Universitat de Lleida

Seed predators and weed seed predation for weed control in winter cereals

Bàrbara Baraibar Padró

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Seed predators and weed seed predation for weed control in winter cereals

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to obtain the degree of Doctor by the University of Lleida

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Bàrbara Baraibar Padró

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A les formigues,

per demostrar que les petites contribucions individuals

són les que fan gran qualsevol projecte.

Contents

Summary

Seed predation can cause significant losses of weed seeds in agricultural systems and can, thus, contribute to weed control. Knowledge on the identity and relative contribution to weed control by various seed predators, and on factors limiting seed predation is currently lacking. This study aimed at casting light on these aspects for the specific case of winter cereal fields in semi-arid north-eastern Spain. This area is traditionally managed without irrigation and with tillage. However, an ever increasing proportion of the arable land is being irrigated and the remainder of the rain fed land is managed without tillage. The impact of tillage and irrigation on weed seed predators and seed removal rates were, therefore, studied. The study showed that in the rain-fed area, *Messor barbarus* harvester ants are contributing substantially to weed control by removing large quantities of weed seeds during spring and summer. Tillage during summer decreased predation rates and buried most of the weed seeds located on the soil surface, thus preventing further seed removal. Tillage also decreased the number of harvester ant nests compared to no-till fields. The expansion of the area that is managed with minimum and no-till should result in high natural weed control level over a large area. In contrast, inundative irrigation completely eliminated harvester ants, and led to the almost complete loss of this ecosystem service. Although carabid beetles and rodents were present in the field edges, predation rates in the field interior were extremely low. Causes for the lack of seed predation are still unknown and should be further investigated.

Densities of harvester ant nests varied enormously between fields; concomitant weed seed predation rates are expected to vary accordingly. Causes for this variability could not be identified. Harvester ant nest density did not correlate with the most common soil characteristics, topographic variables or crop and management practices, with the exception of the number of years of no-till. Harvester ant density was highest after 11-12 years of no-till. Other than that, no recommendations could be formulated to increase nest densities in those areas were they are low.

Success of weed seed predation as an ecosystem service also depends on the ability of predators to respond in a direct density dependent way to increasing seed densities. The density dependent response of granivorous rodents to seed patches with varying density was investigated in winter cereal fields of north-eastern Germany. Rodents responded in a direct density dependent way to increasing seed densities and are, therefore, expected to effectively control weed patches. The density dependent

response by harvester ants and granivorous rodents in cereal fields in NE Spain are currently being investigated.

It is feasible that harvester ants occasionally destroy crop seeds and cause crop damage. Yield loss caused by *M. barbarus* was, however, negligible (0.4 % of yield), and was explained by nest density, nest size and number of years without tillage. Based on these results, damage caused by harvester ants was more than offset by the benefits with regard to weed control. However, occasional higher yield losses (max. 9.2%) were recorded and the conditions leading to higher losses should be investigated further.

This study exemplifies both the strength and vulnerability of an ecosystem service. High weed seed predation by harvester ants is occurring naturally in rain-fed cereals in north-eastern Spain and contributes substantially to weed control. However, this service can easily be lost as illustrated by the absence of seed predation in the flood irrigated areas and the response of harvester ants to excessive tillage. Existing densities of harvester ant nests could be preserved by limiting the level of soil disturbance. In semi-arid regions, cereal production is marginally cost effective due to limited water availability and, therefore, preserving natural weed control by harvester ants is needed in order to preserve the sustainability of the system.

Resum

La depredació de llavors pot causar pèrdues significatives de llavors de males herbes en sistemes agrícoles i, per tant, pot contribuir al control de les arvenses. Actualment, el coneixement existent sobre la identitat i la contribució relativa dels diferents depredadors de llavors, i dels factors que limiten aquesta depredació és escàs. Aquest estudi té com a objectiu contribuir a augmentar aquest coneixement pel cas específic del cereals d'hivern a les zones semi-àrides del nord-est espanyol. Tradicionalment, aquesta zona ha estat de secà i caracteritzada per un intens treball del sòl. Però, amb el temps, una superfície creixent d'aquesta zona ha anat transformant-se al regadiu; i a la restant zona de secà, la sembra directa ha anat creixent en superfície. Per aquest motiu, es va estudiar l'impacte d'aquestes dues transformacions en la depredació de llavors de males herbes. L'estudi ha mostrat que en les àrees de secà, les formigues recol·lectores de l'espècie *Messor barbarus* estan contribuint d'una manera substancial al control de males herbes al emportar-se grans quantitats de llavors de males herbes durant els mesos de primavera i estiu. El conreu del sòl a l'estiu va fer decréixer les taxes de depredació i va provocar l'enterrament de la majoria de les llavors que es trobaven a la superfície del sòl, impedint, d'aquesta manera, la continuació de la depredació. Igualment, el conreu del sòl també va fer disminuir la densitat de nius de formigues als camps conreats en comparació amb els camps de sembra directa. L'expansió de l'àrea en sembra directa hauria de donar lloc a unes taxes elevades de control natural de les males herbes en una àmplia zona. Per contra, el reg per inundació va eliminar completament les formigues recol·lectores i va portar casi a la completa pèrdua d'aquest servei de l'ecosistema. Encara que caràbids i ratolins eren presents als marges dels cultius, les taxes de depredació a l'interior dels camps van ser extremadament baixes. Les causes d'aquesta falta de depredació encara no són conegudes i haurien de ser estudiades en el futur.

Les densitats de nius de formigues recol·lectores varien enormement entre camps i, per tant, s'espera que les taxes de depredació variïn en conseqüència. Les causes d'aquesta variabilitat no van poder ser identificades. La densitat de nius de *M. barbarus* no es van poder correlacionar amb les característiques del sòl més comunes, amb paràmetres topogràfics ni amb practiques de maneig, excepte amb el nombre d'anys des de l'adopció de la sembra directa. La densitat de nius de *M. barbarus* va ser màxima després de 11 – 12 anys de sembra directa. A part d'això, no es van poder

formular recomanacions per incrementar les densitats de nius en aquelles zones en les que són baixes.

L'èxit de la depredació de llavors de males herbes com a servei de l'ecosistema també depèn de l'habilitat dels depredadors de respondre d'una manera directament denso-dependent a densitats creixents de llavors. La resposta a diferents densitats de llavors per part de ratolins granívors va ser investigada en camps de blat del nord-est d'Alemanya. Els ratolins van respondre a densitats creixents de llavors d'una forma directament denso-dependent i per tant, s'espera que puguin ser capaços de controlar d'una manera efectiva els rodals de males herbes. Les respostes a densitats creixents de llavors per part de ratolins i formigues recol·lectores en les condicions del nord-est de l'estat espanyol estan essent investigades actualment.

Es possible que les formigues recol·lectores puguin, ocasionalment, destruir llavors de cultiu. Tanmateix, les pèrdues de rendiment causades per *M. barbarus* van ser negligibles en la majoria dels casos (0.4% del rendiment) i poden ser explicades per la densitat de nius, la mida d'aquests i el nombre d'anys que el camp porta en sembra directa. Ocasionalment, es van registrar pèrdues de rendiment més altes (9.2% del rendiment). Les causes d'aquestes pèrdues han d'esser estudiades en detall en el futur.

Aquest estudi exemplifica la fortalesa i la vulnerabilitat d'un servei del ecosistema. A les zones de secà del nord-est espanyol, s'estan donant, d'una forma natural, altes taxes altes de depredació de llavors de males herbes que contribueixen substancialment al control d'aquestes herbes. Tanmateix, aquest servei es pot perdre fàcilment tal com il·lustren l'absència de depredació de llavors en les àrees regades a manta i la resposta de les formigues recol·lectores a un excessiu treball del sòl. Les densitats de nius de formigues recol·lectores existents podrien ser preservades limitant el nivell de pertorbació del sòl. En regions semi-àrides, on la producció de cereals és marginalment rendible degut a l'escassetat d'aigua, la preservació del control natural de les males herbes dut a terme per les formigues recol·lectores és necessària per preservar la sostenibilitat del sistema.

Resumen

La depredación de semillas puede causar pérdidas significativas de semillas de malas hierbas en sistemas agrícolas y, por lo tanto, puede contribuir al control de dichas hierbas. Actualmente, el conocimiento existente acerca de la identidad y contribución relativa de los depredadores de semillas, y de los factores que limitan esta depredación es escaso. Este estudio tiene como objetivo contribuir a incrementar dicho conocimiento para el caso específico de los cereales de invierno en las zonas semi-áridas del noreste español. Tradicionalmente, esta zona ha sido de secano y caracterizada por un intenso laboreo del suelo. Sin embargo, la superficie de regadío ha ido incrementándose en la zona y, en la zona de secano restante, la siembra directa también ha ido en aumento. Por este motivo, se estudió el impacto de estas dos transformaciones en la depredación de semillas de malas hierbas. El estudio ha mostrado que, en las zonas de secano, las hormigas granívoras de la especie *Messor barbarus* están contribuyendo de una forma sustancial al control de malas hierbas, al llevarse grandes cantidades de semillas de malas hierbas durante los meses de primavera i verano. El laboreo del suelo en verano redujo las tasas de depredación de semillas y provocó el enterramiento de la mayoría de las semillas presentes en la superficie del suelo, lo que impidió, en gran medida, la continuación de la depredación. De la misma forma, el laboreo del suelo también disminuyó la densidad de nidos de hormigas en los campos cultivados en comparación con los campos de siembra directa. La expansión del área en siembra directa debería dar lugar a tasas elevadas de control natural de malas hierbas en una amplia zona. Contrariamente, el riego por inundación eliminó por completo a las hormigas granívoras y llevó a la casi completa desaparición de este servicio del ecosistema. Aún cuando carábidos y pequeños roedores estaban presentes en los márgenes de los cultivos, las tasas de depredación en el interior de los campos fueron extremadamente bajas. Las causas de esta falta de depredación son aún desconocidas y deberían ser estudiadas en el futuro.

Las densidades de nidos de hormigas granívoras varían enormemente entre campos y, por lo tanto, se espera que las tasas de depredación también varíen en consecuencia. Las causas de dicha variabilidad no pudieron ser identificadas. Las densidades de nidos de *M. barbarus* no se pudieron correlacionar con las características del suelo más comunes, con parámetros topográficos ni con las prácticas de manejo del cultivo, exceptuando en número de años desde la adopción de la siembra directa. Las densidades de nidos de *M. barbarus* fueron máximas después de 11-12 años de siembra

directa. A parte de esto, no se pudieron formular recomendaciones para incrementar las densidades de nidos en aquellas zonas en las que son bajas.

El éxito de la depredación de semillas de malas hierbas como servicio del ecosistema depende también de la habilidad de los depredadores para responder de una forma directamente denso-dependiente a densidades crecientes de semillas. La respuesta a diferentes densidades de semillas por parte de roedores granívoros fue investigada en campos de trigo del noreste de Alemania. Los roedores respondieron a densidades crecientes de semillas de una forma directamente denso-dependiente, por lo que se espera que puedan ser capaces de controlar de una forma efectiva, los rodales de malas hierbas. Las respuestas a densidades crecientes de semillas por parte de roedores y hormigas granívoras en condiciones del noreste español están siendo investigadas en la actualidad.

Es posible que las hormigas granívoras puedan, ocasionalmente, destruir semillas de cultivo. Sin embargo, las pérdidas de rendimiento causadas por *M. barbarus* fueron insignificantes en la mayoría de casos (0.4% del rendimiento) y pueden ser explicadas por la densidad de nidos, su tamaño y el número de años de siembra directa del campo. Ocasionalmente, se registraron pérdidas de rendimiento más elevadas (9.2% del rendimiento). Las causas de estas pérdidas deben ser estudiadas en más detalle en el futuro.

Este estudio ejemplifica la fortaleza y la vulnerabilidad de un servicio del ecosistema. En las zonas de secano del noreste español se están dando, de forma natural, altas tasas de depredación de semillas de malas hierbas, que están contribuyendo sustancialmente al control de las malas hierbas. Sin embargo, este servicio puede perderse fácilmente tal como muestran la ausencia de depredación de semillas en las áreas regadas a manta y la respuesta de las hormigas granívoras a un excesivo laboreo del suelo. Las densidades de nidos de hormigas existentes podrían ser preservadas limitando el grado de perturbación del suelo. En regiones semi-áridas, donde la producción de cereales es marginalmente rentable debido a la escasez de agua, el mantenimiento del control natural de las malas hierbas por parte de las hormigas granívoras se hace necesario para preservar la sostenibilidad del sistema.

CHAPTER 1

General introduction

General introduction

BACKGROUND

Seed bank studies have shown that 70 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 and Norquay, 1997; Gerowitt and Bodendörfer, 1998). Seed predation seems to be responsible for the larger part of these losses (Westerman *et al.*, 2003; Davis *et al.*, in prep.) and can, therefore, contribute substantially to weed control. Combined with other non-chemical control tactics, seed predation could reduce reliance on herbicides (Liebman and Davis, 2000; Westerman *et al.*, 2005) and, thus, reduce environmental and monetary costs. Particularly farmers in arid and semi-arid areas would benefit from cost reductions, because here cereal production is marginally cost effective due to limited water availability (Austin *et al.*, 1998). Using weed seed predation for weed control requires gaining knowledge about the main seed predators, how they find and exploit weed seeds and which factors enhance or limit seed predation.

In semi-arid north-eastern Spain (Lleida, Catalonia), the identity of the main seed predators is unknown, although harvester ants and granivorous rodents are likely to be among them (Díaz, 1992a, b, Spafford *et al.*, 2006). It is also unknown if they contribute to weed control and, if so, how much, and whether seed predation is limited by crop and soil management factors; these factors could be used to manage natural weed control by seed predation. Currently, arable production in the area is undergoing two major changes. First, the area that is irrigated will soon increase from 143000 ha (41% of the agricultural land) to 228000 ha (65% of the agricultural land) due to an expansion of the irrigation channel network. Secondly, in the remaining rain-fed area the use of minimum and no-till is increasingly being accepted and adopted. Given the enormous scale at which these changes occur, it is worthwhile to investigate the consequences in terms of natural weed control by seed predators.

Tillage and irrigation may affect harvester ants and granivorous rodents in different ways because of differences in biology and foraging behaviour. Harvester ants may be particularly vulnerable to tillage because the location of colonies of many species of harvester ants is permanent and nests are rarely relocated during the live span of a colony (up to 15-20 years). Any tillage operation is likely to partially destroy nest structure and decrease seed predation rates. Low predation rates by *Messor capitatus*

Latr. harvester ants in croplands of central Spain may have been caused by periodical mouldboard ploughing, which disrupted the soil structure and destroyed ant nests (Díaz, 1991). Irrigation is likely to limit survival chances of harvester ant colonies and decrease ant densities. High soil moisture content may increase the susceptibility to fungal diseases and the germination of stored seeds, which are no longer available as a food source to the ants. In the case of inundative irrigation, colonies will be temporarily flooded and may drown.

Granivorous rodents are more mobile than harvester ants and may be able to seek out suitable habitats when unfavourable conditions, such as tillage, occur. However, tillage can still affect seed predation by rodents by influencing canopy cover, which conceals rodents from predators (Tew *et al.*, 2000). In rain-fed areas, water scarcity allows only one crop per year and fields are left bare most of the time. Protection from predators can only come from crop residues and substrate unevenness, like crevices, holes or soil clods (Mandelik *et al.*, 2003). Tillage decreases the availability of crop residues and substrate unevenness (Brust and House, 1988; Díaz, 1992 a), which could result in lower seed predation rates (Mittelbach and Gross, 1984; Tew and Macdonald, 1993; Cromar *et al.*, 1999; Gallandt *et al.*, 2005). In contrast, in minimum and no-till systems, where stubble is not buried and some residue cover is maintained, rodents have some protection from predators, and seed predation rates may be higher than in conventionally tilled fields (Booman *et al.*, 2009; Brust and House, 1988). The effect of irrigation on seed removal rates by rodents is unknown. Rodents should not directly be affected by inundative irrigation, because some of them may be able to relocate their burrow systems to non-flooded areas, such as field edges. However, irrigation allows continuous cropping throughout the year, causing canopy cover to be available during most of the time. Therefore, predation rates by rodents are expected to be higher than in the rain-fed area.

Besides tillage and irrigation, other management practices and environmental factors may influence seed predator densities. Differences in densities of seed predators within and between fields may result in spatial variability in seed predation rates at the level of fields or landscape. Identifying the main factors influencing differences in harvester ant density within and between fields and identifying management practices that could lead to higher nest densities could serve as a basis for recommendations to farmers who would like to conserve and maximize natural weed control. Nests of harvester ants are linked to a specific location and could, therefore, be more vulnerable to local management and the local environment than the more mobile rodents. For example, soil characteristics, such as moisture content, texture or aggregates distribution, or topographic parameters, such as field altitude and slope, may determine harvester ant establishment success or survival, and therefore, nest density.

Seed predation rates can also vary at the within-field scale (Spafford *et al.*, 2006). Weed seeds in crop fields often occur in patches, either around weed patches or distributed along a track created by tillage and harvesting machinery (Blanco-Moreno *et al.*, 2005; Heijting *et al.*, 2009). High density weed patches are usually the focus of weed control tactics, because here crop yield is most affected. If predators respond in a direct density-dependent manner to seed densities, weed patches would suffer disproportional seed losses, resulting in the gradual elimination of weed patches. The impact on weed population dynamics would be larger than when predators respond in a density-independent or inversely density-dependent way. Density dependence was studied in winter cereal fields of Rostock (Mecklenburg-Vorpommern, Germany). In this area, the main seed predators are carabid beetles and granivorous mice (Daedlow *et al.*, 2007). Only the response of granivorous rodents to patches with different seed densities was studied.

Enhancing or preserving high densities of harvester ants and granivorous rodents within cereal fields for weed control can raise concerns with regard to potential damage to cereal seeds. Granivorous mice have been reported to cause crop damage in the tropics and in Australia (Brown *et al.*, 2003 and references therein), but they have been seldom associated with crop damage in Europe or North America (Clark and Young, 1986). Some ant species, such as the fire ant *Solenopsis invicta* Buren, can damage crops, such as potatoes, maize and sorghum in the United States and Asia (Adams *et al.*, 1988; Drees *et al.*, 1991). Furthermore, there is anecdotal evidence that harvester ants can cause yield losses in cereals in NE Spain, however, this has not been investigated yet. Therefore, this study also addresses these concerns.

OBJECTIVES OF THE THESIS

The main objectives of this thesis were:

1. Determine whether seed predation occurs in semi-arid winter cereal fields.
2. Determine the main seed predators and their relative contribution to seed predation.
3. Understand if and how tillage and irrigation affect seed predators and seed predation rates.

4. Identify crop management and environmental factors that influence harvester ant density in rain-fed cereals.
5. Determine the type of density dependent response to differences in seed density within fields.
6. Estimate yield losses caused by harvester ants in rain fed cereals.

METHODOLOGY AND OUTLINE OF THE THESIS

To answer Objectives 1 – 3, observational research was conducted in nine cereal fields near Lleida (Spain). Predation rates by vertebrate and invertebrate seed predators were assessed using seeds in Petri dishes as feeding stations. Seed predation per two days was measured once a month during a period of 1.5 years. Three of the nine fields were located in an irrigated area and the remaining six in a rain-fed area nearby. Fields in the dryland area were paired such that one of the two was managed without tillage and the other with tillage. Results of this study are reported and discussed in Chapters 2 and 3.

To meet Objective 4, harvester ants nest densities after crop harvest were assessed in 40 commercial winter cereal fields and related to edaphic and topographic parameters, and crop management practices using regression analyses (Chapter 4). Soil samples and topographic measures were taken for each of the fields. Sampling data was supplemented by a survey among farmers, which provided information on the field management, such as the kind of fertilizers and straw management used.

The density dependent response (Objective 5) of granivorous rodents was investigated in four winter cereal fields near Rostock (Germany). Large weed seed patches (15 m ×15 m) were created artificially by applying four weed seed densities to the plots and determining the number of seeds on the soil surface before and after exposure to the rodents (Chapter 5).

Damage caused by harvester ants (Objective 6) was assed in the same 40 commercial cereal fields used for studying Objective 4. Fields were visited a week prior to crop harvest and the area damaged by ants, seen as void of crop (damage at sowing) or crop void of spikes (damage at harvest), was measured around 10 randomly selected nests in each field (Chapter 6).

In Chapter 7 results from the preceding chapters are integrated and jointly discussed, leading to the main conclusions.

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CHAPTER 2

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

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

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Abstract

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 (g g^{-1} 2-$days^{-1}$) was followed from April 2007 until June 2008, using Petri-dishes and exclosure 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

1. 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 and Norquay, 1997; Gerowitt and 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.

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, 1992 a,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 and 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 exclosures.

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 (Azcárate and 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.

2. 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 ℃ (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).

2.1. 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.) Trinex 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 (l0 cm × 11 cm × 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 Batlle, 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 and 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 asses 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.

2.2. 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 and 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 *et al.*, 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 ($< 0{\cdot}4\ m^2$), 2 ($0{\cdot}4$–$1\ m^2$), 3 (1–$2\ m^2$) and 4 ($> 2\ m^2$).

2.3. Statistical analysis

2.3.1. 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 ($P < 0{\cdot}01$), 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.

2.3.2. 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 and Engel, 2005) in genstat (version 10). Because different fields had been used in 2007 and 2008, analyses were conducted for the 2 years separately.

3. Results

3.1. 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; $p < 0{\cdot}01$). This difference was related 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 ($\chi^2 = 3{\cdot}20$; d.f. = 3; $p = 0{\cdot}361$); 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 (0–10 m; 362 ha^{-1}), suggesting that harvester ants avoided field edges.

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

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}).

3.2. Seed removal in dryland fields

3.2.1. 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.

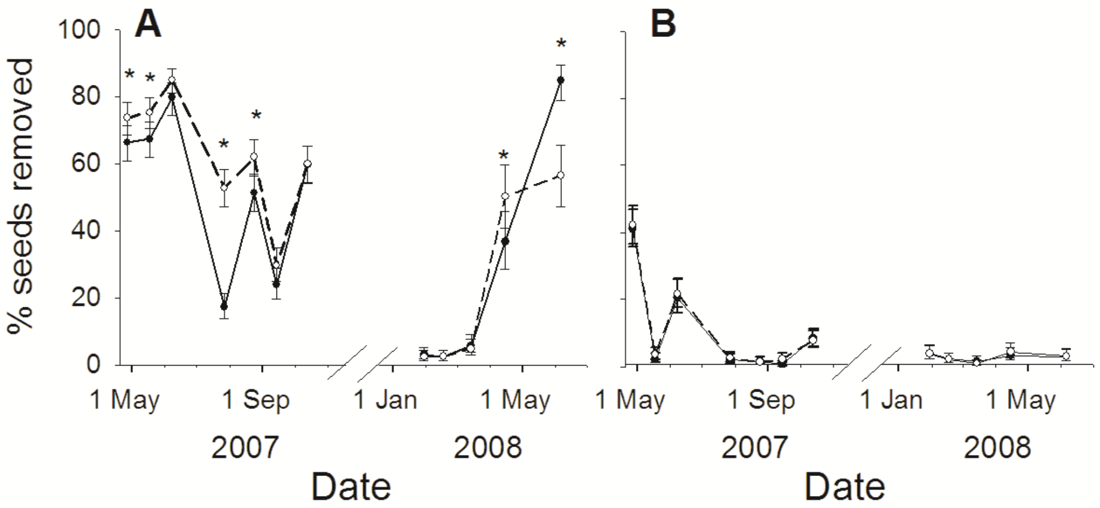

Fig. 1. Percentage of seeds removed by invertebrates (A) and vertebrates (B) in no-till (---) and conventionally tilled fields (—) in dryland. Asterisks indicate significant differences in seed removal between tillage systems. Bars represent 95% confidence intervals around the mean.

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).

	2007				2008			
Fixed term	Wald	d.f.	Wald/d.f.	*P*	Wald	d.f.	Wald/d.f.	*P*
(A)								
Tillage	61.4	1	61.4	< 0.001	1.1	1	1.1	0.295
Predator	1194.2	1	1194.2	< 0.001	551.5	1	551.5	< 0.001
Month	1353.3	6	225.5	< 0.001	756.1	4	189	< 0.001
Tillage × Predator	5.2	1	5.2	0.023	0.5	1	0.5	0.475
Tillage × Month	34.9	6	5.8	< 0.001	61.7	4	15.4	< 0.001
Predator × Month	328.9	6	54.8	< 0.001	272.4	4	68.1	< 0.001
Tillage × Predator × Month	32.9	6	5.5	< 0.001	11.4	4	2.8	0.022
(B)								
Predator	107.3	1	107.3	< 0.001	4.8	1	4.8	0.028
Month	481.1	6	80.2	< 0.001	110.6	4	27.7	< 0.001
Predator × Month	152.7	6	25.5	< 0.001	21.7	4	5.4	< 0.001

3.2.2. Effect of location

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

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).

	2007				2008			
Fixed term	Wald	d.f.	Wald/d.f.	*P*	Wald	d.f.	Wald/d.f	*P*
(A)								
Location	4.1	1	4.14	0.042	0.87	1	0.9	0.352
Predator	820.6	1	820.64	< 0.001	713.8	1	713.8	< 0.001
Month	717.5	6	119.59	< 0.001	822.9	4	205.7	< 0.001
Location × Predator	0.01	1	0.01	0.918	2.46	1	2.5	
Location × Month	15.3	6	2.56	0.018	22.08	4	5.5	< 0.001
Predator × Month	223.7	6	37.29	< 0.001	286.7	4	71.7	< 0.001
Location × Predator × Month	5.5	6	0.92	0.477	298.5	1	296.6	
(B)								
Location	34.1	1	34.1	< 0.001	298.6	1	298.6	< 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	3.4	0.008
Location × Predator	19.51	1	19.51	< 0.001	20.81	1	20.8	< 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	9.6	< 0.001
Location × Predator × Month	18.15	6	3.02	0.006	132.5	4	33.1	< 0.001

3.3. Seed removal in irrigated fields

3.3.1. 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.

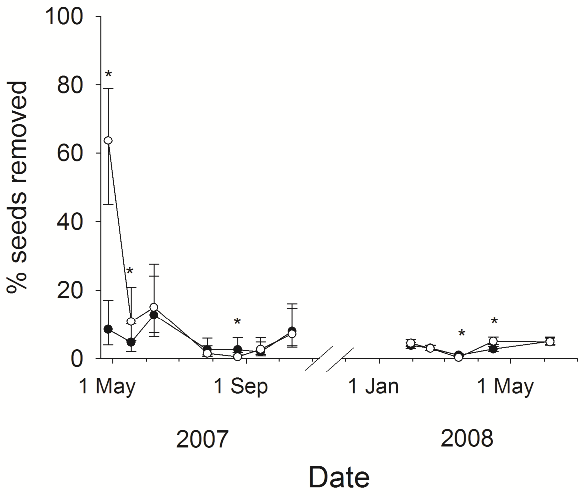

Fig. 2. Percentage of seeds removed by vertebrates (○) and invertebrates (●) in irrigated fields. Asterisks indicate significant differences in seed removal between vertebrate and invertebrate predators. Bars represent 95% confidence intervals around the mean.

3.3.2. 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.

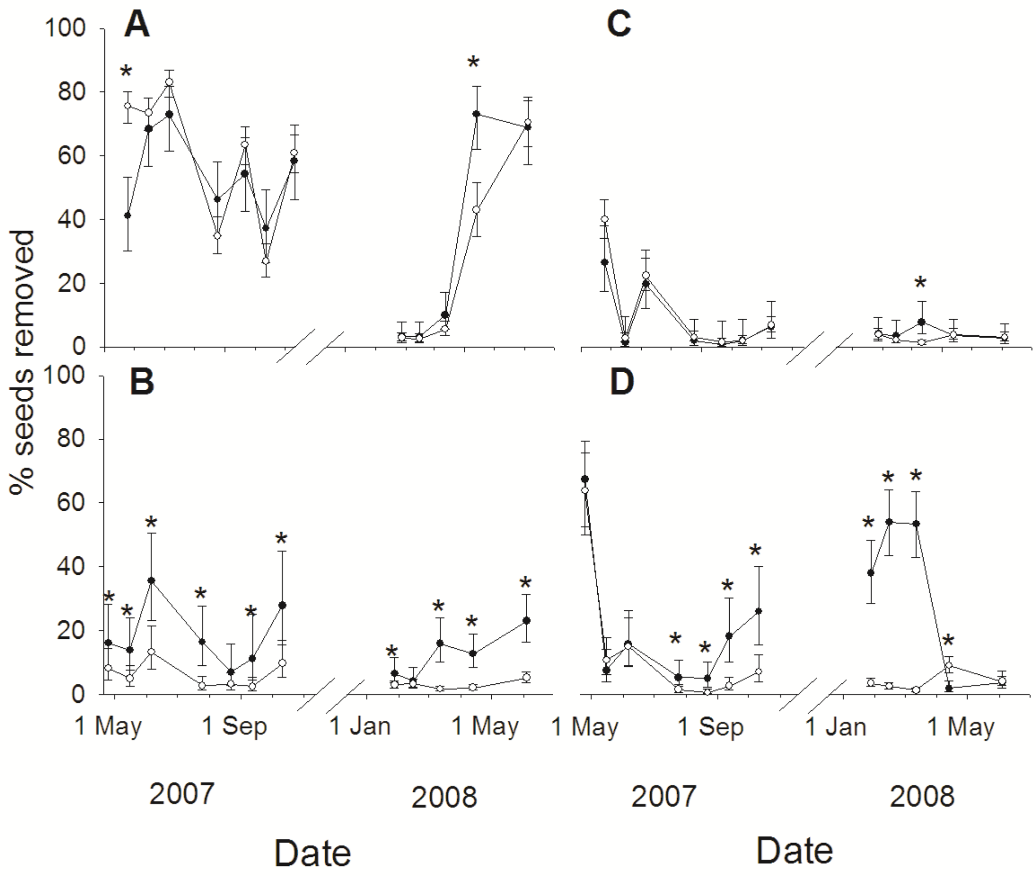

Fig. 3. Percentage of seeds removed from the field interior ○ or the margins ● by invertebrates (A, B) and vertebrates (C, D) in dryland (A, C) or irrigated (B, D) cereal fields. Asterisks indicate significant differences in seed removal between field interior and margin. Bars represent 95% confidence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

4. 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. 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 overestimate 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, 1992 a; 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 farmand 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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Supplementary material.

Table S1. Characteristics of the selected barley and wheat fields, crop variety, and crop management information for 2007 and 2008.

Field No.	Irriga-tion *	Mana-gement **	Crop Variety	Field size ha	Date of tillage	sowing	harvest	herbicide appl.	Herbicides Active ingredients	Dose (g a.i. ha^{-1})
2007										
1A	dryl.	conv.	Dobla	18	27/11/06 + 24/7/07	30/11/06	3/6/07	15/1/07	Clorsulfuron	15
1B	dryl.	no-till	Arlois	4.4	-	20/11/06	25/6/07	13/11/06	Glyphosate + MCPA	528 + 400
								29/4/07	2-4 D + MCPA	75 + 135
2A	dryl.	conv.	Graphic	8.2	30/10/06 + 2/7/07	12/11/06	25/6/07	-	-	-
2B	dryl.	no-till	Hispanic	6.5	-	16/10/06	20/6/07	7/10/06	Glyphosate	630
								15/2/07	Clorsulfuron	15
3A	dryl.	conv.	Hispanic	4.4	5/11/07 + 27/7/07	17/11/06	17/7/07	-	-	-
3B	dryl.	no-till	Hispanic	3.9	-	16/10/06	20/6/07	7/10/06	Glyphosate	630
								15/2/07	Clorsulfuron	15
4	irrig.	-	Arlois	6.5	-	28/11/06	25/6/07	13/11/06	Glyphosate + MCPA	528 + 400
								28/4/07	2-4 D + MCPA	75 + 135
5	irrig.	-	Arlois	1	-	28/11/06	5/7/07	13/11/06	Glyphosate + MCPA	528 + 400
								28/4/07	2-4 D + MCPA	75 + 135
6	irrig.	-	Arlois	2.6	-	28/11/06	5/7/07	13/11/06	Glyphosate + MCPA	528 + 400
								28/4/07	2-4 D + MCPA	75 + 135

Continuation of **Table S1**.

Field No.	Irriga-tion *	Mana-gement **	Crop Variety	Field size ha	Date of tillage	sowing	harvest	herbicide appl.	Herbicides Active ingredients	Dose (g a.i. ha^{-1})
						2008				
1A	dryl.	conv.	Prestige	18	1/10/07	1/11/07	9/8/08	-	-	-
1B	dryl.	no-till	Culma	4.4	-	25/10/07	18/7/08	1/10/07	Glyphosate + MCPA	720 + 300
7A	dryl.	conv.	Prestige	4.2	1/10/07	1/11/07	9/8/08	-	-	-
7B	dryl.	no-till	Culma	7	-	25/10/07	18/7/08	1/10/07	Glyphosate + MCPA	720 + 300
8A	dryl.	conv.	Graphic	2	10/10/07	7/11/07	8/8/08	-	-	-
8B	dryl.	no-till	Culma	1	-	25/10/07	18/7/08	1/10/07	Glyphosate + MCPA	720 + 300
9	irrig.	-	Sarina ***	1.3	4/12/07	11/12/07	18/7/08	-	-	-
10	irrig.	-	Sarina ***	1	11/12/07	19/12/07	5/8/08	-	-	-
11	irrig.	-	Culma	1	-	15/11/07	3/7/08	20/11/07	Glyphosate + MCPA	720 + 600

* Dryl.= dryland; Irrig.= Irrigated; ** Conv. = conventionally tilled; *** wheat instead of barley

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CHAPTER 3

Unravelling the process of weed seed predation: developing options for better weed control

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Unravelling the process of weed seed predation: developing options for better weed control

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Abstract

Seed predation can cause significant losses of weed seeds in agricultural systems and can, thus, contribute to weed control. The removal of *Lolium multiflorum* and *Vicia villosa* seeds by harvester ants, *Messor barbarus*, and granivorous rodents, *Mus spretus,* in six cereal fields in NE Spain was separated into three sequential processes, namely 1) the probability of finding a seed cache (cache encounter rate), 2) the percentage of seeds utilized once a seed cache has been found (seed exploitation rate) and 3) seed selection if multiple species are present (preference). Identifying the most important behavioural component and factors that drive it may help to better understand and manage seed predation.

Seed cache encounter rate correlated well with overall seed removal rate caused by harvester ants ($r^2 = 0.91$), or rodents ($r^2 = 0.82$). Once found, seed exploitation rates were high and fairly constant from spring to autumn for harvester ants, and low throughout the season for rodents. Harvester ants removed almost all *Lolium multiflorum* seeds from caches found, while the exploitation of *V. villosa* seeds varied across the season. In the case of rodents, cache encounter rate, but not exploitation rate, could be explained by canopy cover provided by the crop. *Lolium multiflorum* seemed to be preferred in early 2007, whereas *V. villosa* was in 2008.

The adoption of no-till or minimum tillage systems together with the establishment of field edge vegetation are likely to encourage seed cache encounter and exploitation rates by both harvester ants and rodents, thus leading to increased weed control in semi-arid cereals.

Keywords: Harvester ants, granivorous rodents, seed encounter, seed exploitation, seed preference, no-till, field edge.

1. Introduction

Seed predation can cause significant weed seed losses in agricultural systems and can, thus, contribute to weed control (Westerman *et al.*, 2003). Several studies have measured predation to gain a better understanding of its impact on weed population dynamics in agro-ecosystems and to develop strategies to maximize it (e.g. Westerman *et al.*, 2003, Heggenstaller *et al.*, 2006; Baraibar *et al.*, 2009). Field estimates of seed removal rates are often derived from experiments with artificial seed caches. The observed overall removal rates result from three sequential processes, namely 1) the probability of finding a seed cache (encounter rate), 2) the percentage of seeds utilized once a seed cache has been found (exploitation rate) (Hulme, 1994) and 3) seed selection (preference) based on nutritional value, palatability, easiness to handle, etc. However, it is usually unknown whether, for example, low predation rates are predominantly due to low encounter rate, low exploitation rate or low preference.

Knowing how seed predators find, utilize and select seeds can help to better understand spatial and temporal variability in observed predation rates and explain why certain weed species persist despite high overall seed predation pressure. Ultimately, this knowledge may provide predator-specific clues as to how to manipulate each component of seed predation for better weed control.

In semi-arid cereals in north-eastern Spain, the harvester ant *Messor barbarus* L. and the Algerian mouse, *Mus spretus* Lataste, are the main weed seed predators (Baraibar *et al.*, 2009). Seed removal rates by both predators change over the year. In the case of harvester ants, seed removal rates are high in spring and summer, with a temporary trough in autumn, caused by a temporary shift in workforce allocation (reproductive phase), and low in winter, due to temperature constraints. Tillage after cereal harvest has an immediate effect on seed removal rates and a long-lasting effect via a decline in harvester ant population development. Seed removal rates by rodents are low throughout the season, probably because of low mouse densities due to insufficient foraging and nesting sites (Díaz, 1992a) and water shortage during summer (Newsome *et al.*, 1976).

In this study, existing data (Baraibar *et al.*, 2009) was used to identify which behavioral component(s) is or are responsible for the observed trend in overall seed removal, and to determine whether the relative importance of the components is constant or changes over the season.

In the case of the foraging behaviour of harvester ant, seasonal changes in overall seed removal rates were expected to stem from changes in cache encounter rate and seed preference. Harvester ants send out scouts to identify the location of food sources (Gordon, 2002). Once a food source is encountered, a foraging trunk trail is formed via a pheromone trail and the resulting mobilization of workers should lead to high exploitation rates (Avgar *et al.*, 2008). Seed cache encounter rate is, therefore, directly linked to the proportion of workers allocated to scouting. This proportion may decrease when more workers are needed for other tasks, such as nest cleaning and construction (after rain and soil disturbances), and attending brood (reproductive phase), or when outside temperatures limit foraging (Gordon, 1986). Seed preference by harvester ants is influenced by seed characteristics, such as seed size (Azcarate *et al.*, 2005) and seed coat toughness (Oliveras *et al.*, 2008), which are fixed per species; by seed abundance (Reyes-López and Fernández-Haeger, 2002a) and by the availability of preferred and non-preferred seeds (Risch and Caroll, 1986). In addition, the state of filling of the granaries may influence seed preference. In spring, when the granaries are empty, seeds of larger mass are preferred, whereas towards the end of the season, when the granaries are full, preference disappears or smaller seeds are preferred (Reyes-Lopez and Fernández-Haeger, 2002b).

In the case of the foraging behaviour of the Algerian mouse, seasonal changes in overall seed removal rates were expected to stem mainly from changes in cache encounter and exploitation rates. Canopy cover by the crop is related to overall removal rate (Heggenstaller *et al.*, 2006), probably because of a lower risk of rodents being predated (Plesner Jensen and Honess, 1995). When fields are bare and exposed, such as after crop harvest or when a crop fails to establish due to poor weather conditions in spring, low cache encounter and seed exploitation rates are expected. Rodents select seeds based on carbohydrate and protein levels (Jenkins and Ascanio, 1993), metabolic water balance (Frank, 1988) and seed size and shape (Henderson, 1990). Changes in relative humidity and in nutritional requirements of rodents may cause changes in seed preference over a season (Tew *et al.*, 2000).

2. Materials and methods

2.1. Experimental site and design

Trials were conducted near Vilanova de Bellpuig (41°36′56″N 0°57′54″E, Lleida), a village in the semi-arid region in the north-east of 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. Trials were conducted in 2007 and 2008 and have been described in detail by Baraibar *et al.* (2009). In short, six rainfed barley (*Hordeum vulgare*) fields were paired, such that one field was no-till and the other conventionally tilled. Tillage influenced seed removal rates, however, preliminary analysis showed that tillage did not affect the relative importance of the various processes leading to overall seed removal. Therefore, data from tilled and no-till fields were lumped and jointly analysed. After barley harvest in June, fields were left fallow until seeding in late autumn. Weather data was obtained for Golmés, Pla d'Urgell, 4 km away from the experimental fields (Servei Meteorològic de Catalunya, 2010).

In each field, seed predation was measured via feeding stations that were located in a rectangular grid of 24 – 25 points, 5 × 5, 6 × 4 or 3 × 8 (rows × columns), depending on the shape of the field. Stations were spaced 10 meters apart. Each feeding station consisted of two, 9 cm diameter Petri-dishes, containing seeds, and was designed to measure either invertebrate or vertebrate seed removal (Díaz, 1992a, b). The vertebrate dish was placed on top of a 20 cm high tube, that was pushed 10 cm deep into the soil, and that was coated on the outside with fluon (Polytetrafluoroethylene, BioQuip Products Inc., Rancho Dominguez, California, USA) to keep out insects. The invertebrate dish was placed on the ground surface. It had four openings on the side and was covered by an exclusion cage to keep out vertebrates.

Two grams of non-treated *Lolium multiflorum* Lam. (3.95 ± 0.033 mg seed^{-1}) and 2 g of non-treated *Vicia villosa* Roth seeds (31.3 ± 0.239 mg seed^{-1}) (Semillas Batlle, Bell-lloc, Spain) were mixed and placed in each dish once a month from April to October 2007 and from January to June 2008 (except May 2008). Seeds were similar in size, shape and weight to seeds present in the study area, such as those of *L. rigidum* Gaudin, *V. peregrine* L., *V. sepium* L., *Galium aparine* L., or *Convolvulus arvensis* L. After a 48 hours exposure, remaining seeds were sieved apart and weighed to calculate percentage of seeds removed.

2.2. Calculation of seed removal components

Total seed removal, *T*, as used in Baraibar *et al.*, (2009), was defined as:

$$T = \frac{R_{L.m.} + R_{V.v.}}{I_{L.m.} + I_{V.v.}} \qquad (1)$$

with $R_{L.m.}$and $R_{V.v.}$ the weight of *L. multiflorum* and *V. villosa* seeds removed (g) and $I_{L.m.}$ and $I_{V.v,}$ the initial weight of seeds of these two species (2 g each). Seed removal was averaged over N observations;

$$\overline{T} = \frac{1}{N}\sum_{i=1}^{N}\left(\frac{R_{L.m.}+R_{V.v.}}{I_{L.m.}+I_{V.v.}}\right)_i \qquad (2)$$

Seed cache encounter, C, was defined as

$$C = \frac{M}{N} \qquad (3)$$

with M the number of observations in the subset of data that satisfy the condition; $R_{L.m.} \geq 0.1 \times I_{L.m.} \vee R_{V.v.} \geq 0.1 \times I_{V.v}$. That is, dishes were considered ‘found’ if 10% or more of the *V. villosa* seeds or 10% or more of *L. multiflorum* seeds were missing. The boundary of 10% was based on work by Heggenstaller *et al.* (2006), who found that between 2 and 6% of the seeds were lost from seed cards due to wind, rain, handling and inadequate adhesion. Here, a slightly more conservative boundary was chosen, which minimized the risk that observations were classified as ‘found’, when in reality they had not been found. Seed exploitation, E, was calculated the same way as total seed removal, T, except that it applied to and was averaged over the subset of observations, M, that satisfied the above-mentioned condition;

$$\overline{E} = \frac{1}{M}\sum_{j=1}^{M}\left(\frac{R_{L.m.}+R_{V.v.}}{I_{L.m.}+I_{V.v.}}\right)_j \qquad (4)$$

Seed preference, P, was expressed as the weight of seeds of one species removed, x_1, relative to the seeds of both species removed, x_1+x_2;

$$P_{x1} = \frac{R_{x1}}{R_{x1}+R_{x2}} \qquad (5)$$

P was averaged over M observations;

$$\overline{P}_{L.m.} = \frac{1}{M}\sum_{j=1}^{M}\left(\frac{R_{L.m.}}{R_{L.m.}+R_{V.v.}}\right)_j \quad \text{for } \textit{L. multiflorum} \qquad (5a)$$

and

$$\overline{P}_{V.v} = \frac{1}{M}\sum_{j=1}^{M}\left(\frac{R_{V.v.}}{R_{L.m.}+R_{V.v.}}\right)_j \quad \text{for } \textit{V. villosa} \qquad (5b)$$

The relationships between total seed removal, T, seed cache encounter, C, seed exploitation, E, and seed preference, P, can be described as;

$$\overline{T} \approx C \times \overline{E} \qquad (6)$$

$$\overline{T}_{L.m.} \approx C \times \overline{E} \times \overline{P}_{L.m.} \times 2 \quad (6a)$$

$$\overline{T}_{V.v.} \approx C \times \overline{E} \times \overline{P}_{V.v.} \times 2 \quad (6b)$$

Background seed losses from the (*N-M*) dishes not found by predators were included in *T*, but not in *E* or *P*, hence the approximation. Graphs presenting components of seed predation use *T*, *C*, *E* and *P* expressed as percentages.

3. Results

3.1. Components of seed removal by harvester ants

Overall seed removal by harvester ants, *T*, correlated well with cache encounter rate, *C* (r^2 = 0.91; *P* <0.001), (Fig. 1A), and less well with exploitation rates, *E* (r^2 = 0.58; *P* = 0.02), (Fig. 1A) or preference for *L. multiflorum*, $P_{L.m.}$, and *V. villosa*, $P_{V.v.}$ (r^2 = 0.60 and 0.44; *P* = 0.01 and 0.07, respectively), (Fig. 1C).

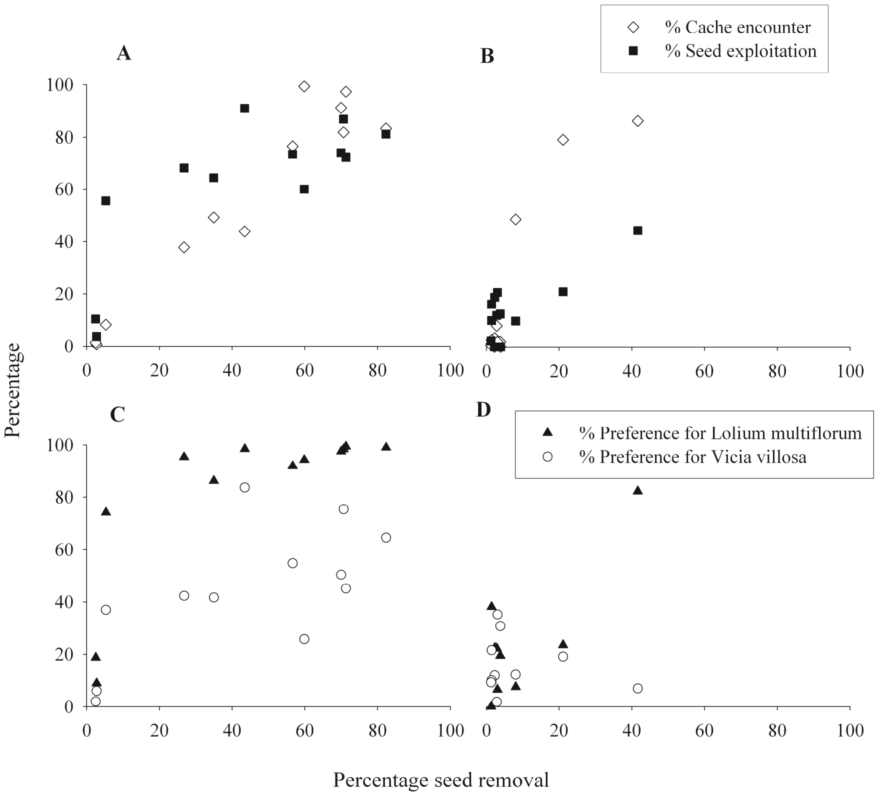

Fig. 1. The percentage seed cache encounter, seed exploitation (A, B), preference for *Lolium multiflorum* and preference for *Vicia villosa* (C, D), as a function of the percentage seed removal for invertebrates (A, C) and vertebrates (B, D).

There was a close visual match between patterns of *T* and *C* (Fig. 2A), and less so with *E* (Fig. 2B), $P_{L.m.,}$ and $P_{V.v.}$ (Fig. 2C). This means that temporal changes in overall removal rates, *T,* by harvester ants appear to be mainly caused by differences in cache encounter rates, *C*. Seed cache encounter rate also contributed most to *T* and its relative importance was constant over the season. Once a dish was found, a relatively stable proportion of seeds was taken (*E* = 0.6 – 0.8 in 2007; *E* = 0.9 in 2008), except in early 2008 when low temperatures inhibited harvester ant activity. *Lolium multiflorum* seeds were almost always completely removed ($P_{L.m}$ = 0.9 – 1.0), except in winter. In contrast, removal of *V. villosa* seeds, $P_{V.v}$, varied between 0.25 and 0.8. As expected, low $P_{V.v}$ occurred after rain events (May, October), after harvest and tillage (July) and during the reproductive phase of the harvester any colonies (September).

3.2. Components of seed removal by granivorous rodents

Overall seed removal rates by rodents correlated with cache encounter rate, *C* (r^2 = 0.82, P<0.001), (Fig. 1B), exploitation rates, *E* (r^2 = 0.65, P = 0.008), (Fig. 1B) and with preference for *L. multiflorum*, $P_{L.m.}$ (r^2 = 0.66, P = 0.009), (Fig. 1D), but correlated poorly with preference for *V. villosa*, $P_{V.v}$ (r^2 = 0.04, P = 0.44), (Fig. 1B). There was a visual match between the temporal patterns of *T* and *C* (Fig. 3A), but not with the other behavioural components (Fig. 3B and C). This means that temporal changes in total seed removal, *T,* by granivorous rodents were mainly caused by changes in cache encounter rates, *C*. Again, seed cache encounter rate was the largest component and contributed most to explaining seed removal by granivorous rodents throughout the season. In contrast to harvester ants, the proportion of seeds exploited by rodents was low (*E* = 0.1 – 0.2). Because cache encounter rates, *C*, in particular before harvest, were high, low overall removal rates were mainly caused by low seed exploitation rates, *E*. The number of dishes found was too low to draw solid conclusions with regard to preference, in particular after crop harvest. However, in April 2007, almost all seeds taken were *L. multiflorum* ($P_{L.m}$ = 0.8), while later in the season preference was less pronounced. In 2008, preference shifted from *L. multiflorum* to *V. villosa*.

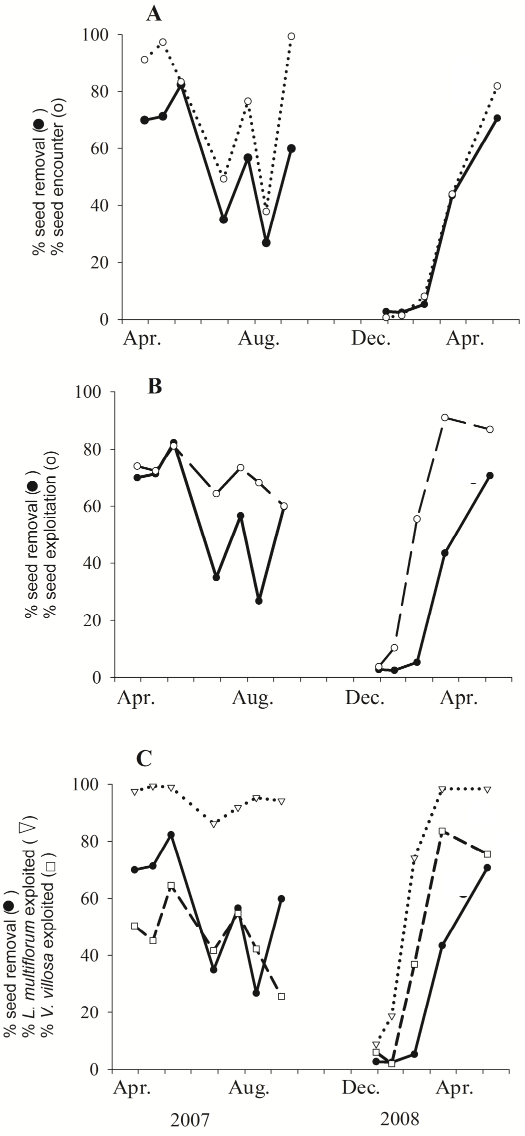

Fig. 2. The percentage overall seed removal and the percentage seed cache encounter (A), the percentage seed exploitation (B), and the percentage preference for *Lolium multiflorum* and *Vicia villosa* (C) of invertebrate seed predators over time. Data on overall seed removal was obtained from Baraibar *et al.* (2009).

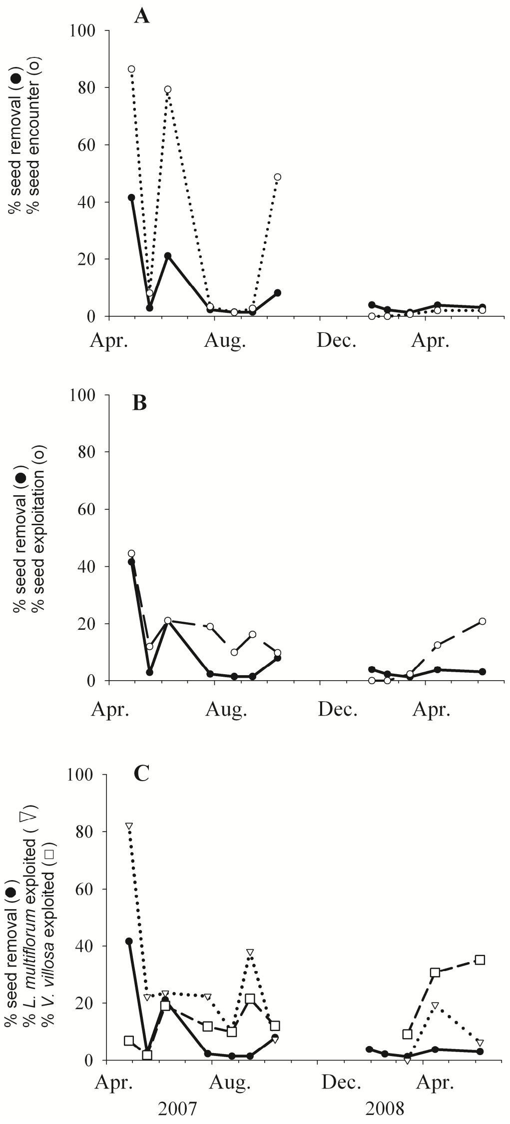

Fig. 3. The percentage overall seed removal and the percentage seed cache encounter (A), the percentage seed exploitation (B), and the percentage preference for *Lolium multiflorum* and *Vicia villosa* (C) of vertebrate seed predators over time. Data on overall seed removal was obtained from Baraibar *et al.* (2009).

4. Discussion

As expected, overall seed removal rate, *T*, by granivorous ants was mainly determined by the proportion of seed caches located, *C*. When cache encounter rate is high, high overall removal rates, *T*, are to be expected. If the objective is to enhance seed predation in agro-ecosystems the focus should be on how factors that limit cache encounter rates can be managed by farmers. Seed cache encounter is limited by many factors, of which some could be managed to some extent.

The spatial distribution of nests may determine seed cache encounter probability. Foraging by *M. barbarus* can reach 30 m around the nest (Cerdan, 1989), but foraging efficiency decreases with increasing distance from the nest. Díaz (1992b) reported a 50% decrease in foraging efficiency at distances more than 1.5 m from the nest for *Messor capitatus* Latreille, a close relative of *M. barbarus*. Assuming a regular nest distribution and nests of identical size, e.g., 4000 workers per nest (Díaz, 1992b), nest density should ideally be around 1200 nests per ha. Densities up to 1100 nests of *M. barbarus* per ha are feasible in no-till dryland cereals (Baraibar *et al.*, unpublished data: Chapter 4). However, a clumped or aggregated distribution of nests will result in some areas probably being more intensely searched for seeds than others.

The location and distribution of new nests is determined by two distinctive processes. The first process is site selection by first-year queens that emerge, fly, mate, land and dig into the soil, all within a single day in autumn. The locations where queens land are largely random, but the opportunities to dig into the soil and establish a nest may fluctuate within and between fields, as a function of, for example, soil (surface) conditions (Johnson, 1992), intraspecific competition (Kawecki, 1992), and queen size (Wiernasz and Cole, 2003). The second process is selective survival of first-year queens and young colonies. The shallow nests of young colonies are particularly vulnerable to soil disturbances, such as tillage and ploughing. Nests of *Messor capitatus* were scarce in mouldboard ploughed cropland probably because of the periodical destruction of the top part of the nest, and because of changes in soil structure, which may affect the survival chances of colonies (Díaz, 1991). In reduced or no-till systems, soil disturbance is low(er), thus positively influencing the survival chances of young colonies. Interestingly, many farmers in the area till following harvest, because they believe that tillage followed by summer showers will induce weed emergence and, thus, lower the weed seed bank. However, tillage can increase the weed seed bank, because it prevents seed predation (Hulme, 1994). In Germany, Dicke and Gerhards (2006) showed that seed predation in no-till fields was higher than weed emergence in tilled fields.

Other factors that influence site selection and nest survival include soil texture and moisture (Johnson, 1992, 1998), organic matter and phosphorus content (Milks *et al.*, 2007), the degree of water-logging, soil compaction, slope of fields (Crist and Williams, 1999) and intra- and interspecific competition (Gordon and Kulig, 1996). However, most of these factors cannot be controlled by farmers.

Harvester ant mobility and foraging activity could be enhanced by increasing soil temperature and moisture content of the soil surface (Johnson 1998; Azcarate *et al.*, 2007). Soil temperatures could be increased by removing mulches or straw from the soil surface (Nkem *et al.*, 2002), albeit, at the expense of loosing soil moisture. The pending climate change, with rising temperatures and lower precipitation, may bring about such changes, however, high temperatures in summer may become limiting.

Seed removal rates by rodents were explained by a mixture of seed cache encounter rate, C, seed exploitation rate, E, and seed preference for *L. multiflorum*, $P_{L.m}$. As expected, cache encounter rate was high when the crop provided cover, but lower when cover was lacking. Once a cache was located, rodents seemed to exploit a constant percentage of seeds regardless of whether cover was available or not. This suggests that seed cache encounter rate could easily be manipulated by increasing cover, but exploitation rate could not. Hulme (1994) found that seed cache encounter rate correlated with rodent population size in the vicinity of the seed source, and that the spatial variation in seed exploitation rates correlated with the spatial distribution of rodents. Thus, the most straightforward way to enhance both cache encounter and seed exploitation rates seems to be to increase rodent population size.

Providing cover throughout the year may enhance rodent populations and, thus, predation rates. Fields are bare during most of the year, and, therefore, vegetation in field boundaries and hedgerows may be essential for maintaining small mammal populations (Pollard and Relton, 1970). In the area studied, field margins are narrow (max. 0.5 m wide) and the vegetation consists almost exclusively of annuals, which dry out or are burned after crop harvest. The resulting habitat quality for rodents after harvest is, therefore, poor. Wider field margins and shrubs and trees, which provide cover at times when the fields are bare, could enhance populations of granivorous rodents (Bence *et al.*, 2003). Currently, farmers in the area view field margin vegetation as a source of weed infestation and a drain of water. They are unaware of the potential benefits for weed control. Finally, inside no-till fields, maintaining stubble may provide some cover and safety, resulting in higher seed removal rates (Booman *et al.*, 2009).

Providing free water during the summer period may also contribute to increasing populations of granivorous rodents in semi-arid regions. Rodent densities and survival chances were higher when rodents had access to free water compared to controls without water (Newsome *et al.*, 1976).

It seems that predation by harvester ants and granivorous rodents can be enhanced in two ways. The first is the adoption of minimum or no-till systems, which are readily adopted in the semi-arid regions of north eastern Spain anyway, mainly because of fuel and water savings. The second involves the expansion or recovery of ecological infrastructures, such as field edge vegetation, which is slightly more problematic.

There is little cause for concern that enhancing or stimulating populations of harvester ants or granivorous rodents could lead to higher levels of crop damage. Harvester ants can collect cereal seeds after sowing in autumn, if temperatures permit, and if seeding was done superficially. Harvester ants can also collect ripe cereal seeds in summer, prior to harvest. However, damage caused by harvester ants is usually negligible (Baraibar, unpublished data: Chapter 6). Rats and granivorous mice do cause crop damage in the tropics and in Australia (Brown *et al.*, 2003 and references therein). However, granivorous mice are seldom associated with crop damage in Europe or North America, and are generally considered beneficial (e.g., Clark and Young, 1986).

This study highlights the importance of seed cache encounter rate as a key component of seed predation, and identifies various management options that could enhance seed cache encounter rate. Eliminating the factors that restrict cache encounter should lead to increased weed seed predation rates and to improved weed control. However, confirmation of the validity and practicality of the various options under field conditions is required first.

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CHAPTER 4

Harvester ant (*Messor barbarus* L.) density as related to soil properties, topography and management in semi-arid cereals

Harvester ant (*Messor barbarus* L.) density as related to soil properties, topography and management in semi-arid cereals

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Summary

Harvester ants are important weed seed predators in semi-arid cereal fields. They consume large amounts of weed seeds that otherwise would enter the soil profile. Populations of harvester ants vary considerably across fields and so do concomitant weed seed predation rates, but causes of variability are largely unknown. Understanding the factors that affect ant density may help to identify areas with high natural weed seed control and management factors that could help to enhance ant densities in areas where they are currently absent or densities low. *Messor barbarus* ant density was approximated by nest density and nest size, and these were correlated to different edaphic (moisture content, bulk density, aggregate distribution, organic matter, texture and soil strength), topographic (field altitude, slope and orientation) and crop management factors (fertilizer use and straw management) of 34 no-till and 6 minimally tilled cereal fields. No-till fields had been managed without tillage for a period of 1-25 years. The number of years since conversion to no-till explained 14.2% of variability in ant density. Densities of *M. barbarus* ants and nests increased with increasing number of years of no-till, reached a peak at 11-12 years, after which densities decreased again. None of the soil characteristics, topographic variables or other management practices could explain nest densities. A number of possible explanations for this lack of relationships are discussed. An alternative explanation is proposed based on the life cycle of harvester ant colonies. The abandonment of yearly tillage may have allowed the establishment of a large cohort of similarly aged colonies, which started to compete for limited resources only after twelve years. The results of this study do not allow us to classify fields according to the level of natural weed seed predation, or to formulate recommendations in order to enhance natural weed control. Maybe other factors, such as the availability of resources, in particular food (seeds), may play a more important role in determining ant density than do edaphic, topographic or management factors.

Keywords: colony establishment, colony survival, colony growth, nest size, years of no-till

1. Introduction

In north-eastern Spain, like in other semi-arid regions of the world, harvester ants are important seed predators. When present in arable fields, harvester ants are the main weed seed predators and can contribute substantially to weed control (Spafford *et al.*, 2006; Baraibar *et al.*, 2009). Harvester ant density varies between locations and it is likely that weed seed predation rates will vary accordingly (Azcarate and Peco, 2003; Baraibar *et al.*, 2009). Understanding the factors that determine harvester ant density and spatial variability between fields may be useful to identify areas where natural weed seed control contributes to weed management, and to identify management factors that could help to enhance ant densities in those areas where harvester ants are currently absent or densities low. Direct measures of ant density are difficult, because of the subterranean life style and the difficulty to obtain estimates of population density for insects that forage in columns (trails) (Schlick-Steiner *et al.*, 2006 and references therein). As an alternative, harvester ant density was estimated using a combination of nest density and size (Milks *et al.*, 2007).

Messor barbarus L. is one of the most common species of harvester ant in NE Spain. Three processes largely determine its density and spatial distribution: 1) nest initiation by foundress queens, 2) survival of colonies, and 3) colony growth.

Once a year, colonies cease normal activity and start producing reproductive males and females, which are released after the first autumn rains. Winged female ants fly up, mate, land, and search for a site to dig into the soil. The place where a young queen lands is largely random, but nest establishment rate may differ within and between fields, because of differences in soil (surface) characteristics (Johnson, 1992), queen mortality rate due to aggression by workers from other colonies (Kawecki, 1992), ant predators, such as spiders or lizards (Gordon and Kulig, 1996), and size of the queen, which determines the probability of survival through the initial stages of colony formation (Wiernsaz and Cole, 2003). Usually, less than one percent of the young queens manages to establish a new nest (Gordon and Kulig, 1996). Once established, survival probabilities of nests remain low until they are two years old, and are largely determined by the degree of soil disturbance and by intraspecific competition with older neighboring colonies (Johnson, 2001). Survival of older colonies is determined by competition for space and resources with other colonies, and by longevity of the queen. If nest density is high, foraging areas of different colonies will frequently overlap. Repeated encounters between workers of different nests may trigger wars, which is usually fatal to one of the competitors. Growth of the colony depends on food availability, which influences productivity of the queen (Smith, 2007), and the rate with which workers die. Usually, colonies grow with age until they reach a stable size at the age of approximately five (Gordon, 1995). *M. barbarus* queens can live as long as 15-20 years, after which the entire colony dies.

External factors influencing *M. barbarus* colony establishment, survival and growth, include soil properties, topographic characteristics, such as field altitude, slope and orientation and management practices, such as tillage, type and amount of fertilization and straw management.

Digging success of young queens, and colony establishment and growth are influenced by soil strength, texture and soil moisture content of the top soil (Wiernasz and Cole, 1995; Johnson, 1998; Enzman and Nonacs, 2010). Soil strength is a measure of the capacity of a soil to withstand forces without experiencing failure, whether by rupture, fragmentation or flow and it is correlated to soil moisture (Laboski *et al.*, 1998). Soil strength is one of the factors that determines the ease with which ants can tunnel the soil and construct chambers (Boulton *et al.*, 2005). Survival probability of colonies is influenced by texture and bulk density, because they are involved in the regulation of temperature and moisture content of the colony (Ali *et al.*, 1986; Johnson, 1998). It is currently unknown how densities of *M. barbarus* are influenced by soil type, but densities are expected to be higher in soils that facilitate the establishment of new queens and chamber construction, such as those with low clay content, high organic matter and low bulk density, than in compacted or sandy soils (Johnson, 1992; Milks *et al.*, 2007).

Altitude, slope and orientation of a field in which a nest is located influence the number of hours that the ant nest is exposed to sunshine, which in turn influences soil temperature (Crist and Williams, 1999). The need for heat regulation to ensure colony survival may determine the location of the nests because ant activity and brood development are controlled by soil temperature (Wang *et al.*, 2001; Azcarate *et al.*, 2007). Low temperatures decrease nest survival probabilities and result in lower ant densities in elevated and north facing sites than in lowlands (Crist and Wiens, 1996; Wang *et al.*, 2001).

Soil disturbance, including tillage, can destroy or damage nests of young and old colonies, respectively. The harvester ant *Messor capitatus* Latr. was completely absent from fields in central Spain that had been yearly mouldboard-ploughed (Díaz, 1991).

Nest densities of *M. barbarus* were higher in no-till than in minimally tilled fields in NE Spain (Baraibar *et al.,* 2009). Multiple years of no-till lead to increased proportions of stable macro-aggregates and organic matter, to increased porosity (Alvaro-Fuentes *et al.,* 2009, So *et al.,* 2009), and to an increase in soil inhabiting insects and earthworms (Neave and Fox, 1998; Edwards and Lofty, 1982). Increases in earthworm densities are attributed to lack of soil disturbance and greater ease of digging in soil in no-till than in tilled fields. For similar reasons, ant densities are likely to increase with decreasing tillage intensity.

Manure, such as pig slurry and broiler litter, is widely used as fertilizer in cereal fields in north-eastern Spain. The type and amount of manure used can alter soil physical and chemical properties such as pH, aggregate stability and concentration of metals (Adeli *et al.,* 2007; Diez *et al.,* 2004) and alter queen survival rates or colony growth. Leaving straw on the soil surface after harvest in June may help to regulate soil temperature and moisture during the hot summer months (House and Parmelee, 1985), and may, therefore, favour harvester ant activity. However, large amounts of straw on the soil surface can hamper queen establishment in autumn, which could result in lower ant nest density.

The purpose of this study was to identify the main factors influencing differences in harvester ant density between fields and to identify management practices that could lead to higher nest densities, as a basis for recommendations to farmers who would like to conserve and maximize natural weed control.

2. Materials and methods

2.1. Study area and nest sampling

Observations were made in the rain-fed semi-arid area of Agramunt (Lleida), north-eastern Spain. Average temperature is 13.9 ºC with hot summers (mean T. 23.8 ºC) and cool winters (mean T. 4.7 ºC). Average rainfall is 428 mm, concentrated in spring and autumn (Servei Meteorològic de Catalunya, 2010). Main crops are wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa*), triticale (× *Triticosecale* sp.) and, less frequently, oil seed rape (*Brassica napus* L.).

Observations and sampling were done in 40 commercial winter cereal fields within a radius of 10 km around the village of Agramunt. No-till is widely adopted in the area (Montcunill, 2009). Thirty-four of the selected fields were managed without tillage for a period varying from 1 to 25 years, and the remaining six were minimally tilled, which included a tillage operation around September with a vertical working depth of 15-20 cm.

In each of the 40 fields, *M. barbarus* nests were counted in a 50 m × 50 m section (2500 m^2), using a 10 m × 10 m grid, after crop harvest in 2008 and 2009. In principle, the location of the 50 m × 50 m section was chosen randomly, except when (part of) the field was located on a sloop. In that case, the section was preferentially selected on a steep part of the field. Nests were marked using spray paint to prevent double counting. Counting was done from sunrise until temperatures limited ant activity (*i.e.*, around 35 °C). Nests were only included if ant activity was detected, to prevent the inclusion of dead or abandoned nests. Counts were transformed to nest density, N [# nests.ha^{-1}]. Nest size, S, was determined for 10 random nests per field, using a subjective scale that ranged from 1 (small) to 5 (large), based on the area occupied by the colony, the number of entrances, worker size and the number of active ants. A proxy of ant density per hectare, A, was calculated by multiplying nest density, N, times average nest size, S.

2.2. Soil characteristics

Soil characteristics were determined using soil samples taken from each of the fields in December 2008 (19 fields) and January 2010 (21 fields). In the case of moisture content and soil strength, samples were taken simultaneously from all fields on 28 and 29 April 2009. Soil variables measured were: 1) moisture content, 2) soil strength, 3) bulk density, 4) aggregate distribution, 5) organic carbon and 6) texture. We sampled three points per field, located on a diagonal across the 50 m × 50 m plot. In the case of samples to determine bulk density, we took three samples per point (9 per field). In the case of samples to determine texture components, we analyzed a composite sample from the three points sampled per field.

Moisture content (%) was measured for every 25 cm soil layer, from 0 to 100 cm deep, with a 5.5 cm diameter soil core. Samples were weighed, dried in a stove at 105 ºC for 48 hours and weighed again. Soil strength was measured as the pressure ($MPa.cm^{-2}$) required to enter the soil profile. We used a hand-held penetrograph (Stiboka penetrograph, Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands), which plots the resistance to penetration as a function of soil depth, to a depth of 80 cm. Because there is no information available with regard to the soil strength that is limiting tunnelling by harvester ants, we calculated the depth at which soil penetration resistance became ≥ 1, 2, 3 and 4 MPa.cm^{-2}.

Bulk density (g.cm^{-3}) was assessed from 0 to 15 cm depth, using the clod method (Campbell and Henshall, 1991). Stable soil aggregate distribution was determined for the 0 – 5 cm and 5 – 10 cm soil layers with the dry sieving method (White, 1993). A series of three sieves (0.05, 0.25, and 2 mm pore size) was used to obtain four aggregate fractions: (i) <0.05 mm ($Agg_{<0.05}$), (ii) 0.05 to 0.25 mm ($Agg_{0.05-0.25}$), (iii) 0.25 to 2 mm ($\mathrm{Agg}_{0.25-2}$) and (iv) > 2mm ($Agg_{>2}$). The weight of each fraction was determined for each depth (hereinafter $Agg^{soil\ depth}_{fraction\ \ size}$). Soil organic carbon, from which percentage organic matter is calculated, was measured for the top 25 cm of the soil according to the wet oxidation method of Walkley and Black (Nelson and Sommers 1982). Textural components (% clay, % sand and % silt) at 0 – 25 cm and 25 – 50 cm depth ($Clay^{soil\ depth}$, $Sand^{soil\ depth}$, $Silt^{soil\ depth}$ hereinafter) were determined using the sieve-pipette method (Gee and Bauder, 1986). Texture and organic matter were analysed by the Laboratory Applus Agroambiental (Sidamon, Lleida).

2.3. Topographic and management variables

We determined field orientation, slope and altitude, with a GPS with sub-metric precision (Trimble® GeoXH™ hand-held, GeoExplorer® 2005), by taking coordinates and slope in the four corners of the 50 m × 50 m plot for each field. We calculated field altitude as the average value of the four points. Slope was calculated between the highest and the lowest point.

Information regarding crop type, cultivar, sowing date, seeding rate and depth, seeding distance, the number of years since conversion to no-till, timing of tillage and machinery used, frequency, timing and type of herbicides and fertilizer used, and straw management were provided by the farmers.

2.4 Data analysis

There were three dependent variables, namely number of nests per hectare, N, mean nest size, S, and ant density, A. Nest size was used as an explanatory variable in the analysis of N.

The independent variables included 20 soil variables, namely aggregates ($Agg_{<0.05}$, $Agg_{0.05-0.25}$, $\mathrm{Agg}_{0.25-2}$ and $Agg_{>2}$) at two depths, three textural components (clay, silt and sand) at two depths, bulk density (*BD*), organic matter (*OM*) and depth at which soil strength was 1, 2, 3 and 4 MPa; three topographic variables, namely field altitude (*Alt*), orientation (*O*) and slope (*Sl*); two management variables, namely fertilizer used (pig slurry, compost, broiler litter, synthetic fertilizers) and straw management (straw removed, straw left in the field); and number of years of no-till (*NT*). Because there were 26 independent variables and only 40 measures of the dependent variables, the first step was to reduce the number of explanatory variables. Biplots and Pearson's correlation matrixes were used to identify 1) explanatory variables that were closely correlated and 2) explanatory variables that correlated well with the dependent variables. In particular among the soil variables redundancy was high. From sets of soil variables that were highly intercorrelated, one variable was maintained, namely the one that was best correlated with the dependent variables *A*, *N* or *S*. Most explanatory variables were not normally distributed, and, therefore, variables were transformed. Those that were expressed as percentages were arcsine square root transformed; bulk density, slope, altitude and depth at which soil strength was 1, 2, 3 and 4 MPa were square root transformed. However, transformed variables are difficult to interpret biologically when significant in regression analyses, and, therefore, the selection procedure was completed with both transformed and untransformed variables.

Generalised linear regression was used to relate *N*, *S* and *A* to untransformed variables that were maintained. Initially, the poisson distribution was assumed (log-link), however, this resulted in high dispersion parameters (80-120), which suggested that the poisson distribution was inappropriate. The use of a gamma distribution avoided overdispersion and resulted in normally distributed residues. Therefore, the gamma distribution (reciprocal-link) was used in all further GLM. First, the best model(s) explaining *A*, *N* and *S* was selected based on all subset regressions for transformed and untransformed data (procedure RSEARCH, Genstat 12), using the corrected AIC ($\mathrm{AIC_c}$) and R^2_{adj} as selection criterions. The use of $\mathrm{AIC_c}$ is recommended when number of observations (*n*) is small or number of estimated parameters (*k*) is large (Burnham and Anderson, 2002). Next, the final model(s) was selected based on R^2_{adj} and significance of the GLM (GLM procedure, gamma distribution, reciprocal-link; R software, 2009). If differences were not significant between models, the principle of parsimony was applied. Normality of the residuals was tested using the Shapiro Wilk test.

Additionally, a correlation matrix between all soil variables and the number of years of no-till was constructed to select the variables that better correlated with *NT*.

The number of years of no-till was related to the selected untransformed soil variables, using generalised linear regressions. Use of the Poisson distribution gave normal residues and dispersion parameters of around 4.5. Therefore, the poisson distribution (log-link) was used.

3. Results

Average nest density was 468 nests.ha^{-1} and varied between fields from 140 to 1168 nests.ha^{-1}. Average nest size was 1.9, and varied between fields from 1 to 3.20. Average ant density was represented by a unit-less value of 953 ha^{-1}, and ranged form 230 to 2570 ha^{-1}. As an indirect variable ($A = N \times S$), A was significantly correlated with both N ($r = 0.93$) and S ($r = 0.59$).

The variables soil moisture, bulk density and depth at which soil strength was 1, 2, 3 and 4 MPa bore no relationship to any of the dependent variables and correlation coefficients were all <0.08, and were therefore excluded. Organic matter and slope did not correlate with either A or S, had correlation coefficients <0.06, and were therefore excluded. Variables related to soil aggregate distribution, and textural components were highly correlated (i) within each depth, ($Agg_{>2} + Agg_{0.25-2} + Agg_{0.05-0.25} + Agg_{<0.05} = 1$; and % sand + % clay + % silt = 1); and (ii) between depths (Tables 1 and 2). Of these two groups of variables, the better correlated with N ($Agg_{0.25-2}^{5-10}$ and $Silt^{0-25}$), A ($Agg_{<0.05}^{5-10}$, $Silt^{0-25}$) and S ($Agg_{<0.05}^{5-10}$, $Clay^{25-50}$) were selected for the analysis.

Table 1. Correlation matrix for aggregates fractions within and between depths (upper case numbers represent depths at which measures were taken (in cm); lower case numbers represent the size of fraction (in mm)).

	$Agg_{>2}^{0-5}$	$Agg_{0.25-2}^{0-5}$	$Agg_{0.05-0.25}^{0-5}$	$Agg_{<0.05}^{0-5}$	$Agg_{>2}^{5-10}$	$Agg_{0.25-2}^{5-10}$	$Agg_{0.05-0.25}^{5-10}$
$Agg_{>2}^{0-5}$	1.00						
$Agg_{0.25-2}^{0-5}$	-0.91	1.00					
$Agg_{0.05-0.25}^{0-5}$	-0.91	0.68	1.00				
$Agg_{<0.05}^{0-5}$	-0.54	0.18	0.69	1.00			
$Agg_{>2}^{5-10}$	0.87	-0.83	-0.79	-0.33	1.00		
$Agg_{0.25-2}^{5-10}$	-0.82	0.89	0.63	0.18	-0.90	1.00	
$Agg_{0.05-0.25}^{5-10}$	-0.76	0.62	0.83	0.41	-0.89	0.60	1.00
$Agg_{<0.05}^{5-10}$	-0.52	0.36	0.61	0.42	-0.71	0.37	0.88

Table 2. Correlation matrix for textural components within and between depths (upper case numbers represent depths at which measures were taken (in cm)).

	$\mathrm{Clay}^{0\text{-}25}$	$\mathrm{Silt}^{0\text{-}25}$	$\mathrm{Sand}^{0\text{-}25}$	$\mathrm{Clay}^{25\text{-}50}$	$\mathrm{Silt}^{25\text{-}50}$	$\mathrm{Sand}^{25\text{-}50}$
$\mathrm{Clay}^{0\text{-}25}$	1.00					
$\mathrm{Silt}^{0\text{-}25}$	-0.34	1.00				
$\mathrm{Sand}^{0\text{-}25}$	-0.21	-0.85	1.00			
$\mathrm{Clay}^{25\text{-}50}$	0.54	0.07	-0.38	1.00		
$\mathrm{Silt}^{25\text{-}50}$	-0.04	0.79	-0.80	0.04	1.00	
$\mathrm{Sand}^{25\text{-}50}$	-0.20	-0.73	0.87	-0.47	-0.90	1.00

Variables that correlated with N were: NT ($r = 0.10$), $Silt^{0\text{-}25}$ ($r = 0.28$), $Agg^{5-10}_{0.25-2}$ ($r = 0.19$), slope (Sl; $r = 0.14$) and organic matter (OM; $r = 0.12$). Variables that correlated well with A were: NT ($r = 0.14$), $Silt^{0\text{-}25}$ ($r = 0.24$), $Agg^{5-10}_{<0.05}$ ($r = 0.18$) and altitude (Alt, $r = 0.12$). Variables that correlated with S were: NT ($r = 0.22$), Alt ($r = 0.22$), $Clay^{25\text{-}50}$ ($r = 0.17$) and $Agg^{5-10}_{<0.05}$ ($r = 0.31$). Visual inspection of biplots suggested a curvilinear relationship between N and NT, and A and NT, therefore, the quadratic term of NT was included in regressions involving these two dependent variables.

There were a number of competing models that described A, N and S equally well (Table 3). Models with highest R^2_{adj} were obtained for untransformed data. All optimal models retained the curvilinear relationship with NT ($NT + NT^2$). Models describing N and A contained NT and NT^2 only because addition of other variables did not significantly improve the regression (Table 3). In the case of A, more elaborate models, which included $Agg^{5-10}_{<0.05}$ and $Silt^{0\text{-}25}$ had higher R^2_{adj} but regressions were not significant ($p > 0.05$). Also in the case of N, more elaborate models, which included $Silt^{0\text{-}25}$, nest size, S, and $Agg^{5-10}_{0.25-2}$ had higher R^2_{adj} but, again, regressions were not significant ($p > 0.05$). In the case of S, the three competing models included NT, NT^2 and $Agg^{5-10}_{<0.05}$, and were significant ($p<0.05$), and two of them also included $Clay^{25\text{-}50}$ or N. The principle of parsimony was applied and the simplest model was selected.

Table 3. Best models explaining ant density, A, nest density, N, and nest size, S.

Var. expl.	MODEL	AICc	R^2_{adj}	Regr (p-value)	Significance of the coefficients (p-value)	
A	$NT + NT^2$	45.9	14.2	0.004	NT NT^2	0.012 0.009
A	$NT + NT^2 + Agg^{5-10}_{<0.05}$	46.0	17.3	0.11	NT NT^2 $Agg_{(<0.05)}$	0.007 0.005 0.07
A	$NT + NT^2 + Silt^{0\text{-}25} + Agg^{5-10}_{<0.05}$	46.4	20.1	0.07	NT NT^2 $Silt^{0\text{-}25}$ $Agg^{5-10}_{<0.05}$	0.01 0.006 0.11 0.03
N	$NT + NT^2$	46.4	12.6	0.007	NT NT^2	0.01 0.01
N	$NT + NT^2 + Agg^{5-10}_{0.25-2}$	46.2	16.4	0.10	NT NT^2 $Agg^{5-10}_{0.25-2}$	0.006 0.009 0.08
N	$NT + NT^2 + Silt^{0\text{-}25} + Agg^{5-10}_{0.25-2}$	46.0	20.5	0.07	NT NT^2 $Silt^{0\text{-}25}$ $Agg^{5-10}_{0.25-2}$	0.009 0.01 0.08 0.06
N	$NT + NT^2 + Agg^{5-10}_{0.25-2} + S$	47.0	18.1	0.09	NT NT^2 $Agg^{5-10}_{0.25-2}$ S	0.01 0.02 0.08 0.18
N	$NT + NT^2 + Silt^{0\text{-}25} + Agg^{5-10}_{0.25-2} + S$	46.8	22.8	0.07	NT NT^2 $Silt^{0\text{-}25}$ $Agg^{5-10}_{0.25-2}$ S	0.01 0.03 0.07 0.06 0.14
S	$NT + NT^2 + Agg^{5-10}_{<0.05}$	46.3	21.0	0.01	NT^2 N $Agg^{5-10}_{<0.05}$	0.06 0.01 0.008
S	$NT + NT^2 + Clay^{25\text{-}50} + Agg^{5-10}_{<0.05}$	46.1	24.8	0.02	NT NT^2 $Clay^{25\text{-}50}$ $Agg^{5-10}_{<0.05}$	0.09 0.02 0.27 0.01
S	$NT + NT^2 + N + Agg^{5-10}_{<0.05}$	47.7	21.3	0.02	NT NT^2 N $Agg^{5-10}_{<0.05}$	0.17 0.05 0.28 0.01

Models containing NT and NT^2 explained 14.2% of the variance in A and 12.6% of the variance in N. The model describing S contained NT, NT^2 and small sized particles ($Agg^{5-10}_{<0.05}$) and explained 21% of the variance in nest size. The relationships can be described by the following set of equations:

$$A = 669.2 + 85.85\,NT - 3.86\,NT^2$$

$$N = 329.87 + 36.65NT - 1.54\,NT^2$$

$$S = (0.58 - 0.013NT + 0.00079\,NT^2 - 0.032\,Agg^{5\text{–}10}_{<0.05})^{-1}$$

A and *N* increased until a maximum was reached after 12 years since the adoption of no-till, and decreased afterwards (Fig. 1). To see if the curvilinear relationship between the dependent variables and *NT* was caused by a particular soil variable, biplots between all soil variables and *NT* were checked for curvilinear relationship with an optimum at 12. However, none of the soil variables had an optimum at 12 years of *NT*. See, for example, the relationships between bulk density and organic matter, and *NT* (Fig. 2). It is also possible that harvester ants have an optimum at intermediate values of some soil variable, but that this soil variable is linearly related to *NT*. Variables that better correlated with *NT* included: organic matter ($r = 0.23$), $Agg^{5\text{–}10}_{0.25\text{–}2}$ ($r = 0.36$), bulk density ($r = 0.15$), *Alt* (r=0.18), $Sand^{0\text{-}25}$ ($r = 0.23$), $Clay^{25\text{-}50}$ ($r = 0.23$) and $Sand^{25\text{-}50}$ ($r = 0.22$). The GLM model that gave the best relationship contained the variables: *OM*, *Alt* and $Clay^{25\text{-}50}$, however, the regression was not significant ($p = 0.17$).

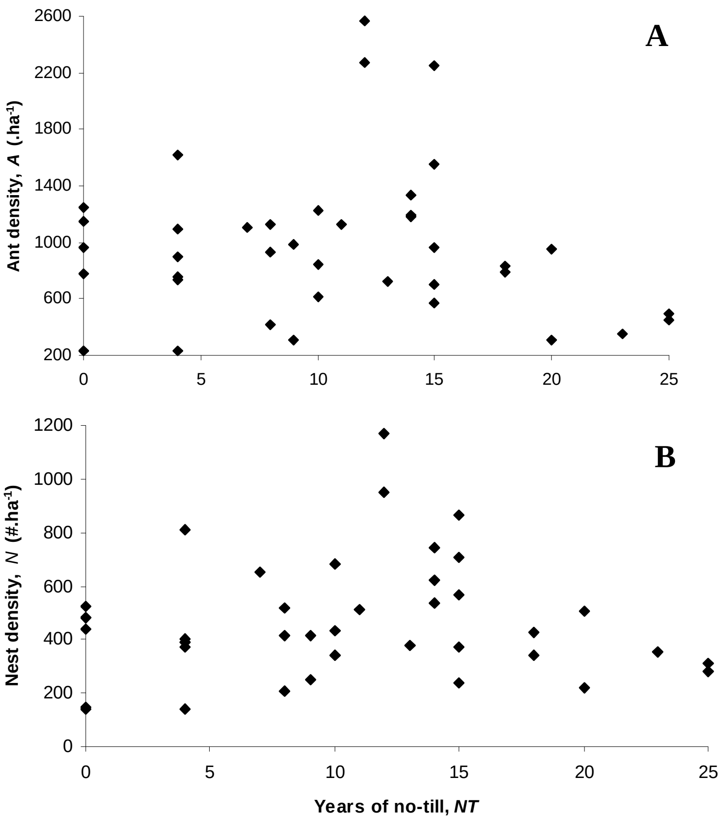

Fig. 1. Correlation between ant density, *A* ($.\text{ha}^{-1}$) (A) and nest density, *N*, ($\#.\text{ha}^{-1}$) (B), and number of years of no-till.

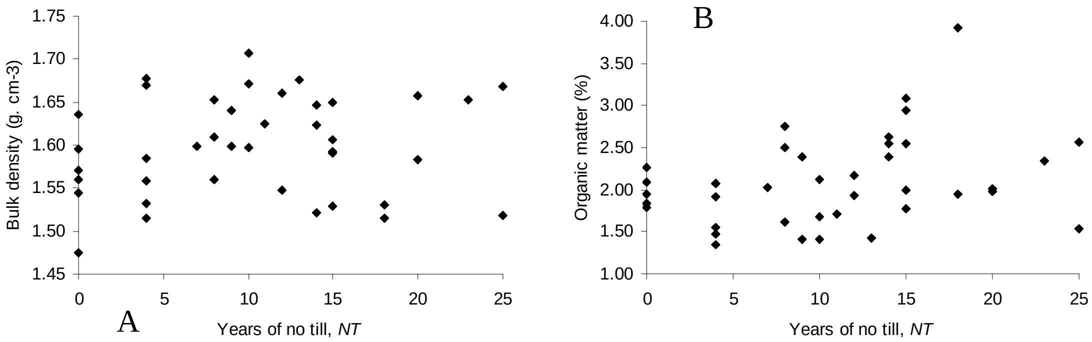

Fig. 2. Scatter plots showing nest density, *N*, as a function of bulk density (A) and nest density, *N*, as a function of organic matter content (B).

4. Discussion

M. barbarus ant density differed between fields. The number of years of no-till, *NT*, seemed to be the only factor that was significantly related to ant densities, *A* and nest densities, *N*. Soil characteristics, topographic parameters or management variables appeared to be unrelated to either *A* or *N*. *NT* and small-sized particles, $Agg^{5-10}_{<0.05}$, explained nest size, *S*. Small-sized aggregates may be easy to tunnel and remove by harvester ants, and may result in large colony sizes (Espinoza and Santamarina, 2010).

A and *N* increased with increasing years of no-till, reaching a peak around year 12 and decreasing afterwards. None of the soil characteristics showed a curvilinear relationship with *NT*. This means that, either soil characteristics do not explain the changes in *A* and *N*, or *A* and *N* are optimal by intermediate values of some soil characteristic. But none of the soil variables, alone or together, were linearly related to *NT*.

Silt content in the first 25 cm of the soil ($Silt^{0-25}$), 0.25-2 mm aggregates from the 5-10 cm soil layer ($Agg^{5-10}_{0.25-2}$) and small-sized particles from the 5-10 cm soil layer ($Agg^{5-10}_{<0.05}$) came close to explaining some of the variability in *A* and *N* (p = 0.11 and 0.07, respectively), but they were finally not selected. Silt-rich and fine soils can retain water much longer, which may benefit nest survival in semi-arid systems (Li *et al.*, 2011).

There are a number of possible explanations for the lack of relationships of *N* and *A* with edaphic, topographic or management factors other than tillage, namely, 1) the wrong set of explanatory variables was included, 2) estimates of ant density and nest density were inaccurate, 3) nest density and nest size are the result of an accumulation of historic events, while most explanatory variables are contemporary, and 4) different steps in the life cycle of an ant colony are influenced by different factors.

Soil chemical components, such as phosphorus, sodium or calcium content were not included in the study and have been reported to correlate to nest densities of other ant species (Milks *et al.*, 2007; Boulton *et al.*, 2005). Sodium, for example, can influence soil hardness and the tendency of a soil to crust and may directly influence colony establishment (Milks *et al.*, 2007). However, most of these soil chemical components are important plant nutrients, which only indirectly influence nest density, by influencing plant richness, densities and seed supply, which is the main food resource for ants (Boulton *et al.*, 2005; Milks *et al.*, 2007). In agricultural fields, soil nutrients are usually not limiting because of fertilization, so soil nutrients are not likely to be limiting harvester ants *via* seed supply.

Nest density and nest size may have been inaccurate estimators of ant density. Sample size for *S* was small. It was not always easy to determine if multiple nest entrances belonged to one or multiple colonies. Furthermore, the nests were counted with a team of people and there may have been differences in assessment between team members. Alternative methods, such as pitfall trapping (Boulton *et al.*, 2005; Bestelmeyer and Wiens, 2001; Rios-Casanova *et al.*, 2006), were considered less accurate to quantify ant populations that forage in trunk trails (Milks *et al.*, 2007).

It is implicitly assumed that observed nest density and size are at an equilibrium. In reality, they are the result of multiple events of establishment, survival and mortality, and growth that occurred over the course of years. Historical events, dating back 15-20 years, may be responsible for bottlenecks in numbers from which the population has not recovered yet. Bottlenecks may be caused for example by harsh winters (Ali *et al.*, 1986; Díaz, 1991), floods (Mertl *et al.*, 2009), or diseases that affected workers or brood.

Explanatory variables may differently affect various stages in the life cycle of a colony. Variables that describe soil surface characteristics (*e.g.*, bulk density, stable aggregates) may influence the success rate of queen establishment, but not subsequent colony survival and growth. Similarly, variables that are decisive for young nest survival (*e.g.* soil disturbance) may be meaningless for the survival and growth of older colonies.

If edaphic, topographic and management factors do not explain ant density satisfactory, it could be that endogenous factors were responsible for the observed curvilinear response to prolonged no-till management instead. It is clear that the first few years after conversion to no-till the number of nests increases. It is likely that initially ant density is lower than the potential carrying capacity of the field, because of the history of tillage. The sudden absence of soil disturbance may have created soil surface conditions that are more favourable for the establishment of young queens, and could have increased survival rate of young colonies. This means that immediately after conversion to no-till, fields will experience a sudden increase in ant colonies, whose queens are all about the same age (same cohort). It is known that with increasing ant densities, intraspecific competition for space and resources increases (Wiernasz and Cole, 1995; Milks *et al.*, 2007). A situation is created where the majority of the queens is of equal age and the colonies of equal strength. The normal elimination of young colonies by larger and older colonies is low and ant (nest) densities may increase above the carrying capacity. Finally (>12 years), a correction takes place through competition, causing lower ant densities. Because of the dominance of one specific cohort and concomitant unstable age distribution, we predict that ant (nest) densities will fluctuate for some time to come.

This study is one of the first to investigate factors influencing harvester ant density in cereal fields. *M. barbarus* (nest) density seems to be unaffected by soil characteristics, topographic factors or management factors, with the exception of tillage. As a result, we were unable to classify fields according to the level of natural weed seed, or to formulate recommendations with regard to measures that could enhance natural weed control. Maybe other factors, such as the availability of resources, in particular food (seeds), may play a more important role in determining ant density than do edaphic, topographic or management factors.

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CHAPTER 5

Density dependence of weed seed predation by invertebrates and vertebrates in winter wheat

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Density dependence of weed seed predation by invertebrates and vertebrates in winter wheat

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Summary

Weed seed predation has the potential to limit weed population growth within agricultural fields. Its success depends in part on the ability of predators to detect weed patches and respond in a direct density dependent way to increasing weed seed densities. To test for a density dependent response to spatial differences in seed density by seed predators, an experiment was conducted in north-eastern Germany in four winter wheat fields during October 2008 and 2009. Seed densities of 0, 1000, 2500 and 5000 seeds.m^{-2} of *Lolium multiflorum* were applied to four adjacent 15 m × 15 m plots in each field. Seed predation was measured in 20 randomly located trays per plot that were accessible to all predators (8 per plot) or excluded vertebrates (12 per plot, covered with cages). Full-access trays were 0.1 m^2 and limited-access trays 0.0225 m^2 large. Trays contained *Lolium multiflorum* on weed seed free soil and crop plants grown to the same stage as those in the fields. Seeds were exposed in the field for 18 days. Remaining seeds were recovered from the soil, using sieves and flotation, and counted. In addition, 20 seed cards were randomly placed in each plot, half of them with vertebrate exclosure cages. Seeds on cards were counted every other day. Seed predators were identified using pitfall traps (invertebrates) and Sherman life traps (vertebrates).

In general, predation rates measured by trays were low (32.7 % per 18 days). They may have been caused by low densities of predators, whose identity differed between fields. Vertebrates responded in a direct density dependent way to increasing seed densities, whereas the response of invertebrates was density independent. Seed predation from seed cards confirmed the density dependent responses obtained using trays. Seed predators only needed a few days to detect and preferably exploit the high density plots. Weed seed patches are likely to persist in fields where invertebrates are the main predators, while they could be better controlled where granivorous rodents predominate.

Keywords: carabid beetles, granivorous rodents, patch size, seed density, seed tray, seed cards

1. Introduction

Weed seed predation is an ecological process that has the potential to limit weed population growth within agricultural fields (Westerman *et al.*, 2006). However, its success depends in part on the ability of predators to respond in a direct density dependent way to increasing weed seed densities (Westerman *et al.*, 2008). Weed seeds are often patchily distributed within a field, due to the pattern of dispersion from the mother plant (Cabin *et al.*, 2000), abiotic conditions such as wind or rain (Burmeier *et al.*, 2010), and management practices, such as tillage or harvesting (Blanco-Moreno *et al.*, 2005; Cousens *et al.*, 2006; Heijting *et al.*, 2009). If seed predators are unable to locate these high seed density areas, or respond inversely density dependent to seed densities, patches are likely to survive and may increase in size and density over the years (Westerman *et al.*, 2008). In contrast, if seed predators respond in a direct density dependent fashion to seed densities, they may be able to limit or reduce growth of weed patches. Several studies have dealt with density dependent response of seed predators with contradictory findings. Some reported density independent responses (Brust and House, 1988; Cummings and Alexander, 2002), while others found a direct density dependent (Cromar *et al.*, 1999, Cabin *et al.*, 2000) or an inverse density dependent response (Cardina *et al.*, 1996; Westerman *et al.*, 2008). Some of the contradictory results may have been caused by the spatial scale at which seed densities differ (*i.e.*, size of patches; Marino *et al.*, 2005, Westerman *et al.*, 2008) relative to the mobility of the predators involved. Patches beyond the action radius of the predator are too large to be treated as a patch (Westerman *et al.*, 2008). Therefore, we designed an experiment at two different spatial scales to try to capture the density dependent response, if any, of the two prevalent groups of seed predators, which differ hugely in mobility and action radius.

In northern Germany, carabid beetles and granivorous rodents are the main weed seed predators (Daedlow *et al.*, 2007). Carabid beetles move at a scale of meters or tens of meters, which allows detection of small patches and individual weed plants (Zhang *et al.*, 1997; Lys and Nentwig, 1992). Granivorous rodents can move several hundred meters during a single night and may be able to distinguish between large differences in seed density at the within or between fields scale (Corp *et al.*, 1997; Tew *et al.*, 2000). They are expected to respond direct density dependently. High density patches decrease searching and foraging time, thus reducing the risk of rodents being predated (Bell, 1991; Hulme, 1993; Cabin *et al.*, 2000) and increase the efficiency of foraging. Carabid beetles are expected to respond independently to differences in seed densities within the duration of the experiment. Their limited mobility inhibits a rapid, selective detection of weed patches if patches are big and far away from each other.

2. Materials and methods

Trials were conducted in October 2008 and 2009 near the city of Rostock (54° 05' N; 12° 07' E), in the state of Mecklenburg-Vorpommern, north-eastern Germany. The climate is influenced by the Baltic Sea, hence it has milder autumns and colder springs compared to other areas at the same geographical latitude. Average annual temperature in the area is 8.4 ºC and average annual rainfall is 591 mm with slightly higher precipitation in summer. Summers are mild (average temperature, *T.* 16.2 ºC) and winters are cold (average *T.* 0.9 ºC) and with frequent snow cover. In October, mean temperature is 9.9 °C and precipitation 43 mm (data 1961-1990, German meteorological service, 2010). In both years of the experiment, weather conditions were typical for October. Mean temperature declined in the course of the experiment and in the second week lowest temperatures were 3 °C and -1°C in 2008 and 2009, respectively.

Predation was measured in the winter wheat (*Triticum aestivum* L.) phase of an oilseed rape (*Brassica napus* L.) – winter wheat – winter barley (*Hordeum vulgare* L.) crop rotation when the crop had 3 to 5 unfolded leaves. Two sets of fields were chosen; in 2008, Dummerstorf and Schlage (Field 1 and 2, respectively) and in 2009, Bandelstorf and Niendorf (Field 3 and 4, respectively). Field sizes were similar to the average size of fields in the region, 75 ha. Fields were close to small woodlots and areas with natural vegetation. Fields were sown between 6 and 12 September, approximately 10 days earlier than the average sowing time in the area. Early sowing fields were chosen to have a well developed crop during the experiment as, generally, seed predators like rodents and carabid beetles, tend to avoid bare soil (Heggenstaller *et al.*, 2006; Navntoft *et al.*, 2006).

L. multiflorum seeds were used because of its demonstrated palatability to vertebrate and invertebrate seed predators (Baraibar *et al.*, 2009), the ease with which large quantities can be obtained and the relatively large size of the seeds, which made them easier to retrieve and handle in the lab. Before applying in the field, seeds were boiled for five minutes in hot water to prevent germination and avoid potential weed problems in subsequent years. Boiling softens the seeds, but does not lead to significant higher or lower predation rates compared with untreated seeds (Daedlow, unpubl.).

2.1. Experimental design

Four adjacent 15 m × 15 m plots were selected in each field, at least 50 m apart from the nearest field edge or semi-natural habitat. Densities of 0 (Control), 1000 (Low), 2500 (Medium) and 5000 (High) seeds.m^{-2} of *Lolium multiflorum* (4.22 ± 0.03 mg seed^{-1}; mean ± SE) were randomly assigned to each plot and manually added. To ensure a uniform coverage of the plot areas, pre-weighed amounts of seeds were applied in strips of 1 m wide and 15 m long. Responses to different seed densities were measured using two methods, namely seed trays and seed cards.

2.2. Seed trays

Seed predation was determined as the percentage seeds removed from eight 0.1 m^2 trays (25 cm × 40 cm × 5 cm) randomly located in each plot. Trays were made of metal mesh (1 cm mesh size) and had the bottom covered with a fine cloth mesh (0.56 mm mesh size) to prevent seeds being lost during the experiment. Each tray contained weed seed free soil, excavated from underneath the ploughing depth and crop plants grown in a greenhouse to 3 to 5 unfolded leaves, about the same stage as those in the fields. Trays were buried into the soil and levelled with the soil surface, leaving a 1 cm wire mesh lip protruding above the soil to limit seed loss due to water movement. Predators could easily climb over the lip (pers. obs.). Known numbers of seeds were added to each tray at the same density of the plot they were in. Trays were accessible to all predators (vertebrates and invertebrates).

To assess the response of invertebrate to different seed densities, twelve 0.0225 m^2 trays (15 cm × 15 cm × 5 cm) were randomly distributed within each plot. They were constructed the same way as the large trays previously described. Seed densities used were, again, 1000, 2500 and 5000 seeds m^{-2}. Small trays were covered with a metal mesh cage (24 cm × 24 cm × 5 cm; mesh size 8.7 mm) and nailed to the soil, to exclude vertebrate predators.

Seeds were exposed in the fields for 18 days, after which time the trays were removed from the field, and remaining seeds were recovered from the soil, using sieves and flotation, and subsequently counted.

2.3. Seed cards

Twenty seed cards (5 cm × 12.5 cm) were placed in each plot. Seed cards where constructed as described in Westerman *et al.* (2003). In 2008, each card contained 40 non-boiled and 40 five minutes boiled *L. multiflorum* seeds. In 2009, only boiled seeds were used (40 per seed card). As no differences were found in seed removal between boiled and non-boiled seeds (Daedlow, unpubl.), only predation rates for boiled seeds were used for the analyses. Cards were exposed in the field: (i) within a cage that excluded vertebrates, but not invertebrate predators (ten per plot) and (ii) without a cage that allowed access for all predators (ten per plot). Exclosure cages (20 cm × 10 cm × 5 cm) were constructed from 1 cm mesh metal screen and fixed to the soil using nails. Locations and exclosure treatments were randomly assigned to each plot. In 2008, cards were not replaced when all seeds had been removed, while in 2009, cards were replaced when the number of remaining seeds fell below 7. Seed cards were exposed in the field the first 16 days of the 18-day-lasting experiment and counted every other day, except for the first counting, which was done after 4 days. In 2008, 37 out of 1120 values were corrected using moving averages as small inconsistencies were observed in the time series. In 2009, after 4 d of exposition, eight seed cards were damaged by wild pigs, thus data from these cards were excluded. New cards were added and data from subsequent counts could be included in the analyses.

2.4. Controls and background seed density

Two kinds of controls were included, namely positive and negative controls. Positive controls measured seed loss from trays caused by other reasons than predation, such as wind or rain. Losses were assessed in three small trays per field. Each tray contained 100 seeds and was surrounded by a fine mesh screen (0.56 mm mesh size) half a meter high, such that wind and rain could enter, but no predators. Negative controls measured potential seed entry from outside the tray caused by wind and rain-splash or seed shed from nearby weeds. They consisted of three large trays per plot, not covered by any exclosure cage, with weed free soil and no seeds added. At the end of the experiment, the trays were removed, the soil was sieved and washed and seeds were counted, when found.

In addition, pre-existing background weed seed densities were determined by sampling the first 2 cm of soil of a 0.1 m^2 area, at three random locations per plot. The soil was sieved and all seeds were recovered. Seeds were identified to species and the sample was weighed.

2.5. Seed predator identity

In 2008 and 2009, invertebrate predators were identified, using pitfall traps. Invertebrates were sampled in twelve dry pitfall traps per field, three in each plot. Traps consisted of a cylindrical polyurethane tube, buried into the soil, such that the edge was levelled with the soil surface. A 250 ml plastic container (8 cm diameter) was placed inside the tube. This construction allowed the replacement of containers without disturbing the surrounding soil. A plastic cover was placed over the traps to prevent flooding of the container after rain. Traps were checked every two days during the duration of the experiment. Insects were identified to species in the field, counted and subsequently released.

In 2009, rodents were sampled, using Sherman live traps. Twenty four Sherman traps were set up within the selected areas in fields 3 and 4. Traps were baited with oat seeds (*Avena sativa* L.) mixed with peanut butter. Synthetic cotton-wool was added as nesting material. Traps were wrapped in bubble-wrap for insulation. Trapping was done around the new moon phase when movement of rodents was least impaired by moonlight (Díaz, 1992a; Plesner Jensen and Honess, 1995). Trapping sessions were conducted from 21 to 25 October 2009, when the percentage of rodent recaptures exceeded 50 %. Trapped rodents were identified, weighed, sexed, ear-tagged, and released.

2.6. Data analysis

Percentage of seeds predated Q from large and small trays and from seed cards were calculated following Abbott (1925):

$$Q = \frac{S_i * C - S_f}{S_i * C} * 100 \qquad [\%.x\ days^{-1}] \qquad [1]$$

where S_i is the initial number of seeds added to each tray or card; C the proportion of seeds recovered from the positive control, S_f the final number of seeds after the exposure period and x the specific exposure period being considered. Percentage of seeds predated by vertebrates (Q_{vert}) was calculated as:

$$Q_{vert} = \frac{S_i * C - S_f}{S_i * C} * 100 - Q_{inv\_plot} \qquad [\%.x\ days^{-1}] \qquad [2]$$

where Q_{inv_plot} is the percentage predation per 18 days by invertebrates averaged over all small trays of each plot.

Data cleansing was done in two steps. First, trays or seed cards in which $Q \leq 0$ were considered not found and were excluded from the analyses. This happened when a higher proportion of seeds was recovered from a tray or card, than from the positive control. Accordingly, seven datasets were excluded from the analysis of predation by invertebrates, one from the analysis of predation by vertebrates and none from the analysis of all predators. A total of 184 of 2240 counts from seed cards were removed in the first step of data cleansing.

Secondly, outliers were removed if their exclusion notably improved the distribution pattern of the residuals and if there was a plausible biological explanation for exclusion. One large and two small trays were excluded from the analyses, because they were presumably not found and exploited by predators; predation rate in the large tray was < 2 %, and the small trays were nearly untouched. Exclusion improved the distribution pattern of the residuals as indicated by the Shapiro-Wilk normality test (large trays before and after the exclusion: $p < 0.00002$ and $p = 0.27$; respectively; small trays before and after the exclusion: $p = 0.00013$ and $p = 0.011$, respectively). Another outlier was removed from the analysis of vertebrate predation rate (equation 2), resulting in an improved distribution pattern of the residuals (Shapiro-Wilk normality test before and after the exclusion: $p = 0.0033$ and $p = 0.76$, respectively). Again, predation rate was less than 2 %, and thus, the tray was considered not found. All data obtained from seed cards were retained in the second step of data cleansing.

To meet the requirements of normality and homogeneity of variance, all response data Q were logit transformed. Transformed predation rates were analysed with mixed effects models, using the package nlme (Pinheiro *et al.* 2010) and lme4 (Bates & Maechler, 2010) of R, v 2.12.0 (R Development Core Team, 2010). Generally, precision of mixed effects models increases with increasing number of units within each random factor (Weisberg, 2005). As variation between fields was larger than between years, and we had more fields than years, the factor field was included as a random factor, but not the factor year. The best model from all possible subsets was selected using Akaike's information criteria (AIC) as a selection criterion (Zuur *et al.*, 2009). Distribution patterns of the residuals were tested using Shapiro-Wilk normality test.

2.6.1. Seed trays

Data were analysed separately for (i) predation by all predators, (ii) predation by invertebrates alone and (iii) predation by vertebrates alone. Some fields harboured only one group of predators, and, therefore, specific analyses were conducted for the specific fields only. Predation by all predators was analysed with the data obtained from all fields. Predation by invertebrates alone was analyzed with the data obtained from fields 1, 2 and 4; predation by vertebrates alone was analyzed with the data obtained from fields 1 and 3.

2.6.2. Seed cards

Seed predation by all predators (without exclosure) and by invertebrates (with exclosure) were analyzed for each counting date separately (duration of exposure *k*: 4, 6, 8, 10, 12, 14 and 16 days). Seed predation was calculated using equation [1], except that the proportion of seeds recovered from the positive control trays, *C*, was linearly interpolated according to the different exposure periods using the following equation:

$$C_{adj} = C + \frac{k * (1 - C)}{m}$$

where *k* is the duration of exposure and *m* the maximal duration of the experiment (18 days).

3. Results

3.1. Seed predator identity

Carabid beetles were the main invertebrate seed predators. Species found in the pitfall traps were predominantly the granivorous *Amara aenea* DeGeer and *Harpalus rufipes* DeGeer and the omnivorous *Calathus cinctus* Motschulsky. Other species trapped are listed in Table 1. Activity-density was low in all fields (Table 1). *H. rufipes* activity-density was significantly higher ($p < 0.05$) in fields 2 and 4 than in the other fields.

Table 1. Total carabid catches from twelve pitfall traps over 18 days of trapping during 2008 (Field 1 and 2) and 2009 (Field 3 and 4). Complete names referred to in the text.

Carabid species	Field 1	Field 2	Field 3	Field 4
H. rufipes	15	129	49	104
A. aenea	7	3	35	70
C. cinctus	17	8	104	36
P. strenuous			74	151
P. melanarius	3		1	22
C. melanocephalus			6	2
H. hirtipes	1			
T. quadristriatus	1			
P. dorsalis	3			
B. properans	3			
H. distinguendes		4		
L. pilicornis		3		
B. tetracolum		3		
C. convexus		1		

Apodemus sylvaticus L. was the main vertebrate predator trapped in field 3, with 10 unique individuals per 96 trap nights. A single *Apodemus agrarius* Pallas was trapped in field 4.

3.2. Controls and background seed densities

Less than 5 % of the seeds (4.1 ± 0.7 %; mean ± SE) were removed by other causes than predation (positive control). Only 4 ± 0.7 seeds per tray per 18 days entered from outside the tray (negative control). Background seed density was 0.11, 0.38, 0.29 and 0.48 g m^{-2} in fields 1, 2, 3 and 4, respectively and did not significantly differ between fields ($p > 0.05$). These seed densities are low compared to the weight of seeds added, which ranged from 4.2 g m^{-2} (1000 seeds.m^{-2}) to 21 g m^{-2} (5000 seeds.m^{-2}). The most abundant species found was *Brassica napus* L., followed by *Chenopodium album* L.

3.3. Density dependence response measured using seed trays

In general, seed predation was relatively low (32.7 % ± 1.8). Vertebrates accounted for most of the seed losses in fields 1 and 3, whereas invertebrates did so in fields 2 and 4, as confirmed by trapping (see section Seed predator identity).

3.3.1. All predators

Data from 95 out of 96 trays could be used for analyses after data cleansing. Best model selection resulted in a random intercept mixed model with a linear and a quadratic term for plot seed density as fixed effect and field as random factor (Table 2). Predation rates were 24.2 %, 34.7 % and 31.1 % in the low, medium and high density plots, respectively, indicating that predation increased from low to medium but not from medium to high seed density.

Table 2. The effects of plot density on seed predation measured by seed trays (logit transformed values of random intercept mixed models; *p* value and significance of the terms).

	Predation measured by seed trays					
	All predators (N=4)		Invertebrates (N=3)		Vertebrates (N=2)	
Fixed effects:						
Intercept	-1.737	***	-1.417	***	-1.494	***
Plot density	$7.0*e^{-4}$	**			$1.5* e^{-4}$	*
Plot density^2	$-1.0*e^{-7}$	**				
Random effects (SD):						
Intercept (Field)	0.801		0.755		0.520	
Residual	0.587		0.908		0.661	

Significance of the terms, **p* < 0.05, ***p* < 0.01, ****p* < 0.001. *N* is the number of fields included in the analysis.

3.3.2. Invertebrate predators

Data from 99 out of 108 trays could be used for analyses after data cleansing. The best model to explain the response of invertebrates to seed density at plot level was a random intercept model with only a constant term and field as random factor (Table 2). Invertebrates did not respond to seed densities; they predated a similar percentage of seeds in all plot densities, namely 22.4 %, 11.5 % and 29.8 % in fields 1, 2 and 4, respectively (Fig. 1).

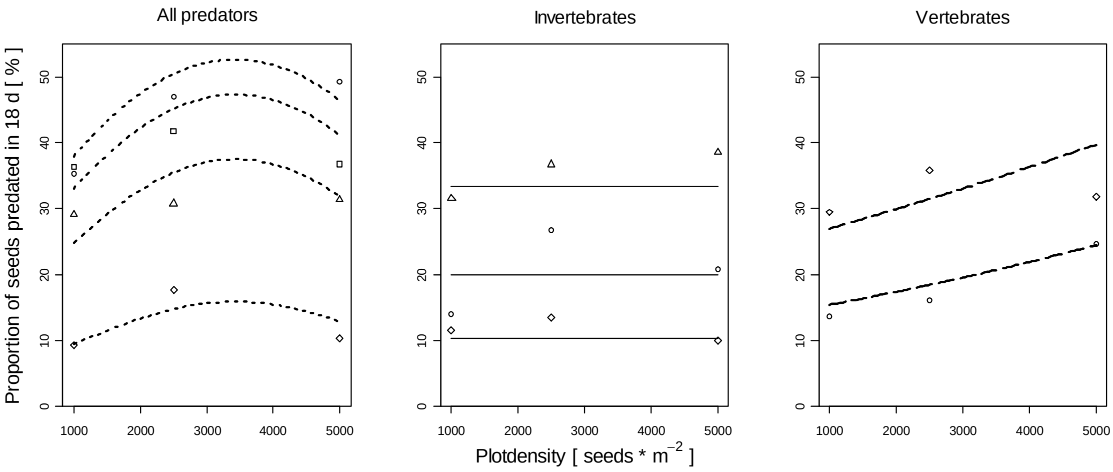

Fig. 1. Seed predation rates, measured with seed trays, as related to seed densities by all predators, invertebrates and vertebrates (Field 1 ○ , Field 2 ◇, Field 3□, Field 4 △). Lines represent the back transformed results of the chosen model.

3.3.3. Vertebrate predators

Data from 46 out of 48 trays could be used for analyses after data cleansing. Best model selection resulted in a random intercept mixed model with a linear term for plot seed density as fixed effect and field as random factor (Table 2). On average, vertebrates consumed 20.6 %, 24.4 %, 31.6 % in the low, medium and high seed density plots, respectively. Differences between plot densities were significant ($p = 0.02$) (Fig. 1).

3.4. Density dependence response measured using seed cards

Thanks to repeated counting, the results of the seed cards revealed the patterns of seed predation over time. For all exposure periods, best model selection resulted in random intercept mixed models. In general, estimates by seed cards confirmed that predation rates were influenced by increasing seed densities in a direct density dependent way. In addition predators responded to differences in seed densities within few days. For example, in the high seed density patch, 35 % of the seeds were predated within 4 days after exposure, whereas in the low seed density patch only 19 % of seeds were predated during the same time period. Seed cards showed slightly higher seed predation rates and a greater effect of seed density compared to the seed trays (Table 3; Fig. 1, 2). The vertebrate exclosure treatment did not significantly reduce predation rates after 4 and 6 days of exposition, but it did from day 8 onward. This indicates that up to 6 days after exposure, invertebrates were the main seed predator, but that from day 8 onward seed predation by invertebrates suddenly decreased, possibly due to low temperatures that occurred on 23 and 19 October in 2008 and 2009, respectively.

Table 3: The effects of plot density and exclusion treatment (exclosure, open) on seed predation measured by seed cards at different exposure periods (logit transformed values of random intercept mixed models, *p* values and significance of the terms).

Exposition	**4 d**		**6d**		**8d**		**10d**		**12d**		**14d**		**16d**	
S-W Test *p*-value	0.06		0.05		0.50		0.0004		0.26		0.15		0.03	
Fixed effects:														
Intercept	-1.99	***	-1.43	***	-0.10	n.s.	-0.05	n.s.	-0.28	n.s.	-0.15	n.s.	0.52	n.s.
Density	$3.9\ e^{-4}$	*												
Density^2	$-3.2\ e^{-8}$	n.s.	$4.9\ e^{-8}$	***	$4.4\ e^{-8}$	**	$2.5\ e^{-8}$	n.s.	$3.7\ e^{-8}$	***	$3.2\ e^{-8}$	**		
Exclusion	-0.22	n.s.	-0.24	n.s.	-0.84	**	-1.13	***	-0.54	**	-0.75	***	-1.42	***
Exclusion × Density^2	$-5.5\ e^{-8}$	***	$-6.8\ e^{-8}$	***	$-7.1\ e^{-8}$	***	$-4.9\ e^{-8}$	*	$-4.9\ e^{-8}$	**	$-3.6\ e^{-8}$	*		
Random effects (SD):														
Intercept (Field)	0.71		0.53		0.90		0.79		0.65		0.67		0.88	
Residual	1.35		1.44		1.78		1.86		1.38		1.42		1.67	

Significance of the terms, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

S-W Test *p*-value: *p*- values of the Shapiro Wilk Test applied on the residuals of each model chosen; $p > 0.05$ indicates normal distribution.

After 4 days of exposition, the best model contained a linear and quadratic term for the fixed effect plot density, indicating a density dependent response (Table 3). Analyses of predation rates after longer exposure time showed a stronger density dependent response, leading to models which only contained a quadratic term. In all cases, the interaction between seed density and exclosure treatment (invertebrates, all predators) was significant ($p < 0.05$), indicating that seed predators exhibited different responses to seed densities. Seed predation rate decreased rapidly and variance rose after 10 days of exposure, probably due to low temperatures and frost, in 2008 and 2009, respectively. The resulting best model for 10 days of exposition contained the same factors as the best models after 6 or 8 days, but the values of the Shapiro-Wilk normality test were lower. For exposure periods of 12 and 14 days, Shapiro-Wilk normality test values rose again and predation rates remained low (Fig. 2). However, the best models still contained the same factors as the models for shorter exposure periods, namely a strong density dependent response to increasing seed densities, a clear influence of the exclosure cages and a significant interaction between exclosure treatment and seed density. The best model for exposure period of 16 days showed that seed density did not influence seed predation rate anymore.

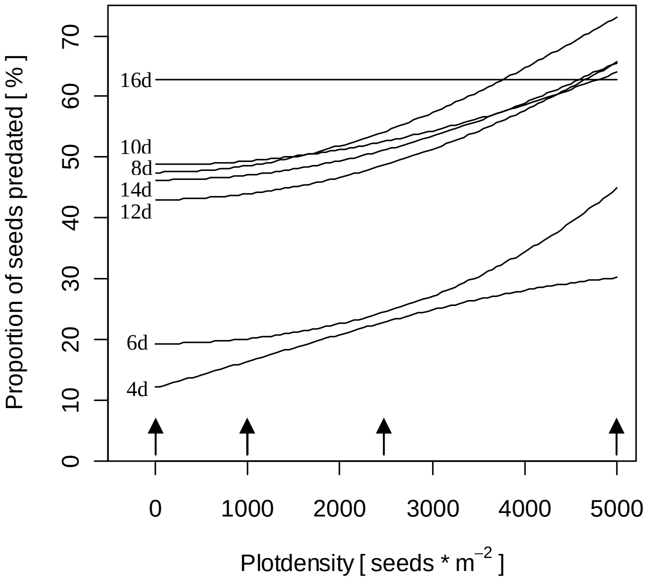

Fig. 2. Back transformed data on proportion of seeds predated, measured with seed cards, by all predators at different exposure periods (4, 6, 8, 10, 12, 14 and 16 days). Back transformed data of chosen models. Arrows represent densities at which predation rates were measured.

4. Discussion

The results of this study indicate that vertebrate and invertebrate predators differ in their response to seed densities, thus confirming our expectations.

Vertebrates, mainly granivorous rodents, were able to detect the 15 m × 15 m patches and foraged preferably in the high seed densities, whereas invertebrates did not respond to seed densities. The response was the result of seeds applied and not influenced by pre-existing seeds, because these were negligible in all plots.

Patches of a large size may be easier to locate by rodents, because of the high mobility of these predators (Corp *et al.*, 1997). In addition, rodents can detect high seed density patches by using olfactory and visual cues (Hulme, 1993). Rodents search large areas to forage and this study indicates that they are able to distinguish between the qualities of areas as big as 225 m^2 (15 m × 15 m). Once a high seed density patch is located, predators can respond functionally or numerically. Functional response relates to the proportion of prey consumed by individual predators while numerical response relates to the changes in the density of predators (Holling, 1959). In the case of rodents, the response is probably the result of a combination of functional and numerical responses (Abramsky, 1983). The observed direct density dependent response means that rodents can readily locate and forage from large weed seed patches, such as those occurring naturally in fields or created by tillage and harvesting machinery. Thus, direct density dependent response may contribute to limit weed populations build up within cereal fields of northern-Germany.

Seed predation caused by granivorous rodents in this study was low. Therefore, the effect of the observed direct density dependent response to seed densities is probably limited. A possible cause for the low predation rate is the lack of suitable habitat for rodents, which may have led to the low densities measured. The poor canopy cover available at the time of the experiment (3 to 5 unfolded leaves) probably inhibited rodent movement (Tew *et al.*, 2000; Baraibar *et al.*, 2011). Rodents usually abandon the field and move to the field edges when crop cover is not available within fields (MacDonald *et al.*, 2000). Rodent predation is expected to increase with increasing crop development.

Although no attempt was made to quantify rodent densities, the low numbers of rodents trapped may reflect a low population density in the area. It is known that high management intensity and large fields reduce rodent densities (Tew *et al.*, 1992). Intense and repeated herbicide and insecticide spraying, especially during the oilseed rape phase of the oilseed rape – winter wheat- winter barley rotation, may decrease food availability. Rodents are known to consume insects as a part of their diet. Insecticide spraying may increase mortality of invertebrates and indirectly affect rodent population (Menalled *et al.*, 2007; Navntoft *et al.*, 2006). The oilseed rape phase of the rotation may constitute a bottleneck for rodent populations survival and growth. However, proof for this hypothesis is currently lacking.

Low predation rates may also be partially caused by the season. The experiment was conducted after soil cultivation in a young crop, hence background seed densities were low. This was intended to reduce the influence of background seed densities on the response of predators to seed densities. After a period of high food availability in late summer, it is likely that, at the time of the experiment, predators had already finished storing and accumulating seeds for the winter. The experimentally added seeds were an unexpected and an artificial food resource and may have caused lowered response in activity density and predation rates.

Invertebrates, mainly carabid beetles, were not able to detect differences in seed densities at the plot level; they responded density independent to the applied seed densities. Large patch size, low mobility of these predators and the short duration of the experiment may explain why invertebrates were unable to respond numerically to seed densities (Zhang *et al.*, 1997; Westerman *et al.*, 2008). In addition, temperatures near zero between days 8 and 10 after the beginning of the experiment decreased predation rates by invertebrates, probably because invertebrates were either killed or their activity limited. Invertebrates neither cache seeds for winter storage nor can they build up large fat reserves as rodents do. In addition, low temperatures reduce invertebrates activity and limit the time available for foraging. Therefore, their ability to respond functionally to increased seed availability is limited (Westerman *et al.*, 2008). It can be assumed that carabid beetles respond to different seed densities in patches smaller than those created by a single or few weeds. We would expect this effect, if seeds are longer exposed than in the experiment. However, both assumptions still need to be tested.

The results of this study suggest that large weed seed patches are likely to persist in fields where invertebrates are the main predators, while they could be successfully controlled where granivorous rodents are present. Patch size seems to be crucial in determining the extent to which predators are able to detect high seed density areas and respond to them. The different identity of seed predators reported in this study suggests that the impact of seed predation on weed population dynamics may differ between fields in Mecklenburg-Vorpommern region. If direct density dependent responses are to be maximized, measures to increase rodent populations should be encouraged.

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CHAPTER 6

Assessing yield losses caused by granivorous ants, *Messor barbarus* L., in winter cereals

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Assessing yield losses caused by granivorous ants, *Messor barbarus* L., in winter cereals

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Summary

Harvester ants, *Messor. barbarus* L., are important seed predators in semi-arid cereal fields of NE Spain, and can contribute substantially to weed control. However, occasionally they harvest newly sown crop seeds at sowing in autumn, or ripe cereal grains close to harvest in summer, causing yield losses.

A preliminary study was conducted in 34 commercial winter cereal fields to measure yield loss, and to identify factors that influence it. The area affected by ants was measured ten days prior to the anticipated harvest date. Ant colony size, nest density, crop height, weed densities and temperatures at sowing were assessed.

At sowing, harvester ants did not cause yield losses (0.2% of potential yield on average). At harvest, yield losses were generally low as well (0.6%) although occasionally higher losses were recorded (max. 9.2%). Yield losses significantly increased with increasing nest density, nest size and with number of years of no-till. The results of this study show that in 2009 yield losses caused by *M. barbarus* were insignificant and more than offset by the benefits provided by the destruction of weed seeds.

Keywords: yield loss at sowing; yield loss at harvest; damage; nest density; colony size; no-till

1. Introduction

Messor barbarus (L.) is one of the main species of harvester ants in the semi-arid region of north-eastern Spain. It plays a role in weed control, because it collects and destroys a large proportion of the newly shed weed seeds, thus limiting the build up of weed populations (Atanackovic, 2010; Baraibar *et al.*, 2009). However, under certain circumstances and in some years, farmers report yield losses caused by ants. Here, we investigated if and when harvester ant-induced yield losses occur and estimated their magnitude.

Damage can occur at sowing in late autumn or close to harvest in summer. Harvester ants can collect crop seeds that are superficially drilled or simply scattered over the soil surface at sowing (Campbell, 1982). At harvest, harvester ants cut grains or entire ears straight from the cereal plants.

It is likely that the density of harvester ants, which can be estimated by nest density and colony size, will influence yield losses. Nest density seems to be influenced by the number of years that a field has not been tilled (Baraibar, unpubl.: Chapter 4). In the last 25 years, many farmers in the region have adopted no-till or minimum till in order to save costs, increase water use efficiency and improve yield of rainfed cereals (Cantero-Martínez *et al.*, 2007). Harvester ants are favoured by these techniques, reaching high densities and large colony sizes (Baraibar *et al.*, 2009). Big nests have more ants and, thus, need more food. Furthermore, large colonies have a higher proportion of workers devoted to foraging than smaller colonies (Tschinkel, 1998), and more “soldiers”, which are better able to harvest crop seeds (Baraibar, personal observation).

Winter cereals in north-eastern Spain are usually sown at the beginning of November, when temperatures start to decrease and relative humidity is high (Servei Meteorològic de Catalunya, 2010). The combination of low temperatures and high relative humidity leads colonies of harvester ants to close down for winter hibernation (Azcarate *et al.*, 2007). The minimum threshold temperature reported for *M. barbarus* activity is 9 ºC (Azcarate *et al.*, 2007). However, occasionally temperatures remain high deep into November, or temporally rise again, causing a burst in harvester ant activity, which may result in the harvesting of newly sown crop seeds. In addition, seeds that are not buried at drilling are more likely to be harvested, because, in general, seed predators do not dig for seeds, but remove seeds available on the soil surface (Hulme, 1994).

Cereal type (wheat, barley, triticale) and variety may differ in the rate of maturation and in architecture, which may influence the timing and the ease with which ants gain access to the grains and can cut ears off the plant. Architectural differences could include, for example, hairs on the stem, the height at which the ears are formed, or the thickness of the stem. In certain years, densities of alternative seed sources at harvest, in particular weed seeds, may be insufficient to satisfy the needs of all colonies. In this case, harvester ants may engage in the more energy-consuming strategy of collecting crop seeds off the plant.

This study is a first attempt to quantify crop losses caused by granivorous ants both at sowing and at harvest. In addition, the relationship between some of the factors that could influence yield losses, namely nest density and colony size, number of years of no-till, date of sowing and harvest, crop height, temperatures after sowing and weed abundances were explored.

2. Materials and methods

2.1. Experimental site and design

This research took place in 2009 in the area of Agramunt, a village in semi-arid north-eastern Spain. Long-term average temperature is 13.9 ºC and average rainfall is 428 mm, concentrated in spring and autumn (1971 – 2000; Servei Meteorològic de Catalunya, 2010). Yield loss was assessed in 34 commercial cereal fields that had been sown to cereals between 2 October and 25 November 2008. Twenty nine fields had been planted with barley (*Hordeum vulgare* L.), four with wheat (*Triticum aestivum* L.) and one with triticale (×*Triticosecale* Wittm.). Twenty eight of the fields were managed without tillage for periods between 1 and 25 years, and 6 with minimum tillage. Minimum tillage included a tillage operation at the beginning of autumn, prior to sowing; working depth of 15-20 cm. Preliminary analysis showed that tillage did not directly affect yield losses caused by ants, neither at sowing nor at harvest. Therefore, data from minimally tilled and no-till fields were combined and jointly analysed.

In each field, an area of 50 × 50 m was marked permanently, and used to assess 1) area affected by ants, 2) ant colony size, 3) ant nest density, 4) crop height and 5) weed density.

Yield loss was assessed between 12 and 22 June 2009, ten days before the anticipated crop harvest (22 - 29 June). In three fields, harvest did not occur on the anticipated harvest date, but two weeks later, namely on 6 (one field) and 12 July (two fields). Therefore, in these three fields yield loss was assessed twice; prior to the anticipated and the real harvest. Damage assessed at the later date was used in the analyses. The surface area affected by the ants was measured for ten randomly selected nests within the 50 × 50 m area. The area affected by each nest at sowing, A_s, was distinguished from the area affected at harvest, A_h, by the visible symptoms; seeds harvested at sowing resulted in an area surrounding the nest that was void of crop, while damage at harvest was characterized by the removal of ears from crop rows at and adjacent to the nest. Causes other than ants, such as fatal germination or seedling mortality due to insects (*e.g.* the beetle *Zabrus tenebroides* (Goeze)), cannot completely be excluded as causes for crop failure at sowing. However, the spatial coincidence with ant nest presence strongly suggests a causal relationship. The number of rows and the length of the row(s) affected were measured, and converted to calculate the average area affected, $\overline{A}_s$ and $\overline{A}_h$ (ha nest^{-1}).

The size of the ten selected *M. barbarus* colonies was estimated, using a subjective scale that ranged from 1 (small) to 5 (large), based on the area occupied by the colony, the number of entrances, worker size and the number of active ants. The average nest size, $\overline{S}$, was calculated.

After crop harvest, all *M. barbarus* nests in the 50 × 50 m area were counted, using a grid spaced 10 m apart, and marked with spray-paint to prevent double counting. Counts were converted to numbers of nests per hectare, N.

The height at which ears were formed was measured next to the ten nest, and averaged to produce the average crop height, $\overline{H}$.

Weed densities were assessed in 30 random locations within the 50 × 50 m area in May 2009 by identifying and counting all weeds along one meter between two cereal rows. Weed counts were averaged and converted to numbers per square meter, $\overline{W}$ (m^{-2}).

The number of days (T_d) and the number of hours (T_h) with temperatures above 9 ºC after sowing were determined, using hourly and average daily temperatures (ºC) from October to December 2009 for Tàrrega, 17 km away from the experimental fields (Servei Meteorològic de Catalunya, 2010).

Finally, the farmers provided information on crop type, crop variety, sowing date, sowing depth, D, number of years of no-till, NT, and yield, Y.

2.2. Data analysis

Damage was expressed as the yield loss, YL, caused by harvester ants, and was calculated as;

$$YL = \overline{A} \times N \times Y \text{ [kg ha}^{-1}\text{]}$$

with Y, the crop yield obtained in that field (kg ha^{-1}), as provided by the farmer.

Generalized linear regression (Genstat 12) was used to relate YL_s to the explanatory variables N, $\overline{S}$, crop, NT, T_d and T_h, and D; and YL_h to the explanatory variables N, $\overline{S}$, crop, NT, $\overline{H}$, Y and $\overline{W}$. First, the best model(s) explaining YL_s and YL_h were selected based on all subset regressions (procedure RSEARCH), using R^2_{adj}, Cp and AIC as selection criterions. Next, the final model was selected based on R^2_{adj} and significance of the GLM (GLM procedure, log-link, free dispersion).

3. Results

3.1. Yield loss at sowing

Averaged over all fields, yield loss at sowing, YL_s, was 6.7 kg ha^{-1}, or 0.2% of potential yield. In most of the fields, YL_s was negligible (< 18 kg ha^{-1} or 0.6%) and only in two fields was YL_s higher, namely 46 and 49 kg ha^{-1} or 1.6%. Sixty-six percent of the nests did not cause any yield loss at sowing while 32.9% affected an area smaller than 0.5 m^2 (Fig. 1, black bar).

Yield loss at sowing was best described by the variables: nest density, N, average nest size, $\overline{S}$, and the number of years of no-till, NT (Table 1). Yield loss at sowing increased with increasing nest density, nest size and number of years of no-till. The model explained 73.5% of the variation. The regression equation to predict YL_s is as follows:

$$Log(YL_s) = -3.56 + 0.003\,N + 1.43\,\overline{S} + 0.06\,NT$$

Table 1. Generalised linear regression analysis (GLM) on yield loss at sowing, YL_s, caused by harvester ants *Messor barbarus*, as influenced by nest density (N), average nest size ($\overline{S}$) and number of years of no-till (NT).

	Df	Mean Deviance	Deviance ratio	P value
Nest density (N)	1	180.9	56.43	<.001
Nest size ($\overline{S}$)	1	87.45	27.28	<.001
Years of no-till (NT)	1	17.09	5.33	0.029
Residual	28	3.21		
Total	31	12.1		

3.2. Yield loss close to harvest

Averaged over all fields, yield loss at harvest, YL_h, was 18.5 kg ha^{-1} or 0.6%. In most fields, YL_h was negligible, namely < 30 kg ha^{-1}. Only in two fields losses were higher, namely 238 and 274 kg ha^{-1}, representing 8 and 9.2% of the average yield, respectively. Eighty-two percent of the nests did not cause any yield loss at harvest (Fig. 1, white bar).

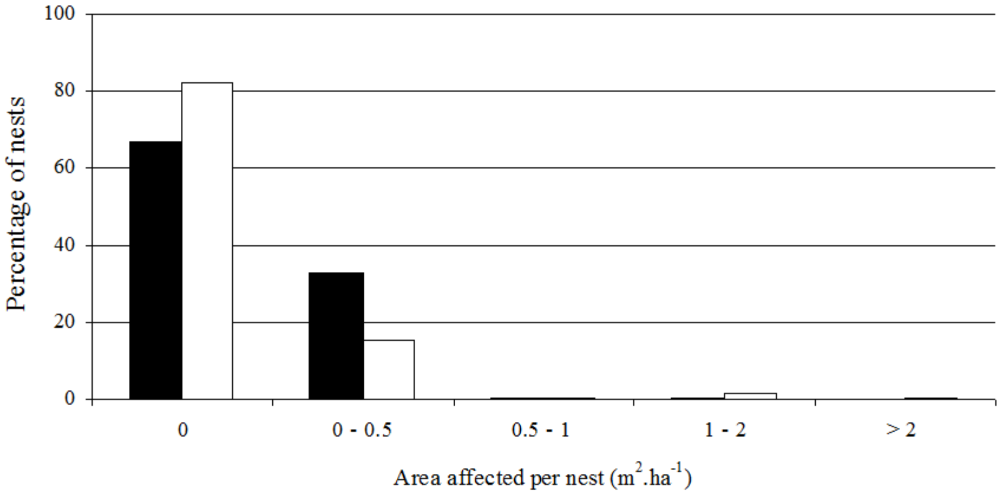

Fig. 1. Frequency distribution of nests of all fields according to area affected per nest (m^2.ha^{-1}) at sowing (black bar) and close to harvest (white bar).

There were a number of competing models that correctly described YL_h. All models included N, $\overline{S}$ and NT. More elaborate models, which included crop height, $\overline{H}$, and yield, Y, had a minimal AIC and a maximum R^2_{adj}. However, we opted for a smaller model including $N, \overline{S}$, and NT, because the addition of H or Y did not significantly improve the regression (Table 2). Yield loss at harvest increased with increasing nest density, nest size and number of years of no-till (Fig. 2). The model explained 64.8 % of the variation. The regression equation to predict YL_h is as follows:

$$Log(YL_h) = -8.67 + 0.007\,N + 2.63\,\overline{S} + 0.08\,NT$$

Yield loss at harvest was more than three times higher in the three fields that were harvested late (60.11 ± 68.57 ($\overline{x}$ ± sem)) than in fields harvested earlier. This was mainly caused by a large increase in the level of damage in one field.

Table 2. Generalised linear regression analysis (GLM) on yield loss close to harvest, YL_h, caused by harvester ants *Messor barbarus*, as influenced by nest density (*N*), average nest size ($\overline{S}$) and number of years of no-till (*NT*).

	Df	Mean Deviance	Deviance ratio	*P* value
Nest density (*N*)	1	1238.52	166.6	<.001
Nest size ($\overline{S}$)	1	1049.49	141.17	<.001
Years of no-till (*NT*)	1	32.03	4.31	0.047
Residual	28	7.43		
Total	31	81.55		

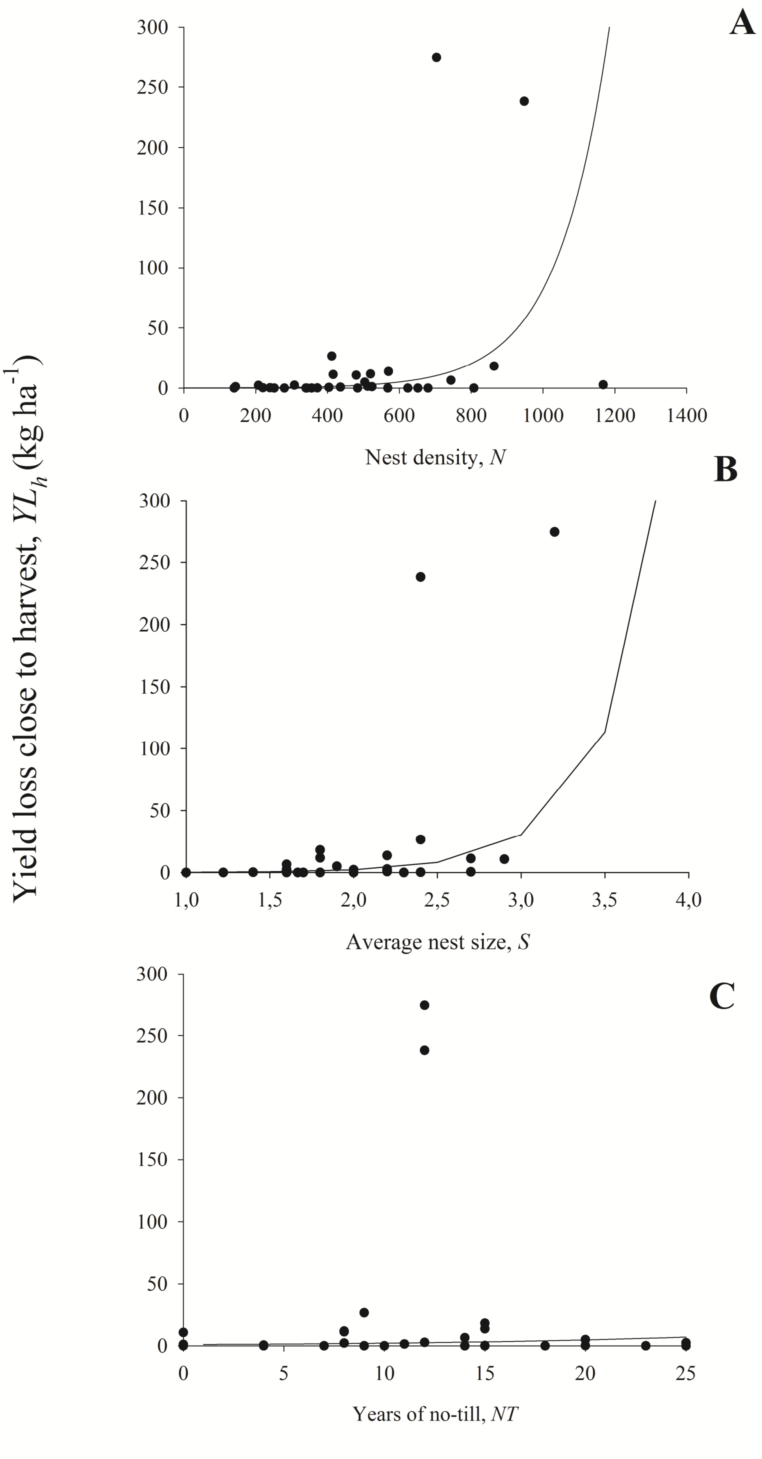

Fig. 2. Regression lines and observed yield losses close to harvest, YL_h, and nest density, *N* (A), average nest size, $\overline{S}$, (B), and years of no-till, *NT* (C).

4. Discussion

In general, yield losses by harvester ants were small, and economically insignificant.

Losses at sowing were affected mainly by harvester nest density, *N*, average nest size, $\overline{S}$, and number of years of no-till, *NT*. The combination of *N* and $\overline{S}$ can be regarded as an estimate of harvester ant density. In the case of the fire ant, *Solenopsis invicta* Buren, which is known to cause damage to crops such as potatoes, soybeans, corn and sorghum, in the United States, Australia and some Asian countries, correlations were found between crop losses and the number of ants caught per bait trap (Adams *et al.*, 1988), and colony size (Drees *et al.*, 1991). Nest density of *M. barbarus* increases with increasing number of years of no-till, reaching a maximum after 10 – 12 years (Baraibar, unpubl.: Chapter 4). The reason for the growth in the number of colonies is probably the lack of soil disturbances. Soil disturbances destroy the shallow nests of young colonies, destroy the nest entrances of older colonies, force workers to allocate time to reconstruction rather than gathering seeds, and bury surface seeds, which are no longer available to the ants. In soils without tillage, harvester ant colonies may have higher survival and growth rates. Foraging efficiency is related to ant nest density (Baraibar *et al.*, 2011), and it is, therefore, likely that seed consumption will be higher in the case of high ant densities and large colonies.

Contrary to expectations, T_d and T_h, the number of days or hours after sowing with temperatures > 9 ºC, did not contribute to explaining variability in yield losses caused by harvester ants at sowing, YL_s. Apparently, the duration of the period with temperatures > 9 ºC was unimportant. A single day with some hours with temperatures > 9 ºC, which occurred in all fields, seems to be sufficient to induce damage. This suggests that the ants do not require much time to gather the seeds.

Seed burial usually prevents seed harvesting and consumption by predators (Drees *et al.*, 1991; Brown *et al.*, 2003). Superficial drilling could put seeds at risk of exposure. However, during model selection, sowing depth was not selected as an explanatory variable. It is possible that the seeding depth provided by the farmers was inaccurate and that, in reality, seeds were more superficially planted, due soil compaction, presence of stones, dense crop stubble, etc. Another possibility is that, although the seeds were delivered at the required depth, the seeding furrow did not close after seeding, resulting in exposure to harvester ants.

Yield losses caused by harvester ants close to crop harvest were explained by nest density, *N*, average colony size, $\overline{S}$ and number of years of no-till, *NT*. High nest density may increase competition among colonies for food, forcing colonies to harvest seeds off the crop. On average, large nests (category 5) caused more damage than small nests. *Messor barbarus* has three castes of workers, namely *minor*, *media* and *major*, which usually perform different tasks within the colony. For *Pogonomyrmex badius* Latreille, another species of granivorous ants, Tschinkel (1998) reported an increase in the number and size of *major* workers as the colony grows. Because only the mandibles of these big workers are strong enough to successfully cut the ears of cereals (Baraibar, personal observation), this could provide a plausible explanation for the fact that colony size is related to yield losses close to harvest.

In the three fields that were harvested late, yield loss tended to be higher than in remaining fields that were harvested two weeks earlier. Possible explanations include 1) a longer exposure period of the cereals to the ants, and 2) more mature cereal grains. In June and July, colonies of *Messor* spp. have a high production of new workers, which can lead to a rapid increase in the foraging activity (Díaz, 1992). A delay in harvest date would allow these ever increasing numbers time to increase harvest rate. Similar results were obtained for the fire ant, *Solenopsis invicta*. Longer exposure increased the proportion of wheat, corn and sorghum seeds damaged in laboratory experiments (Morisson *et al.*, 1997). The spikes of fully mature and dry crops may be easier to bite through and harvest. However, proof for either hypotheses is currently lacking.

Most seeds of important weeds in semi-arid winter cereals, such as *Lolium rigidum* G., *Bromus diandrus* Roth and *Papaver rhoeas* L., are shed prior to harvest (Atanackovic, 2010). The availability of these weed seeds on the soil surface was expected to reduce yield loss close to harvest because climbing cereal plants is much more energy and time consuming than foraging seeds on the soil surface (Azcarate *et al.*, 2005; Heredia and Detrain, 2005). However, there was no relationship between weed density and the yield loss caused by ants at harvest. We realize that weed density alone may not suffice as a proxy for seed availability. Weed species distribution on the field may have influenced weed seed availability close to the ant nests and determined the need to harvest crop seeds. Burial of the smallest seed species may have reduced seed availability on the soil surface and may have increased yield loss. Therefore, it would have been better to quantify the number of weed seeds available to ants prior to harvest (e.g., Westerman *et al.*, 2003; Atanackovic, 2010).

We could not confirm that wheat was more prone to damage by harvester ants than barley, as claimed by local farmers, because of insufficient wheat fields in our survey. Nor could we confirm if differences in yield losses were caused by crop varieties. Expanding the survey, to include replications of the various crops and cultivars, could also be a useful way to investigate whether structural differences or differences in the rate of maturation influence the level of crop damage caused by harvester ants.

There are various ways to prevent ant-induced yield losses. Early crop harvest could in some cases reduce yield loss, although this recommendation is based on the fate of a single field only. There was no evidence for the hypothesis that high temperatures in autumn increased yield losses at sowing. Nevertheless, fields sown in October or the first half of November tended to have higher yield losses than fields sown during the second half of November. So, delaying sowing until temperature drops below 9 ºC could help to prevent yield losses at sowing. Both recommendations need to be tested first.

A third option involves reducing harvester ant population density. Spraying insecticides, to reduce harvester ant populations, is not suitable because it would only eliminate worker ants that are on the soil surface. Spraying does not affect the queen, which is buried deep in the colony, and which is responsible for the survival and growth of the colony (Cerdan, 1989). Spraying might be effective if it is done on the day of the release of the reproductives, which are released yearly following the first autumn rains. Killing new queens would reduce the density of nests. However, the prediction of the exact day the flights take place is difficult, hence, spraying cannot be timed. The use of ant bait insecticides could be an alternative option to control ants. Worker ants take the bait to the nest and feed the queen; the death of the queen causes the death of the colony. Cereal and product prices largely determine the cost-effectiveness of this treatment. The estimated cost of an ant bait application is currently justified in fields with more than 150 kg ha^{-1} of yield loss. However, no chemical products are registered against harvester ants in grain crops. A more readily adoptable option to decrease harvester ant density is a year of intense cultivation because soil disturbance reduces the survival chances of ants nests, in particular the shallow colonies of young nests.

In summary, this study indicated that yield losses caused by the harvester ant *M. barbarus* were generally low in 2009. Harvester ants contribute to weed control in semi-arid cereal systems (Baraibar *et al.*, 2009). At least in 2009, yield losses caused by harvester ants were more than offset by the benefits provided by the destruction of weed seeds.

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CHAPTER 7

General discussion and main conclusions

General discussion

This study revealed that seed predation in dryland cereals is completely different from seed predation in irrigated cereals within the same region (Catalonia, NE Spain). In the rain-fed areas, seed predation is substantial and must contribute to weed control, whereas in irrigated areas, seed predators have almost completely disappeared, resulting in negligible levels of natural weed control.

In the following two sections, the consequences of these differences, in terms of natural weed control in cereal fields, will be discussed. A third section deals with the consequences of direct density dependent seed predation to weed control.

Natural weed control by seed predation in rain-fed areas

In the rain-fed areas of Lleida (Catalonia), winter cereals are usually grown in monoculture, because few other crops are productive in the dry climate. Insect pests and diseases occur infrequently and usually do not cause yield losses, so weeds are the main yield reducing factor. Diversified crop rotations, cover crops or intercropping, which are effective non-chemical means against weeds (Davis and Liebman, 2000), cannot be used because of water scarcity. Therefore, weed control relies heavily on herbicides, tillage, and other cultural practices such as delayed sowing or increased seeding rate (Gonzalez-Andujar and Fernandez-Quintanilla, 2004).

This study clearly showed that seed predation is occurring naturally and must be responsible for substantial weed seed losses. The period of high seed predation rates coincides with the main period of weed seed shed, namely from April to June (Chapter 2; Atanackovic *et al.*, *in prep.*). Based on these results, harvester ants could remove 65 to 95% of all weed seeds produced yearly (Atanackovic *et al.*, *in prep.*). No published studies on seed predation in agroecosystems have ever reported such consistently high annual predation rates (see references in Davis *et al.*, submitted). Seed losses of this magnitude contribute substantially to weed control.

The main seed predator is the harvester ant *Messor barbarus*. Existing nest densities (approx. 400 nests.ha^{-1}) seem to suffice to guarantee high predation rates. Therefore, in order to maintain high levels of natural weed control, nest densities should be kept at the current level.

Tillage was the only factor investigated in this study that influenced harvester ants nest densities and weed seed predation rates. Because ploughing was much shallower and did not involve soil inversion, *M. barbarus* was not eliminated by ploughing, as in the case of *M. capitatus* in central Spain (Díaz, 1991). Nevertheless, harvester ants may have suffered from tillage. For example, tillage after harvest influenced the predation rates directly, and indirectly by reducing the duration of seed exposure to seed predators. Late autumn tillage can affect the reproduction success of harvester ant populations, but the timing of tillage is crucial. If tillage occurs after the mating flight, it will probably kill most of newly established queens. If tillage occurs before the mating flight, more queens are likely to survive. The fact that more and more farmers within the study area are adopting no-till suggests that natural weed control via seed predation will increase in the rain fed region of Catalonia.

Harvester ant density varied enormously between fields (140 - 1168 nests.ha^{-1}). Causes of this variability are still unknown. Nest density appeared to be uncorrelated to any of the soil or topographic characteristics tested. Only the number of years without tillage seemed to explain 14.2 and 12.6 % of the variation in ant and nest densities, respectively (Chapter 4). Future research should investigate the causes of variability in nest density, such that management options can be designed to enhance ant densities in area where they are currently too low (e.g. < 400 nests.ha-1).

In 2009, cereal yield losses caused by *M. barbarus* were low (Chapter 6). However, under certain circumstances, such as delayed crop harvest, crop damage can be substantial. Riper grains combined with high ant activity in June seem to be a possible cause for high yield losses at a late harvest date. If these results are confirmed, some agri-environmental schemes, aimed at preserving threatened species of steppe birds and based on delaying crop harvest, may need to be reconsidered. Yield losses caused by harvesting of seeding material in autumn can easily be prevented by delaying the date of cereal sowing until temperatures are too low for harvester ant activity.

Natural weed control by seed predation in irrigated areas

The situation with regard to weed seed predation in cereals in the irrigated area is completely different from that in the rain-fed area. Cereals are grown as part of a rotation, which includes alfalfa and maize, and usually have higher yields than in the rain-fed area. The higher soil and air moisture content causes more problems with regard to fungal diseases and a higher incidence of insect pests than in the rain-fed area. Nevertheless, weeds are still the main yield reducing factor.

Seed predation in the irrigated area was almost negligible. Except for a peak in seed predation by granivorous rodents in spring (April-May), the absence of harvester ants led to the almost complete loss of weed seed predation. The current expansion of the irrigated area will probably result in the total loss of harvester ants over a large area in Catalonia. In order to maintain natural weed control, other animals will have to replace the harvester ants. Although granivorous rodents (e.g., *Mus spretus*) and carabid beetles are present, they do not contribute much to weed seed predation. Future research will have to elucidate why these predators consume so few weed seeds within the irrigated cereal fields.

Density dependent response

In north-eastern Germany, seed predation rates by granivorous rodents were higher inside than outside patches with high seed density. The direct density dependent response observed indicates that rodents could limit the expansion of weed patches in winter cereal fields. Unfortunately, predation rates were very low (32.4 % per 18 days) and the impact of seed predation on weed population dynamics is, therefore, low. The density dependent response by harvester ants and granivorous rodents in semi-arid cereals in north-eastern Spain are currently being studied (Atanackovic *et al.*, *in prep.*; Rouphael 2010).

MAIN CONCLUSIONS

This study exemplifies both the strength and vulnerability of an ecosystem service. High weed seed predation by harvester ants is occurring naturally in rain-fed cereals in north-eastern Spain and contributes substantially to weed control. However, this service can easily be lost as illustrated by the absence of seed predation in the flood irrigated areas and the response of harvester ants to excessive tillage. Existing densities of harvester ant nests could be preserved by limiting the level of soil disturbance. In semi-arid regions, cereal production is marginally cost effective due to limited water availability and, therefore, preserving natural weed control by harvester ants is needed in order to sustain the system.

The main results of this study are:

For the rain-fed area:

- *Messor barbarus* harvester ants are the main seed predators and are contributing substantially to natural weed control. The period of high predation rates coincides with the period of maximum weed seed shed, thus maximizing weed seed mortality.
- In order to maintain high levels of natural weed control, harvester ant densities should be maintained at the current level.
- Tillage should be avoided because it reduced the density of harvester ant nests and concomitant seed predation rates. In addition, tillage after crop harvest buried most weed seeds, which very likely escaped predation by harvester ants.
- Causes of variability in ant nest densities between fields are unknown. *M. barbarus* ant and nest densities did not correlate with common soil characteristics, topographic variables or crop and management practices, except for the number of years of no-till. Harvester ant density was highest after 11-12 years of no-till. Other than that, no recommendations could be formulated to increase nest densities in those areas were they are low.
- Granivorous rodents in rain-fed fields were scarce and did not contribute much to weed seed predation.
- Crop yield losses caused by harvesting of seeding material in autumn or cereal ears in summer by *M. barbarus* were negligible. However, causes of occasional higher crop losses close to harvest should be investigated further. In general, it seems that yield losses caused by harvester ants are more than offset by the benefits provided by the predation of weed seeds.

For the irrigated area:

- Harvester ants were completely absent in flood irrigated fields. The loss of this species led to the almost complete loss of weed seed predation.
- Harvester ants were replaced by carabid beetles and granivorous rodents. Although densities of granivorous rodents were high in the field edges, seed removal rates within the fields were low except for a short period of time in spring. Causes of low predation rates within irrigated fields are unknown and need to be investigated.

Density dependent response:

- Granivorous rodents in NE Germany responded in a direct density dependent manner to increased weed seed densities and, thus, have the potential to limit the expansion of weed patches in winter cereal fields.
- Unfortunately, seed predation rates were exceptionally low (32.7 % per 18 days) and the causes for this need to be investigated.

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Conclusions

Les principals conclusions d’aquest estudi són:

Per l’àrea de secà:

- Les formigues recol·lectores *Messor barbarus* són els principals depredadors de llavors i estan contribuint substancialment al control natural de males herbes. El període on les taxes de depredació son més altes coincideix amb el període de màxima pluja de llavors, pel que la mortalitat de llavors de males herbes es veu maximitzada.
- Per mantenir els alts nivells de control natural de les arvenses, les densitats de formigues recol·lectores s’haurien de mantenir al nivell actual.
- El conreu del sòl hauria d’evitar-se quan fos possible perquè redueix la densitats de nius de formigues recol·lectores així com les taxes de depredació. A més, el conreu del sòl després de la collita del cereal enterra la majoria de les llavors de males herbes, i d’aquesta manera, poden escapar a la depredació per part de les formigues.
- Les causes en la variabilitat en la densitat de nius entre camps encara es desconeixen. Les densitats de nius de *M. barbarus* no es van correlacionar amb les característiques del sòl més comunes, ni amb variables topogràfiques ni amb practiques de maneig; excepte el nombre d’anys en sembra directa. La densitat de nius de *M. barbarus* va ser màxima després de 11 – 12 anys de sembra directa. A part d’això, no es van poder formular recomanacions per incrementar les densitats de nius en aquelles zones en les que són baixes.
- Les poblacions de ratolins granívors en les àrees de seca van ser molt baixes i no van contribuir gaire a la depredació de llavors de males herbes.
- Les pèrdues de rendiment causades per *M. barbarus*, tant per la recollida de llavors de cultiu a la tardor o d’espigues de cereal abans de la collita, van ser negligibles. Tanmateix, les causes que condueixen ocasionalment a pèrdues més altes abans de la collita haurien d’investigar-se en detall en el futur. En general, sembla que les pèrdues causades per les formigues recol·lectores queden compensades pels beneficis de la depredació de llavors de males herbes.

Per les àrees de regadiu:

- Les formigues recol·lectores van desaparèixer completament dels camps regats per inundació. La pèrdua d'aquesta espècie va portar a la casi completa pèrdua de la depredació de llavors de males herbes.
- Les formigues recol·lectores van ser substituïdes per caràbids i ratolins granívors. Encara que les densitats de ratolins granívors van ser altes als marges, les taxes de depredació a l'interior dels camps van ser baixes, excepte per un curt període de temps a la primavera. Les causes que expliquen aquestes baixes taxes de depredació són encara desconegudes i han de ser investigades en detall.

Respostes denso-dependents:

- Els ratolins granívors del nord-est d'Alemanya van tenir una resposta directament denso-dependent a densitats creixents de llavors de males herbes, i per tant, tenen el potencial per limitar l'expansió de rodals de males herbes en camps de cereals d'hivern.
- Malauradament, les taxes de depredació van ser excepcionalment baixes (32.7% en 18 dies), pel que s'haurien d'investigar les causes.

Conclusiones

Las principales conclusiones de este estudio han sido:

Para las zonas de secano:

- Las hormigas granívoras de la especie *Messor barbarus* son las principales depredadoras de semillas y están contribuyendo de una forma sustancial al control natural de las malas hierbas. El periodo en el que se dan las tasas más elevadas de depredación coincide con el periodo de máxima dispersión de semillas, por lo que cabe esperar que la mortalidad de semillas de malas hierbas sea máxima.
- Para mantener los niveles de depredación de semillas altos, las densidades de hormigas granívoras deberían mantenerse en el nivel actual.
- El laboreo del suelo debería ser evitado en lo posible ya que reduce la densidad de nidos de hormigas y las concomitantes tasas de depredación. Además, el laboreo después de la cosecha del cereal entierra la mayoría de las semillas de malas hierbas y evita en gran medida, que éstas puedan ser depredadas.
- Las causas de la variabilidad en la densidad de nidos de hormigas entre campos son aún desconocidas. Las densidades de nidos de *M. barbarus* no pudieron ser correlacionadas con las características del suelo más comunes, con parámetros topográficos ni con las prácticas de manejo del cultivo, exceptuando en número de años desde la adopción de la siembra directa. Las densidades de nidos de *M. barbarus* fueron máximas después de 11-12 años de siembra directa. A parte de esto, no se pudieron formular recomendaciones para incrementar las densidades de nidos en aquellas zonas en las que son bajas.
- Las poblaciones de roedores granívoros en las zonas de secano fueron muy escasas y contribuyeron escasamente a la depredación de semillas de malas hierbas.
- Las pérdidas de rendimiento causadas por *M. barbarus* tanto en el momento de la siembra, como en el de la cosecha fueron insignificantes. Sin embargo, las causas que ocasionan pérdidas más elevadas de rendimiento antes de la cosecha, aún de forma ocasional, deben continuar siendo estudiadas. En general, parece que las pérdidas de rendimiento causadas por hormigas granívoras son compensadas por los beneficios que proporciona la depredación de semillas de malas hierbas.

Para las zonas de regadío:

- Las hormigas granívoras desparecieron por completo en los campos regados por inundación. Esta desaparición causó la pérdida casi completa de la depredación de semillas.
- Las hormigas granívoras fueron reemplazadas por carábidos y roedores granívoros. Sin embargo, aunque las densidades de roedores fueron altas en los márgenes de los cultivos, la depredación de semillas en el interior de los campos fue baja, excepto por un corto periodo de tiempo en primavera. Las causas de las bajas tasas de depredación aún no han sido clarificadas y necesitan ser investigadas en el futuro.

Respuestas denso-dependientes:

- Los ratones granívoros en el noreste de Alemania tuvieron una respuesta directamente denso-dependiente a densidades crecientes de semillas y, por lo tanto, tienen el potencial de limitar la expansión de los rodales de malas hierbas en campos de cereales de invierno.
- Lamentablemente, las tasas de depredación fueron excepcionalmente bajas (32.7% en 18 días) y sus causas aún deben ser investigadas.

Curriculum vitae

Bàrbara Baraibar graduated as Agronomic Engineer in 2004 at the “Escola Tècnica Superior d’Enginyeria Agrària” (ETSEA) of the University of Lleida. In 2005 she got a master’s degree in Organic Agriculture from the University of Barcelona. At the end of the master’s she got a fellowship to work in the Research Institute for Organic Farming (FiBL) in Frick, Switzerland, for 4 months where she participated in the ongoing research within the Entomology, Annual Crops and Communication groups. In 2006 she obtained a PhD grant from the University of Lleida and started working on her thesis entitled “Seed predators and weed seed predation for weed control in winter cereals”. In 2007 she obtained a PhD grant from the “Generalitat de Catalunya” (FI grants). During her thesis work she has attended several national and international congresses where she has presented her research results. She has worked within the Crop Health group of the University of Rostock (Germany) and within the Crop and Environmental Sciences Division of the International Rice Research Institute (IRRI) in Los Baños (Philippines). She has taught during 3 years on the subjects: “Weed Control” and “Organic and Sustainable Agriculture” and on a summer course on Organic Farming at the University of Lleida. She speaks fluent Spanish, Catalan and English and basic German.

Refereed scientific papers

Baraibar, B., P.R. Westerman, Carrión, J. Recasens (2009). Effects of tillage and irrigation in cereal fields on leed seed removal by seed predators. *Journal of Applied Ecology,* 46, 380–387.

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Oral presentations:

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