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Stacked Crop Rotations Exploit Weed-Weed Competition for Sustainable Weed Management

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Crop rotation has long been considered one of the simplest and most effective tools for managing weeds. In this paper, we demonstrate how crop rotations can be strategically arranged to harness a novel mechanism of weed suppression: weed-weed competition. Specifically, we consider how crop stacking, or increasing the number of consecutive plantings of a single crop within a rotation, can decrease the size of the weed seed bank, by forcing weeds to compete with each other in similar environments for longer periods of time, while still reaping the traditional benefits of crop rotation. Using an annual plant model, we investigate the theoretical effects of stacked crop rotations on weeds that have different life-history strategies and phenology. Our results show that when weeds compete within a season, stacking can reduce the weed seed bank compared to rotations without stacked crops. Although more research is needed to fully understand the effects of crop stacking on other aspects of the system, such as insect pests and diseases, our research suggests that crop stacking has the potential to improve weed suppression without additional inputs, and their associated costs and externalities. More generally, improving management by changing the temporal arrangement of disturbances is a novel, process-based approach that could likely be applied to other weed management practices, such as mowing and herbicide application, and which could involve mechanisms other than weed-weed competition. Leveraging this new application of existing ecological theory to improve weed management strategies holds great promise.

Key words: Autocorrelation, canola, disturbance, maize, Reciprocal-Yield Law, soybean, wheat.

Ecological theory can be used to develop cropping systems and inform weed management strategies. Effective management strategies can improve weed suppression and decrease reliance on traditional control tactics such as herbicides. There is also potential to reduce environmental impacts, increase provisioning of ecosystem services, and ultimately lead to a more sustainable agriculture. Community ecology research is relatively common in the weed science literature, and assembly theory has recently been applied to characterize weed community responses to different management practices and environmental conditions (Booth and Swanton 2002; Ryan et al. 2010; Storkey et al. 2010). Theoretical frameworks have advanced our knowledge and improved management strategies, though more work is needed before weed community dynamics can be effectively predicted and manipulated. Ecological theory has also contributed to the development of ecological weed management, which is focused largely on exploiting ecological phenomena to manage weed population dynamics and reduce weed-crop competition (Bastiaans et al. 2008; Liebman and Davis 2000; Liebman and Gallandt 1997; Liebman and Staver 2001). Here, we build on recent theoretical research on the role of disturbance in maintaining species diversity and describe a novel, and often overlooked, mechanism of weed suppression that can be leveraged to improve cropping system sustainability: weed-weed competition. Weed-weed competition arises when weeds affect each other (via inter- or intraspecific competition) within the crop matrix; leveraging this weed-weed interaction can allow for better weed control overall.

Pickett and White (1985) define a disturbance as ''any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.'' By this definition, the production of a crop in an agroecosystem, including the biological effects of the crop as well as any ancillary management activities, may be considered a type of disturbance to weed populations. Since the work of Pickett and White, many steps have been

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Table 1. Illustration of stacking number for the maize-soybean-wheat crop rotation. Note that each crop appears the same number of times on average over a 12-yr period, but that the autocorrelation differs for the different stacking numbers.

Stacking number	Rotation length	Crop sequence[a]
S	yr	
1	3	M-S-W-M-S-W-M-S-W-M-S-W
2	6	M-M-S-S-W-W-M-M-S-S-W-W
4	12	M-M-M-M-S-S-S-S-W-W-W-W

[a] Abbreviations: M, maize; S, soybean; W, wheat.

taken toward understanding the role of disturbance in species coexistence. For example, several coauthors of this paper have explored different mechanisms of coexistence (Miller and Chesson 2009) and the importance of considering multiple aspects of the disturbance regime such as intensity, frequency, and timing (i.e., seasonality) (Miller et al. 2011; Miller et al. 2012a,b; Roxburgh et al. 2004; Shea et al. 2004; Zhang and Shea 2012). Using a simple annual plant model that accounts for reductions in fecundity from increased density, Garrison et al. (2012) demonstrated that manipulating the temporal autocorrelation of disturbance occurrences could be used to control population densities in plant communities without increasing management costs. Briefly, temporal autocorrelation is a measure of the similarity of a variable measured at consecutive times (e.g., successive cultivation of the same crop, which affects plant competition). We expand on this previous work and explore the potential for weed suppression from manipulating the autocorrelation of disturbance caused by the production of crops in a rotation. In our model, the crop acts as a disturbance to the weeds. Thus, planting the same crop for multiple years increases the autocorrelation of the cropping process, relative to changing crops every year, even if on average the same number of crops is present for the same amount of time over the long term (see Table 1 for an example).

Crop rotation has long been considered a powerful tool for managing weeds. For example, Leighty (1938) (quoted in Gallandt 2009) stated: ''Rotation of crops…is the most effective means yet devised for keeping land free of weeds. No other method of weed control, mechanical, chemical, or biological, is so economical or so easily practiced as a well-arranged sequence of tillage and cropping.'' From an ecological perspective, the effectiveness of rotating crops stems from the fact that dissimilar crops have different ecological niches and impose diverse stresses and mortality factors, reducing the ability of weed communities to adapt and populations to expand (Liebman and Staver 2001). For organic growers, or in situations where control tactics are limited (e.g., vegetable production) or are no longer effective (e.g., farms with herbicide resistant weeds), implementing strategic crop rotations can be a practical, process-based cultural weed management practice that reduces the need for direct control tactics such as cultivation and herbicides. For example, Davis et al. (2012) compared a maize (*Zea mays* L.)-soybean [*Glycine max* (L.) Merr.] rotation (2 yr), a maize-soybean-small grain/red clover (*Trifolium pratense* L.) rotation (3 yr), and a maize-soybean-small grain/alfalfa (*Medicago sativa* L.) rotation (4 yr) in a 9-yr field experiment in Iowa and found that weed suppression was similar despite herbicide inputs being six to 10 times lower in the 3- and 4-yr rotations compared to the 2-yr rotation. As Mohler (2009) stated: ''Rotation planning is a key way organic growers can substitute brain power for labor and purchased inputs.''

Previous research has illustrated the weed suppression benefit of diversifying crop rotations with weed suppressive or ''cleaning'' crops such as cereals or alfalfa. Westerman et al. (2005) used matrix models to compare weed population dynamics in a 2-yr (maize-soybean) and reduced-input 4-yr (maize-soybean-triticale [× *Triticosecale* Wittmack]-alfalfa) crop rotation and showed that despite only 18% of the herbicide input of the 2-yr rotation, population growth of a common summer annual weed could be nearly halted in the 4-yr rotation because of increased stressors and mortality factors. Numerous empirical studies also support the notion that diversifying crop rotations with cereal crops decreases summer annual weed populations (e.g., Doucet et al. 1999; Schreiber 1992). One criticism of this approach is that weed suppressive crops such as cereals are typically less profitable than maize or soybean, and thus diversifying crop rotations with these crops can reduce short-term profitability. However, altering the sequence of a particular set of crops would have minimal impacts on profitability, and could have a profound effect on weed population dynamics, in part due to soil weed seed bank legacy effects (Eyre et al. 2011; Ryan et al. 2010). For example, Doucet et al. (1999) reported greater weed populations in plots where maize was grown the previous year compared to where soybean or wheat were grown. Similarly, Anderson (2005, 2009) observed the weed suppression benefits of two cool season and then two warm season

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crops in a long-term field experiment in the Central Great Plains. Using a simulation model, Anderson (2004) demonstrated the weed suppressive effect of a strategic crop rotation sequence of two warm season crops followed by two cool season crops. The mechanistic basis for enhanced weed suppression from this crop rotation is related to the rapid loss of viable seed in the soil weed seed bank during the first 2 yr after seed rain. Thus, by preventing summer annual weed seed additions to the soil seed bank for 2 yr, summer annual weed populations quickly decrease, with the same effect occurring for winter annual weeds during the opposite phase of the rotation.

In this paper, we present a heuristic theoretical model to illustrate a different, yet complementary, mechanism of weed suppression that can be influenced by strategically sequencing crops in a rotation. We demonstrate the role of weed-weed competition and investigate the potential applications of manipulating autocorrelation via changing crop rotation patterns. To many, utilizing weed-weed competition as a management tactic may seem academic or impractical because of the underlying assumption that weeds are present at sufficient levels that they compete with one another. However, this concept has been suggested for its potential role in sustainable weed management (Munier-Jolain et al. 2002), and may be particularly relevant in organic cropping systems where weeds tend to be more abundant (McCloskey et al. 1998). Recent empirical research has also shown how disturbance timing can influence weed-weed competition and mediate weed community composition in no-till planted soybean (Nord et al. 2012).

A relatively simple way to manipulate autocorrelation is to change the number of consecutive plantings of a single crop before switching to the next crop in the rotation—a practice known as crop stacking (Derksen et al. 2002). Table 1 lists several stacked rotations and illustrates how increasing stacking number increases autocorrelation. Generally, more environmental variation tends to allow multiple species to coexist, because no one species can dominate in many different environments (Chesson 2000). With stacked rotations, the environment within which weeds compete changes less frequently, hence weed-weed competition intensifies, leading to a decline in overall weed density. Moreover, despite limited research, stacked crop rotations (e.g., maize-maize-soybean-soybean-wheat-wheat) have been discussed at grower meetings and promoted in trade magazines (e.g., Hagny 2001). Beck (2003) described stacked rotations as a way to confuse pests and introduce diversity without necessarily introducing new crops and has reported that two consecutive plantings can lead to improved agronomic and economic outcomes. Expanding upon this work, we consider rotations with two or more consecutive plantings of a single crop species, and define the number of these consecutive plantings as the "stacking number" of the rotation.

Materials and Methods

Model. To determine the effects of stacking number on weed density, we developed an annual plant model, derived from the Reciprocal Yield Law (Ellner 1985; Miller et al. 2011; Shinozaki and Kira 1956). The law assumes an inverse relationship between population density of mature weeds in the community and weed seed yield. This assumption is a highly simplified description of plant competition, but it has strong predictive power in many diverse real systems (Maxwell and O'Donovan 2007; Radosevich 1987). High seed yields result in high degrees of competition among seedlings, which ultimately leads to reduced adult fecundity. The strength of this inverse relationship is represented by a competition term, α_{jk}. A high value of this parameter represents weed *k* seeds being strong competitors against weed *j* seeds.

Our model incorporates three life history parameters: seed bank survival rate (s), germination rate (G), and seed yield (Y). Our model of seed bank survival leads to decay of the seed bank over time, though the germination rate G does not decrease with an individual seed's age. In our implementation of the model, Y has units number of seeds m^{-2}. Using a standard notation, we let X_{jt} represent the number of seeds of weed species *j* at time *t* in the weed seed bank. We define $X_{j,\ t+1} = \lambda_{jt}X_{jt}$, where λ_{jt} (here, the "growth rate") is defined by

$$\lambda_{jt} = \left(1 - G_j\right)s_j + \frac{G_j Y_j D_{jt}}{C_{jt}}.$$

C_{jt} represents the effect of competition and is defined as

$$C_{jt} = \alpha_{jj}G_j X_{jt} + \alpha_{jk}G_k X_{kt}.$$

From an ecological perspective, this equation describes the impact on species *j* of all germinating weeds in a given year, adjusted by the competition parameters α_{jk}. Note that the coefficient of the first term, α_{jj}, represents the effect of intraspecific

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competition, as our model allows for both intra- and interspecific weed-weed competition, at different strengths. Also, our model assumes that all seeds germinate at the same time, soon after crop planting, though warm season and cool season weeds emerge at different times. Finally, D_{jt} represents the decrease in seed yield of weed species j at time t due to disturbance caused by a certain cropping system, and is explained in detail below.

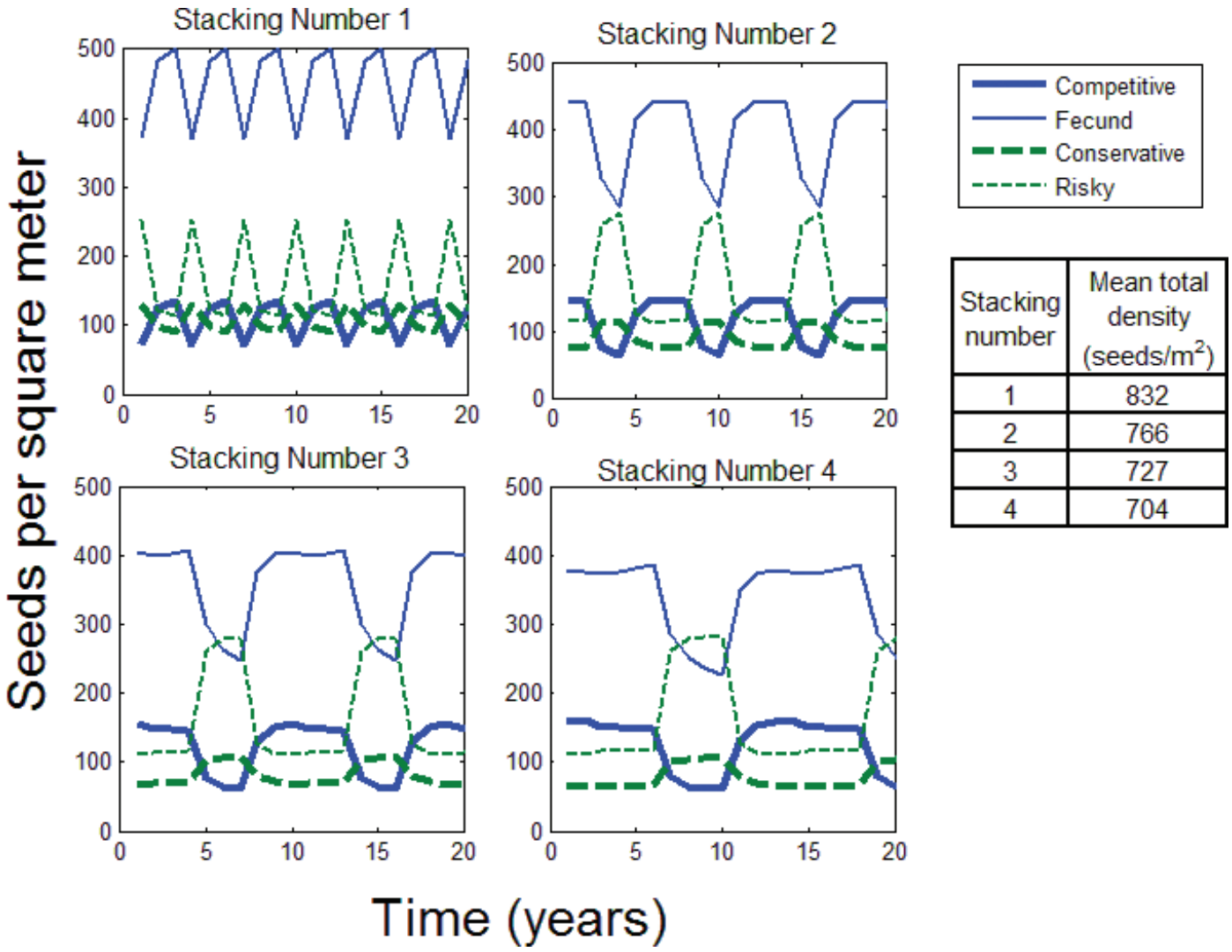
Disturbance Process. Weed life cycles are disturbed by the impacts that come with crop production. In this case, the disturbance is caused by a combination of effects including physical effects such as primary tillage to prepare seed beds, cultivation or herbicide applications that directly target weeds, and harvesting operations and biological effects such as competition from the crop. All these processes can adversely affect the seed yield of weed species. In this paper, we consider three specific crop rotations: soybean-wheat (S-W: one warm season crop and one cool season crop), maize-soybean-wheat (*Triticum aestivum* L.) (M-S-W: two warm season crops and one cool season crop), and maize-soybean-wheat-canola (*Brassica napus* L.) (M-S-W-C: two warm season crops and two cool season crops).

We examine the effects of these different crop rotations on an example community of four weed species, which we name according to the strategies described by their life history traits: "competitive," "fecund," "conservative," and "risky." The parameters for our example weed community are for illustrative purposes and do not represent specific species. The presence of seeds of the competitive species has a strong, negative impact on the ability of seeds of the fecund species to survive to maturity, while the fecund species has a much higher seed yield. Giant ragweed (*Ambrosia trifida* L.) is an example of a competitive species that is capable of reducing soybean yield by 52% from just 1 individual m^{-2}, whereas horseweed [*Conyza canadensis* (L.) Cronq.] is an example of a fecund species that is capable of producing 200,000 seeds $plant^{-1}$ (Davis et al. 2005). The conservative strategy represents a species with a low germination rate and high seed bank survival, indicating that its population is less sensitive to disturbance caused by crop production. Common chickweed [*Stellaria media* (L.) Vill.] is an example of a conservative species with 50% of seeds persisting in the soil seedbank after 3 yr (Davis et al. 2005). On the contrary, the risky species has low seed bank survival and high germination rate, which lets it capitalize on "good" years (from the point of view of resource availability for the weed), though it suffers more damage from crop competition. Downy brome (*Bromus tectorum* L.) is an example of a risky species with germination that can be reduced from 99 to 2% after just 1 yr of burial in soil (Burnside et al. 1996). For purposes of illustration, we assume that the competitive and fecund weeds grow in the summer, while the conservative and risky weeds grow during the winter. In principle, these strategies can be manifest in any season, but we present our main results in terms of this fixed example community.

The disturbance regime in our model is controlled by two types of parameter: Stacking number (S) and the intensity of damage inflicted by crop c on weed j (I_{cj}). The stacking number is equal to the number of consecutive plantings of a single crop before moving to the next distinct crop in the rotation. To illustrate the concept of stacking, we show the disturbance regime of a maize-soybean-wheat crop rotation for stacking numbers one through four in Table 1.

The intensity (I_{cj}) is defined as the proportion by which the seed yield (of weed j) is reduced by the disturbance (crop c). As described earlier, this is a measure of the response of weed species (in terms of seed yield) to all features of the cropping system. The value of the intensity largely depends on the phenology of the weeds and crops. Previous research on the effects of crop rotations has shown that integrating cool season crops (e.g., winter wheat) into a rotation dominated by warm season crops (e.g., maize and soybean) can effectively reduce summer annual weeds (Anderson 2009). This is because different crops provide different opportunities for weeds, and in this case warm season crops provide opportunities for warm season weeds and vice-versa. Thus, the same disturbance does not affect all weeds uniformly, and the intensity can be different for each weed and crop pair. This assumption has been well supported empirically from some crop-weed pairs, though parameter values are unknown for many crop systems and weed pests (Clay et al. 2005). Finally, crop disturbance is defined as $D_{jt} = (1-I_{cj})$, where I_{cj} is dependent on the type of crop planted at time t. Thus, D_{jt} reduces the seed yield of weed j by I_{cj} percent. For the purposes of illustrating the benefits of crop stacking, our parameters are chosen to reflect damage to weeds by cropping practices but do not reflect extreme weed suppression that would result from high rates of pesticide use. Additionally, I_{cj} parameters were chosen to reflect that fact that cool season crops have a stronger effect on warm

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Stacking number	Mean total density (seeds/m^2)
1	832
2	766
3	727
4	704

Figure 1. Steady state dynamics of the number of seeds per square meter (10 cm depth) vs. time for the competitive, fecund, conservative, and risky species under a maize-soybean-wheat rotation for stacking numbers one through four. As the stacking number increases, the mean total density of the weed population decreases. The largest marginal decrease occurs moving from stacking number one to stacking number two. (Color for this figure is available in the online version of this paper.)

season weeds, relative to cool season weeds. A list of model assumptions is included in Table A1 in the online appendix.

Analysis Methods. We use MATLAB to simulate this model for the three crop rotations listed earlier for stacking numbers one through four for 1,000 yr. Total mean number of weed seeds (to which we refer as density, for brevity and as this is a nonspatial model) is calculated by averaging the total yearly densities from time step 400 to time step 1,000 (to eliminate the effect of transient dynamics).

Results and Discussion

In our four weed species example community, increasing the stacking number of a maize-soybean-wheat crop rotation from one to four while holding all other components of the model constant decreases the total number of weed seeds by 15% (Figure 1). The figure also shows that stacking does not qualitatively change weed community composition; species ranking according to mean density is unchanged. However, stacking increased the maximum density of the risky species. This creates more competition for the fecund species, resulting in a decrease in the total mean weed density (Figure 1). While this decrease in the seed bank (15%) is not large from an absolute perspective, it can be part of a "many little hammers" approach to weed management, as described by Westerman et al. (2005).

This trend is not unique to the maize-soybean-wheat crop rotation; it also occurs with the shorter soybean-wheat and longer maize-soybean-wheat-

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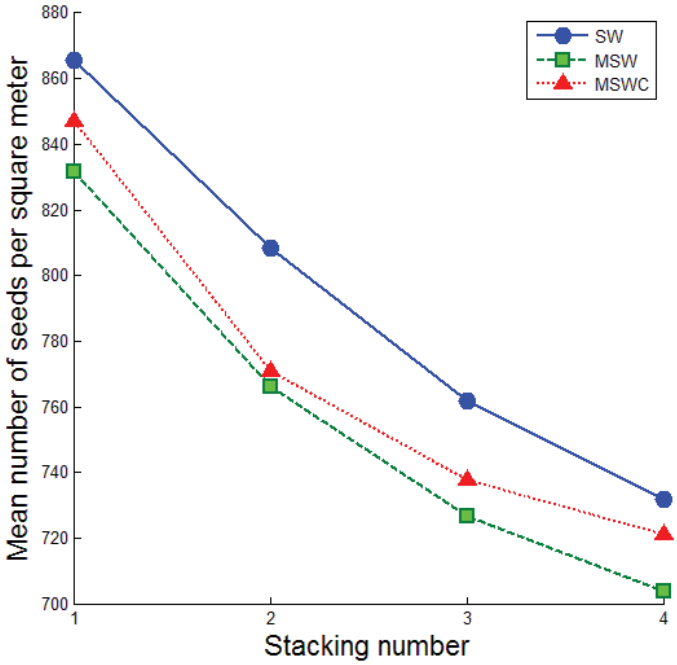


Figure 2. Mean total number of weed seeds per square meter for stacking numbers one through four for the soybean-wheat, maize-soybean-wheat, and maize-soybean-wheat-canola rotations. Increasing the stacking number decreases the total number of weeds in the seed bank regardless of the type of rotation. For all three rotation types, the greatest marginal benefit occurs when changing from stacking number one to stacking number two. (Color for this figure is available in the online version of this paper.)

canola rotations (Figure 2). In all cases, increasing the stacking number decreases mean total number of weed seeds in the seed bank. It is interesting to note that the largest benefit of stacking occurs with a change from a stacking number of 1 to 2. Across all rotations, changing from a single stack to a double stack (e.g., soybean-wheat to a soybean-soybean-wheat-wheat) results in a larger decrease in weed seed density than changing from a double stack to a triple stacked rotation, and so on.

To understand why stacking reduces weeds in our model, we consider the maize-soybean-wheat crop rotation with three subsets of our four weed community: competitive and fecund (two warm season weeds), conservative and risky (two cool season weeds), and fecund and risky (one warm season weed and one cool season weed). In cases where the weeds have the same seasonality, increasing the stacking number can decrease the mean total number of seeds for the weeds (Figures 3A and 3B). However, this relationship is lost when weeds do not grow during the same season (e.g., one warm season weed and one cool season weed, regardless of the weed strategy). In this case, increasing the stacking number has no bearing on mean total density (Figure 3C). Thus, these results show that interspecific competition among weed species is crucial to the weed-reducing impact of stacking crop rotations in our simulation.

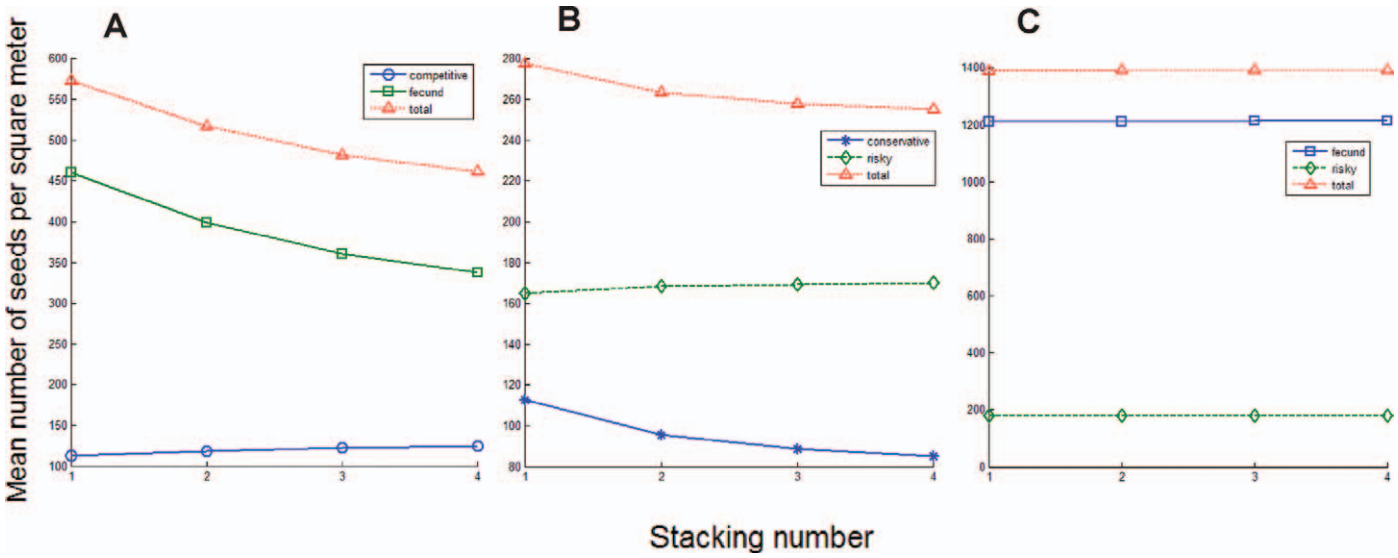


Figure 3. The four-species weed community is broken down into three subsets of two species each. Panels show (A) the competitive and fecund weeds, (B) the conservative and risky weeds, and (C) the fecund and risky weeds. For each subset, the mean total number of seeds per square meter and the mean number of seeds per square meter for each individual species is plotted for stacking numbers one through four. The rotation type is maize-soybean-wheat. In panels (A) and (B), the two weeds are of the same seasonality. In these cases, increasing the stacking number can decrease the mean total weed density. In panel (C), the two weeds are not of the same seasonality. In this case, stacking has no effect on weed density. Thus, interspecific competition among weed species is vital to the success of reducing weed density with stacked crop rotations. (Color for this figure is available in the online version of this paper.)

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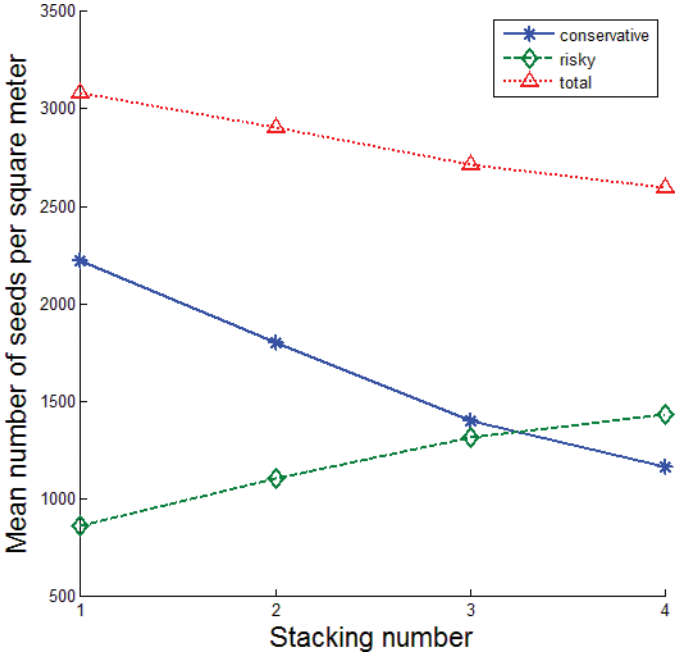


Figure 4. Using a more extreme parameter set (i.e., "more conservative" and "more risky"), the mean total number of seeds per square meter and the mean number of seeds per square meter for each individual weed species are plotted for stacking numbers one through four. The rotation type is maize-soybean-wheat. Under these more extreme parameters, the mean total weed density decreases at a faster rate (contrast with Figure 3b). (Color for this figure is available in the online version of this paper.)

If we consider a different hypothetical species set, with life-history strategies marked by more extreme parameter values, we observe more dramatic results (Figure 4). For example, we evaluated the effect of life-history trait strength by changing parameters to make our conservative and risky species more extreme exemplars of those life history strategies (a complete list of parameter values for all simulations can be found in Table 2 for easy comparison). Under these more extreme parameters, mean total abundance decreases at a faster rate as stacking number increases. Furthermore, the relative mean density of each species switches at higher stacking numbers; as the stacking number increases the risky species density exceeds that of the conservative species. This may be especially important if one weed species causes more damage than the other, or is difficult to control by other means (e.g., due to herbicide resistance). In this example, if the conservative species is a more damaging weed than the risky species, stacking is doubly useful: it decreases the total mean density and specifically targets the most detrimental weed. With extreme weed parameters, we also observed an interaction between stacking and crop rotation on weed suppression. For stacking numbers one and two, the soybean-wheat crop rotation resulted in the lowest mean total weed seed density (Figure 5). However, for stacking numbers three and four, the maize-soybean-wheat-canola rotation resulted in the lowest weed density (Figure 5).

Given that our findings are based on a simulation model, and not empirical evidence, careful interpretation that considers our assumptions and the limitations of crop stacking is important. As outlined in Table A1, there are a number of assumptions inherent to our model that may magnify the importance of weed-weed competition relative to other mechanisms of weed suppression (such as shifts in crop phenology and timing of management practices). Furthermore, crop production problems can arise when a single species is planted consecutively on a plot of land, such as increased risk of crop insect pests and disease and decreased soil health. Our model does not consider these issues, which means that the approach may have reduced benefit for high stacking numbers (S); for this reason, and because higher stacking numbers are unlikely to be economically robust, we restrict our stacking to a maximum of four. Additionally, our results show unequivocally that the greatest marginal benefit comes at low stacking numbers; changing from 1 to 2 yr of a certain crop perforce changes the autocorrelation more than changing from two to three stacks, so a stacking number of five would have very little benefit over a stacking number of four. Although we used a specific set of parameters to generate these results, our model shows that stacking is effective for many different assumptions on crop and weed parameters, which cover a wide range of weed life-history strategies (see online appendix, Figures A1 and A2). Additionally, our results suggest that crop stacking can reduce the weed seed bank for a large variety of seed densities, because Figures 1–5 cover an entire order of magnitude of seed densities. We also note that our model is sensitive to changes in crop intensity (I) (Figure A3). As crop intensity encompasses all aspects of the disturbance regime, not only the competition from crops, managers may be able to manipulate intensity by integrating physical or chemical disturbances, as well as biological factors such as crop planting density. For instance, it has been shown empirically that spatially uniform, high density cropping systems may suppress weed density (Olsen et al. 2012; Weiner et al. 2010), and this can be accounted for by suitably changing intensity parameters in our model. Finally, for some weed species that have low inter- and intraspecific

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Table 2. Parameter values for all model simulations presented.

Figure	Rotation	Weeds present	Seed yield	Seed bank survival rate	Germination rate	Competition parameters	Intensity parameters[a] I			
							M	S	W	C
			Y, seeds m^{-2}	s	G	α				
1	M-S-W	Competitive	210	0.85	0.85	$\begin{bmatrix} 1.00 & 0.85 & 0.01 & 0.01 \\ 0.70 & 1.00 & 0.01 & 0.01 \\ 0.01 & 0.01 & 1.00 & 0.45 \\ 0.01 & 0.01 & 0.40 & 1.00 \end{bmatrix}$	0.20	0.25	0.65	
		Fecund	900	0.60	0.10		0.22	0.23	0.67	
		Conservative	300	0.70	0.20		0.70	0.65	0.25	
		Risky	360	0.20	0.70		0.68	0.67	0.23	
2	S-W	Competitive	210	0.85	0.85	$\begin{bmatrix} 1.00 & 0.85 & 0.01 & 0.01 \\ 0.70 & 1.00 & 0.01 & 0.01 \\ 0.01 & 0.01 & 1.00 & 0.45 \\ 0.01 & 0.01 & 0.40 & 1.00 \end{bmatrix}$	0.20	0.25	0.65	0.67
	M-S-W	Fecund	900	0.60	0.10		0.22	0.23	0.67	0.65
	M-S-W-C	Conservative	300	0.70	0.20		0.70	0.65	0.25	0.20
		Risky	360	0.20	0.70		0.68	0.67	0.23	0.22
3a	M-S-W	Competitive	210	0.85	0.85	$\begin{bmatrix} 1.00 & 0.85 \\ 0.70 & 1.00 \end{bmatrix}$	0.20	0.25	0.65	
		Fecund	900	0.60	0.10		0.22	0.23	0.67	
3b	M-S-W	Conservative	300	0.70	0.20	$\begin{bmatrix} 1.00 & 0.45 \\ 0.40 & 1.00 \end{bmatrix}$	0.70	0.65	0.25	
		Risky	360	0.20	0.70		0.68	0.67	0.23	
3c	M-S-W	Fecund	900	0.60	0.10	$\begin{bmatrix} 1.00 & 0.01 \\ 0.01 & 1.00 \end{bmatrix}$	0.22	0.23	0.67	
		Risky	360	0.20	0.70		0.68	0.67	0.23	
4	M-S-W	Conservative	3,000	0.70	0.20	$\begin{bmatrix} 1.00 & 1.50 \\ 0.50 & 1.00 \end{bmatrix}$	0.73	0.63	0.10	
		Risky	3,600	0.20	0.70		0.63	0.73	0.10	
5	S-W	Competitive	210	0.85	0.80	$\begin{bmatrix} 0.30 & 4.00 \\ 0.20 & 3.00 \end{bmatrix}$	0.15	0.05	0.60	0.60
	M-S-W	Fecund	12,000	0.60	0.10		0.05	0.15	0.50	0.60
	M-S-W-C									
A1	S-W	Competitive	17.5	0.85	0.80	$\begin{bmatrix} 0.30 & 4.00 \\ 0.20 & 3.00 \end{bmatrix}$	0.63	0.73	0.15	0.10
	M-S-W	Fecund	1,000	0.60	0.10		0.73	0.63	0.15	0.10
	M-S-W-C									
A2	S-W	Conservative	250	0.70	0.20	$\begin{bmatrix} 1.00 & 0.50 \\ 0.10 & 1.00 \end{bmatrix}$	0.10	0.10	0.90	0.90
	M-S-W	Risky	300	0.20	0.70		0.75	0.85	0.08	0.12
	M-S-W-C									
A3a	S-W	Conservative	3,000	0.70	0.20	$\begin{bmatrix} 1.00 & 1.50 \\ 0.50 & 1.00 \end{bmatrix}$	0.08	0.12	0.80	0.80
	M-S-W	Risky	3,600	0.20	0.70		0.12	0.08	0.70	0.90
	M-S-W-C									
A3b	S-W	Conservative	3,000	0.70	0.20	$\begin{bmatrix} 1.00 & 1.50 \\ 0.50 & 1.00 \end{bmatrix}$	0.08	0.12	0.80	0.85
	M-S-W	Risky	3,600	0.20	0.70		0.12	0.08	0.70	0.90
	M-S-W-C									
A3c	S-W	Conservative	3,000	0.70	0.20	$\begin{bmatrix} 1.00 & 1.50 \\ 0.50 & 1.00 \end{bmatrix}$	0.08	0.12	0.80	0.90
	M-S-W	Risky	3,600	0.20	0.70		0.12	0.08	0.70	0.90
	M-S-W-C									

[a] Abbreviations: C, canola, M, maize; S, soybean; W, wheat.

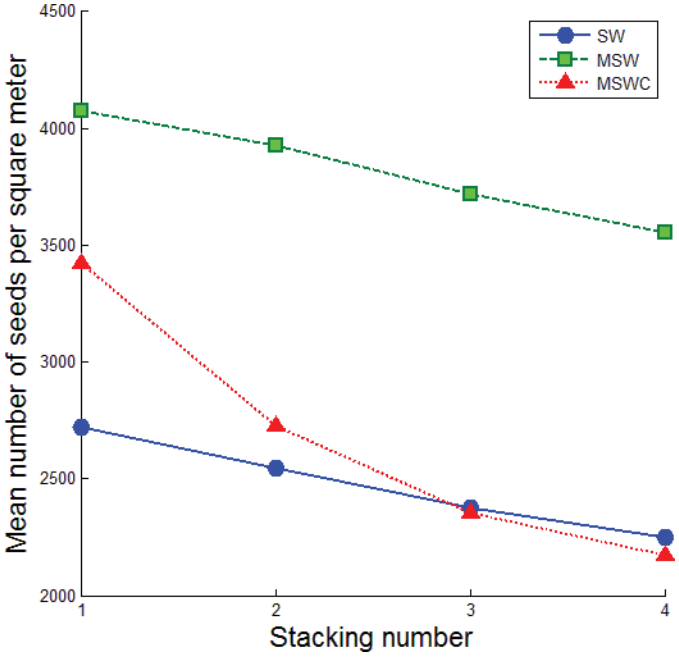


Figure 5. For more extreme parameters (i.e., "more competitive" and "more fecund"), the mean total number of weed seeds per square meter is plotted for stacking numbers one through four for the soybean-wheat, maize-soybean-wheat, and maize-soybean-wheat-canola rotations. The rotation with the lowest weed density is not constant across stacking number, suggesting that different rotations respond differently to stacking, and the optimal rotation may change with the stacking number. (Color for this figure is available in the online version of this paper.)

competition, the densities needed for weed-weed competition to be effective may be beyond economic damage thresholds. There is one aspect of our model that likely underestimates the beneficial effects of crop stacking; in reality, seed viability and germination rate decay nonlinearly over time. Adding nonlinear seed viability to our model would likely show even more benefits from stacked rotations.

Despite these limitations, our results suggest that stacking might be an environmentally friendly alternative or complement to the use of herbicides or soil tillage. While other weed management tactics might carry a financial and/or environmental burden, crop stacking can be implemented at minimal additional cost. Regardless of the number of consecutive plantings of a single crop within a crop rotation, the total cost and benefit remains constant, as the same proportions of each crop are planted. Moreover, stacking might be effective for managing weeds that have developed a resistance to herbicides or in organic cropping systems where herbicide use is prohibited. Finally, though we have discussed our model crops as representing single species, they are formally distinguished only by their impacts on the weed communities, and thus can also be described as general crop functional types. From this perspective, it is not necessary to plant the same exact crop (e.g., maize) for multiple years to attain the weed suppression benefits of from crop stacking. Rather, if different crops are available that have similar impacts on weeds, they could be alternated within the stacked rotation. This would allow the benefits of stacking, while preventing buildup of species-specific insect pests and pathogens.

Conclusions

A great deal has been learned about the weed suppression benefits of strategically sequencing crops in a rotation (Anderson 2004; Bohan et al. 2011). Here we contribute to that growing literature by examining the potential to manipulate crop rotation patterns, specifically crop stacking, as a tool to manage weed density. Our work is framed very generally, as a heuristic, and is not intended to provide specific recommendations. Nevertheless, we demonstrate that stacking crop rotations may be used to reduce overall weed density. The driving force behind the success of stacking in our model is the exploitation of weed-weed competition and the manipulation of this interaction by altering the autocorrelation of disturbance caused by crop production. Essentially, stacked rotations force weeds to compete more strongly with each other, because each switch to a different crop type can change which weed performs better. With higher stacking numbers, the effects of a certain competitive arena have time to accumulate, and keep overall weed populations lower. Despite its simplicity, the concept of utilizing weed-weed competition as a weed management strategy is relatively novel. There have, however, been other notable theoretical investigations of the effects of crop rotation on weed populations (Mertens et al. 2002). Though that model did not feature density dependence or weed-weed competition, it also showed that stacked rotations can reduce weed populations, via mechanisms that are distinct from those discussed here. We interpret the results of Mertens et al. (2002) as complementary to ours; together our work illustrates that there are multiple mechanisms that may lead to decreased weed densities under stacked rotations. Our work also has broader implications. A key concept underlying our work is manipulation of disturbance autocorrelation, and our methods can likely be applied to other weed management tactics, such as mowing and herbicide application, and exploit mechanisms other than weed-weed competition. In addition to explor-

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ing the role of disturbance autocorrelation in other process-based management strategies, future research should focus on verifying our results by integrating weed-weed competition and crop stacking into existing system-specific models. In addition to further model testing, empirically testing the effect of crop stacking in long-term field experiments will be necessary, both to fully demonstrate the beneficial effects of crop stacking, and to ensure that this management approach does not interfere with existing management tactics. Through a combination of such ongoing empirical and theoretical agro-ecological research, we can decrease management costs and environmental impacts, and improve overall cropping system sustainability.

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Literature Cited

Anderson RL (2004) Sequencing crops to minimize selection pressure for weeds in the Central Great Plains. Weed Technol 18:157–164

Anderson RL (2005) A multi-tactic approach to manage weed population dynamics in crop rotations. Agron J 97:1579–1583

Anderson RL (2009) A 2-year small grain interval reduces need for herbicides in no-till soybean. Weed Technol 23:398–403

Bastiaans L, Paolini R, Baumann DT (2008) Focus on ecological weed management: what is hindering adoption? Weed Res 48:481–491

Beck D (2003) An Emphasis on Rotations. http://www.notill.org/KnowledgeBase/03_emphasisrotations_Beck.pdf. Accessed August 3, 2012

Bohan DA, Powers SJ, Champion G, Haughton AJ, Hawes C, Squire G, Cussans J, Mertens SK (2011) Modeling rotations: can crop sequences explain arable weed seedbank abundance? Weed Res 51:422–432

Booth BD, Swanton CJ (2002) Assembly theory applied to weed communities. Weed Sci 50:2–13

Burnside OC, Wilson RG, Weisberg S, Hubbard KG (1996) Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. Weed Sci 44:74–86

Chesson P (2000) Mechanisms of maintenance of species diversity. Ann Rev Ecol System 31:343–366

Clay SA, Kleinjan J, Clay DE, Forcella F, Batchelor W (2005) Growth and fecundity of several weed species in corn and soybean. Agron J 97:294–302

Davis AS, Hill JD, Chase CA, Johanns AM, Liebman M (2012) Increasing cropping system diversity balances productivity, profitability and environmental health. PLoS ONE 7:e47149

Davis AS, Renner KA, Dyer L, Mutch D (2005) Integrated weed management guide: One year's seedling. East Lansing, MI: Michigan State University Extension. 112 p

Derksen DA, Anderson RL, Blackshaw RE, Maxwell B (2002) Weed dynamics and management strategies for cropping systems in the Northern Great Plains. Agron J 94:174–185

Doucet C, Weaver SE, Hamill AS, Zhang J (1999) Separating the effects of crop rotation from weed management on weed density and diversity. Weed Sci 47:729–735

Ellner S (1985) ESS germination strategies in randomly varying environments. II. Reciprocal Yield-Law models. Theoretical Popul Biol 28:80–116

Eyre MD, Critchley CNR, Leifert C, Wilcockson SJ (2011) Crop sequence, crop protection and fertility management effects on weed cover in an organic/conventional farm management trial. Europ J Agron 34:153–162

Gallandt E (2009) Managing Weeds With Crop Rotation. http://gallandt.wordpress.com/. Accessed August 3, 2012

Garrison A, Miller AD, Roxburgh SH, Shea K (2012) More bang for the land manager's buck: disturbance autocorrelation can be used to achieve management objectives at no additional cost. J App Ecol 49:1020–1027

Hagny M (2001) Stand tall with stacked rotations. Leading Edge: The Journal of No-Till Agriculture 1:13–17

Leighty CE (1938) Crop rotation. Pp 406–430 *in* Patrick AL, ed. Soils and Men: Yearbook of Agriculture 1938. Washington, DC: USDA, Government Printing Office

Liebman M, Davis AS (2000) Integration of soil, crop and weed management in low-external-input farming systems. Weed Res 40:27–47

Liebman M, Gallandt ER (1997) Many little hammers: ecological management of crop-weed interactions. Pp 291–343 *in* Jackson LE, ed. Ecology in Agriculture. San Diego, CA: Academic Press

Liebman M, Staver CP (2001) Crop diversification for weed management. Chapter 7 *in* Liebman M, Mohler CL, Staver CP, eds. Ecological Management of Agricultural Weeds. Cambridge: Cambridge University Press

Maxwell BD, O'Donovan JT (2007) Understanding weed-crop interactions to manage weed problems. Pp 17–34 *in* Upadhyaya MK, Blackshaw RE, eds. Non-Chemical Weed Management: Principles, Concepts, and Technology. Oxfordshire, UK: CAB International

McCloskey MC, Firbank LG, Watkinson AR, Webb DJ (1998) Interactions between weeds of winter wheat under different fertilizer, cultivation and weed management treatments. Weed Res 38:11–24

Mertens SK, van den Bosch F, Heesterbeek J (2002) Weed populations and crop rotations: exploring dynamics of a structured periodic system. Ecol Appl 12:1125–1141

Miller AD, Chesson P (2009) Coexistence in disturbance prone communities: how a resistance-resilience trade-off generates coexistence via the storage effect. Amer Natural 173:E30–E43

Miller AD, Reilly D, Bauman S, Shea K (2012b) Interactions between frequency and size of disturbance affect competitive outcomes. Ecol Res 27:783–791

Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversity-disturbance relationships. Proc National Acad Sci 108:5643–5648

Miller AD, Roxburgh SH, Shea K (2012a) Timing of disturbance alters competitive outcomes and mechanisms of coexistence in an annual plant model. Theor Ecol 5:419–432

Mohler CL (2009) The role of crop rotation in weed management. Pp 44–46 *in* Mohler CL, Johnson SE, eds. Crop Rotation on Organic Farms. A Planning Manual. Ithaca, NY: Natural Resource, Agriculture, and Engineering Service

https://doi.org/10.1614/WS-D-13-00037.1 Published online by Cambridge University Press

Munier-Jolain NM, Chauvel B, Gasquez J (2002) Long-term modelling of weed control strategies: analysis of threshold-based options for weed species with contrasted competitive abilities. Weed Res 42:107–122
Nord EA, Ryan MR, Curran WS, Mortensen DA, Mirsky SB (2012) Effects of management type and timing on weed suppression in soybean no-till planted into rolled-crimped cereal rye. Weed Sci 60:624–633
Olsen JM, Griepentrog H-W, Nielsen J, Weiner J (2012) How important are crop spatial pattern and density for weed suppression by spring wheat? Weed Sci 60:501–509
Pickett S, White P (1985) The Ecology of Natural Disturbance and Patch Dynamics. New York, NY: Academic. 472 p
Radosevich SR (1987) Methods to study interactions among crops and weeds. Weed Techno 1:190–198
Roxburgh SH, Shea K, Wilson JB (2004) The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359–371
Ryan MR, Smith RG, Mirsky SB, Mortensen DA, Seidel R (2010) Management filters and species traits: weed community assembly in long-term organic and conventional systems. Weed Sci 58:265–277
Schreiber MM (1992) Influence of tillage, crop rotation, and weed management on giant foxtail (*Setaria faberi*) population dynamics and corn yield. Weed Sci 40:645–653
Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecol Letters 7:491–508
Shinozaki K, Kira T (1956) Intraspecific competition among higher plants VII. Logistic theory of the CD effect. J Instit Polytech Series D 7:35–72
Storkey J, Moss SR, Cussans JW (2010) Using assembly theory to explain changes in a weed flora in response to agricultural intensification. Weed Sci 58:39–46
Weiner J, Andersen SB, Wille WK-M, Griepentrog H-W, Olsen JM (2010) Evolutionary agroecology: the potential for cooperative, high density, weed suppressing cereals. Evolut Appl 3:473–479
Westerman PR, Liebman M, Menalled E, Heggenstaller AH, Hartzler RG, Dixon PM (2005) Are many little hammers effective? Velvetleaf (Abutilon theophrasti) population dynamics in two- and four-year crop rotation systems. Weed Sci 53:382–392
Zhang R, Shea K (2012) Integrating multiple disturbance aspects: management of an invasive thistle, *Carduus nutans*. Ann Botany 110:1395–1401

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