin than from the interior (March,

vertebrates, 8% and 1%, respectively; Fig. 3C), (April, invertebrates, 73% and 43%, respectively; Fig. 3A). Vertebrate seed removal rates did not correspond to rodent numbers; on both trapping sessions, rodents were more frequently captured in

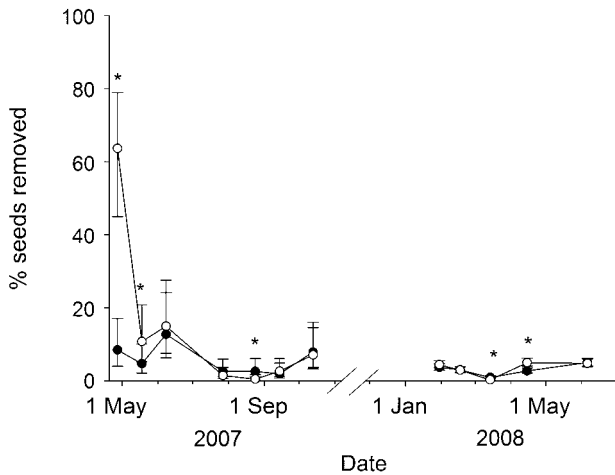


Fig. 2. Percentage of seeds removed by vertebrates (○) and invertebrates (●) in irrigated fields. Asterisks indicate significant differences in seed removal between vertebrate and invertebrate predators. Bars represent 95% confidence intervals around the mean.

the margin than in the field interior, while seed removal rates were similar in both June and August 2007 (Fig. 3C). Apparently, rodents used the field interior only for foraging, while they nested in the margins.

SEED REMOVAL IN IRRIGATED FIELDS

Predator type

Seed removal in irrigated fields was significantly influenced by predator type, sampling date and their interaction (Table 2B). Seed removal rate was high in April 2007 and low thereafter (Fig. 2). Vertebrates removed significantly more seeds than invertebrates in April (2007, 64% and 8%; 2008, 5% and 3%)

and May (2007, 11% and 5%, respectively). The peak in vertebrate activity in spring was not repeated in 2008 due to poor crop development in 2008. However, there may have been a peak in seed removal by vertebrates in May 2008, which we did not detect due to excessive rain. Invertebrates removed more seeds than did vertebrates in August 2007 (3% and 1%) and in March 2008 (1% and < 1%, respectively), but in both cases, the effect was minimal.

Effect of location

In the irrigated fields, vertebrate and invertebrate predators removed significantly more seeds from the field margin than from the field interior on almost all dates in both years (Table 3B; Fig. 3B,D). However, vertebrates removed equal numbers of seeds from field margin and interior during the April–June period when the crop canopy was well developed (Fig. 3D). Here, differences in seed removal rate (Fig. 3D) corresponded well with differences observed in rodent numbers: there were similar rates and numbers in the field margin and interior in June, but higher rates and numbers in the field margin than in the field interior in August. It seems that in irrigated fields, rodents retreated to the field margins after crop harvest and remained there over winter. Field margins were important to invertebrates, probably carabids, during the entire year.

Discussion

Seed predation assays, such as those used in this study, can yield valuable information as to when and where seed predators are active and which type of predator is active (Westerman *et al.* 2003b). The interpretation of the outcome of these assays in terms of total seed loss is more complicated but necessary to evaluate the potential impact on weed population dynamics.

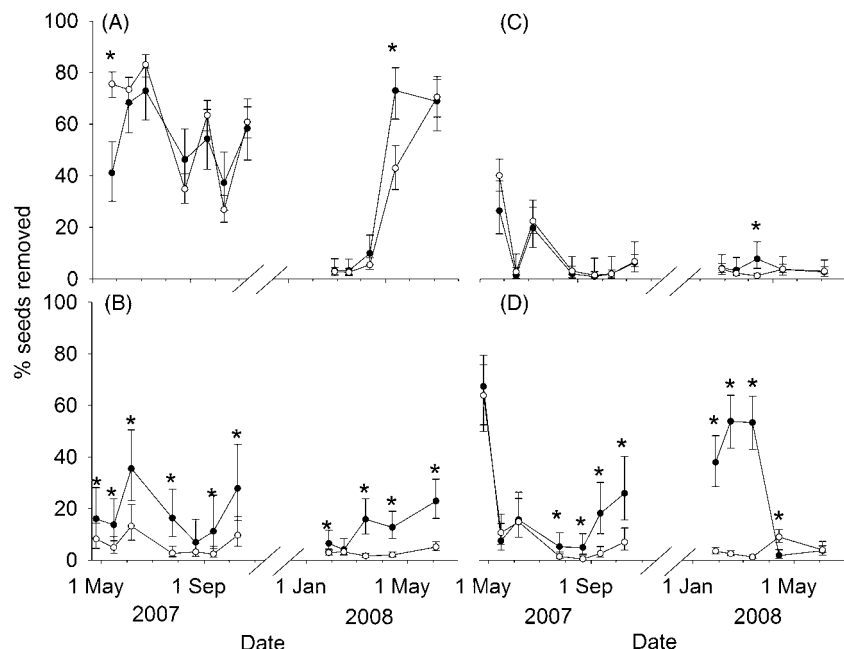


Fig. 3. Percentage of seeds removed from the field interior (○) or the margins (●) by invertebrates (A, B) and vertebrates (C, D) in dryland (A, C) or irrigated (B, D) cereal fields. Asterisks indicate significant differences in seed removal between field interior and margin. Bars represent 95% confidence intervals around the mean.

The proportion of weed seeds consumed from artificial seed caches over a short-term period depends on: (i) predator numbers and activity, which change continuously due to birth and death, immigration and emigration, social interactions, and responses to environmental and seasonal variables; and (ii) the relative food abundance which changes from day to day due to seed shed and seed burial, and changes in the availability of alternative food sources. The arithmetic mean of short-term predation rates may therefore under- or over-estimate annual seed losses due to predation, depending on seed abundance. For this reason, Westerman *et al.* (2006) suggested using seed availability on the soil surface as weights when averaging short-term predation rates.

Results obtained from the dryland cereals, however, are easy to interpret, because seed removal rates were high during the entire period of weed seed shed (mid-April to end-August). When accumulated over the season, they may cause a strong weed suppressive effect. Harvester ants, *M. barbarus*, were responsible for most seed removal. However, seed removal rates were much lower in irrigated cereals. No harvester ants were observed in any of the irrigated fields, and irrigation is likely to be responsible for their absence because ant colony survival is poor when fields are periodically flooded. Granivorous rodents replaced harvester ants in the irrigated fields. The rodents, however, were not nearly as effective in collecting weed seeds as the harvester ants. It is not entirely clear why, because rodents are effective seed predators in other agro-ecosystems (Westerman *et al.* 2003b; Heggenstaller *et al.* 2006). Seed predation activity by rodents is closely linked to canopy cover (Díaz 1992a; Heggenstaller *et al.* 2006). However, canopy cover cannot explain the poor rodent performance in the irrigated fields in May–June 2007. It is possible that the canopy was denser in other crops, as the irrigated area provided a lush habitat of small fields with diverse crops, and ample vegetation. Alternatively, the rodents, although present and foraging in cereal fields, did not consume weed seeds. Granivorous rodents are generalists and their diet can include insects (Hansson 1971). However, the rodents also refrained from collecting seeds during winter when insect availability was low. Detailed behavioural and dietary studies are required to cast light on why the granivorous rodents did not consume weed seeds, and what they were eating instead.

The results of this study raise the more general questions as to how well generalist seed predators can replace specialist seed predators, and how much functional redundancy there is for seed predation. The fact that neither rodents nor any other seed predators were able to fully fill the gap caused by the elimination of harvester ants suggests that at least in this agro-ecosystem, there is little overlap in functions. The difference between seed removal rates between dryland and irrigated fields also means that weed seeds that would otherwise have been destroyed by predators can now enter the seed bank and contribute to future weed problems. The loss of effective seed predators may provide a partial explanation for the higher weed pressure in irrigated compared to dryland cereals. However, confirmation of our findings by long-term estimates of weed seed removal is required.

Small but important differences in invertebrate seed removal rate were observed between conventional and no-till dryland cereals, with higher levels of seed removal in no-till fields from April–August 2007. This corresponded with a significantly higher harvester ant nest density in no-till compared to conventional fields. More importantly, tillage in the conventional fields limited the duration of seed exposure to predators, which starts with weed seed shed in May. Seed predators usually avoid digging for buried seeds to save time and energy; predation chances are therefore higher for surface seeds (Hulme 1994). Interestingly, no-till has traditionally been associated with increased weed pressure due to a concentration of weed seeds near the soil surface from which germination chances are higher. However, in this particular dryland system, weed pressure should decrease in the absence of tillage, as was confirmed by farmers in the area. Moreover, no-till is mainly adopted to improve soil quality and reduce costs; weed control is just an additional service.

Harvester ants have been reported to cause crop damage by harvesting seeding material (Andersen 1991). In Catalonia, harvester ants can also cause damage, but here they gather cereal grains right off the ear, prior to harvest, probably as a result of food shortage at that time. However, the extent of the yield losses seems to vary between areas and years. It is currently unknown which sets of environmental conditions or crop management decisions lead to enhanced weed control and which to yield losses, and whether the two can be combined or not.

Field margins were important stable habitats to rodents in both dryland and irrigated fields, and to invertebrates, probably carabids, in irrigated fields. However, harvester ants avoided field margins. No management recommendation could be formulated because our data on the contribution of field margins to weed seed removal were inconclusive. More research is required to determine if and how improved field margin management can help to optimize natural weed control.

Intensification of agricultural practices since the 1960s has resulted in reduced self-regulation and increased reliance on external input for the control of pests, diseases and weeds (Altieri 1999). Attempts are underway to reverse the trend and reduce the dependence on pesticides by restoring and facilitating functional biodiversity. However, it appears difficult to determine in retrospect the role of each component of the intensification process that led to decline or loss of functions (e.g. increases in farm- and field-scale, mechanization, chemical pesticides, mineral fertilizers, high-yielding crop varieties).

Here, we document an ongoing process of agricultural intensification via irrigation that is accompanied by an alarming loss of functionality. We are under no illusion that the results of this study will have consequences for the irrigation network under construction in the study area; plans are too advanced and financial benefits too great. Nevertheless, awareness of the role of harvester ants in weed control and associated changes in herbicide use and dependency should be taken into consideration in future

plans particularly in cases where financial benefits of irrigation are lower or environmental costs higher. Harvester ants are common in arid and semi-arid climates around the world, and therefore, our results are relevant to all regions where irrigation is an issue.

We also documented the consequences of an ongoing process of agricultural de-intensification via no-till in rain-fed cereals, where weed pressure should decrease because of increasing harvester ant populations and prolonged weed seed exposure to predators. Awareness of the services provided by harvester ants may become an additional incentive to adopt no-till techniques, provided that crop damage by harvester ants can be managed.

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References

- Agencia Estatal de Meteorología (2008) Valores Climatológicos Normales. Lleida/Estación 2. <http://www.aemet.es/es/elclima/datosclimatologicos/valoresclimatologicos?l=9771c&k=cat>. Date of last access: 23 December 2008.
- Altieri, M.A. (1999) The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment*, **74**, 19–31.
- Andersen, A.N. (1991) Seed-harvesting ant pests in Australia. *Applied Myrmecology: A World Perspective* (eds R. K. Vander Meer, V. Jaffe & A. Cedenio), pp. 35–39. Westview Press, Inc., Boulder, CO, USA.
- Azcárate, F.M. & Peco, B. (2003) Spatial patterns of seed predation by harvester ants (*Messor* Forel) in Mediterranean grassland and scrubland. *Insectes Sociaux*, **50**, 120–126.
- Cardina, J., Norquay, H.M. (1997) Seed production and seedbank dynamics in subthreshold velvetleaf (*Abutilon theophrasti*) populations. *Weed Science*, **45**, 85–90.
- Cerdá, X. & Retana, J. (1994) Food exploitation patterns of two sympatric seed-harvesting ants *Messor bouvieri* (Bond.) and *Messor capitatus* (Latr.) (Hym., Formicidae) from Spain. *Journal of Applied Entomology*, **117**, 268–277.
- Díaz, M. (1991) Spatial patterns of granivorous ant nest abundance and nest site selection in agricultural landscapes of Central Spain. *Insectes Sociaux*, **38**, 351–363.
- Díaz, M. (1992a). Rodent seed predation in cereal crop areas of Central Spain: effects of physiognomy, food availability, and predation risk. *Ecography*, **15**, 77–85.
- Díaz, M. (1992b) Spatial and temporal patterns of granivorous ant seed predation in cereal crop areas of central Spain. *Oecologia*, **91**, 561–568.
- Gerowitt, B. & Bodendörfer, H. (1998) Long-term population development of *Viola arvensis* Murr. in a crop rotation. I. Field experiments. *Journal of Plant Diseases and Protection*, **105**, 641–654.
- Hansson, L. (1971) Small rodent food, feeding and population dynamics. *Oikos*, **22**, 183–198.
- Heggenstaller, A.H., Menalled, F.D., Liebman, M. & Westerman, P.R. (2006) Seasonal patterns in post-dispersal seed predation of *Abutilon theophrasti* and *Setaria faberi* in three cropping systems. *Journal of Applied Ecology*, **43**, 999–1010.
- Hulme, P.E. (1994) Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology*, **81**, 645–652.
- Keen, A. & Engel, B. (2005) GENSTAT IRREML procedure. *Biometris GENSTAT Procedure Library Manual* (eds P.W. Goedhart & J.T.N.M. Thissen), pp. 41–44. Biometris, Wageningen, The Netherlands.
- Levey, D.J. & Byrne, M.M. (1993) Complex ant–plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology*, **74**, 1802–1812.
- Loman, J. (1991) The small mammal fauna in an agricultural landscape in southern Sweden, with special reference to the wood mouse *Apodemus sylvaticus*. *Mammalia*, **55**, 91–96.
- MacMahon, J.A., Mull, J.F. & Crist, T.O. (2000) Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics*, **31**, 265–291.
- Plesner Jensen, S. & Honess, P. (1995) The influence of moonlight on vegetation height preference and trappability of small mammals. *Mammalia*, **59**, 35–42.
- Servei Meteorològic de Catalunya (2008) Butlletins Climàtics. http://www.meteocat.com/mediamb_xemec/servmet/marcs/marc_clima.html. Date of last access: 23 December 2008.
- Tattersall, F.H., Macdonald, D.W., Hart, B.J., Manley, W.J. & Feber, R.E. (2001) Habitat use by wood mice (*Apodemus sylvaticus*) in a changeable arable landscape. *Journal of Zoology, London*, **255**, 487–494.
- Watson, S.J., Mauchline, A.L., Brown, V.K. & Froud-Williams, R.J. (2003) Post-dispersal losses of *Stellaria media* and *Polygonum aviculare* seeds in spring barley (*Hordeum vulgare*). *Aspects of Applied Biology*, **69**, 203–208.
- Westerman, P.R., Wes, J.S., Kropff, M.J. & Van de Werf, W. (2003a) Annual losses of weed seeds due to predation in organic cereal fields. *Journal of Applied Ecology*, **40**, 824–836.
- Westerman, P.R., Hofman, A., Vet, L.E.M. & van der Werf, W. (2003b) Relative importance of vertebrates and invertebrates in epigeic weed seed predation in organic cereal fields. *Agriculture, Ecosystems & Environment*, **95**, 417–425.
- Westerman, P.R., Liebman, M., Menalled, F.D., Heggenstaller, A.H., Hartzler, R.G., & Dixon, P.M. (2005) Are many little hammers effective? Velvetleaf population dynamics in two- and four-year crop rotation systems. *Weed Science*, **53**, 382–392.
- Westerman, P.R., Liebman, M., Heggenstaller, A.H. & Forcella, F. (2006) Integrating measurements of seed availability and removal to estimate weed seed losses due to predation. *Weed Science*, **54**, 566–574.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Crop Management.

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