

Weeds in field margins: a spatially explicit simulation analysis of Canada thistle population dynamics

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Field margin weeds may contribute to the invasion and persistence of weeds in arable fields. Experimental studies of this hypothesis, however, have been inconclusive. We examined the role of field margin weed populations with a spatially explicit simulation model of Canada thistle population dynamics. We measured the contribution of field margin populations to weed pressure in the field across a wide range of parameter values and compared the weed control value of efforts applied to the field margin to that of similar efforts applied to the field. Under most combinations of parameter values, field margin weeds contributed little to weed pressure in the field, suggesting that controlling field margin weeds may often be of little value. Two conditions appeared to be necessary for field margin weeds to influence weed population dynamics within the field: the presence of unoccupied weed habitat, which increased the importance of dispersal to population growth, and high dispersal rates of field margin weeds relative to field weeds, which increased the relative contribution of field margin weeds to dispersal.

Nomenclature: Canada thistle, *Cirsium arvense* (L.) Scop. CIRAR.

Key words: Metapopulation, source–sink, dispersal, patchiness.

Field margin weed populations may contribute to the invasion and persistence of weed populations in adjacent arable fields (Boatman 1989; Kleijn 1997; Marshall and Smith 1987). For this reason, noxious weed laws require the control of many weed species that occur in both cropland and noncropland. Consequently, both farmers and government agencies spend large sums of money each year controlling weeds in noncropland. Weed control in noncropland also has environmental costs. For example, field margins actively managed for weeds contain lower levels of plant and animal diversity (Kleijn 1997). Despite the high costs and potential benefits associated with managing weeds in noncropland, little work has been done to determine the circumstances under which field margin weeds influence weed populations in adjacent fields.

Field margin weeds can influence field weed population dynamics only when immigration is important to the growth of field weed populations. Insight into the importance of immigration can be gleaned from spatial models of plant population dynamics. Spatial models have focused on the role of dispersal in allowing plants to escape from crowding (Howe and Smallwood 1982), in invading new habitats (Shigesada and Kawasaki 1997), and in reducing local variation in abundance (Hastings and Harrison 1994; Levin 1976; Levin et al. 1984; Venable and Brown 1988). Models of weed populations have suggested that dispersal rates are important both in determining the speed of an invasion (Auld and Coote 1980; Ballaré et al. 1987; Maxwell and Ghera 1992; Weiner and Conte 1981) and in escaping from density dependence by migrating to areas with less intraspecific competition (Ballaré et al. 1987; Perry and Gonzalez-Andujar 1993; Schippers et al. 1993).

Dispersal can also serve to recolonize extinct local populations, a role elucidated by the development of metapopulation models. These models assume multiple local populations interconnected by migration and subject to extinc-

tion; they find that equilibrium population size depends on the balance between extinction and recolonization rates (Levins 1969). Recent metapopulation models of plant populations have found dispersal to increase mean population size by allowing for the recolonization of unoccupied habitat following local extinction (Perry and Gonzalez-Andujar 1993; Tilman et al. 1997). In sum, dispersal (and, consequently, immigration from the field margin) is most likely to be important where a weed is invading a field, where density dependence is strong, or where local extinction is common.

Source–sink models, a subset of metapopulation models, have been used to address questions similar to the one posed in this paper: Can source populations (field margin populations), which persist independently, enable the persistence or growth of sink populations (field populations) by supplying immigrants (Hanski and Simberloff 1997; Pulliam 1988, 1996)? For organisms with extremely high fecundities and dispersal rates (e.g., marine invertebrates), small source populations may support much larger sink populations (Quinn et al. 1993). Plants have lower rates of reproduction and dispersal than marine invertebrates but also have been found to have sink populations (Janzen 1983; Kadmon and Shmida 1990; Keddy 1981). Sink populations of desert annuals, for example, may be several times larger than adjacent source populations (Kadmon and Shmida 1990; Shmida and Ellner 1984). Similarly, a source–sink model of an annual weed found that seed input from the field margin might account for as much as 75% of the weed seedbank in the area within 10 m of the field edge (Fogelfors 1985). Source–sink models therefore suggest that field margin populations might strongly affect weed population size but that the area over which they do so may be limited by fecundity and dispersal distance.

Empirical studies of weeds in field margins have focused on spatial patterns of weed abundance. Studies of weed or

seed distribution in relation to field margins have found that the weed/seed abundance of certain species can be substantially higher near the field margin than in the center of the field (Hume and Archibold 1986; Jones and Naylor 1992; Marshall 1989; Wilson and Aebischer 1995). In all cases, this edge effect was found to decrease quickly with distance from the edge. Cultivation may increase dispersal distance for non-wind-dispersed species, thereby extending the influence of the field margin; within 1 yr, however, few seeds travel further than 10 m from the field margin (Fogelfors 1985). Finally, according to Marshall's (1989) observations, relatively few weeds thrive in both fields and field margins. Taken together, empirical studies suggest that field margin weed populations are of little importance to the population dynamics of most field weeds but could play a more important role in the dynamics of a small subset of species.

In this paper we attempt to further narrow the question of when field margin weed populations are important with a spatially explicit metapopulation model. This model allows us to study the effects of field margin populations on field populations across a wide array of different conditions. Specifically, we examine the role of field margin populations in the context of three different scenarios concerning the spatial distribution of the weed within the field. In the first, the weed is present throughout the entire field. This scenario (referred to as complete occupancy) represents a weed that is well dispersed through its potential habitat. In the second scenario (invasion), the weed is initially present in only one patch in the center of the field and in the field margin. Invasion situations might exist either because weeds have never invaded a particular field or because management practices have changed, resulting in a newly favorable environment for the weed population. In the third scenario (extinction), the weed is absent from portions of the field because random extinctions periodically eliminate weed patches. This scenario represents situations in which control efforts and environmental variation result in the complete elimination of patches of weeds. In each of the above scenarios, we focus on how the presence of field margin weeds changes the amount of effort needed to keep the field population within acceptable levels.

Our purpose is to improve theoretical understanding of the role of field margin weeds in weed population dynamics. The results of interest consist of the behavior of modeled weed populations together with mechanistic explanations for that behavior. These mechanistic hypotheses can then serve as a framework to ground future empirical studies. Because of the generality of our theoretical questions (e.g., Under what assumptions about dispersal do field margin weeds increase weed abundance in the field?), a believable model structure is more important than the exact correspondence of the model to the circumstances of any particular weed population. We have taken two steps to try to ensure that our model behaves, qualitatively, like real weed populations. First, we base the model on a particular weed species, Canada thistle, a common weed of cultivated fields, field margins, and other ruderal habitats; this gives us a reference point from which to evaluate the structure and parameters of the model. Second, we use the resultant estimates of parameter uncertainty to set bounds for sensitivity analyses. These sensitivity analyses allow us to test whether the behavior of the model is robust.

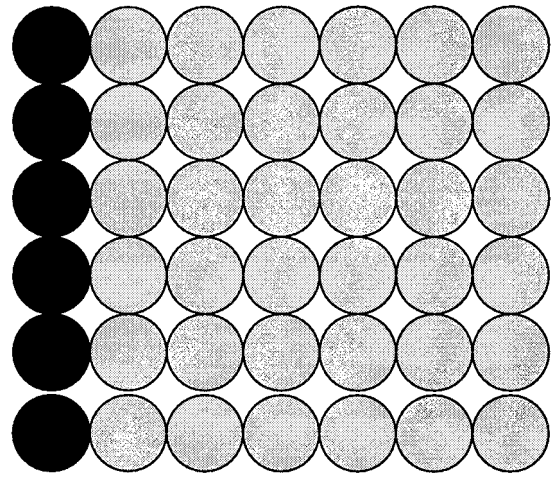


FIGURE 1. Map of the spatial layout of the model. Field margin patches are black and field patches are gray.

Materials and Methods

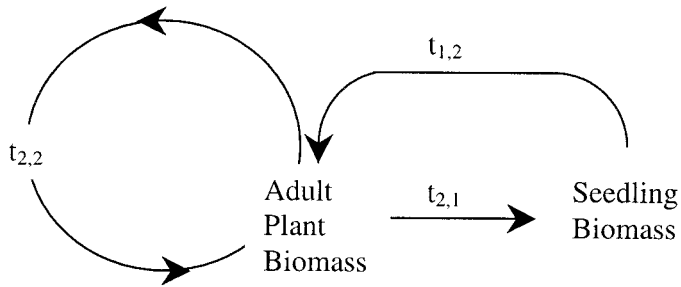
Model Structure

The population dynamics of Canada thistle are simulated using a spatially explicit metapopulation model built using the RAMAS GIS simulation program (Akçakaya 1998). The simulated environment consists of 36 circular patches 10 m in diameter in a six by six array (representing a field 60 by 60 m) adjacent to six similar patches in a one by six array (representing a field margin 10 by 60 m; Figure 1). The size of the array was chosen to allow for the presence of spatial patterns within the field while minimizing the practical difficulties of modeling large numbers of populations.

Growth and reproduction within individual patches is accomplished by multiplying a matrix of transition values by a vector describing the number of grams of Canada thistle per patch in each of two life history stages: adult plants and seeds/seedlings (Figure 2). Seeds and seedlings are condensed into a single stage to represent the occurrence of seed production, seed dispersal, and seedling growth within one time step (1 yr). For each patch, prior to matrix multiplication, each value in the matrix is chosen randomly from a log-normal distribution around a fixed mean and standard deviation (Table 1). The mean for a given transition value represents the average number of grams of one stage produced, in a single time step, by 1 g of that stage or the other stage. The random variation around that mean represents environmental variation that causes transition values to change over time. Within a patch, variations in individual transition values are perfectly correlated and, thus, vary in synchrony.

Among patches, variations in transition values ranged from independent to highly correlated. Factors that cause growth rates to vary over time (e.g., climate) might be expected to act over spatial scales larger than that of an individual patch. Independent variation among patches would thus be inappropriate. For this reason, we added varying degrees of correlation among the randomly chosen transition values of individual patches. The degree of correlation (C) between the vital rates of two patches i and j depends on the distance (D_{ij}) among patches such that

$$C_{ij} = a \exp(-D_{ij}^c/b), \quad [1]$$



$$\begin{bmatrix} 0 & t_{2,1} \\ t_{1,2} & t_{2,2} \end{bmatrix} \begin{bmatrix} N1_{(t)} \\ N2_{(t)} \end{bmatrix} = \begin{bmatrix} N1_{(t+1)} \\ N2_{(t+1)} \end{bmatrix}$$

$$N1_{(t+1)} = t_{2,1}N2_{(t)}$$

$$N2_{(t+1)} = t_{1,2}N1_{(t)} + t_{2,2}N2_{(t)}$$

FIGURE 2. Model diagram, depicting the life cycle of Canada thistle (*Cirsium arvense*, divided into plant and seed/seedling stages) and associated transition matrices and column vectors. N1 and N2 are the stage abundances of seedlings and plants, respectively.

where a , b , and c are parameters of the function. The resulting matrix of patch correlations is then used to calculate correlated random transition values (Akçakaya 1998). After matrix multiplication, ceiling-type density dependence is simulated by multiplying the resulting stage abundances by

$$K(t)/N_p, \quad [2]$$

where $K(t)$ is the maximum patch biomass, chosen randomly at each time step for each patch from a log-normal distribution with a fixed mean and standard deviation, and N_p is the patch biomass. Variation in maximum biomass is proportional to variation in transition values and represents the same environmental variation. Both parameters are varied to ensure that patches are subject to variation at all stages of growth. Canada thistle control follows population growth. Individual Canada thistle patches are controlled when they

exceed a threshold density, at which point a fixed percentage (representing the efficacy of the herbicide) of the biomass of the patch is removed.

Dispersal occurs among patches and is limited to the seed/seedling stage, reflecting an assumption that vegetative dispersal is important to the growth of individual patches but unimportant, relative to seed dispersal, in the creation of new patches. This assumption is most applicable to conservation tillage systems but may be questionable in tilled cropland, where movement by machinery may lead to rapid rates of vegetative dispersal (Donald 1990). Relaxing this assumption might be expected to have two principal effects: increasing dispersal within the field or changing the shape of the dispersal function. Although we evaluated the effects of elevated field dispersal, the scale of the patches in our model kept us from examining the extensive but short-distance movement that would be expected from vegetative dispersal.

Dispersal rates are nonrandom and based on distance according to the function

$$M_{ij} = q \exp\left(\frac{-D_{ij}^s}{r}\right), \quad [3]$$

where M_{ij} is the proportion of the population dispersing from patch i to patch j , D_{ij} is the distance between i and j , and q , r , and s are constants based on the dispersal ability of the species. Seeds that move beyond the edge of the field are lost, (i.e., these seeds are no longer part of the simulation). Following dispersal, the abundance of each patch is adjusted to account for emigration and immigration and then used as the initial abundance for the subsequent year.

Parameterization

Model parameters and bounds for sensitivity analyses were based on field data and values from the literature (Table 1). Where these were not available, parameters were hypothesized based on information from other species or from our understanding of the system. Bounds for sensitivity analyses reflect the degree of certainty in parameter estimates; where estimates are less certain, bounds are wider. Specifically, estimates of transition matrix elements were taken from field studies of Canada thistle in no-till corn (*Zea*

TABLE 1. Parameter estimates and upper and lower bounds used in sensitivity analyses.

Parameter ^a	Lower bound	Parameter estimate	Upper bound
Growth and density dependence ^b			
$t_{2,1}$ (seed set)	0.00103	0.103	1.03
$t_{1,2}$ and $t_{2,2}$ (seedling and plant growth, respectively)	1.3	2.22	15
Maximum biomass (shoots m ⁻²)	15	25	55
Environmental variation			
Coefficients of variation ($t_{2,1}$, $t_{1,2}$, $t_{2,2}$, maximum biomass)	0.25, 0.166, 0.125,	0.50, 0.33, 0.25, 0.25	1.00, 0.66, 0.50, 0.50
Correlation parameters (a, b, c)	1, 2, 0.5	1, 5, 0.5	1, 25, 0.5
Degree of correlation among neighboring populations (%)	20	53	88
Dispersal			
Dispersal parameters (q, r, s)		2, 0.7, 0.5	
Dispersal rates (relative to median)	/100	1	*10
Proportion of seeds migrating to each adjacent population (10 m)	0.000021	0.002183	
Field dispersal (relative to median dispersal rates)	0.01	1	

^a See text, Equations 1 and 3, respectively, for correlation and dispersal functions.

^b See Figure 2 for a description of growth rates.

TABLE 2. Dispersal distances for Asteraceae species with plumed achenes. Numbers preceded by “~” are estimated from figures.

Species	Seed fall (within distance)		Maximum dispersal distance (m)	Wind speed (km h ⁻¹)	Height of release (m)	Reference	Type of study
	(%)	(m)					
<i>Picris capillaris</i>	93	(~3.5)		6.9	0.4	Jongejans and Schippers 1999	Wind tunnel/model
	95	(4.37)		21.6	0.4		
	95	(14.31)		43.2	0.4		
<i>Crepis capillaris</i>	95	(~6)		21.6	0.4	Jongejans and Schippers 1999	Wind tunnel/model
<i>Senecio jacobea</i>	89	(5)	14	7–15	0–1.5	McEvoy and Cox 1987	Field
<i>Cirsium vulgare</i>	91	(1.5)			1	Michaux 1989	Field
<i>Arnica montana</i>	95	(3.75)	~6	23.4	0.35	Strykstra et al. 1998	Wind tunnel
	99	(5)		23.4	0.35		
<i>Heterotheca latifolia</i>			30	18.8		Plummer and Keever 1963	Field
			15	9.4			
<i>Cirsium arvense</i>						This study	Model
Lower bound	99.98	(10)					
Median	98.32	(10)					
Upper bound	83.20	(10)					

mays)–soybean [*Glycine max* (L.) Merr.] rotations (N. Jordan and S. Huerd, unpublished data). To model the effects of a large field margin population, we applied these transition values to the field margin population as well as the field population, thereby ensuring that field margin patches contained dense Canada thistle populations. Little is known about variation in weed demographic parameters over time. We therefore calibrated our model based on an observed coefficient of variation (CV) of Canada thistle abundance over time of 0.4 (Firbank 1993). To obtain this value in our model, a CV of 0.25 for plant growth had to be used. We hypothesize that seedling growth will vary 50% more than plant growth, because it is not buffered by root carbohydrate reserves, and that seed set will vary twice as much as plant growth based on generally higher variation in fecundities than survival rates reported in the literature (Charron and Gagnon 1991; Lesica and Shelly 1995; Moloney 1988). The resulting CVs of transition values are within the range of those reported for other species (Charron and Gagnon 1991; Ehrlen 1995; Horvitz and Schemske 1995; Lesica and Shelly 1995; Moloney 1988).

Maximum patch biomass is taken from a survey of Canada thistle shoot density in wheat (*Triticum aestivum* L.) fields (Donald and Kahn 1996). Maximum biomass of field margin patches was 55% of that of field patches, reflecting an assumption that some of the field margin would be occupied by plants other than Canada thistle. Although no information was available regarding the spatial correlation of growth rates, reasonably high levels of correlation might be expected based on the homogeneity of agricultural environments and climatic effects at the scale of an individual field. The high and low bounds of the correlation function parameters (Table 1) correspond, respectively, to 20% correlation and 88% correlation of growth rates between neighboring patches.

Canada thistle is wind dispersed. Although Canada thistle dispersal has not been studied directly, Sheldon and Burrows (1973) estimate its maximum dispersal distance to be 11.4 m, based on a measured terminal velocity of 21.6 cm s⁻¹ and a wind speed of 16.41 km h⁻¹. The dispersal patterns of other Asteraceae species with similar dispersal structures have been studied in more detail (Table 2). Given the rel-

atively low terminal velocity of Canada thistle achenes (Bakker 1960; Sheldon and Burrows 1973), one would expect it to be one of the more effective dispersers. Its dispersal ability may be limited, however, by a tendency for the pappus to break off, leaving the achene attached to the receptacle (Bakker 1960; Bostock and Benton 1979). Bakker (1960) found that only 9.9% of Canada thistle plumes collected 10 m from parent plants were attached to achenes. We have therefore chosen dispersal rates in the middle of the range observed for Asteraceae species (Table 2). Because of the large uncertainties inherent in measuring dispersal and the desire to encompass the dispersal characteristics of a variety of weed species, we have also chosen to vary the dispersal parameter widely in our sensitivity analyses. Our median, high, and low dispersal distances correspond to 1.7, 16.8, and 0.017%, respectively, of seeds dispersing beyond the boundaries of a parent patch (10 m or more). With median dispersal and growth rates, an average of 819 seeds move from a field margin patch to the adjacent field patch in a single time step; 30 seeds move from the same field margin patch to a patch 30 m away.

Model Output

Starting with the assumption that farmers will control Canada thistle populations in the field, the relevant measure of the importance of field margin populations is the effect these populations have on the effort farmers must expend to control field populations. The effect of field margins on necessary control efforts can be gauged by comparing models with and without dispersal from the field margin. We measured necessary control effort as the quantity of Canada thistle biomass that must be removed in order to keep the population below a threshold level (5 shoots m⁻²). Our primary dependent variable, Canada thistle biomass removed, is a measure of the degree to which the combined mass of the field patches exceeds the threshold mass. The lower the population growth during a particular time step, the less Canada thistle biomass must be removed. Canada thistle biomass removed is thus considered to be indicative of the rate or frequency of herbicide application needed to keep the population under control.

TABLE 3. Parameters specific to individual Canada thistle (*Cirsium arvense*) distribution scenarios.

Parameter	Complete occupancy			Invasion			Extinction		
	Lower bound	Median	Upper bound	Lower bound	Median	Upper bound	Lower bound	Median	Upper bound
Intensity of patch control (% of Canada thistle biomass removed)	25	65	85	25	65	85	25	50	75
Extinction probability	0	0	0	0	0	0	0	50	85
Distribution of initial abundance among patches	All field patches occupied			One field patch occupied			18 randomly chosen field patches occupied		
Initial abundance (mean number of shoots per occupied patch)	0.122	1.22	12.2	4.91	491	4,910	0.055	0.55	5.5

In addition to presenting the difference in necessary control effort between models with and without dispersal from the field margin, we gauge the relative worth of focusing control efforts on field margin Canada thistle vs. field Canada thistle by examining a third type of model, in which the control efforts that could have been applied to the field margin are instead applied to an area of the field of the same size. We thus compare three model types, all of which include patch control (i.e., the truncation of patch size at the infestation threshold [see Model Structure]). The first model type, *Patch Control*, includes no additional control and represents the situation in which the field margin is present, but no actions are taken to control it. In *Field Margin Control and Patch Control*, all dispersal from the field margin patches is cut off, representing control of field margin patches by herbicides or mowing. In the third type of model, *Field Control and Patch Control*, control efforts (which remove 50% of Canada thistle biomass in affected patches) are applied randomly to an area of the field equivalent to the area of the field margin (one-sixth of the field).

The assumption underlying the comparison of field control and field margin control models is that farmer effort may be approximated by area covered without reference to the type of control being applied. To test whether the results were sensitive to the spatial pattern of the field control, pattern was varied independently of the intensity of control. Two approaches were used: control of the entire field but with one-sixth the effectiveness of the field control, and control of the entire field once every 6 yr. Field Control and Patch Control is the only model type in which additional control efforts are applied within the field. To allow comparison of farmer effort following the three types of additional control represented by the three models, the field control portion of the harvest is not included in the Canada thistle biomass removed.

Sensitivity Analyses

Initial explorations of model behavior suggested that the relative effectiveness of these different control strategies depends on the number of unoccupied patches. As discussed in the introduction, three different scenarios of patch occupancy have corollaries in real weed populations and are potentially of interest. We therefore performed sensitivity analyses on all model parameters under three different assumptions about occupancy.

1. Complete occupancy. Extinction is rare enough that most patches are occupied at all time steps.

2. Invasion. Occupancy is low because the weed has not yet invaded.

3. Extinction. Occupancy is low because of frequent extinctions. Under this scenario, each local patch had a 0.125 chance of extinction each year, resulting, on average, in local extinction once every 8 yr. To reduce occupancy, it was also necessary to reduce dispersal among field patches; otherwise, field patches immediately recolonize extinct patches and occupancy is complete. Such a situation might arise from cropping systems that reduce seed production. Because lower dispersal results in lower growth rates, it was also necessary to lower the intensity of patch control to obtain a viable Canada thistle population under the extinction scenario.

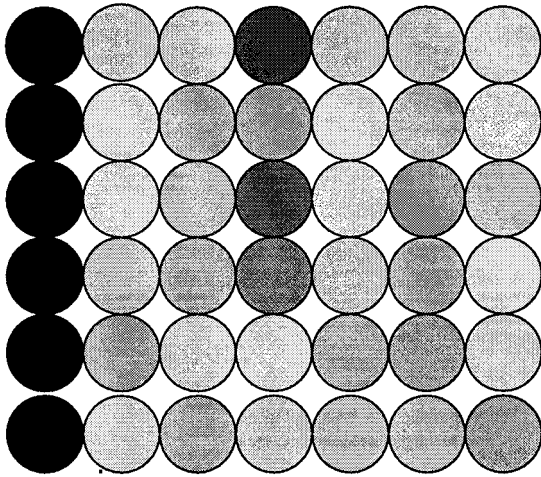
These three basic scenarios thus differ in terms of initial abundance/distribution, extinction rates, and the intensity of control efforts (Table 3; Figure 3). In sum, we performed sensitivity analyses on the relative merit of three different control strategies under each of three different occupancy scenarios. Sensitivity analyses involved varying parameters independently, within ranges based on the degree of uncertainty in each parameter estimate (Table 1). For each scenario, we present results only for those parameters that influenced the importance of the field margin.

Results

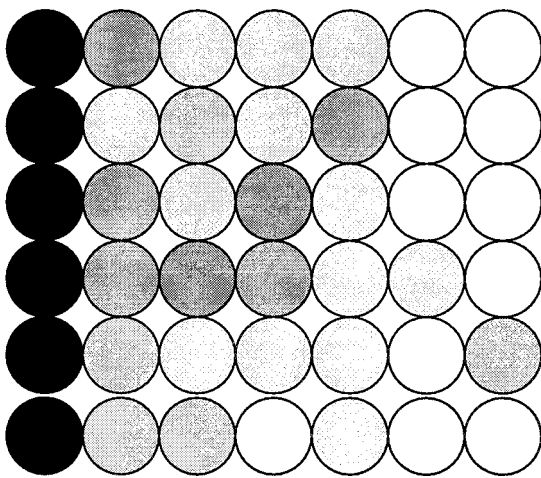
Basic Scenarios

When mean parameter values were used, the three different occupancy scenarios had similar results. Where occupancy is complete, seeds from the field margin populations had no discernible effect on the growth of the field populations, and control efforts applied to the field were most effective in reducing the necessary control effort (Figure 4; deterministic results for this simulation are presented in Appendix 1). Where occupancy is low because the weed has not yet invaded, necessary control effort increases as the weed invades the field. Dispersal from the field margin increases the speed of this invasion (and therefore the rate of increase in Canada thistle control), but only for a few years, after which the rate of invasion is similar with or without control of the field margin (Figure 5). The rate of invasion is slowest when control efforts applied to the edge are instead applied to the field (Figure 5). Finally, although random extinction reduces both the rate of increase in and the equilibrium levels of control effort (Figure 6), field margin control again does little to reduce necessary control efforts. These results are robust to changes in the spatial pattern of

A) COMPLETE OCCUPANCY



B) INVASION



C) EXTINCTION

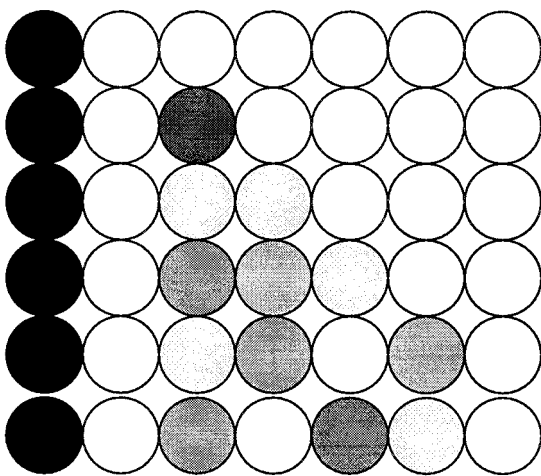


FIGURE 3. The model in action: examples of population densities after 12 yr under the three different occupancy scenarios. Field population densities of Canada thistle (*Cirsium arvense*) range from < 1 shoot m^{-2} (light gray)

control in the field control models. Control of the entire field once every 6 yr and annual control that is one-sixth as effective result in qualitatively similar patterns (results not shown).

Sensitivity Analyses

Complete Occupancy

In the complete occupancy scenario, the relative effectiveness of the three control strategies was not sensitive to variation in any of the model parameters (Figure 7).

Invasion

Sensitivity analyses of the invasion scenario revealed that there are conditions under which controlling field margin weeds greatly reduces necessary control effort in the field. Where weeds in the field have little dispersal ability of their own but weeds in the field margin have high dispersal rates (e.g., where control efforts reduce seed production in the field), seeds from the field margin can greatly speed the invasion process (Figure 7B). Under such conditions, control can be more effective when applied to the edge than when applied to the field. The difference in necessary control efforts between Patch Control and Field Margin Control models is most pronounced early in the invasion process. If dispersal rates are universally high or universally low, the presence of the field margin speeds the invasion only slightly, and control efforts applied to the edge are less effective than similar efforts applied to the field (Figures 5 and 7E).

The greater influx of seeds adjacent to the field margin can lead to a situation in which the field margin is important to weed patches at the edge of the field (Figure 8A), even where it is not important to the weed population as a whole (Figure 5). This edge effect declines sharply with distance from the field margin (Figure 8B), although this decline is less pronounced with higher dispersal rates (results not shown).

Extinction

As in the invasion scenario, the field margin is most important to field population growth when there is a large discrepancy between the dispersal abilities of the two populations; that is, where the field patches have little ability to recolonize extinct patches in their midst. In such situations, controlling field margin weeds can be more effective in reducing subsequent control efforts than similar amounts of control applied to the field (Figure 7C). If dispersal rates are equalized, however, either by increasing the field dispersal (Figure 6) or by decreasing edge dispersal (Figure 7F), the importance of the field margin population decreases, reducing in turn the effectiveness of control strategies aimed at field margin weeds.

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to more than 7 shoots m^{-2} (dark gray). Field margin population densities were 13.7 shoots m^{-2} . Simulations were run with median parameter estimates (Tables 1 and 3) and no control of field margin populations.

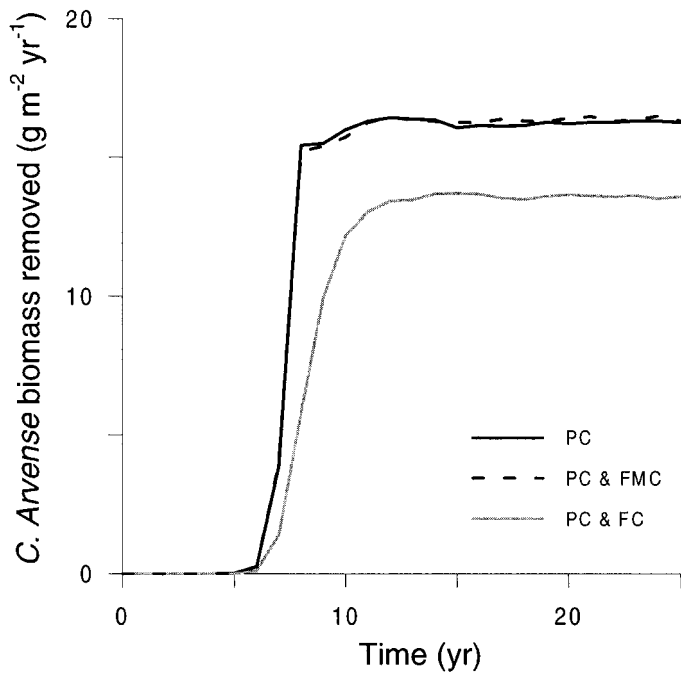


FIGURE 4. Patch control removal rates necessary to keep the field population at acceptable levels in the complete occupancy scenario. Patch control alone (PC) is compared to patch control plus field margin control (PC & FMC) or additional field control (PC & FC).

Discussion

Weed populations in field margins may sustain populations in adjacent fields (Marshall and Smith 1987; Theaker et al. 1995). Given the economic and environmental costs of weed control in nonarable land, however, it is important to practice such control only when it is effective in reducing weed populations within adjacent fields. Several hypotheses about when field margin weed control may or may not be effective can be drawn from our simulations.

Relative Dispersal Abilities of Field and Field Margin Weeds

Controlling field margin weeds was only advantageous (i.e., more effective than similar measures applied to the field) if weeds in the field margin had substantially higher dispersal rates than their counterparts in the field (Figures 7B and 7C). Where dispersal rates were universally high or universally low, immigrants to any given patch from the field margin were insignificant relative to the larger number from within the field (Figures 4–6 and 7d-f). Because dispersal declines rapidly with distance, the primary sources of immigrants for a given location are nearby patches rather than patches with high seed production. Field patches were closer to one another than they were to field margin populations, and this more than offset the much larger number of seeds produced in field margin populations. Although lower growth rates can limit seed production within the field, making immigrants from the field margin more important, this effect is counterbalanced by the associated decrease in growth potential for each immigrant.

Field margin populations become more important, however, as their dispersal rates (or seed set) increase relative to those of field populations (Figures 7a-c). Such discrepancies

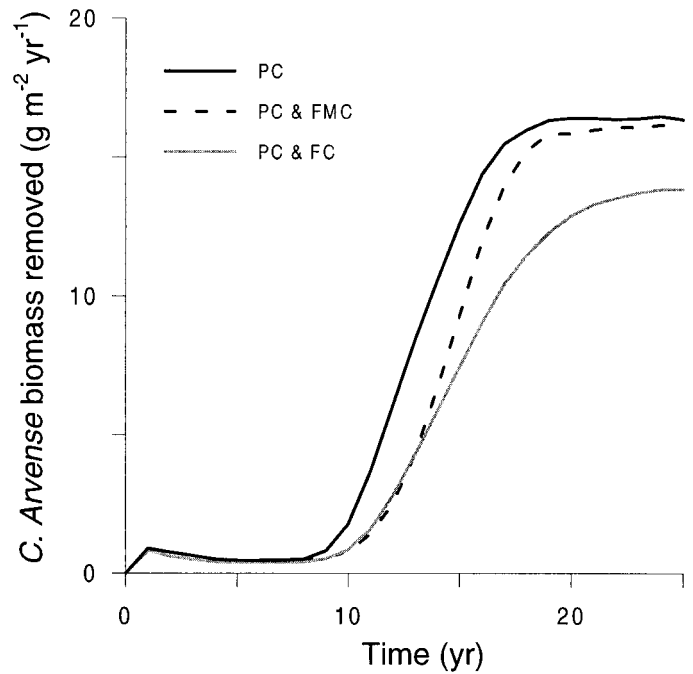


FIGURE 5. Patch control removal rates necessary to keep the field population at acceptable levels in the invasion scenario. Patch control alone (PC) is compared to patch control plus field margin control (PC & FMC) or additional field control (PC & FC).

in dispersal rates could arise from impediments to seed production or dispersal within the field (e.g., tall crops would limit wind dispersal). Conversely, for many species, dispersal may be facilitated by cultivation or combining (Howard and Cussans 1991; Rew and Cussans 1997), leading to higher dispersal rates within the field than between the field margin

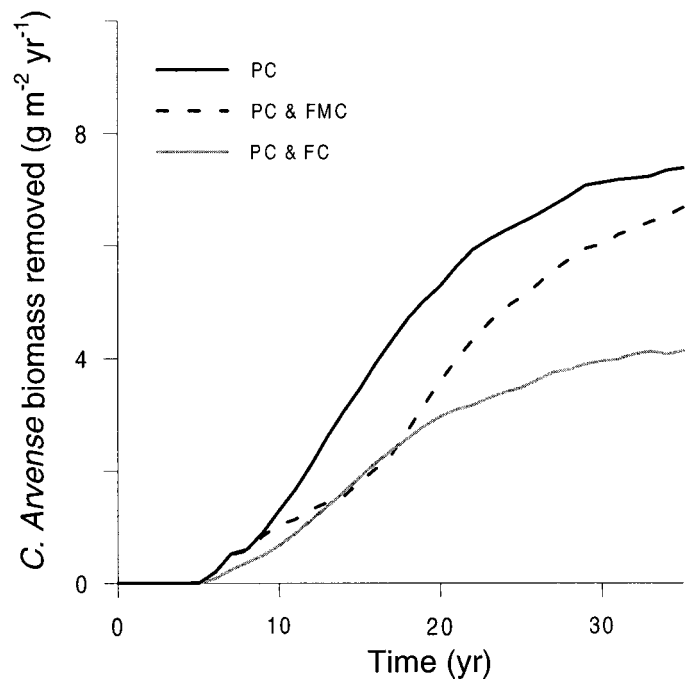


FIGURE 6. Patch control removal rates necessary to keep the field population at acceptable levels in the extinction scenario. Patch control alone (PC) is compared to patch control plus field margin control (PC & FMC) or additional field control (PC & FC).

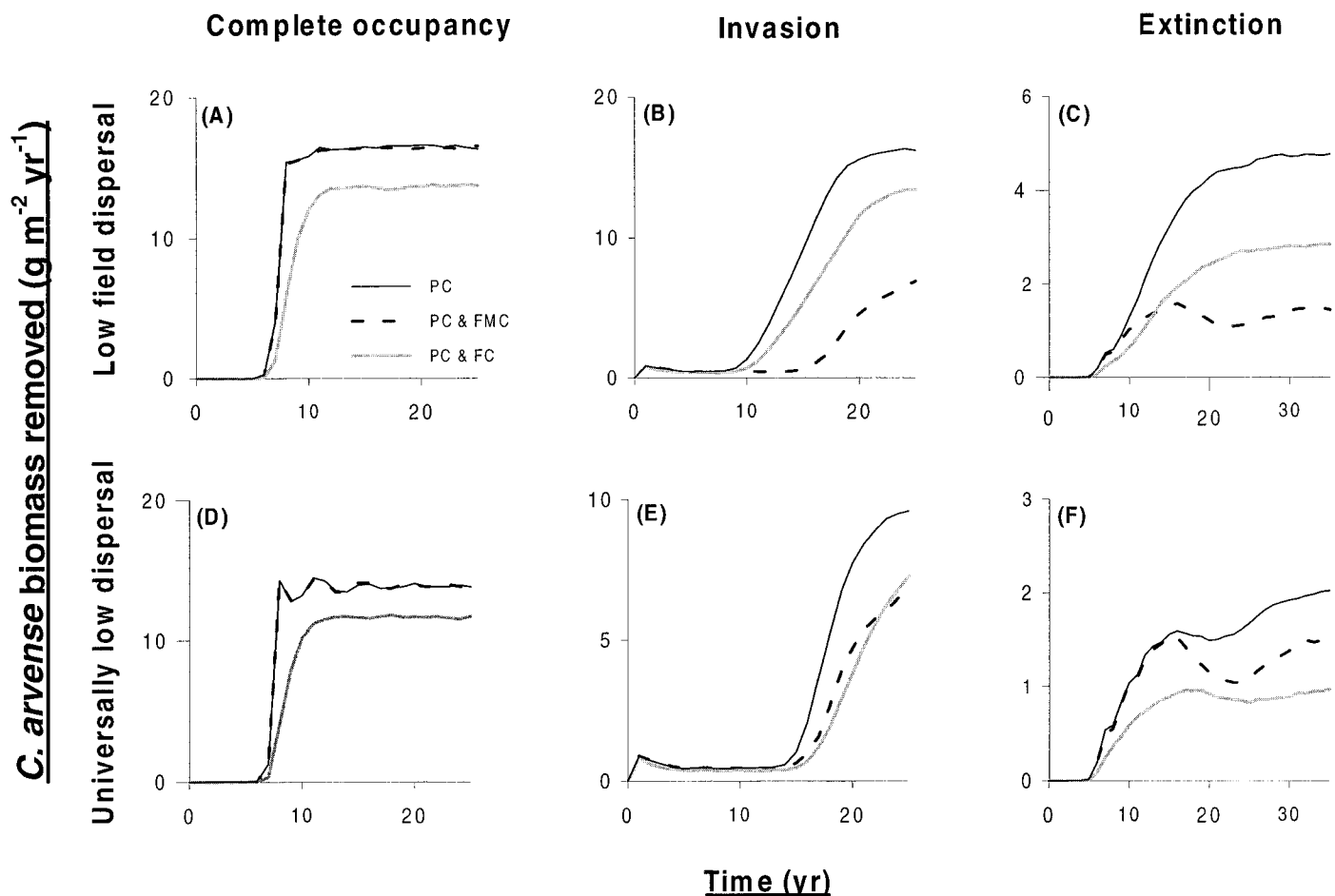


FIGURE 7. Necessary removal rates under the three different invasion scenarios with either low dispersal from field populations but high dispersal from field margin patches (a–c) or low dispersal rates in both field and field margin patches. Patch control alone (PC) is compared to patch control plus field margin control (PC & FMC) or additional field control (PC & FC).

and the field. Under such conditions, one would expect field margin weeds to have little effect on population dynamics within the field. The vegetative dispersal of Canada thistle, which can be facilitated by field operations, may be an example of this latter situation: high dispersal rates within the field would decrease the relative contribution of field margin patches to total immigration. The inclusion of vegetative dispersal in the model might therefore be expected to reduce the effect of field margin weeds on population dynamics within the field.

Habitat Occupancy

Given higher dispersal abilities of field margin weeds than field weeds, a second condition must be met for the field margin to have a substantial effect over a large portion of the field. Potential habitat for the weed in question must be unoccupied. This condition exists because very few seeds travel long distances. If those few seeds land in existing patches, their effect on growth will be negligible. Source-sink models suggest that, given sufficiently high rates of reproduction and dispersal, immigrants from the field margin could comprise a large portion of the weed population within the field (Kadmon and Shmida 1990; Quinn et al. 1993). Our results suggest, however, that Canada thistle dispersal rates are too low for these immigrants to act as a direct

subsidy to the field population. Rather, for immigrants from the field margin to substantially increase population size within the field, they must create new, growing patches.

At first glance, unoccupied habitat seems to be present for most weed species. Weeds are, in general, patchily distributed (Cardina et al. 1995; Marshall 1988; Mortensen et al. 1993; Wallinga 1995). A closer look, however, suggests that patchiness need not be indicative of unoccupied habitat and, consequently, that the cause of the patchiness may determine the importance of dispersal from the field margin. The three causes that have been suggested in the literature are represented by the three basic scenarios used in this model.

1. Weeds are patchy because much habitat is not suitable for population persistence.
2. Weeds are patchy because they have not yet fully invaded a field.
3. Weeds are patchy because they have gone extinct in some areas.

In the first case, habitat might be unsuitable because of underlying environmental conditions (e.g., weeds that exist only in wet areas of a field), patchy control efforts, or an interaction between the environment and control efforts (Dieleman et al. 1997). Insofar as environmental heterogeneity causes weed patchiness, the weed exists in all available

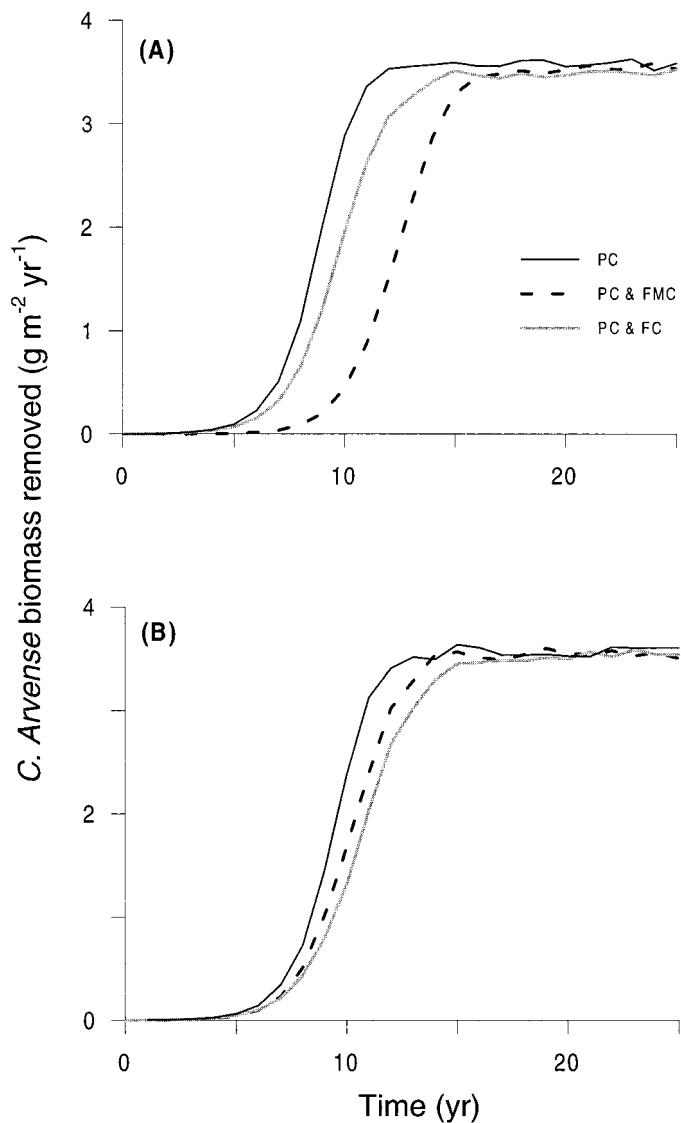


FIGURE 8. Patch control removal rates necessary to control Canada thistle (*Cirsium arvense*) patches 10 and 20 m from the nearest field margin patch (A and B, respectively). Patch control alone (PC) is compared to patch control plus field margin control (PC & FMC) or additional field control (PC & FC).

habitats. In our models, this situation is represented by the complete occupancy scenario, in which the field margin has no effect on the weed population dynamics in the field (Figures 4, 7A, 7D).

Conversely, where patchy distributions result from incomplete invasion or extinction, control of field margin weeds is potentially beneficial (Figures 7B and 7C). The invasion scenario represents any situation in which a weed is invading an area of favorable habitat that is large relative to its dispersal abilities. Such situations are not limited to the arrival of new weeds. They also include instances in which changing management practices make habitat more favorable to a weed already present within a limited area of the field. Our results suggest that the presence of field margin weeds can increase the speed of such invasions, resulting in (temporarily) large differences in the amount of weed control necessary to contain the invasion (Figure 7B).

Extinction in weed populations would be caused by tem-

poral variation in the environment (including control measures). A series of bad years or effective control efforts might cause local patches to go extinct. Inasmuch as extinction dynamics cause weed patchiness, the potential exists for field margin control to be beneficial on an ongoing basis (Figure 7C). This result is in accord with those of other metapopulation models (Levins 1969; Perry and Gonzalez-Andujar 1993; Tilman et al. 1997). As in these models, the importance of dispersal stems from its role in recolonizing extinct weed patches. Where field margin emigrants account for a large proportion of this recolonization, their presence can greatly increase equilibrium population size (Figure 7C).

In both the invasion and extinction scenarios, the size of the edge effect is very sensitive to the relative dispersal rates of the field and field margin populations (Figures 7E and 7F). Furthermore, although we were not able to model this situation, the importance of the field margin would also be expected to depend on the relative scales of extinction and colonization. If dispersal distances are small relative to the areas over which extinction occurs, the weed will be repeatedly faced with the invasion scenario, suggesting that the field margin could be important to population growth. As the scale of extinction decreases relative to that of dispersal, however, the limited dispersal ability of field weeds would be more effective in recolonizing extinct patches, and dispersal from the field margin would be less important in keeping potential habitat occupied.

Given the different results obtained under the complete occupancy, invasion, and extinction scenarios, it is worth considering to what extent each hypothesis might account for observed weed patchiness. Inasmuch as weed patches reflect patchiness in underlying environmental conditions, weeds occupy available habitat (the complete occupancy scenario). Spatial correlations between soil characteristics and weed populations suggest that a patchy environment may cause weed patchiness (Andreasen et al. 1991; Dieleman et al. 1997). Studies showing stability of weed patches over time are also in agreement with this hypothesis (Gerhards et al. 1997; Wilson and Brain 1991) but have not been conducted over time frames longer than 10 yr. Furthermore, a recent model of an annual weed has shown that stable patches can be generated randomly (Wallinga 1995), suggesting that such patches may not always reflect environmental heterogeneity.

Evidence for incomplete invasion as a cause of weed patchiness consists of direct observations of weed invasions (e.g., Chancellor 1985) and shifts in weed communities with changing management practices (Holzner and Immen 1982). Such observations do not provide us with insight into the relative importance of incomplete invasion. Given the frequency with which management practices change, however, and the slow speed at which invasions occur in this (Figure 5) and other models (Auld and Coote 1980; Fogelfors 1985; Maxwell and Ghera 1992), the invasion scenario could be quite common.

Evidence for extinction as a cause of weed patchiness is limited to the few studies that have tracked the persistence of weed populations over time. Patches have been found to be stable over 5 to 10 yr at the field scale (Gerhards et al. 1997; Wilson and Brain 1991) but to vary at either small spatial scales (Benoit et al. 1992) or large temporal scales (Chancellor 1985). It seems likely that each of the above

hypotheses accounts for some of the patchiness observed in weed populations. Determining their relative importance is an empirical task: one that is crucial to the advancement of our understanding of the spatial dynamics of weed populations.

Localized Edge Effects

Even if a weed appears from its distribution to be invading a field from the field margin, the actual effect of the margin may be limited to the edge of the field. Under conditions in which controlling the edge would do little to slow an invasion at the field scale (Figure 5), it could slow it substantially for those patches closest to the field margin (Figure 8). Similar results have been found with a simple analytical model of an annual weed (Fogelfors 1985).

That the importance of the field margin may be limited to the portion of the field adjacent to the edge is also suggested by empirical studies. Three studies of seed movement found only small numbers of seeds moving more than 7, 12.5, or 3 m into the field (Hume and Archibold 1986; Jones and Naylor 1992; Rew et al. 1996). Patterns of weed abundance also suggest limited movement of field margin weeds. Field margin weeds have been found to have elevated abundance only within the first 2 to 4 m of the field, and few of these apparent invaders are also important field weeds (Marshall 1989; Wilson and Aebischer 1995). Furthermore, even when important field weeds are particularly abundant in the field margin and decrease in abundance with distance into the field, it cannot be assumed that the field margin is "fueling" the persistence of the weed in the field (Cousens and Mortimer 1995). Rather, the extra seed input may simply be increasing the local abundance of a weed that would be common in the absence of the field margin population (Figures 5 and 8).

It has been suggested that few weed species thrive in both field margins and fields (Marshall 1989). For those species that do, this study suggests two conditions that appear to be necessary for field margin populations to influence field populations strongly: differential dispersal abilities and unoccupied but favorable habitat. For many weed species, therefore, the field margin may be of little consequence. It is particularly unlikely that the field margin would be important for weeds that disperse well in the field (e.g., species that are spread by combine harvesters or tillage). Exceptions to these generalizations might be expected following changes in management practices (the transition to no-till agriculture is a current example) and with weeds that disperse more effectively from the field margin than within the field. In such instances, controlling field margin weeds may prevent or slow weed population growth in the field.

The restricted number of instances in which field margin weeds are likely to be a problem suggests that it may be possible to reduce management of weeds in nonarable land without negative consequences in adjacent arable land. Recent work on the ability of diverse perennial plant communities to exclude weeds provides further grounds for optimism (Kleijn 1997; Knops et al. 1999; Smith and MacDonald 1992). Such plant communities might not only reduce the need for weed control within field margins, but also greatly increase the biological diversity of agricultural landscapes.

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Literature Cited

- Akçakaya, H. R. 1998. RAMAS GIS: Linking Landscape Data with Population Viability Analysis. Version 3.0. Setauket, NY: Applied Biomathematics. pp. 1–6.
- Andreasen, C., J. E. Jensen, and J. C. Streibig. 1991. Soil properties and plant nutrients affecting the occurrence of *Poa annua*, *Stellaria media* and *Viola arvensis* on arable land. Pages 395–402 in Brighton Crop Protection Conference—Weeds. Surrey, Great Britain: British Crop Protection Council.
- Auld, B. A. and B. G. Coote. 1980. A model of a spreading plant population. *Oikos* 34:287–292.
- Bakker, D. 1960. A comparative life history study of *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. Pages 185–200 in J. L. Harper, ed. *The Biology of Weeds*. Oxford, Great Britain: Blackwell Scientific Publications.
- Ballaré, C. L., A. L. Scopel, C. M. Ghersa, and R. A. Sanchez. 1987. The population ecology of *Datura ferox* in soybean crops: a simulation approach incorporating seed dispersal. *Agric. Ecosyst. Environ.* 19: 177–188.
- Benoit, D. L., D. A. Derksen, and B. Panneton. 1992. Innovative approaches to seedbank studies. *Weed Sci.* 40:660–669.
- Boatman, N. D. 1989. Selective weed control in field margins. Pages 785–794 in Brighton Crop Protection Conference—Weeds. Surrey, Great Britain: British Crop Protection Council.
- Bostock, S. J. and R. A. Benton. 1979. The reproductive strategies of five perennial Compositae. *J. Ecol.* 67:91–107.
- Cardina, J., D. H. Sparrow, and E. L. McCoy. 1995. Analysis of spatial distribution of common lambsquarters (*Chenopodium album*) in no-till soybean (*Glycine max*). *Weed Sci.* 43:258–268.
- Chancellor, R. J. 1985. Maps of the changes in the weeds of Boddington Barn field over twenty years (1961–1981). Yarnton, UK: Agricultural and Food Research Council Weed Research Organization Technical Rep. 84. pp. 1–38.
- Charron, D. and D. Gagnon. 1991. The demography of northern populations of *Panax quinquefolium* (American ginseng). *J. Ecol.* 79:431–445.
- Cousens, R. and M. Mortimer. 1995. *Dynamics of Weed Populations*. Cambridge, Great Britain: Cambridge University Press. pp. 237–238.
- Dieleman, J. A., D. A. Mortenson, and D. D. Buhler. 1997. Multivariate approaches for linking field-scale variability of soil properties and weed populations. *Weed Sci. Soc. Am. Abstr.* 37:46.
- Donald, W. W. 1990. Management and control of Canada thistle (*Cirsium arvense*). *Rev. Weed. Sci.* 5:193–250.
- Donald, W. W. and M. Kahn. 1996. Canada thistle (*Cirsium arvense*) effects on yield components of spring wheat (*Triticum aestivum*). *Weed Sci* 44:114–121.
- Ehrlén, J. 1995. Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. *J. Ecol.* 83:297–308.
- Firbank, L. G. 1993. Short term variability of plant populations within regularly disturbed habitat. *Oecologia* 94:351–355.
- Fogelfors, H. 1985. The importance of field edge as a spreader of seed-propagated weeds. Pages 178–189 in *The 20th Swedish Weed Conference*. Uppsala, Sweden: Department of Plant Husbandry and Research Information Centre, Swedish University of Agricultural Sciences.
- Gerhards, R., D. Y. Wyse-Pester, and G. A. Johnson. 1997. Characterizing spatial stability of weed populations using interpolated maps. *Weed Sci.* 45:108–119.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. A. Hanski and M. E. Gilpin, eds. *Metapopulation Biology: Ecology, Genetics, and Evolution*. San Diego, CA: Academic Press.
- Hastings, A. and S. Harrison. 1994. Metapopulation dynamics and genetics. *Annu. Rev. Ecol. Syst.* 25:167–188.
- Holzner, W. and R. Immonen. 1982. Europe: an overview of weed flora and vegetation. *Geobotany* 2:203–226.
- Horvitz, C. C. and D. W. Schemske. 1995. Spatiotemporal variation in

- demographic transitions of a tropical understory herb: projection matrix analysis. *Ecol. Monogr.* 65:155–192.
- Howard, C. L. and G. W. Cussans. 1991. The dispersal of weeds: seed movement in arable agriculture. Pages 821–828 in Brighton Crop Protection Conference—Weeds. Surrey, Great Britain: British Crop Protection Council.
- Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13:201–228.
- Hume, L. and O. W. Archibald. 1986. The influence of a weedy habitat on the seed bank of an adjacent cultivated field. *Can. J. Bot.* 64:1879–1883.
- Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* 41:402–410.
- Jones, N. E., and R.E.L. Naylor. 1992. Significance of seed rain from set aside. Pages 91–96 in J. Clarke, ed. *Set-Aside*. Surrey, Great Britain: British Crop Protection Council.
- Jongejans, E. and P. Schippers. 1999. Modeling seed dispersal by wind in herbaceous species. *Oikos* 87:362–372.
- Kadmon, R. and A. Shmida. 1990. Spatiotemporal demographic processes in plant populations: an approach and a case study. *Am. Nat.* 135:382–397.
- Keddy, P. A. 1981. Population ecology on an environmental gradient: *Ca-like edentula* on a sand dune. *Oecologia* 52:348–355.
- Kleijn, D. 1997. Species Richness and Weed Abundance in the Vegetation of Arable Field Boundaries. Ph.D. thesis, Wageningen University, Wageningen, The Netherlands.
- Knops, J., D. Tilman, N. M. Haddad, et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* 2:286–293.
- Lesica, P. and J. S. Shelly. 1995. Effects of reproductive mode on demography and life-history in *Arabis fecunda* (Brassicaceae). *Am. J. Bot.* 82:752–762.
- Levin, S. A. 1976. Population dynamics in heterogeneous environments. *Annu. Rev. Ecol. Syst.* 7:287–310.
- Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* 26:165–191.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15:237–240.
- Marshall, E.J.P. 1988. Field-scale estimates of grass populations in arable land. *Weed Res.* 28:191–198.
- Marshall, E.J.P. 1989. Distribution patterns of plants associated with arable field edges. *J. Appl. Ecol.* 26:247–257.
- Marshall, E.J.P. and B. D. Smith. 1987. Field margin flora and fauna: interaction with agriculture. Pages 23–34 in J. M. Way and P. W. Greig-Smith, eds. *Field Margins: Integrating Agriculture and Conservation*. Surrey, Great Britain: British Crop Protection Council.
- Maxwell, B. D. and C. Ghera. 1992. The influence of weed seed dispersion versus the effect of competition on crop yield. *Weed Technol.* 6:196–204.
- McEvoy, P. B. and C. S. Cox. 1987. Wind dispersal distances in dimorphic achenes of ragwort, *Senecio jacobaea*. *Ecology* 68:2006–2015.
- Michaux, B. 1989. Reproductive and vegetative biology of *Cirsium vulgare* (Savi) Ten. (Compositae: Cynareae). *N. Z. J. Bot.* 27:401–414.
- Moloney, K. A. 1988. Fine scale spatial and temporal variation in the demography of a perennial bunchgrass. *Ecology* 69:1588–1598.
- Mortensen, D. A., G. A. Johnson, and L. J. Young. 1993. Weed distribution in agricultural fields. Pages 113–124 in *Soil Specific Crop Management*. Madison, WI: American Society of Agronomy—Crop Science Society of America—Soil Science Society of America.
- Perry, J. N. and J. L. Gonzalez-Andujar. 1993. Dispersal in a metapopulation neighborhood model of an annual plant with a seedbank. *J. Ecol.* 81:453–463.
- Plummer, G. L. and C. Keever. 1963. Autumnal daylight weather and camphor-weed dispersal in the Georgia Piedmont region. *Bot. Gaz.* 124:283–289.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. *Am. Nat.* 132:652–661.
- Pulliam, H. R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45–69 in O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, eds. *Population Dynamics in Ecological Space and Time*. Chicago, IL: University of Chicago Press.
- Quinn, J. F., S. R. Ring, and L. W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Am. Zool.* 33:537–550.
- Rew, L. J. and G. W. Cussans. 1997. Horizontal movement of seeds following tine and plough cultivation: implications for spatial dynamics of weed infestations. *Weed Res.* 37:247–256.
- Rew, L. J., R. J. Froud-Williams, and N. D. Boatman. 1996. Dispersal of *Bromus sterilis* and *Anthriscus sylvestris* seed within arable field margins. *Agric. Ecosyst. Environ.* 59:107–114.
- Schippers, P., S. J. Terborg, J. M. Groenendaal, and B. Habekotte. 1993. What makes *Cyperus esculentus* (yellow nutsedge) an invasive species?—A spatial model approach. Pages 495–504 in Brighton Crop Protection Conference—Weeds. Surrey, Great Britain: British Crop Protection Council.
- Sheldon, J. C. and F. M. Burrows. 1973. The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. *New Phytol.* 72:665–675.
- Shigesada, N. and K. Kawasaki. 1997. *Biological Invasions: Theory and Practice*. New York: Oxford University Press. pp. 114–132.
- Shmida, A. and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58:20–55.
- Smith, H. and D. W. MacDonald. 1992. The impacts of mowing and sowing on weed populations and species richness in field margin set-aside. Pages 117–122 in J. Clarke, ed. *Set-Aside*. Farnham, Surrey, UK: The British Crop Protection Council.
- Strykstra, R. J., D. M. Pegtel, and A. Bergsma. 1998. Dispersal distance and achene quality of the rare anemochorous species *Arnica montana* L.: implications for conservation. *Acta Bot. Neerl.* 47:45–56.
- Theaker, A. J., N. D. Boatman, and R. J. Froud-Williams. 1995. Variation in *Bromus sterilis* on farmland: evidence for the origin of field infestations. *J. Appl. Ecol.* 32:47–55.
- Tilman, D., C. L. Lehman, and P. Kareiva. 1997. Population dynamics in spatial habitats. Pages 3–20 in D. Tilman and P. Kareiva, eds. *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton, NJ: Princeton University Press.
- Venable, D. L. and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131:360–384.
- Wallinga, J. 1995. The role of space in plant population dynamics: annual weeds as an example. *Oikos* 74:377–383.
- Weiner, J. and P. T. Conte. 1981. Dispersal and neighborhood effects in an annual plant competition model. *Ecol. Model.* 13:131–147.
- Wilson, B. J. and P. Brain. 1991. Long term stability of distribution of *Alopecurus myosuroides*, Huds. Within cereal fields. *Weed Res.* 31:367–373.
- Wilson, P. J. and N. J. Aebischer. 1995. The distribution of dicotyledonous arable weeds in relation to distance from the field edge. *J. Appl. Ecol.* 32:295–310.

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APPENDIX 1. Deterministic output of numbers of Canada thistle (*Cirsium arvense*) shoots and seeds after 25 yr using median parameter values (Tables 1 and 3) and Patch Control model type. Simulation included migration from the field margin and excluded variation in transition values and maximum biomass. During the 25th time step, 4.6 shoots m⁻² were harvested from field patches.

Population	Shoots	Seeds
(Column, row) ^a	m ⁻²	
1, 3 (field margin)	24.00	3,667
2, 3	2.83	1,164
3, 3	2.52	1,037
4, 3	2.46	1,012
5, 3	2.45	1,004
6, 3	2.44	1,001
7, 3	2.42	988
Average of all field patches	2.48	1,020

^a Refer to Figure 1 for populations corresponding to column and row numbers.