

Controlling annual weeds in cereals by deploying crop rotation at the landscape scale: *Avena sterilis* as an example

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Abstract. Weed control through crop rotation has mainly been studied in a nonspatial context. However, weed seeds are often spread beyond the crop field by a variety of vectors. For weed control to be successful, weed management should thus be evaluated at the landscape level. In this paper we assess how seed dispersal affects the interactions between crop rotation and landscape heterogeneity schemes with regard to weed control. A spatially explicit landscape model was developed to study both short- and long-term weed population dynamics under different management scenarios. We allowed for both two- and three-crop species rotations and three levels of between-field weed seed dispersal. All rotation scenarios and seed dispersal fractions were analyzed for both completely homogeneous landscapes and heterogeneous landscapes in which more than one crop was present. The potential of implementing new weed control methods was also analyzed. The model results suggest that, like crop rotation at the field level, crop rotation implemented at the landscape level has great potential to control weeds, whereby both the number of crop species and the cropping sequence within the crop rotation have significant effects on both the short- and long-term weed population densities. In the absence of seed dispersal, weed populations became extinct when the fraction of each crop in the landscape was randomized. In general, weed seed densities increased in landscapes with increasing similarity in crop proportions, but in these landscapes the level of seed dispersal affected which three-crop species rotation sequence was most efficient at controlling the weed densities. We show that ignoring seed dispersal between fields might lead to the selection of suboptimal tactics and that homogeneous crop field patches that follow a specific crop rotation sequence might be the most sustainable method of weed control. Effective weed control through crop rotation thus requires coordination between farmers with regard to cropping sequences, crop allocation across the landscape, and/or the fraction of each crop across the landscape.

Key words: aggregated crop patches; *Avena sterilis*; crop rotation; population dynamics; regional stochasticity; seed dispersal; southern Spain; spatially explicit landscape model; weed management.

INTRODUCTION

Crop rotation can be defined as the alternation of crops on the same field in a recurring sequence (Thenail et al. 2009). This is qualitatively different from crop succession, which is a more flexible framework in which farmers apply a combination of sequences based on agronomic rules (Joannon et al. 2008). Crop rotation has been shown to be a successful method for weed control and has positive effects on many biotic and physical soil factors (Liebman and Dyck 1993). This success is achieved by the heterogeneity created by the different crops and their management systems (Joannon et al. 2008), which impose different types and intensities of biotic and abiotic stresses on weeds (Liebman and Dyck 1993). In more recent years, weed control has

mainly been through herbicide use (Saavedra et al. 1989), but control methods such as crop rotation are regaining interest due to the increased pressure to develop sustainable control methods that have a limited environmental impact. An effective crop rotation deployment might thus limit, and in some cropping years even eliminate, the need for herbicide applications to control the dominant weed species.

In existing crop rotation models, the effects of the weed control established by the rotation are either introduced via individual weed life cycle parameters (González-Andújar and Fernández-Quintanilla 1991, 1993) or through the development of more complex matrix models (Jordan et al. 1995, Mertens et al. 2002, Westerman et al. 2005, van den Berg et al. 2010). Mertens et al. (2002) studied how different crop rotation sequences, crop fractions, and lengths in a two-crop species rotation affect the growth rate of the weed species *Persicaria maculosa* (formerly named *Polygonum persicaria*). Although the model incorporated a lot of

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biological detail, it ignored the spatial aspect of seed dispersal between fields. However, Auld and Coote (1980) showed that the weed population growth rate is strongly influenced by seed dispersal, which stresses the need to take seed dispersal mechanisms into account when developing weed control strategies (Ghersa and Roush 1993). Moreover, there is a need to understand how dispersal processes and management practices interact (Thill and Mallory-Smith 1997).

The agricultural landscape can be thought of as fields interconnected by seed dispersal driven by both agronomic factors and other human activities (Benvenuti 2007). If weed seeds spread beyond the crop field, attempts to control the weed population through within-field crop rotation might be ineffective (Helenius 1997). This is because metapopulation theory predicts that, although crop rotation deployed at the field level ensures an increased environmental stochasticity and presumably an increased weed extinction rate at the field level (Hanski 1991), the mean regional stochasticity might be unaffected, rendering the crop rotation ineffective at the regional scale (Helenius 1997). González-Andújar et al. (2001) studied how decisions at the field level influence weed control at the landscape level and concluded that to achieve effective control, weed population dynamics should be integrated at different spatial scales.

The main aim of this study was to evaluate the interaction between different crop rotation sequences at the field level and the relative proportion of these crop species in the landscape in the presence of different levels of seed dispersal and the effectiveness of weed control for the dominant weed species. Both short- and long-term seed population dynamics were analyzed. The study is motivated and illustrated by the specific example of the weed species *Avena sterilis* L.

A. sterilis is the dominant cereal-infesting grass weed in the south of Spain (González-Andújar and Saavedra 2003) and is difficult to control due to its seed dispersal (Thill and Mallory-Smith 1997) and its dormancy strategies (Sánchez del Arco et al. 1995). Although *A. sterilis* control currently focuses mainly on control by herbicides (Saavedra et al. 1989), weed management through crop rotation has been studied both experimentally (Fernández-Quintanilla et al. 1984, Navarrete and Fernández-Quintanilla 1996) and theoretically (González-Andújar and Fernández-Quintanilla 1991, 1993). We will show that the omission of between-field seed dispersal from crop rotation models, such as the models developed by Mertens et al. (2002) and van den Berg et al. (2010), might lead to the selection of suboptimal weed control strategies.

MATERIALS AND METHODS

Model construction

The agricultural landscape was discretized into a two-dimensional square lattice with absorbing edges consisting of $V \times V$ cells with $V = 100$ cells. Each cell represented a farm field of 1 ha in which an independent

weed seed population developed. Note that field sizes of <2 ha are frequent in the south of Spain (Junta de Andalucía 2010) and other European countries. For example, mean field sizes in six French regions were found to be 2.1, 1.7, 1, 2.1, 3.5, and 1 ha, respectively (Colbach et al. 2009). Once the weed seed population was established in each cell, the seeds were distributed over the landscape following some specific rules.

Crops were initially allocated across the farmland in a random manner, according to the number of crop species in the rotation and their frequency in the landscape. Such a randomized crop distribution results in the aggregation of individual fields containing the same crop species. These aggregations thus can be thought of as larger fields and can therefore account for the variability in field sizes observed in the agricultural landscape. Crop distribution was subsequently changed yearly following the rotation sequence so that in each weed growing season only one of the crops in the rotation appeared in each cell. For example, in the case of the two-crop species rotation WSWS, where W and S denote different crops, cells initiated with crop W will contain crop S in year two, followed by crop W in year three and so on, whereas cells initiated with crop S follow the opposite alternation pattern.

Crop species of the rotations.—We studied rotations of both two and three crops. Because the model was parameterized for *A. sterilis*, we studied rotations that are commonly used in Andalusia to control this species, i.e., the two-crop species rotation of winter wheat (W) and sunflower (S) (Jurado-Expósito et al. 2005) and the three-crop species rotation that also incorporates legumes (L) (Saavedra et al. 1989).

Landscape scenarios (LS).—Each cropping sequence was evaluated under different landscape scenarios based on the relative proportion of the crops across the landscape, i.e., the level of crop evenness (sensu Magurran 2004). The resultant landscapes varied broadly from completely homogeneous, in which only one crop was present each year, to heterogeneous with a maximum crop evenness, in which case all crops were simultaneously present in the landscape in equal proportions and with an initial random distribution. Percentage contributions of each crop to the landscape's spatial pattern are given in Table 1. Note that heterogeneity is introduced by two factors: (1) the number of crop species involved in the rotation and (2) crop evenness, which measures the relative proportion of crops in the landscape, whereby an increasing value means that the relative crop proportions are increasingly equal. The process of farmers rotating their crops according to agronomic factors without applying a consistent rotation sequence was simulated by landscape scenarios 1 and 7, LS1 and LS7, respectively (Table 1), whereby the proportional distribution of the crops in the landscape was allocated at random. In all other cases, the farmers were assumed to apply a consistent rotation scheme as outlined in the next section, with the

TABLE 1. Initial landscape-level crop distribution whereby the different landscape scenarios result in different levels of heterogeneity.

| Landscape scenario (LS) | Crops at the landscape level (%) | | |
|-------------------------|----------------------------------|-----------|--------|
| | Wheat | Sunflower | Legume |
| Two-species rotations | | | |
| 1 | random | random | |
| 2 | 0 | 100 | |
| 3 | 25 | 75 | |
| 4 | 50 | 50 | |
| 5 | 75 | 25 | |
| 6 | 100 | 0 | |
| Three-species rotations | | | |
| 7 | random | random | random |
| 8 | 0 | 100 | 0 |
| 9 | 0 | 0 | 100 |
| 10 | 20 | 60 | 20 |
| 11 | 20 | 20 | 60 |
| 12 | 33 | 33 | 33 |
| 13 | 60 | 20 | 20 |
| 14 | 100 | 0 | 0 |

proportional distribution of the crops in the landscape as a result of local decisions.

Cropping sequences.—Rotation lengths of more than six years are not exceeded in practice (Mertens et al. 2002) and short sequences of similar crops are recommended when trying to control other weeds or diseases associated with these crops and when trying to maintain soil properties and nutrients (Liebman and Dyck 1993). We thus considered crop rotations of up to six years in length, whereby crops appeared in the same field for a maximum of two consecutive years.

We studied two qualitatively different types of rotations. Cyclic permutations, distinguished by letters in Table 2, are rotations with an identical cropping sequence, but initiated with a different crop. For example, rotations WWSS and WSSW are cyclic permutations. Such rotations have identical long-term dynamics with identical growth rates or mean seed densities, but differ in some other characteristics such as the short-term population growth rate (Mertens et al. 2002). All other rotations studied were “essentially different” (Mertens et al. 2002) and are distinguished by numbers in Table 2. Essentially different rotations differ in both their short-term and long-term dynamics. Column 2 of Table 2 specifies the rotation sequence followed by cells that were initiated with a winter wheat crop. Cells initiated with an alternative crop followed the same rotation scheme, but in such a way that the landscape scenario remained constant over each rotation cycle.

Population model.—The *A. sterilis* seed bank in a given cell at the beginning of crop season t is denoted by $N_t[x, y]$ with $x \in \{1, \dots, V\}$ and $y \in \{1, \dots, V\}$. The seed population size at the end of crop season t , i.e., after reproduction, is given by

$$M_t[x, y] = N_t[x, y]f(N_t[x, y]) \tag{1}$$

with reproduction, $f(\cdot)$, following Mortimer et al. (1989), i.e.,

$$f(N_t[x, y]) = \lambda g(1 - c_j)(1 + agN_t[x, y])^{-b}$$

with

$$j = \{W, S, L\} \tag{2}$$

and with g the proportion of seeds germinating, λ the seed production of an individual plant, a and b parameters determining self regulation, and c_j the level of weed control in crop j (Table 3). *A. sterilis* seeds start emerging in late October with around 75% of seedling production in the next two months (Aibar et al. 1991). Crops sown after this time can reduce *A. sterilis* population by means of pre-planting tillage, whereby established seedlings are destroyed (Fernández-Quintanilla et al. 1984). Moreover, weed seeds that emerge late in the growing season, i.e., after tillage operations, produce seeds at a much reduced capacity due to strong competition with the crop (Fernández-Quintanilla et al. 1984), leading to a reduced weed seed rain. Winter wheat (generally sown in October or November) does not significantly contribute to the pre-planting tillage death of *A. sterilis*, but pre-planting tillage applied to legume (generally sown in December or January) and especially sunflower crops (generally sown in March) can result in a substantial seedling death and seed production reduction of *A. sterilis*. Such crop-specific weed “control” was denoted by parameter c_j , which implicitly affected both the weed seedlings’ survival and their seed production capacity at maturity (Cousens and Mortimer 1995). The winter wheat crop was used as the reference crop, leading to $c_W = 0$, whereas the weed

TABLE 2. Rotation scenarios studied whereby different numbers indicate essentially different rotations and different letters indicate cyclic permutations.

| Rotation scenario | Cropping sequences for different initial crops | | |
|-------------------------|------------------------------------------------|---------------|------------|
| | Wheat (W) | Sunflower (S) | Legume (L) |
| Two-species rotations | | | |
| 1 | WSWS | SWSW | |
| 2(a) | WWSS | SSWW | |
| 2(b) | WSSW | SWWS | |
| Monoculture 1 | WWWW | SSSS | |
| Three-species rotations | | | |
| 3 | WSLWSL | SLWSLW | LWSLWS |
| 4 | WLSWLS | SWLSWL | LSWLWS |
| 5(a) | WWSSLL | SSLLWW | LLWSSS |
| 5(b) | WSSLLW | SLLWWS | LWWSSL |
| 6(a) | WWSLLS | SLLSWS | LSWWSL |
| 6(b) | WSLLSW | SWWSLL | LLSWSW |
| 7(a) | WWLSSL | SLWWLS | LSSLWW |
| 7(b) | WLSSLW | SSLWWL | LWWLSS |
| 8(a) | WWLLSS | SSWWLL | LLSSWW |
| 8(b) | WLLSSW | SWWLLS | LSSWWL |
| 9(a) | WSSWLL | SWLLWS | LLWSSW |
| 9(b) | WLLWSS | SSWLLW | LWSSWL |
| Monoculture 2 | WWWWWW | SSSSSS | LLLLLL |

control exerted by the other crops relative to the control exerted by winter wheat was fixed according to the survey of Fernández-Quintanilla et al. (1984) (Table 3).

A constant crop-specific fraction, d_j , of the total number of seeds produced in a parent cell was assumed to disperse over the landscape following the von Neumann neighborhood method, whereby seeds were equally distributed over all four directions and over a distance of a single ring of neighboring farms or cells. Due to the machinery associated with winter wheat crops, *A. sterilis* seeds spread beyond the field boundary of these crops (Shirliffe and Entz 2005), but this is not the case for sunflower and legume crops (i.e., $d_W \geq 0$ and $d_S = d_L = 0$). The three different fractions of seed dispersal that were studied, i.e., $d_W = 0$, $d_W = 0.014$, and $d_W = 0.12$, are based on field observations for winter wheat crops (Steinmann and Klingebiel 2004, Shirliffe and Entz 2005). Because *A. sterilis* seeds are subject to dormancy (Sánchez del Arco et al. 1995), the model also incorporated a persistent seed bank, sN_t , with s being the fraction of seeds surviving from one generation to the next. The seed bank in the next generation was thus given by

$$N_{t+1}[x, y] = M_t[x, y] - E_t[x, y] + I_t[x, y] + sN_t[x, y] \quad (3)$$

with $E[x, y]$ and $I[x, y]$ the emigrating and immigrating weed seeds from the parent cell to its neighboring cells and vice versa.

Model analysis

The model was implemented in Microsoft Excel, using Visual Basic macros. For all scenarios studied, the initial weed seed bank density was set to the weed seed density found in cereal crops infested with *A. sterilis*, i.e., 16 seeds/m² (derived from 4 plants/m²) (Saavedra et al. 1989) and each scenario was replicated 10 times. Model outputs in the form of the number of weed seeds in a given cell at the end of a crop growing season ($N_{t+1}[x, y]$) were derived at every time step, representing a complete crop growing season. To avoid equivocal results disguising the true model behavior, the method of Perry and González-Andújar (1993) was used to derive the integer equivalents of the output values, such that

$$N_{t+1}[x, y] = \text{floor}(N_{t+1}[x, y] + U) = \lfloor N_{t+1}[x, y] + U \rfloor \quad (4)$$

with U being a random number between 0 and 1. The landscape-wide average seed density, \hat{N} , was subsequently calculated from

$$\hat{N} = \left(\sum_{x=1}^V \sum_{y=1}^V N_{t+1}[x, y] \right) V^{-2}. \quad (5)$$

The long-term seed bank dynamics were restricted to the asymptotic phase, where trends have settled down to a fixed pattern and are independent of initial conditions (Caswell 2001). Because the rotations studied have different cycle lengths, the mean seed

TABLE 3. Parameter values for *Avena sterilis* in winter wheat crops.

| Parameter | Symbol | Value | Units |
|--------------------------|-----------|-----------------|-------------|
| Germination | g | 0.25† | 1 |
| Potential fecundity | λ | 32.15‡ | seeds/plant |
| Parameter a | a | 0.004‡ | 1 |
| Parameter b | b | 1‡ | 1 |
| Survival | s | 0.15† | 1 |
| Control of weeds | | | |
| Wheat | c_W | 0 | 1 |
| Sunflower | c_S | 0.99§ | 1 |
| Legume | c_L | 0.93¶ | 1 |
| Seed dispersal fractions | | | |
| Wheat | d_W | 0; 0.014#; 0.12 | 1 |
| Sunflower | d_S | 0 | 1 |
| Legume | d_L | 0 | 1 |

† *A. sterilis* germination and seed bank survival rates under Mediterranean conditions (Sánchez del Arco et al. 1995).

‡ Parameters estimated according to González-Andújar and Fernández-Quintanilla (1993) for *A. sterilis* growing in winter barley.

§ The weed control parameter can be estimated from the experiment of Fernández-Quintanilla et al. (1984). Two randomized block design field experiments were performed to evaluate effects on *A. sterilis* demography, with two and four cropping systems over four and two years, respectively. Sequences were winter wheat monoculture and fallow–spring barley rotation in the first experiment and winter barley and spring barley monocultures and fallow–winter barley and sunflower–winter barley rotations and vice versa in the second experiment. For each plot, seed bank and panicle densities were measured annually at the beginning and end of the weed life cycle. The sunflower control parameter c_S was estimated from $N_{t+1} = N_t \lambda g (1 - c_S) (1 + ag N_t)^{-b} + s N_t$, with N_t and N_{t+1} the 2-year average weed seed bank densities in sunflower at the beginning and end of the weed life cycle, respectively (from Fernández-Quintanilla et al. 1984), and all other parameters set to their default value.

¶ No literature available; estimated according to the *A. sterilis* seed bank in spring barley (Fernández-Quintanilla et al. 1984) and $N_{t+1} = N_t \lambda g (1 - c_L) (1 + ag N_t)^{-b} + s N_t$, with N_t and N_{t+1} the 4-year average weed seed bank densities in spring barley at the beginning and end of the weed life cycle, respectively (from Fernández-Quintanilla et al. 1984), and all other parameters set to their default value.

Seed fraction found 100 m from the parent position for *Avena fatua* (Shirliffe and Entz 2005).

|| Seed fraction found beyond the farm boundaries (each subfield was 1 ha) for *Anisantha sterilis* (formerly *Bromus sterilis*) (Steinmann and Klingebiel 2004), which has a seed shape similar to *A. sterilis*.

bank density, \bar{N} , for a given rotation was calculated over a common cropping period, p , of 12 years:

$$\bar{N} = \frac{\sum_{i=1}^p \hat{N}_i}{p}. \quad (6)$$

This ensured that the results for different rotation scenarios could be compared directly and that the fraction of each crop species in the total rotation sequence remained constant.

The short-term weed seed dynamics, on the other hand, do depend on the initial conditions. Therefore, for the crop rotation that resulted in the largest decrease in

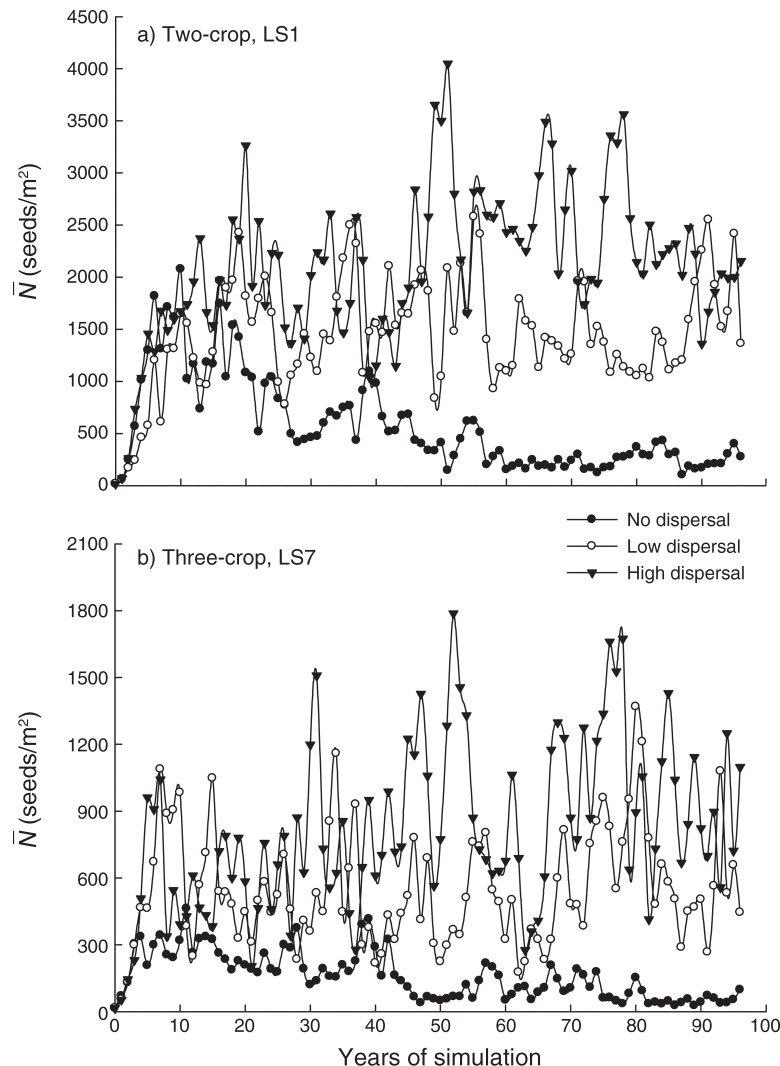


FIG. 1. Mean *Avena sterilis* seed population density dynamics for different seed dispersal fractions (no dispersal, $d_w = 0$; low dispersal, $d_w = 0.014$; high dispersal, $d_w = 0.12$) for (a) the two-crop species succession system and landscape scenario 1 (LS1) and (b) the three-crop species succession systems and LS7.

the long-term weed seed densities, we also studied the short-term population dynamics.

RESULTS

Crop succession: landscape scenarios 1 and 7

For crop succession, whereby crop allocation across the landscape occurred at random, the weed seed densities depicted stochastic behavior in the presence of seed dispersal, whereas in the absence of dispersal, *A. sterilis* decreased markedly (Fig. 1) and eventually became extinct after a time period exceeding 100 years (results not shown). Furthermore, increased dispersal fractions led to increased seed densities. The results were qualitatively the same for the two- and three-crop species rotations (Fig. 1a, b), although landscapes with

less diversity, involving fewer crop species, resulted in higher weed seed densities (Fig. 1).

Long-term population dynamics: all rotation scenarios and landscape scenarios 2–6 and 12–14

For homogeneous landscapes (LS2, LS6, LS14), in which every year only one crop species was present, and for all monoculture scenarios, the mean long-term weed seed densities were unaffected by seed dispersal events (Tables 4 and 5). This is a direct consequence of the constant crop-specific weed seed dispersal fractions resulting in a homogeneous regional seed spread. Seed densities increased with increased crop evenness in the landscape and increased seed dispersal fractions (Tables 4 and 5). Obviously, in the absence of dispersal the mean seed population density is unaffected by the landscape

TABLE 4. Mean equilibrium *A. sterilis* seed densities for the two-crop species rotations, different seed dispersal fractions, and landscape scenarios 2–6 (defined by relative fractions of wheat and sunflower).

| Rotation scenario | Example, wheat as initial crop | <i>A. sterilis</i> density (seeds/m ²) by landscape scenario (LS) and dispersal fraction (d_w) | | | | | | | | | | | | | | |
|-------------------|--------------------------------|----------------------------------------------------------------------------------------------------------------|-------|------|------------------|-------|------|------------------|-------|------|------------------|-------|------|------------------|-------|------|
| | | 2 (0% W, 100% S) | | | 3 (25% W, 75% S) | | | 4 (50% W, 50% S) | | | 5 (75% W, 25% S) | | | 6 (100% W, 0% S) | | |
| | | 0 | 0.014 | 0.12 | 0 | 0.014 | 0.12 | 0 | 0.014 | 0.12 | 0 | 0.014 | 0.12 | 0 | 0.014 | 0.12 |
| Monoculture 1 | WWWW | 0 | 0 | 0 | 2114 | 2113 | 2099 | 4228 | 4227 | 4205 | 6341 | 6340 | 6320 | 8456 | 8454 | 8445 |
| 1 | WSWS | 1452 | 1452 | 1448 | 1452 | 1519 | 1955 | 1452 | 1542 | 2110 | 1452 | 1519 | 1955 | 1452 | 1452 | 1448 |
| 2(a) | WWSS | 1246 | 1476 | 1473 | 1304 | 1646 | 2328 | 1362 | 1702 | 2569 | 1420 | 1646 | 2330 | 1477 | 1476 | 1473 |

Note: SEs are not included because of their small values (<1%).

scenario (Tables 4 and 5). The absence of dispersal often led to local field-level population extinction, which explains why certain results deviate from this general finding (see Rotations 2(a) and 5(a)–8(a)). Such extinction events could be avoided by increasing the initial seed bank density above the default density, in which case the mean seed densities were indeed constant across all fragmentation scenarios (results not shown).

In general, the equilibrium weed densities decreased with the number of crops involved in the rotation and winter wheat monocultures were thus least effective with respect to *A. sterilis* control (Tables 4 and 5). Note, however, that the weed populations became extinct in monocultures of sunflower (Table 4; LS2) and legume (results not shown). Overall, Rotation 1 resulted in better *A. sterilis* control than Rotation 2 and this difference in control ability was more significant for landscapes with increased crop evenness and increased seed dispersal fractions (Table 4). For three-crop rotations, it is less clear which management scenario is optimal (Table 5). In the absence of seed dispersal, Rotation 8 was the most efficient rotation. However, in heterogeneous landscapes and in the presence of either low ($d_w = 0.014$) or high ($d_w = 0.12$) seed dispersal fractions, Rotation 4 and Rotations 3, 4, and 9, respectively, all became more efficient in controlling *A. sterilis* than Rotation 8. For LS12, Fig. 2 provides a graphical representation of the changes in which rotation sequence is optimal when the seed dispersal

fraction is increased. Equilibrium weed densities are only given for permutation (a), because the long-term population dynamics are identical for cyclic permutations (Tables 4 and 5).

Results for the essentially different rotation scenarios, i.e., Rotations 3 and 4, Rotations 5 and 8, and Rotations 6 and 7, show that a rotation with legume phases followed by sunflower phases performs better than rotations with sunflower phases followed by legume phases (Table 5). More generally the results reveal that the best weed control is achieved when crops are deployed within a rotation in order of increasing level of weed control, before changing back to the crop with the lowest weed control ability at the start of the next rotation cycle (Table 5).

Table 6 reveals that *A. sterilis* population densities changed noticeably between individual phases of the rotations. Years or phases with high seed bank densities tended to coincide with years in which winter wheat was grown. This result was more pronounced for rotations with two consecutive wheat phases, in which case weed densities were much higher in the second wheat phase as compared to the other rotation phases, although these differences were less clear for Rotations 7 and 8. The results were qualitatively the same for all seed dispersal fractions and all landscape scenarios, whereby the long-term seed densities for LS8 and LS9 were similar to those for LS14, and densities for LS10 and LS11 were similar to those for LS13 (results not shown).

TABLE 5. Mean equilibrium *A. sterilis* seed densities for the three-crop species rotations, different seed dispersal fractions, and landscape scenarios 12–14 (defined by relative fractions of wheat, sunflower, and legume).

| Rotation scenario | Example, wheat as initial crop | <i>A. sterilis</i> density (seeds/m ²) by landscape scenario (LS) and dispersal fraction (d_w) | | | | | | | | |
|-------------------|--------------------------------|----------------------------------------------------------------------------------------------------------------|-------|------|--------------------------|-------|------|-------------------------|-------|------|
| | | 12 (33% W, 33% S, 33% L) | | | 13 (60% W, 20% S, 20% L) | | | 14 (100% W, 0% S, 0% L) | | |
| | | 0 | 0.014 | 0.12 | 0 | 0.014 | 0.12 | 0 | 0.014 | 0.12 |
| Monoculture 2 | WWWWW | 2818† | 2834 | 2862 | 5637 | 5650 | 5661 | 8456 | 8455 | 8445 |
| 3 | WSLWSL | 258 | 309 | 740 | 258 | 296 | 624 | 258 | 258 | 257 |
| 4 | WLSWLS | 174 | 196 | 402 | 174 | 190 | 336 | 174 | 174 | 173 |
| 5(a) | WWSSLL | 273 | 598 | 1500 | 306 | 533 | 1271 | 338 | 338 | 336 |
| 6(a) | WWSLLS | 211 | 420 | 1241 | 236 | 375 | 998 | 261 | 261 | 260 |
| 7(a) | WWLSSL | 156 | 334 | 1303 | 175 | 293 | 1030 | 193 | 193 | 192 |
| 8(a) | WWLLSS | 123 | 257 | 1064 | 143 | 228 | 783 | 163 | 163 | 163 |
| 9(a) | WSSWLL | 226 | 278 | 647 | 226 | 265 | 542 | 226 | 226 | 225 |

† SEs are not included because of their small values (<1%).

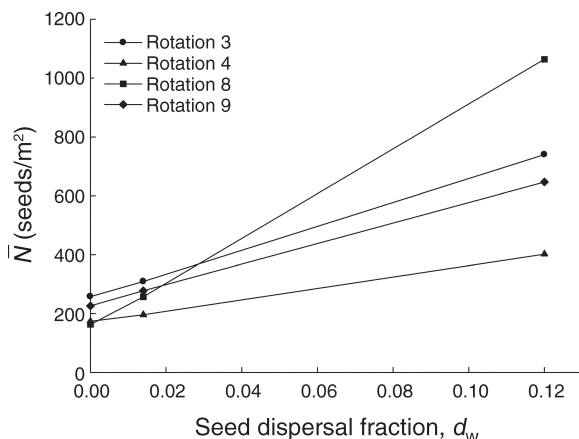


FIG. 2. Equilibrium *A. sterilis* seed population densities for the four three-crop rotations that were most efficient at controlling the long-term weed densities (i.e., Rotations 3, 4, 8, and 9 in LS12) as a function of the seed dispersal fraction, d_w .

Short-term population dynamics for optimal long-term management strategies: Rotations 1, 8(a), and 8(b) and landscape scenarios 2, 6, and 9

For rotations involving two crops, Rotation 1 within a homogeneous landscape (LS2 and LS6) resulted in the lowest long-term seed densities (Table 4). Analysis of the short-term population dynamics of these two scenarios revealed that for LS2, as compared to LS6, it took longer for the population dynamics to reach equilibrium because the seed population established at a lower rate (Fig. 3a). For rotations involving three crops, Rotation 8 combined with LS8, LS9, and LS14 resulted in the lowest long-term seed densities (Table 5). A comparison between these three landscape scenarios revealed that LS9 was most efficient in retarding the population dynamics (results not shown). Further analysis comparing the short-term population dynamics for the cyclic permutations of Rotation 8 in combination with LS9 showed that permutation (a) resulted in lower short-term weed seed densities than permutation (b) (Fig. 3b).

DISCUSSION

Methods developed in this paper allowed for the quantification of the effect of landscape on weed dispersal and the resultant weed population dynamics for different crop rotation scenarios. Results showed that the heterogeneity introduced by the variability in the proportion of crops in the landscape facilitates weed seed exchange between fields of different crops, leading to increased weed seed populations, and that the rotation sequence that is most efficient in reducing the weed seed population strongly depends on the level of weed seed dispersal. This stresses the need to plan weed control strategies at the landscape level as opposed to planning at the field level only. Model results are discussed in detail in the next few paragraphs, where we focus on the management implications at both the field and the landscape level.

Management implications at the landscape level

Model results revealed that the presence of dispersal and a randomized crop proportion in the landscape resulted in the persistence of *A. sterilis* with temporal changes in abundances and with average abundance depending on the fraction of seeds that dispersed. However, *A. sterilis* populations became extinct in the absence of seed dispersal (Fig. 1). A survey by Saavedra et al. (1989) showed that *A. sterilis* remains associated with cereal crops and that it is the most widely distributed weed, which suggests that dispersal indeed largely contributes to the persistence of *A. sterilis*. It is thus important to increase our understanding of how weed seed dispersal can be decreased at the landscape level.

Thill and Mallory-Smith (1997) point out that tillage operations, contaminated seed stock, and combine harvesters are the main drivers for dispersal of wild oat seeds. Cleaning tillage and harvesting equipment before entering a new field, especially when the soil is wet, helps to reduce the number of adhered seeds and limits seed spread from one field to another (Thill and Mallory-Smith 1997). Other desired tactics to avoid weed seed introduction and dispersal are the use of

TABLE 6. Equilibrium *A. sterilis* seed densities for individual years within the different crop rotations, a seed dispersal fraction of $d_w = 0.014$, and a homogeneous spatial distribution (LS14).

| Rotation scenario | Example, wheat as initial crop | <i>A. sterilis</i> density (seeds/m ²) by cropping year | | | | | | | | | | | |
|-------------------|--------------------------------|---------------------------------------------------------------------|-------------|------------|------------|------------|-----------|------|------|------|------|------|-----|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| 1 | WSWS | 2475 | 428 | 2475 | 428 | 2475 | 428 | 2475 | 428 | 2475 | 428 | 2475 | 428 |
| 2(a) | WWSS | 975 | 4114 | 682 | 135 | 975 | 4114 | 682 | 135 | 975 | 4114 | 682 | 135 |
| 3 | WSLWSL | 579 | 116 | 76 | 579 | 116 | 76 | 579 | 116 | 76 | 579 | 116 | 76 |
| 4 | WLSWLS | 304 | 177 | 39 | 304 | 177 | 39 | 304 | 177 | 39 | 304 | 177 | 39 |
| 5(a) | WWSSLL | 211 | 1433 | 262 | 56 | 38 | 27 | 211 | 1433 | 262 | 56 | 38 | 27 |
| 6(a) | WWSLLS | 141 | 1017 | 193 | 120 | 78 | 18 | 141 | 1017 | 193 | 120 | 78 | 18 |
| 7(a) | WWLSSL | 87 | 656 | 321 | 68 | 15 | 11 | 87 | 656 | 321 | 68 | 15 | 11 |
| 8(a) | WWLLSS | 62 | 474 | 252 | 151 | 33 | 8 | 62 | 474 | 252 | 151 | 33 | 8 |
| 9(a) | WSSWLL | 701 | 138 | 31 | 242 | 146 | 94 | 701 | 138 | 31 | 242 | 146 | 94 |

Notes: Densities for the shortest repeatable unit of the rotation are given in bold. SEs are not included because of their small values (<1%).

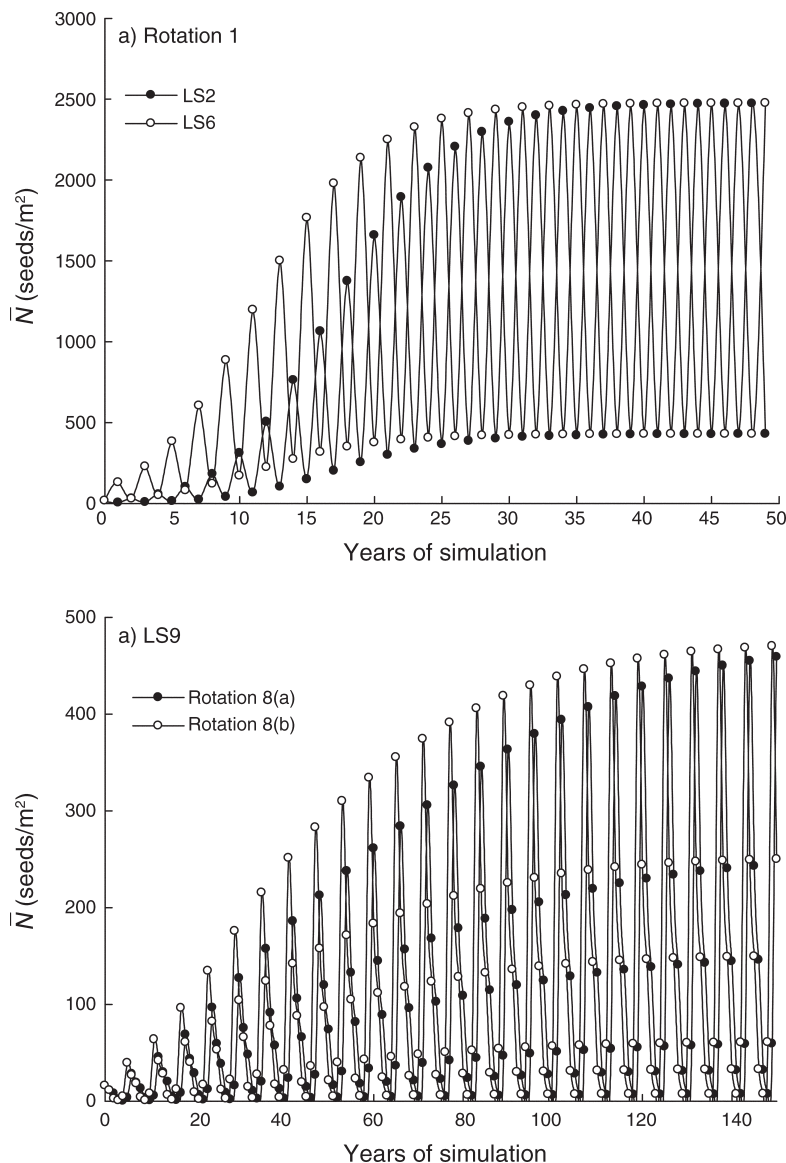


FIG. 3. Short-term *A. sterilis* population dynamics for the rotation and landscape scenarios that were most efficient in controlling the long-term weed population densities: (a) Rotation 1 under LS2 and LS6; (b) the cyclic permutations of Rotation 8 for LS9.

certified crop seeds and clean manure. Most farmers, however, conserve and grow their own crop seeds and, despite the seed cleaning procedures applied, the contamination by weed seeds was shown to be much higher than expected by the farmers (Michael et al. 2010). Furthermore, the direct weed seed dispersal through combine harvesters can be reduced by connecting a chaff collector to the back of the harvester (Shirtliffe and Entz 2005), turning off the chaff-spreaders when the harvester is passing through weed patches (Thill and Mallory-Smith 1997), or avoiding harvesting on windy days. Although some initial work has been done on understanding the nature of dispersal vectors (Benvenuti 2007) and some ideas for slowing

down human-related seed spread have been proposed (Thill and Mallory-Smith 1997), more work within this area is required.

The model analysis also highlighted a significant interaction between dispersal processes and which crop rotation was optimal with respect to weed control. Although this phenomenon was not evident in rotations of two crop species, it was clearly manifested in rotations of three crop species. For example, Rotation 8 (e.g., WWLLSS) was most efficient at decreasing the weed population in the absence of dispersal, but Rotation 4 (e.g., WLSWLS) obtained the best control in the presence of seed dispersal. This suggested that the omission of landscape-level dispersal processes from

models developed to establish suitable weed management practices might lead to the selection of suboptimal rotation and landscape schemes.

Two practical approaches can be derived from the results of the spatial analysis. Firstly it was shown that agricultural landscapes for which the proportion of each crop present is very similar, independently of the spatial allocation of these crops, favored increased weed densities in the region. This suggests that, from a regional weed management point of view, it would be beneficial to achieve uneven crop proportions within the wider landscape. Such unequal crop proportions are of course limited by consumer demands, but are achievable as long as the market absorbs the crop production fluctuations between years. The approach will require coordination between farmers with regard to crop rotation sequences, but not their specific allocation. Although coordinated management tactics at the landscape level have been proposed previously by other authors (González-Andújar et al. 2001, Dauer et al. 2009) and would offer a suitable alternative approach to help combat the weed problem, such a coordination is a new approach and it could prove difficult for farmers to cooperate together (Colbach et al. 2001).

Secondly, this study showed that homogeneous landscapes achieved the best *A. sterilis* control. This is an incongruous solution from a sustainable farmland management point of view (Benton et al. 2003), due to the need to diversify crops on a yearly basis in order to meet consumer demands and to prevent rapid spread of other pests and reduce the crop-specific risks associated with adverse environmental conditions. Other cropping patterns should thus be considered. When crops occur in aggregated patches that follow a specific rotation sequence, all crops could still be simultaneously present within the landscape. This ensures that the requirements for landscape-wide crop diversity are still met, whereas on a more local scale the homogeneous landscape within the aggregated patches helps to reduce weed populations. This approach, however, does require that farmers cooperate with regard to cropping sequences and landscape-level crop allocation. As mentioned previously, such coordination might be difficult to achieve because crop allocation has previously been shown to be affected by decisions of other farmers (Cutforth et al. 2001).

Management implications at the field level

The number of crop species involved in the rotation had a significant effect on the field-level equilibrium *A. sterilis* densities. Rotations of two crop species resulted in a weed population reduction of up to 83% and rotations of three crop species resulted in reductions of up to 98% as compared to the weed densities found in wheat monocultures (Tables 4 and 5). That rotations of three crops generally perform better than rotations of two crops is not surprising, considering that dispersal has such a large effect on the weed seed densities and the

fact that in the three-crop rotation, no dispersal takes place in two out of three rotation phases. However, the additional benefits that can be achieved by carefully choosing the rotation order should not be underestimated. For most landscape and dispersal scenarios, altering the crop order can lead to further weed seed bank density reductions of up to 18% and 74% for the two- and three-crop rotations, respectively. Crop diversification through rotation, however, does not always reduce weed seed production (Westerman et al. 2005) and is in fact related to the frequency of rotation phases with crops that are successful at controlling the weed (Mertens et al. 2002). Data analysis of the national-scale farmland data sets from Great Britain revealed that crop sequences can be simplified into crop management classes to predict their effects on weed seed bank abundances, whereby the salient descriptors of the crop management classes are crop type, sowing season, and the weed group target for herbicide control (Bohan et al. 2011). Like Mertens et al. (2002), we have shown that crop order, regardless of crop frequency, is also a crucial factor in determining the asymptotic growth rate of the weed population. The very high interannual variability in the equilibrium seed bank densities resulted in annual growth rates ranging from 0.17 to 7.9, whereby the highest weed densities occurred in the wheat phases of the rotation, especially when wheat crops were sown in two consecutive years of the rotation. In phases with such increased weed densities, additional management practices such as herbicide application ought to be considered.

The highest level of weed control is achieved when the crop order within a rotation scenario is such that crops are deployed in order of increasing level of weed control before changing back to the crop with the lowest weed control ability at the start of the next rotation cycle. These results are in accordance with previous findings by Mertens et al. (2002) and van den Berg et al. (2010). Deploying the crops in order of increasing levels of weed control results in the highest possible weed seed density reduction, ensuring a much reduced seed density at the beginning of the wheat phases and, consequently, a much lower weed seed population growth rate in the wheat phases where control is limited. A sensitivity analysis for the control parameters in the sunflower and legume crops was performed for landscape scenarios LS6 and LS14 and both the two- and three-crop rotation scenarios, whereby the control parameters were varied between the minimum and maximum estimates derived from the study by Fernández-Quintanilla et al. (1984). When, in independent simulation, the weed control parameter values were set to their minimum values (i.e., $c_S = 0.98$ and $c_L = 0.85$), the crop rotation ranking in relation to their effectiveness in decreasing the weed seed bank density changed slightly for the three-crop species rotations. When the weed control values were set to their maximum values (i.e., $c_S = 1$ and $c_L = 0.99$), the weed populations became extinct for the three-crop species

rotations, whereas for the two-crop species rotations a different rotation became optimal (see Appendix).

A detailed comparison of Rotation 8 and Rotation 9 for a high seed dispersal fraction and landscape scenario 12 reveals clear consequences of the interaction between within-field and landscape-level crop deployment. In this case, Rotation 9 proves to be more efficient at controlling the weed population than Rotation 8, but it is not immediately clear why. Because in the wheat (W) phases no weed control occurs, there is a large local increase in weed seed density during these phases, which will consequently result in a large seed rain into neighboring fields due to the dispersal associated with wheat crops. This is especially important in LS12, because in this case these neighboring fields are likely to be in the wheat phase during the following growing season. It is thus beneficial that the wheat phases are more frequently rotated with other crops to avoid multiple successive wheat phases (i.e., WSSWLL provides better control than WWLLSS).

The crop with which the rotation was initiated strongly affected the population dynamics of the transient phase, revealing that studies on the short-term population behavior for different cyclic permutations could complement studies of long-term population behavior when developing appropriate management strategies (see also Mertens et al. 2003). For rotation and landscape scenarios resulting in high yearly seed density variability, it can take a long time for the densities to reach equilibrium. Because farmers and advisors tend to make decisions based on short-term outcomes rather than long-term predictions, the seed densities established during the transient phase should be taken into consideration when new crop rotation schemes are designed (Mertens et al. 2002, 2003) and the crop with which the rotation is initiated should thus be chosen with care.

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SUPPLEMENTAL MATERIAL

Appendix

Sensitivity analysis for the control parameters (*Ecological Archives* A022-055-A1).